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Mimicry, Aposematism, and related Phenomena

Mimetism in Nature and the History of its Study

Spilogale putorius
in the aposematic display

Lincom München

Contents

Introduction

The history of the research of mimetic phenomena in nature (and the interpretation of the external appearance of organisms generally) has not been studied in depth so far, even though it is an absolutely pivotal theme in biology, as was noted by **Mayr** (1982), for example. A certain hint of a historical overview of this research area, albeit not very extensive, none-the-less clear and deep, can by found in certain texts by **Heikertinger** (1921-27, 1954). Research of mimicry as exemplary instances of evolutionary theory was pursued by **W. C. Kimler** (1982) in his dissertation, which was partially published later in year 1983. This work is an example of Anglo-Saxon point of view, which disregardes almost all continental work on the subject and interprets only the most important Anglo-Saxon authors between the era of natural theology, **Bates** (1862a), and Neo-Darwinian syntheses of the British population's genetics in the style of reports on the linear progression of science (this method of research is applicable only when considering main-stream British and American research, which gives the impression of cumulation of knowledge). All other approaches, for example **Hingston** (1933), lead in a different direction, not to mention the continental, especially the German school's approach to mimetic expressions in nature. At the same time **Kimler's** work is not aware of the deeper aspects of mimetic expressions in nature, especially the general problem of forms. However large the extent of knowledge attained by Anglo-Saxon authors in the field of research and theoretical explanations of mimetic phenomena in nature, I consider it necessary to study Continental authors as well, and that for two reasons. First of all, Central European biology and the author himself, belong to this school and intellectual tradition, and secondly the postmodern era characteristically accentuates that, which is often considered marginal. These marginal themes have a tendency to become central, if only because central themes lost their potential for development due to intensive exploitation. The materials for this study were gathered from 1985 to 1995, first in Vienna and later in Prague, Leiden, and Amsterdam. The study is complemented by a bibliography (**Komárek**, 1998), and a database of works about mimetic phenomena, which contains around 5000 entries causing it to be the largest piece of work of this kind ever created. While the bibliography only encompasses the years 1800 to 1990 and concentrates only on cases of mimicry, aposematism, and certain important cases of crypsis, the study itself is wider because it encompasses a larger time period and a broader range of themes, especially concerning the history of the interpretation of the exterior appearance of living organisms. For that reason only quotations from the most important texts are cited in this book and in cases of need for a wider referential system the citations will point to the above mentioned *Bibliography* (in the text with a capital '*B*'). Only works concerning skin and wing patterns of animals, which are not included in the *Bibliography*, are referred to in full. The goal of this book is to point out the centrality of the problem of resemblance and mimicry in nature and the dependence on the understanding of this phenomena in the biological paradigm of the given era, the intellectual atmosphere, and the language in which the problem is interpreted. This work can also be interpreted to an extent as an „archeological" study, because the swamp of forgetfulness, into which most written and later duly published works eventually sink can be more easily compared to studying deep layers of an archeological excavation than to the study of recent, easily accessible knowledge. The myth of linearly progressing science, where nothing disappears beyond the horizon, is one of the most flagrant of unconscious modern hypocrisies. Only after concrete work in libraries, directly with historical texts, does the number of particularities and even complete alternative concepts, which have almost entirely disappeared beyond the horizon, become apparent. This research is similar to uncovering material archeologically or paleontologically, material which is difficult to find and also is to an extent fragmentary and which today does not address us directly, but in the best of cases through its „descendants". Therefore, it is often strongly derivative making it difficult to trace back to its roots. This permanent masking of the past in science has the advantage that research starts with an almost entirely clean slate and doesn't drag „deadwood" from the past along with it (this phenomenon is generally acknowledged even outside of scientific history, where early Christianity discards „heathen prattle", the Renaissance „scholastic trash", Communism and Nazism „city-slicker deadwood", etc.). It is always necessary to prepare a clean stage so the next generation has room to make themselves known, and this is only possible by moving the clutter of theses and particularities of the older era „off stage", in other words into the province of forgetfulness. This ends not only in their loss in memory but eventually even their true loss (this doom isn't limited for example to Alexandrian science, but after another „reorganization of libraries" may even afflict older layers of the modern period). Every social structure, including modern science, actively and even unconsciously camouflages and lays shadows on its own past. The past, incorporated into skinny textbooks or brochures, can only be viewed in this metamorphosed and simplified or even caricatured form. No historical study can compensate for studying original historical texts for the serious student (but even these texts represent only a specific concentration and sediment of the history of a certain branch; that which was meant for publication - the past itself is exactly that, past, gone). These modern studies necessarily contains only a selection of information, which the author considers relevant. Historical studies are then necessarily a specific cross-section. Reading historical texts and „getting into" the heart and soul of any branch is necessary to discover and understand that branch, which, in this way, affect the student directly. The history of anything is a process in the same way as the life of an organism is - constantly changing, which significantly complicates grasping it, not only on paper, but in thought as well. Generally speaking, the human mind prefers grasping static images (it is not a coincidence that biology is actually „necrology", it is necessary firstly to „fixate" the studied object, on whichever level), and it is not different with the history of any specific scientific branch. It is not surprising that the three most prominent modern attempts at grasping the world through its changes (**Hegel**, **Marx**, and **Klages**) ended, against all invention and fascination, as social catastrophes. In addition, with every partial historic account, knowledge of the era's thought and social context is, if possible, necessary. Due to the extreme span of the theme, this is always possible only to a certain extent. We can see this even in the roughest interpretation of „broad" history, for example the correlation of **Darwin's** and **Wallace's** rise and the drastic progress of the capitalism of free trade in England in the first half of the 19th century or the loss of prestige of „continental" biology after 1945. A more delicate approach reveals other connections (see also **Komárek**, 1989a). Understandably this work concentrates on themes which are not mainstream and at this time not often studied, instead of those, whose successors are visible in the thoughts of today's scientific community. One of the main reasons for the interest in studying history generally is an effort to pursue that which is in danger of being forgotten, not, on the other hand to pursue that which survives in the general consciousness (in this case in the scientific community) without problems - this also applies to the concentration of interest in the time period up to 1950 (end ends in 1990), that is a period whose protagonists are no longer alive and which is conserved only in books, not in individuals. For that reason, works of the past fifty years are evaluated and described with a certain reserve. First of all, every researcher is bound to his/her work by an exceptional emotional tie, because the work usually took very much time and effort and the researcher viewed the work as completely constitutive for the given branch of research. Secondly the interval of time is much shorter, than is necessary for writing the history of a scientific branch. During the writing of this book another problem arose; should this book be written for those who directly work in the research branch concerned with mimicry (for whom many „technical" terms are a matter of course and who also have certain „fixed" assumptions, which they consider obvious, even though they are not), or for a wider public, especially for those from the ranks of intellectuals oriented towards the humanities. In the end the more or less middle path was selected, which was not always simple and without problems. Reading this requires a certain, actually quite extensive knowledge of living forms, without which the reader will not only misunderstand the book, but also, without an interest in and knowledge of the various forms in the living world the problem of appearance in the ranks of living organisms will not shine through at all and will not appear relevant or important. This work, together with the *Bibliography*, attempts to at least partially make accessible the history of the view on the external appearance of organisms, which have sunk beyond the horizon of memory, and its importance in the framework of scientific and non-scientific contexts in their respective eras. This work is not meant as a description from an enlightened point of view based on a sequence of famous „Oldies" forming a path to cumulative linear progress, but like a part of the „world drama" and its many, on its own logic dependent, twists and turns.

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Defining the scope of interest

The term *mimicry* (from the Greek word *mimésis* - meaning imitation) was first used by **Kirby** and **Spence** in 1817 for the imitation of parts of plants by insects. Today this term denotes a likeness between two animals, which is not caused by kinship or convergent evolution but is typically caused by selective pressure from predators (this will be expanded on later). The range of concern covered in this work concerns the study of the external appearance of animals generally and its interpretation. Here we can divide this appearance into two main categories, which surprisingly are not always distinct from one another. The first category concerns features (both form and color) of the surface which serve to mask the animal. This type of coloration is generally labeled **cryptic** (from the Greek word *kryptos* - hidden; *concealing coloration,* germ. *Tarnfärbung*), if the case concerns a detailed imitation of plants or parts of a plant the term **phytomimesis** (from the Greek word *phýton* - plant) is occasionally used. All color-masking techniques, from the simplest which allow an animal disappear in-between plants or on bare ground, up to the most sophisticated, which imitate with amazing accuracy lichens, flowers, or dried leaves. The second category consists of coloration and surface formations, which serve to make the animal noticeable, which is usually achieved by a combination of bright and contrasting colors, or even by over-dimensioned features that often serve as secondary sexual marks, so-called **exaggerated structures** (germ. *Luxus-* bzw. *Exzessivbildungen*). These „attractor" types of design are generally referred to as **semantic coloration** (from the Greek word *sémeion* - mark). Although theoretically this differentiation can easily be overlooked, general practice is obviously much more complicated. Not only that both types of coloration commonly appear on the same animal - one type on one part of the body and on a different part a different type (sometimes for instance on a part which is hidden in times of resting), but the same coloration can for instance be considered cryptic from a distance or under certain conditions and seem semantic under different conditions. Even though the (arbitrary) distinction between the two types can at times be unclear and is always based on human observers, generally there are very few serious doubts concerning these basic categories. Doubts arise later, when subdividing the semantic colorations into more specific categories, as we will see in the following text. In the context of both categories we will also see feature types, which serve to „deceive" the observer. They allow the animal to become conspicuous (not only optically, but also acoustically, tacitly, olfactorily, etc.) and be considered by observers to be something else (*deception,* germ. *Täuschung*). Besides cryptic deception, which is mentioned above, a second deception exists in the form of one animal imitating another animal species through external appearance, where the imitating animal is often quite distinct from related forms and „stands out" from the rest. The imitated animal is usually called the **model** (germ. *Vorbild*), while the imitator is called the **mimic** (germ. *Nachahmer*). Usually this distinction also does not cause problems (the differences between mimicry and convergence will be dealt with later as will be the individual types of imitation according to their known or presumed purpose). Sometimes the imitation of the model is only partial, in other cases the imitation can occur in places which do not correspond to the natural situation (false heads or some cases of eye-spots). „False" body parts, especially if they serve intraspecific communication, are occasionally called **dummies** (germ. *Attrappen*). Plants are dealt with in a slightly different way: besides cryptic imitations of certain inanimate objects (e.g. some desert plants imitate rocks) we can divide plant imitations into a number of categories: the occurrence of a similarity of leaves or flowers in two or more plants (even here it is very often possible to distinguish between the mimic and the model), imitations of primary crops by weeds and flower mimicry for the luring of pollinating insects: flowers imitate carrion, excrements, fungi, or even females of the pollinating insect species (for example orchids of the genus *Ophrys* imitate female bees of the genus *Andrena*, including reproductive pheromones for luring the males), and lastly various types of dummies found on blooms. Deceptions and pretending in human culture is outside of our primary interest, even though it is such fertile ground. For the more interested I recommend **W. Wickler's** (1968) book, where the mentioned events are described and portrayed in detail, in spite of its neo-Darwinian interpretation and partitioning of an otherwise very confusing muddle. (In this book the viewpoint of the observer is applied with minimal explanative and interpretive machinery and an effort to divide surface and similar phenomena into „natural" categories that are „evident" at first or second glance, with certain paradigmatic assumptions concerning the acceptance of mutual kinship between two species based on „hidden“ signs and their evolutionary affiliation in the past, which have almost universally become part of the intellectual instrumentation. The fact that this has not been the case in the past will be shown in the following chapters.)

Surface, interiority, similarity, and kinship

The term surface and other variations of this word are generally held to be associated with deceit, shallowness or incomplete knowledge in our sub-consciousness and in Indo-European languages generally (this is not so apparent in Anglo-Saxon languages, but the association can be seen in such words as baseness or superficiality). On the other hand, the second connotation associated with this word is completely opposite, which is evident in the Greek word for truth, *alétheia*, meaning to be visible, to clearly stand out. Whatever is true and essential is obvious at first glance, evident, clear as day and apparent at once. In this case light metaphors are interlaced with metaphors of illuminated surfaces. That which is evident at first glance is something which is correct, which does not have to hide and which is not afraid of being seen. The traditional relation to things hidden is similarly ambivalent. We can trace the fact that a thing's nature likes to hide at least as far back as Antiquity. Our attempts to uncover it only cause it to withdraw deeper and deeper into even greater darkness and hiding. Certainly, that which is hidden is in some way not honest, it is something which cannot (yet) stand broad daylight, but at the same time it is the essence, the root of the thing, even if it is somewhat sneaky, vulnerable, and hidden for good reasons. Hidden things such as buried treasure, secret services and the police, state and personal secrets, etc. have always caused people to desire their uncovering or possession, even though the process has always been risky, and in the case of miscarriage even ruinous or deadly. On the other hand, things which are visible constitute a world which is certain, even though it is apparent that often we are dealing with cleverly designed shams, which often, in the best of cases, hide in themselves ambivalent contents, frequently in the sense of the New Testament's whitewashed graves. Nevertheless from time immemorial it has been believed that the external appearance of things and people in some way exposes their internal characteristics. The appearance of external form should always point towards the appearance of internal essence, towards the nature of the object. In relatively recent times **A. Portmann** (1948, 1960) has again discussed the problem of external forms of organisms. According to his view, the external appearance of organisms, including ethological, sound, etc. aspects (so called **proper phenomenon**, *eigentiche Erscheinung*) are genuine expressions of the disclosure of the organism's **centricity**, *Innerlichkeit* (this term originated with the well known embryologist **W. Roux**), which means their hidden aspects. A central term of his biological concept is the **self-display** (*Selbstdarstellung*) of proper phenomena, which he considers an absolutely essential aspect of being of organisms, as essential as reproduction or internal physiology. The addressee of proper phenomena can either be an organism of the same or different species, or even derivatively a person. But a whole range of proper phenomena are address-less, or in other words the addressee is not known and probably does not even exist. The great ingenuity and energy that many organisms use to create their external appearance (complicated structure, the insertion of special pigments, etc.) does not leave room to doubt that the surface of animals (and plants) represents a very important part of that organism, something which is worthwhile to invest into. The adaptive significance of external coloration and design is not denied by **Portmann**, but he is convinced that their meaning is not exhausted by these functional aspects. From Antiquity biology has always stressed the ingenious functionality of organisms - although today we aren't usually astonished by the fact that the nasal cavity opens in the same place as the larynx, which leads to the lungs. This amazing fact was „explained away“ by the theory of natural selection, by which inefficient individuals were eliminated. In any case, the attempt to find a specific purpose or meaning behind every individual structure of an organism has stayed with us since the era of natural theology of the baroque type - today „purpose“ in the sense of survival, energetic profit, and the spreading of one's genome. **I. Kant** (1790) noticed the self-display phenomenon, even before **Portmann**, in the *„Kritik der Urteilskraft“*, § 58 I., II. 2, for which he used the term *Zweckmässigkeit*, meaning purposeness. Purposeness, not in the sense of a functional purpose, but that which signifies an aim at a self-presentational purpose. The scientific explanation of anything actually means the process of bringing that thing into triviality, the elimination of the amazing in something by transplanting that which is in some way special or exceptional into some well-known and predefined scheme, in the today typical case directly into an algorithm. **Portmann** performs this process more or less very considerately. Among **Portmann's** predecessors, not only **Kant** belongs to those who acknowledged the importance of organisms' surfaces and their ornamental character, but these thoughts already appeared in the Hellenistic era in the Alexandrian treatises and in the Roman responses to similar thoughts (**Corpus Hermeticum** V, par. 6, **Cicero**: De officiis I 35, 126, De nat. Deorum II, 164). However, these documents always pertained exclusively to humans and their appearance /classical literature is cited here using standard Latin titles of the respective works and is not separately covered in the bibliography, which is limited to literature that was written after the year 1000/. **Portmann** emphasizes the importance of external symmetry in comparison with internal asymmetry in higher life forms (evident namely in transparent fish and in planktonic snails, where the sack containing the internal organs is obscured by a silver opalescent membrane, which masks the blob of not very symmetric or good-looking internal organs; the problem of transparent organisms is pursued in a similar way by **Schad**, 1981). Certain organisms' surface designs, which are not intended to be seen (e.g. cave organisms, internal parasites, embryos, the young of feeding birds) are poor or non-existent and generally seem incomplete, they evoke the feeling of optical unpleasantness, or something which shouldn't be presented or seen (Portmann's view of organisms can in principle be applied to social institutions, where closer contact with many evokes feeling similar to curiously cutting into a golden pheasant only to have its distasteful entrails fall out). This is connected to the so-called **Oudemans´ phenomenon**, which describes animals with discontinuous surfaces (feathers, scales, overlapping wings of butterflies) (**Oudemans**, 1903) - the coloration of the surface continues only on exposed parts of the overlapping morphological structures, as if it had been painted from the outside. The parts which under normal circumstances are not seen are generally colored neutrally, or parts which are seen under calm circumstances are colored differently from parts which are seen during movement. A close relationship between Portmann's observations and **Peterich's** so-called **biochromatic law** (**Peterich,** 1972, 1973) exists, which formulates rules for the combination of colors on organisms' surfaces (this law applies to plants only in part): warm (from red to yellow-green) and cold (from blue-green to purple) colors aren't found next to each other on the organism's surface, but are at least separated by a strip of some neutral color (from white to black, brown, neutral green - **Portmann** also calls attention to the incomparably larger diversity of organisms' surfaces when compared to the diversity of their internal structures (Any child can differentiate between members of the European duck species according to the coloration and patterns of their feathers, while it is difficult for an educated expert to tell members of this species apart when in possession of only their skeletons or innards). Portmann compares, in **Goethe's** tradition, the living world to a theater, where important is that which is happening on the stage, truths which are not directly apparent for the audience (such as the mechanical instrumentation for the stage, the composition of the paint used for the requisites, etc.) are not without appeal, but they belong to a different category and to interpret the show on their basis is inapt, even though they are also part of the show (in the same way that tools are not, or should not, be central to the performance). Although Portmann does not condemn penetrating backstage as being obscene or impertinent, but he does warn against confining oneself to this way of viewing the world, especially the living world. For Portmann, an essential aspect of an organism's display and it's self-presentation is the ethological angle, where exterior behavior can be explained in the same way as any other morphological structure (here Portmann is following in the footsteps of **K. Lorenz**). The behavior of related species can be homologized and rudiments or atavisms can be found, which shapes it's phylogenesis just the same as any other structure of the organism. For this behavior it is even easier to end up losing the primary function, to turn from the fully functional to a ritual or a representative procedure, which carries a different meaning. Imitation has an especially important role in animal behavior, from primates „aping" some behavior, human and animal acting, to the acoustic imitations of birds (a few works on this subject, but concerning mammals, also exist, eg. **Ralls**, **Fiorelli** & **Gish**, 1985, **Richards**, 1986 or **Nikolskij**, 1981), which mimic the voices and songs of other species or even human voices. Especially these vocal imitations defy functional interpretations (except for a number of textbook examples, such as the blue jay of the genus *Cyanocitta*, which occasionally imitates the voice of predatory birds in order to deter competitors from food sources) and very intensively, almost „crystalically", appear to be self-purposeful. The imitation usually occurs out of playfulness, experimentation, or just „for the fun of it". The outward appearance of organisms, according to Portmann, includes olfactory, touch-sensitive, or for responsive species even electrical field (or stimuli) aspects. Portmann's methods of exegesis of the external appearance of organisms appear closer to methods used by art scholars or structuralists (even though structuralism, with its method of preparing formal outlines from binary opposites from the studied objects in pure form, is not very useful for interpretations of organisms and Portmann only lightly touches this aspect). The complete separation of the human and the natural world in modern times and the completely distinct methods used by the social and natural sciences has made it impossible to view cultural phenomena and its artifacts as a „continuation of Nature using different means". If we were to apply the line of reasoning, today so common in biology, to, for example, the interpretation of paintings on a Greek amphora, the questions asked would no doubt sound strange: Was their goal to lure consumers to the wine, which was available inside? Or, on the other hand, were they intended to repel uncalled visitors, so that they would not drink the wine instead of its lawful owner? Nothing illustrates the break between social and natural sciences, including the difficulty or even impossibility of a meaningful exchange of information between the two branches as clearly as this example. Not that biology is without its own hermeneutics, the opposite is in fact true, biology makes use of hermeneutics very often. The interpretation of organisms' coloration and patterns, in the same way as for example the interpretation of paleontological objects of study, are precisely branches which solely rely on hermeneutics. The only difference is that their exegesis stems from completely different premises than interpretations in the humanities. The opinion that that which needs interpretation is in the first place written text developed in late Antiquity and until the Cartesian revolution even living organisms requested interpretation in the form „What is the meaning of a crow?" (today this question may be formulated for example in this way: Where does the crow belong in the evolutionary tree of the family Corvidae - for people of the post-Cartesian era the crow does not carry any special omen). In the past this was the other way around, the interpretation of organisms, especially in the case of divinations, was quite common (**Portmann** depicts a Babylonian model of a sheep's liver on which young adepts of the prophesy trade learned to identify signs from the innards of sacrificed animals. The sacred oak in Dodone murmured coherently for experienced and initiated interpreters (*theologoi*), the feeding activity of sacred chickens or the direction of flight, the number and species of flying birds was, for the *augures*, a source of information about present and future events. Archaic man felt addressed by the whole of the cosmos, including plants and animals.). **Portmann's** idea that the external appearance of organisms is the most adequate externalization of their „true nature", their intrinsic characteristics, which was based on much older views, clearly describes a very important, existentially archetypal and fundamental human intuitive idea. If there is a crass discrepancy between the external appearance and the internal nature or any similar discord we develop an uneasy feeling. The reason for this being that is that we are unable, on the basis of external features, to correctly judge the internal characteristics of the given individual, thing, institution, animal, or plant. A special combination of feelings, including disenchantment, apprehension, uncertainty, sensationalistic interest and longing to uncover that which is hidden, ensues. It is these moments, neutrally expressed as feelings of excitement, pervade heavily into mythologies, folklore, fiction, and even everyday life. The mythology of Antiquity was filled with deceptions and disguises in various shapes and forms, shamans and dances with masks have been in evidence from the drawings of the Cro-Magnon era up until and including our time. The counterfeiting of documents and money and cases of secret child substitution (this was common for royal families in the Middle Ages) are favorite themes for trivial literature. The Biblical image of the „wolf in sheep's clothing" as an exposition of the Devil, the father of lies and deceptions, or his later hypostasis, filled even religious - political life. The possibility that a harmless country woman is in fact a socially very dangerous witch or that an old and responsible comrade has been, ever since his entry into the Party, in the services of foreign powers, was, during inquisitions or the Moscow processes, a matter which was disquieting for the majority of the population. The level of accuracy and cunning malice in the deceptions and impostures was so high that they could be uncovered and eliminated only by the collective wisdom of the Church or the Party, represented by special trained professionals. It is without doubt that it was the above-mentioned aspect of hidden deceptions, so archetypally effective, that caused the unusual explosion of interest in deceptions in nature in the modern period. This thought could not have originated before the modern era, specifically right after the Cartesian scientific revolution. Up to and including the Renaissance the external appearance of living nature was at least considered to be an expression of the kinship of essence (in addition, the „Book of Nature", when correctly interpreted, cannot deceive, because it is a divine creation, in the same way as the Holy Scripts). The European Middle Ages had, in addition, only a vague notion of original works as opposed to counterfeits - as in the example of writings, the *bona fide* falsification of lost documents, or in art, where the difference between the original and the copy was indiscernible. Due to this world-view, for example, bats were classified together with birds and whales and cuttlefish with fish generally, even though scientists naturally knew the respective anatomical differences and the similarities to other animal groups (this lasted until the end of the Renaissance). Nevertheless, the general shape of the body and movement in certain elements were stronger arguments (The way in which birds understand by this method themselves is in itself interesting. Day-active birds, as is well known, attack owls with an almost passionate hatred /so called *mobbing*/, even though most of them do not constitute a direct danger for the birds. On the other hand, the birds usually cannot attack the owls with any great success. In spite of all neo-Darwinian attempts at interpretation of this phenomenon /e.g. **Curio**, 1978/ it seems, that „irrational" emotions, something like archetypal hatred between day birds and night birds, play an important role. This is seen even clearer in occasionally published papers about occurrences of the mobbing of bats by small day birds /**Campbell**, 1973, **Cundale et al.**, 1988, **Strong & Cuffe**, 1985/ (this author observed this as well) - Here neither predation nor competition can play even the slightest role, the only remaining explanation is the deep archetypal hatred for non-birds, which are too similar not to attract attention and at the same time too different to be accepted as „regular" birds.). Only after the world-view of the Renaissance and its inexhaustible number of affinities, inter-dependencies, and correlations between various objects passed (stars, minerals, plants, animals, parts of the human body, etc.) did the change in thought occur (attention moved from the external appearance to the detailed study of internal anatomy). That which is hidden again begins to become relevant. This conviction spreads hand in hand with the attitude that hidden secrets should be forcefully extracted from nature on the dissection table or, even better, by vivisection (**Bacon's** famous statement, that Nature is like a dirty bitch, who should be hung on the rack and forced to give up her secrets, notably corresponds to the brutal judicious practice of the early modern era). In biology a cult of the secret developed, where hidden structures are very important, eventually these structures are the only important aspect (DNA - the sequence of it's base elements being the most important and most fundamental aspect of an organism). A nice example of this change of view can be seen in chapter 78 of **Pigafetta's** report on **Magellan's** voyage around the world (**Pigafetta**, 1519-1522), where he describes a type of orthopteroid insect from one of the islands around Borneo, which imitates through its external appearance a tree leaf. Pigafetta explains the phenomenon by suggesting that the insect is actually part of this special tree, it is a living leaf, which has feet and can crawl (he was of the opinion that these leaves do not need nourishment and feed only on air). For some time he kept one of these „leaves" in a box (this occurred in 1521). **Bougainville** (1772) describes in the fifth chapter of his book a similar insect from the area of New Britain, which he definitely identified as a bush-cricket with a special „leaf" adaptation and in this way it entered into collections. On a folk-lore level, the system of identifying organisms according to external appearance survived for a much longer time. **Bianki** (1961) describes a Russian folk interpretation of a horsehair worm from the genus *Gordius*; it is considered to be a real horsehair, which has come alive. The author himself has experienced in the Czech Republic an interpretation by which caddisfly (Trichoptera) larvae, which are covered in a camouflaged case, are considered to be sticks that have „come to life".

Similarity is, as is well known, a non-transitive relation and noticing similarity is, as a part of the principle of analogies, the basis of all „right hemisphere intellectual operations" (which means those operations, which can be simulated by computers only by comparing „everything with everything", which is a process completely distinct from the processes of the human psyche and its „insight into appearance"). The experience of noticing an analogy between two things is in some way a pleasurably exciting - suddenly we gain an insight into „how things are", we sense the inner kinship, the affinity. It is not a coincidence that in many European languages the semantic field for „to be similar" is next to the field for „to like, to appeal to, to have a relation to, to have an affinity" (eg. the Polish *podobaç się* = to like, *like,* - *lich* in English and German, etc.) [It is interesting to note that in various languages the word for beauty lies right next to the word for form - latin *formosus*]. We discover a hidden attraction of inner strength between things, their hidden love and mesaliance, so to say, in a sense we see into their private lives (this has always been a favorite activity for humans) /the expression for similarity melts or is very close to the expression for something, which is fitting - the Russian word *udobnyj* - comfortable, and others. In ancient Greece similarity was understood to be a closeness of soul, a similarity of thought, or of association/. Things embody thousands of analogies in an almost incomprehensible mixture. The similarity which is in some way relevant must be allowed to

„stand out", by concentrating on it. The relation of similarities are generally so wide-spread and can include similarities from so many different aspects, that it is very difficult to express them all. Until the Cartesian turnaround in the 17. century all similarities were judged more or less in the same way, the division between accidental and therefor unimportant similarities and on the other hand essential ones was introduced by modern science with its views on causality and later on evolution. One category of similarities has been, since Antiquity, viewed as inferior - the similarity of coloration. The opinion that coloration is secondary and the lack of consideration of coloration in the systematization of objects is perhaps understandable (the relation between a tomato and a male red robin is, in spite of the obvious similarity, quite vague). The world of colors has in any case an exceptional emotional attraction and excitement and there were some attempts to rehabilitate this category (**Goethe**). How would our world-view appear if, for example it were to postulate the law of conservation of color, instead of the law of the conservation of mass?

The amount of various similarities, which appear in the living world, is uncountable, so it is difficult to decide from which side to begin. Maybe through finding analogies between the human or animal body and the plant kingdom (or maybe different animals) or their parts. Occasionally a noticeable amount of imagination is required to notice certain similarities (for example the spotted leaves of the lungwort, *Pulmonaria,* and the structure of the lungs; the somewhat withered leaves of the liverwort, *Hepatica* and the liver), in other situations the similarity makes itself known, so to say: the „hearts" of the flower of the "bleeding heart", *Dicentra*, the „people" seen in the flowers of the man orchid, *Aceras anthropophora.* The popular and scientific names often reflect these similarities, on an optical basis (*Fungia* - a mushroom-like coral, *Ophioglossum* - the snake-tongue fern, *Phallus impudicus* - stinkhorn, *Priapulida* - a phylum of sea organisms) or for example on the basis of smell – stinking goose feet (*Chenopodium vulvaria*). Even animals are sometimes interpreted in this way, the death's head hawkmoth (*Acherontia atropos*) has on its thorax a mark resembling a skull, one Japanese crab actually carries an image of a fully armored samurai (**Fisher**, 1930). **Piepers**, 1903, mentions two more interesting specimens from Java - the chrysalis of the moth *Drepana argenteola* suggests a miniature owl in a sitting position and the fruit of the tree *Anacardium occidentale* a sitting ape. The South American passion-flower plant, *Passiflora* has on various parts of its flower certain attributes of Christ's torture - a cross, a hammer, nails, a crown of thorns, drops of blood - as it was interpreted by the Jesuit **Bosio** (1610). Many butterflies and moths have Latin, Greek, or Hebrew letters or Arabic numbers on their wings. /Especially apparent external appearances of some organisms always provided good material for their popular mythological or hagiographic interpretations: the guinea fowls are sisters changed into birds, who shed tears for King Meleager and who carry these tears on their feathers; the dark hands and face of the hanuman langur (*Semnopithecus*) represent traces of burns, which were caused by Shiva's attempt to punish him for stealing mango; the flowers of carnations, *Dianthus,* are transformed drops of Christ's blood - all of these are examples of „ethiological myths", which represent a different type of „ethiological myth" than later Darwinian explanations for why one species looks a certain way and not differently - the ethiological myth is different in each specific case/. All these types of similarity were very popular until the Cartesian revolution and to an extent even after it. The relation between herbs and certain parts of the human body was the basis of the medical theory of the so called „*signaturae rerum*" (already frequently mentioned by **Paracelsus** - /1493-1541/ - and used according to the principle of analogy - „*similia similibus curantur*"). For example **Giambattista de la Porta** devotes most of his book *Phytognomonica* (1608) to exactly these types of similarity and the interrelations between people, animals, and plants. With the decline of the Renaissance way of thinking, interest in this type of interpretation fell, and after the erosion of the belief in Creationism and the rise of German Romantic sciences in the 19th century it disappeared from the intellectual world completely. In our culture only artists and small children can afford to believe that these similarities are not random occurrences. For a dweller in Ancient Greece the sight of the silver Y-moth, *Autographa gamma*, which has one of the Greek letters on its wings, must have been seen as a definite proof of the prevalent notion of the universal character of the Greek language and alphabet. This type of world-view also gave birth to the following story: **Trajan's** legions, on their way through the forests of Dacia, allegedly found a large mushroom on which was written that they should not continue in their mission. The indicated method of interpreting Nature is not very favorable for understanding fossils, as we do today. If there can be images of people or their organs on plants, why not images of shells, fish, or plants on rocks? Notions of spontaneous generation in Nature without the necessity of physical and informational conti-

De la Porta's table which depicts plants (especially the family Araceae) that have a visual affinity to snakes due to their spotted stems and petioles.

nuity went hand in hand with this - mice in the granary originated in the same way as trilobites in rocks or the skull on the back of the death's head hawkmoth.

The Cosmos was, until the Cartesian turnaround, meaningful, interlaced with many various affinities and Man felt directly addressed by it. The color and shape of older leaves of the liverwort not only indicated an affinity to the liver, but they directly indicated their medical use. The planet Mars was at once associated with iron, roosters, and nettles. The nature of burdocks (*Arctium*) was on one hand associated with plants, but also had something to do with bears - bulk, furriness, „claws" on their inflorescences, etc. Images of Ancient ruins could be seen in smoothed marble or breccia, images of flowers could be found in crystals of antimony or in ice on glass windows. The *de novo* creation of living creatures was quite simple - it was enough just to open the oak gall and in its center was a completely enclosed, „newly created" larvae (the reproductive cycle of the gall wasps /Cynipidae/ was of course not known then). Animals embodied Christian virtues and even vices, they were for instruction, thought, fun, use, and even for warning. This entire system of interrelationships and kinships, which on the one hand gave birth to alchemy, magic, and divination, required a meaningful universe through its aspects, the gods, and obviously could not give rise to a theory of mimicry of the type we know from modern times. Certain examples which we consider mimetic today, were of course described earlier, but they constituted only a small part of the uncountable number of affinities. **G.-B. de la Porta** (1608) describes the similarity between the flowers of the orchid of the genus *Ophrys* and bees and flies right next to the similarity between the flowers of the grain legume, *Lathyrus*, and butterflies. The Cartesian revolution caused the entire system of affinities to be reduced to only a handful, and in the end to only two things: the force of attraction and repulsion, which eventually led to Newtonian physics. The organic interrelations of the Cosmos are replaced by mechanical interdependencies, qualitative aspects of organisms, which mostly cannot be secondarily quantified, loose their importance. The term kinship, which until then had the character of an affinity (kinship between organisms was even recognized by „primitive“ cultures, although their view was a projection of their family structure onto the living world - the sparrowhawk is a cousin of the goshawk). In the strict Creationist perspective of the early period of the modern era, the term kinship was actually based only on similar „building plans“, which the Creator used during Creation. Affinity and even direct affiliation do not have a place in this system, a time-based tree of life depicting the existence of species was unheard of, instead there was something like a close cropped lawn, which depicted the time between creation and the present. By this world-view, kinship, however intuitively intensively felt, was a term colored by vagueness and mysticism. The entire collection of similarities in the living world, whose elements were once considered almost entirely equal to each other, was later radically weeded and only a few were considered significant (eg. the number of stamina for plant classification, which is a criterion resembling numeric mysticism). The requirements for forming exact dichotomous keys were later, more or less without change, projected into the presentation of Lamarck's and Darwin's descendence theory (in biology the word "descendence" is used in a different, basically opposite way from its use in the humanities) and their „tree of life“, which depicts ancestors and descendents according to their affiliation (this picture obviously has its own ancestor in the „*Stammbaum*“ of feudal clans or even earlier in the family trees of ancient gods - in the latter a question similar to today's problem's of cladistics was often asked - if the dendrogram represents real affiliations or only ideal ones). Similarities between organisms is far too common, so the yearned-for „tree“ would instead produce a structure similar to a web. For this reason it is necessary to pronounce those similarities, which unsettle the bridge of dendritic structures, as being only due to adaptation, convergence, which does not require kinship, but is only an adaptation to the given environment (wolf and *Thylacinus*, the "Tasmanian tiger", and fish, dolphins and ichthyosauruses, etc.). For example a penguin is no longer something between a bird and a fish (**Bougainville**, 1772, still understood the penguin in this way and this concept can still be seen in **Lamarck**, 1809, who considered pinnipeds to be the link between amphibians and mammals and woodpeckers to be the link between chameleons and other birds), but a legitimate bird with some specific adaptations. Although most cases are less than trivial, a favorite subject of taxonomical discussions is which features on an organism are adaptive and which are not. Not until 1848 did the English comparative anatomist **R. Owen** (1848) start differentiating between analogous and homologous organs as being organs with the same function, and organs with the same origin, respectively. In the beginning this pertained only to similarities of the following types: coincidental similarities (like the flower of grain legume, *Lathyrus* and butterflies), convergence, and analogy (fish and whales, the wings of birds and butterflies), and true similarities, or structural homologies (the horse and the tapir, the horse-hoof and the nail of the human middle finger). It is unnecessary to stress that in special and non-trivial cases the differentiation between distinct categories was not always simple. Comparative morphology of the first half of the 19th century, especially that of the Germans and French, abundantly used similarities and analogies to explain the anatomical structures of organisms, either within the framework of a specific individual (metamery, chiral similarities within the symmetry on one plane) or within the framework of comparative morphology (e.g. the homologizing of the respective mouth appendages of crustaceans and insects with walking legs). This method of work requires a large capacity for understanding analogies and metaphors and his concept of metamorphosis, which follows in the footsteps of **J. W. von Goethe** (1790), develops ancient archetypal notions of change. Only the above mentioned conceptual system can give birth to the type of discourse, where the existence and rise of mimetic phenomena can present difficulties. An example of a different approach to Nature can be found in an essay by **A. Murray** (1860), which judges that all kinds of similarities in Nature are essentially the same. Murray, an entomologist and eminent anti-Darwinian, saw all similarities, including today's cases of mimicry, convergences, and kinship similarities as being caused by one specific factor, some kind of divine law of mutual attraction between things, something akin to the law of gravity - some of God's creations have a greater, some lesser, affinity to each other and that plays a role in their appearance. The **Duke of Argyll** (1869), who was another serious opponent of **Darwin**, had a similar concept. These concepts where again revived in a transmutated form as so called **nomogenesis**, evolution determined by law, by the Russian zoologist **L. Berg** (1926). This holistic concept describes the biosphere as a single super-organism, where seemingly analogous organisms can evolve (this even includes so-called true mimicry) even over large differences in time, placement in the system, and locality. In this way evolution, complete with a large number of these inter-dependent „rules“, creates similar species in the same way as for example the human right thumb is similar to the thumb on the left hand, without one necessarily descending from the other and also without the need for one to have sprung from the same type of natural selection as the other, but neither is this a question of pure „coincidence“. **Kácha** and **Petr** (1996) revived, in a more holistic way, this concept (without knowledge of Berg's work) for describing similarities in paleontological material concerning trilobites. As is apparent, these problems are not Natures' and live organisms' own (they have of course their own problems, but of a completely different kind), but are caused by the „frictional surfaces“ of a specific conceptual layout of our world, in the sense of **Foucault's** epistémé. These individual conceptual layouts in the frame of their respective argumentations clearly describe living nature „sufficiently“, because they are adjusted to each other and create a meaningful entirety (for example: creation - Creator in Creationism, adaptation - selection - survival in classical Darwinism). It is indeed impossible to imagine observing or understanding living beings and not interpreting them at the same time, but with proper reflection it is possible to minimize this interpretation and most importantly to be aware of the indefiniteness of conceptual layouts, which depends on the frame of thought concerning living beings of the given epoch. It would be somewhat one-sided to pronounce mimetic phenomena as being only a cultural historical category which project into Nature, in which it has no correspondences (e.g. **Heikertinger**, 1954), but it is necessary to have in mind that it is only our internal conceptual layout which allows it to go forth (For most researchers of this specialization such contemplation is wholly foreign - it seems that for science to be successfully carried out, it is necessary not to allow self-reflection and it is necessary to work with abstract categories, which have a complex historical genesis, with the same, or even greater self-evidentness, akin to the handling of the „naive obviousness“ of living beings, like for instance slugs. This situation is not different from successful social existence, where abstract concepts such as „inflation“, „interest rate“, „citizenship“, etc. are dealt with in a similar manner. In the same way, or possibly even more than scientific abstract concepts, these concepts „are“ more, the more they are generally recognized, the more people „believe in them“ and work with them - whereas the functioning of living nature is not very dependent on science, the functioning of society is quite dependent on it's abstract frame).

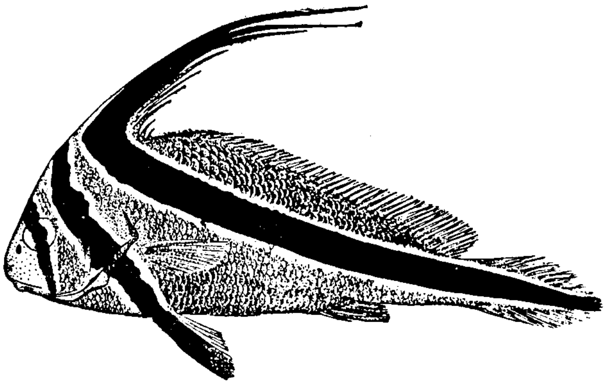
The time-period up to the year 1800

In this era biologists gave the most attention to phenomena, which today fall under the category of **cryptic** phenomena, with most of the research taking place after the Cartesian revolution. Nevertheless, two examples from Antiquity have been recorded. The absolutely oldest mention of adaptive coloration can be found in **Aristotle's** *Mirabilium auscultationes 832(8)* and *Fragmenta varia 371(5)*, which many of his followers included in their own works [**Theophrastus**: *Fragmenta 172(3)*, **Philo Judaeus**: *De ebrietate 174(3)*, **Aelianus**: *De natura animalium II 16(3)*]. Aristotle described an animal, named *tarandos*, from Scythia. This animal, which is about the size of an ox, can beguile hunters by always changing its fur color to match the coloration of the land on which it is or to match the color of the tree under which it lives (most probably this is a distant echo of observations of the changing from summer to winter fur seen on reindeer) - Aristotle also knew about color changes in octopuses and chameleons. The mention itself is interesting because it is the first explicit account of external coloration in the sense of concealment on the specific surface of an organism's habitat, in other words cryptic phenomena as we understand them today. It is also typical that the example does not come from the insect kingdom, which was studied quite sparsely in Antiquity (with the possible exception of social insects), but from the world of large vertebrates. According to Aristotle, the adaptive coloration of the fur also serves to conceal the animal before hunters, so the primary reason is not concealment before natural predators. The third and very typical aspect of this passage is that it is a story or fable, more or less fabricated or strongly twisted through oral repetition, which does not correspond to existing large mammals of northern Russia or of the Ukrainian steppes. It is very characteristic that most new concepts in biological thought emerged firstly as „thoughts in themselves“, in a way completely bare. Examples and arguments were attached to the concept only after some time, and the first few examples are often half-truths or complete fables (this theme will become more apparent later in the text when discussing **Kirby** and **Spence's book**, 1817). This common phenomenon, which occurs not only in the history of discovery and interpretation of adaptive coloration, but also in the whole history of biology (and other sciences), causes quite a bit of skepticism towards the common conception of how observing particularities by inductive method heaps up in the mind of the observer, who then uses them all to postulate a generality - it seems that the process is actually opposite - we could say that a genuine thought slowly surfaces, and only then does it start search for additional arguments from particularities, which at the beginning are partially, or in some cases completely, fictional or inadequate. Only later, after exhaustive searches, are arguments and proofs, which seemed plausible and stood thorough examination, added (a good example of this method can be seen for example in classical Darwinism).

The second mention of cryptic adaptive coloration from Antiquity is in the 8th book of **Pliny's** *Naturalis Historia* and concerns the correlation between the coloration of snakes and the color of the surface on which they live in various countries.

A considerable increase in interest in adaptive coloration, this time concerning insects (insects, with their „machine" character, more closely resemble the early modern period's concept of biological exemplary beings than for example vertebrates), arose in the 17th and 18th century. Some examples of concealing coloration were illustrated by **M. S. de Merian** (1679, 1705), a number of examples are also presented in *Insecten-Belustigungen* by **A. J. Roesel von Rosenhof** (1746-61), where the functionality of the concealment of the various organisms is in depth commented, e.g. the cryptic coloration of the underside of the wings of the central-European brush-footed butterflies, Nymphalidae, or the calm posture of the eyed hawkmoth, later called *Smerinthus ocellata*, during the day, or tropical leaf insects (today the genus *Phyllium*), inchworms which are similar to twigs, etc. It is impossible not to mention the only older mention (from before the era of **A. R. Wallace**), which appears in the 4th part of the before-mentioned book, about so-called aposematical or warning coloration. **Roesel von Rosenhof** on page 197 illustrates and comments on the tiger moth, which was later named *Arctia hebe*, which has a bright black and white coloration on its forewings and a bright black-red coloration on its hindwings. The reflection on the possible meanings of this coloration forces the question of whether or not these wing colors are aimed at predators (bats), but the hypothesis was then discarded because of the argument, that the bats would hunt the moth regardless of the coloration, whether bright or gray. He then comes to the conclusion that the coloration serves both genders for specific identification during twilight (this is an interesting and experimentally unfounded anticipation of the later concept of „species specific" coloration for inter-species recognition and signalization - besides this Roesel von Rosenhof envisioned many other later discoveries, e.g. the male moth olfactory sense for detecting pheromones for locating females). We can also find some references to cryptic adaptations in **Réaumur's** work (1734-42) - e.g. the various cryptic postures of lepidopteran caterpillars. General accounts on concealment coloration in organisms and the resultant protection can be also found in the first part of the poem *Zoonomia* by Darwin's grandfather **Erasmus Darwin** (1794, p. 509) (*„the colours of many animals seem adapted to their purposes of concealing themselves, either to avoid danger or to spring upon the prey"*, on page 511 he mentions the origin of cryptic coloration of bird eggs as being the result of the „imagination of the female", inspired by the surroundings.).

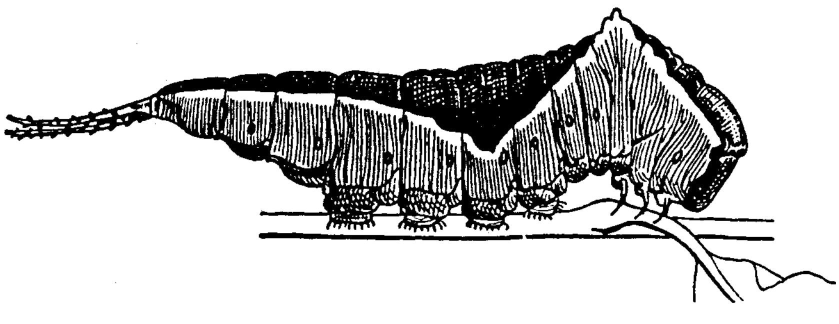
Interest in cryptic adaptations is closely related to another intellectual trend, which was most popular on the Continent in the 17th and 18th centuries: natural theology (**J. Ray**, 1691; **W. Derham**, 1713, 1714; **C. Linnaeus**, 1749, 1750; **F. Ch. Lesser**, 1738, 1744; **H. S. Reimarus**, 1760; **Ch. v. Wolff**, 1725; **Ch. K. Sprengel**, 1793; **W. Paley**, 1802; **J. F. Martinet**, 1777-79; **Ch. Bell**, 1833; **W. Buckland**, 1836). Their intellectual appeal was primarily devoted to pointing out the Creator's power, wisdom, goodness, and foresight by means of describing ingenious adaptations in living nature and in the structure and function of inanimate nature. This type of argumentation necessarily included the silent assumption that wisdom manifests itself through functional purpose. The successfully advancing research of insects supplied one example of remarkable functional design after another, which caused the whole doctrine to be validated over and over again (The constant reaffirmation of the premises of the time's paradigm and doctrines belongs to one of the most popular and never wearisome intellectual activities. The emotional tie to such theses is great and their constant application brings not only „scientific" confirmation but also substantial personal satisfaction.). Natural theology survived the longest in England (on the Continent it was, in its unspoiled form, dead already by the end of the 18th century), surprisingly until Darwin's time. Their method of handling knowledge was similar to all other teachings, which try using some simple formula to describe and squeeze into their systems the whole world, with all of its precarious diversity. The method of argumentation used by natural theology did not encounter many problems when dealing with, for example, pollination, where the ingenuity and goodness of the Creator was apparent for the pious observer. A less suitable object for demonstration of the all encompassing goodness of



Disruptive color pattern on the ribbon fish, *Eques lanceolatus* in combination with the masking of the eye pupil by a dark vertical band that also traverses the length of the iris (according to Cott).

God was, for example, the parasitism of caterpillars by the larvae of the ichneumon wasp, the sight of being eaten alive from the inside was undoubtedly appalling for the observer. But even here it is possible to argue that the victimized caterpillar does not actually feel pain, and that this is the way God made sure that insects won't eat every plant and all the crops, etc. (such forced arguments strongly resemble the desperate attempts by neo-Darwinians to argue away all types of altruism in living nature). In England, a country which was in a way a „social Galapagos", Darwin was confronted with this method of thought and its followers zealously fought against him. Cryptic coloration and various concealment adaptations are especially fundamental objects of interest for natural theology - their functionality and usefulness for their owner is apparent at once (the difficulty lies rather in just finding the animal). Cryptic adaptations (the word adaptation is used here in a broader and more general sense than the neo-Darwinian meaning - as an adjustment to a certain environment or way of life) did not cause difficulties for interpretation even after the Darwinian re-writing of biology - their functionality was again evident and it is more or less simple to see the cause as being natural selection, the selective pressure of predators, which pluck out individuals who are not properly adjusted. Bright coloration, later put into the category of semantic coloration, did not necessarily require a functional explanation in the Creationist model of the world. The Creationist God did not have to explain to anyone His intentions, if the function of some coloration for its bearer is not at first glance apparent, it is possible for the „function" to be merely to please humans. The „function", in the broadest sense of the word, of the coloration might just as well exist for some other unfathomable reason, as is common, generally, for the works of God and gods in general. At this point it is reasonable to undertake a more detailed study of the problem of cryptic coloration, especially because of its simplicity and lucidity, which did not undergo any significant changes during the advancement of research (recounting the history of any branch of study can be arranged either by theme or chronologically, but strictly sticking to either one of these rules fragments the material in the end - for this reason this author eventually decided to combine the two views). We can generally designate those types of external appearances which serve to conceal or cause difficulties in recognition for optically oriented observers as being cryptic coloration (**Wallace**, 1867, understood them in this way and

Disruptive coloration of the caterpillar of the the puss moth, *Cerura vinula*, whose black and white contrasting sections make the organism appear to be made of two parts (according to Cott).

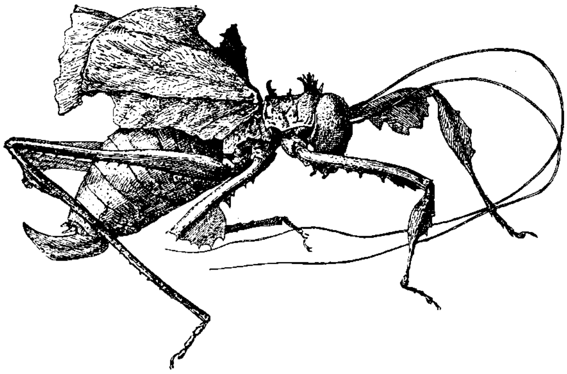


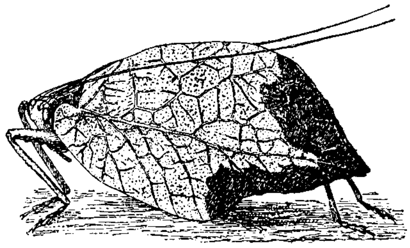
The collective crypsis of the homopterous bug *Ityraea gregoryi* from eastern Africa imitating an inflorescenceof the plants of the family Viciaceae around the twigs (according to Wickler).

used for them the term *concealing colouration*). **Poulton** (1890) divided this coloration into two categories, depending on whether the coloration is primarily meant to puzzle predators and lead them to overlook and spare the prey, or whether it is intended to conceal the predator while it is lying in ambush - the first being **procryptic**, the latter **anticryptic** coloration. Further he distinguished concealment which makes use of foreign objects (some insect larvae, e.g. Trichoptera or Cassidinae), calling it **allocryptic** coloration (from the Greek word *allos* - different). The American painter **A. H. Thayer** (1896, 1909) added two more basic concealment principles, the so-called **somatolysis** (from the Greek words *sóma* - body and *lýein* - to divide) and **countershading** (germ. *Gegenschatten*). The first principle, used intensely for example in military technology, consists of optically breaking the masked object into a number of parts by combining light and dark elements (e.g. the young of pheasants and plovers, many moths). The contrast between elements, additional shading, and similar optical details create the illusion of a number of non-related, often disfigured surfaces, which causes the organism and its form to completely disappear (the masking of the eye or only the pupil using vertical dark stripes, which is characteristic for many vertebrates, also comes under this principle). The principle of countershading then lies in masking bulging surfaces by lightening those parts of an organism which during normal sunshine are in the shade. The resultant optical impression is of a uniform and therefore non-plastic surface (typical instances e.g. most fish and mammals or many caterpillars). It is possible to suitably combine both principles, so for example a sizable butterfly chrysalis seems to be a dry leaf or several similar surfaces without „depth“ (**Süffert**, 1937). We can find numerous examples, illustrations, and more in-depth views of the problem of these two principles for example in **Cott** (1940) or **Süffert** (1932). **Heikertinger** (1919, 1954) distinguishes a delicate division of the category *„unauffällige Trachten“* (he uses the term *Tracht* - garb, costume - instead of the common German expression *Färbung* - coloration intended to accent, not only colorful components and the entire appearance, but also structure - also: to observe in German is *betrachten*), which is divided into *protektive und aggressive Umgebungstracht*, in other words classical cryptic coloration corresponding to Poulton's first two categories and another category called *Mimese* (again protective and aggressive), by which he means being similar to an object which has no importance to predator or the prey. Depending on the imitated object we differentiate between **phytomimesis** (imitation of plants or their parts), **zoomimesis** (imitation by certain parasites of their hosts or the imitation by many insects of ants - these instances are not the subject of this review of one's own crypsis), and **allomimesis** (germ. *Allomimese*), the imitation of inanimate objects (the imitation of dew drops, fallen birds' feathers, surfaces of rocks, bird and mammal feces, etc. which is most common on butterfly and moth wings, or in other cases on insects, spiders, caterpillars, and under special circumstances even plants of the genus *Lithops*,"living stones", which imitate rocks). It was especially allo- and phytomimesis according to the above definitions that attracted in the course of the two centuries of their study the most popularity and enthusiasm. Not surprisingly. The caterpillar form of the inchworm, which imitates dry twigs, including buds and scars from fallen leaves; the aggressive phytomimesis of tropical mantids of the genus *Hymenopus* and *Idolum*, which imitate the flower of orchids; moths or beetles, or even Orthopterans perfectly imitate lichens; the collective cryptic mimesis of the east-African Homopteran *Ityraea*, which imitates many-budded inflorescences, etc. are all fascinating examples (e.g. **Poulton**, 1918). The most amazing examples in this sense are the adaptations of many, especially tropical, Orthopterans, stick insects, butterflies, and moths, whose wings imitate leaves, either living or in various phazes of dying and decomposition, the imitation is also often accompanied by bite marks or marks of skeletation by caterpillars, the mines of endophagous caterpillars or Dipteran larvae in the leaf parenchym including even imitations of their feces, simulations of the sporangia from parasitical or saprophytical fungi including their mycelia, etc. Especially leaf insects (*Phyllium*) enjoyed great popularity, their imitation of leaves goes so far that old or sick individuals become yellow and brown and eventually fall off the branch (the original green color is caused by chlorophyll gained from food). In the same manner, the „dead leaf butterflies“, especially the Asian genus *Kallima*, are one of the essential instruments of argumentation of all Darwinian text-books and of books dealing with adaptive coloration in general („Leaf butterflies“ have a leaf's „middle rib“ on both sides of their wings while the wings are folded, the „leaf moths“ have this pattern on the surface of the upperside of their spread wings between both wing apexes. In the tropics these butterflies constitute a quite numerous group, which is spread throughout various families.). These detailed adaptations, especially in tropical Orthopterans, were studied in the last decades of the 19th century by the Viennese entomologist **Brunner von Wattenwyl**, who worked in the Museum of Natural History. In his works (1873, 83, 97, 99, 1900, 1906) he introduced the term **hypertely** (germ. *Hypertelie* - from the Greek words *hyper* - over, beyond, and *télos* - goal) for describing those cryptic adaptations, which go into such noticeable details - details which, according to him, by far exceed their own goal (meaning to become inconspicuous before predators), farther in fact than is necessary. This phenomenon is really quite apparent, because extremely cryptic are, compared to „slightly cryptic“ species (which survive just as well as their counterparts), quite rare. On the other hand, from a Darwinian standpoint, an adaptation which „goes over the limit“ cannot exist, because as a result of natural selection every species has developed exactly the „correct level“

The leaf butterfly *Kallima inachis* from southeastern Asia is a classical example of „leaf“ adaptation in butterflies and a classical example of the Darwinian concept of mimetism in general (according to Heikertinger).

Two examples of hypertelic crypsis in tropical bush-crickets: on the left *Acridoxena hewaniana* from Gabun, on the right *Pterochroza maculifolia* from Brazil (according to Heikertinger).





necessary for survival (all bearers of weaker adaptations died through the selection process). The fact that this belief is a thing of faith and by definition circular reasoning is something that its believers did not and do not realize. In the same way Brunner von Wattenwyl did not manage to convincingly prove that the opposite is true, that is to prove the hypertely of certain cryptic adaptations in a different way - he only had the instinctive feeling of an experienced systematic entomologist. In any case Brunner von Wattenwyl was later quoted in German literature a few times (**Rádl** 1908, **Handlirsch** 1927, **Heikertinger** 1954), but with the decline of German biology after the WW II all mention of him slowly disappeared (Because of his „different-ness", he didn't appear in Anglo-Saxon literature at all). Attempts to consider cryptic adaptations in a non-Darwinian way were not, broadly taken, very common and they almost always arose from the Continental biological tradition. As early as 1861, **Rössler**, Wiesbaden's court's council and entomologist, mentioned in his article many cryptic adaptations in butterflies, which he considered to be used for concealment from predators, given by Nature but not statically created or evolved through selection. For example he interprets the caterpillar of the eyed hawkmoth, *Smerinthus ocellata,* as imitating withered leaves, where the thorn is the petiole; the „wasp-ness" of the poplar hornet clearwing, *Sesia apiformis,* as imitating a hornet to protect itself from enemies; the buff-tip moth, *Phalera bucephala,* imitating a broken twig.. The wings of butterflies are for him, from the Natural philosopher's standpoint, analogous to the leaves of plants - surface, ribs, straight or jagged edges - there is even an analogy for the plant flowers - their colors are either harmonically combined or contrasted. In the year 1880 **Wagner**, in an article published in the magazine *Kosmos*, attributed a correspondence between the color of an organism and its environment with an instinctive inclination to choose such an environment and surroundings that conform to the organism's exterior appearance (much later certain articles, e.g. **Longstaff** 1906, 1912; **Sargent** 1968, 1969a, b confirm this meaning in the case of butterflies and moths in the sense of the active finding of their resting spots in their micro-habitats). Certain authors from the beginning of the 20th century, for example **Eimer** (1897) or **Piepers** (1903) saw cryptic coloration as a process of „photographing" or suggestion from the environment, which operates through the optical nerves (especially in the case of color „adjusting" to the environment in animals with extensive color-changing abilities - cephalopods, certain fish, for example flatfish, chameleons, certain Orthopterans, etc. - where such a phenomenon really exists and optical perceptions play a very important part). It is essentially the same concept as the one Darwin used to explain the development of instinct - behavior which is often repeated by habit becomes inbred, in a way it is built into the animal's „hardware". In the same way, according to Eimer's and Piepers's concept, cryptic adaptations are something akin to slow or „oozing" color-changing. These notions where indeed, again by **Rádl** (1908) or **Heikertinger** (1954), cited, but mostly they were not taken too seriously within the framework of Continental biology (Heikertinger saw the genesis of cryptic surface designs as a realization of immanent tendencies of the organism and more or less did not accept their adaptive significance in relation to predators in general). On the whole it is possible to say that cryptic adaptations traditionally belonged to the least controversial of topics (and were also the first to be studied in detail). Even the theory of cryptic adaptations has its weak points, for example the desert ochre cryptic coloration of the desert sub-species of the Eurasian eagle owl or certain birds of prey from the same habitat, even though they practically do not have an optically oriented enemy, which would endanger their lives and thereby cause selection to occur - neither is concealment for hunting prey, due to their method of hunt, feasible.

It is interesting that nobody from the Continental school attempted to interpret cryptic phenomena using **Jung's** and **von Pauli's** (**Jung**, 1952) principle of synchronicity, or rather in this case „syntopicity", for which it would be an almost ideal subject (synchronicity is understood by Jung and von Pauli to be the cumulation of phenomena, which require joint interpretation - in this case optical phenomena) in space and time (even various other mimetic phenomena would fit into this thought system very well). It is important to know that Jung's and von Pauli's (and also **Kammerer's**, 1919) principle of **synchronicity** goes against the whole range of modern science with its principle of causality (acausal synchronicity is its complementary principle, which certain non-European cultures, for example the Chinese, accentuated much more, practically exclusively) and if we identify science with the principle of causality, the idea of synchronicity becomes „outside of science" or „non-scientific". Surprisingly, neither von Pauli and Jung nor any of their followers, who usually did not have a biological education, called attention to mimetic phenomena in nature from their perspective: An attempt at re-interpreting mimetic similarities from a Jungian psychological perspective: if we take the term *psýché* as meaning the totality of autonomous dynamics and self-construction of an organism (a middle-ages scholastic saying states that „*anima est forma corporis*"), then mimetic parallelism of the external form would remind us of inter-psychic connections between people who are close to one another, which causes for example the induction of psychic symptoms in otherwise healthy individuals by their sick relations (the well known phenomena *folie* à *deux*). Considering the fact that modern science does not operate with the term *psýché* in this way, the interpretation of mimetic phenomena in this way lies outside its scope of interest, but in any case this analogy seems to be quite useful.

The time-period from 1800-1860

Considering that mimetic analogies, that is an analogy between the external appearance of two relatively non-related organisms, of all groups of animals are more common in the tropics than in the temperate zones, it was possible to see some of the more prominent examples accentuated by the most largest colonial power of that era, Great Britain. British biology from the first half of the 19th century (to an extent the second half as well) was, compared to Continental biology, which was considerably state-financed (in France the series of museums under Paris's *Jardin des Plantes*, in Germany the network of essentially provincial universities), different (besides other things) in the fact that it was basically composed of wealthy amateurs (up until the fifties basically the only professional biologist in England was **R. Owen**). Another very important fact was the close links between this amateur biology (in the style of „*natural history*", meaning systematics, observation, and later even attempts at ecology) and the Church of England. An important entomologist from this social context was for example **W. Kirby**, who will be dealt with later. One more typical characteristic of this British biology was its close ties with colonial quarters, in the first half of the 19th century this primarily included Australia and India, in the second half also Africa. A number of colonial officers exchanged the boredom of the tropics and the traditional „pleasures" of army life for hunting and later organized collecting and field observations of animals and plants, which exceptionally increased not only their horizons, but also the horizons of their colleagues at home, who were kept well supplied with interesting material and observations. In comparison with German and French biology, which concentrated on the study of less exotic organisms, the British had an indisputable advantage for the first studies of mimicry. German biology at the time, just when their romantic natural philosophy was at its apex, was concerned primarily with embryology and animal and plant ontogenesis (the type of viewpoint of the natural philosophers favorable for understanding changes and transformations in general, „static" descriptive branches was also developing, but was considered second-rate). The differentiation between „essential" and „accidental" markings was not possible for this perspective, one which followed in the footsteps of a number of models from Antiquity and the Renaissance, so this perspective did not concern itself with mimetic analogies, which are very rare in the central European area anyway. Of course, the problem of analogies was of interest for romantic biologists, for example **L. Oken**, but it was often understood in a much broader sense and in a metaphorical way, like the analogy between genera and families, if not between greater systematic groups (even analogies between individual plant and animal groups have been „found", and similar, more or less poetic, points of view examples also existed). Some of these accounts were strongly contaminated by numerical, or geometrical mysticism in the form of cyclic, penta-, or hexagrammatical systems of mutual correspondence (e.g. **F. Kaup**, 1844). Although the situation in France was a bit different, the biological discussion was centered on the structural plans of various animal groups and their mutual transformability (therefore they centered on „essential" and not on „accidental" marks), or they worked on historical geology and the applications of **Cuvier's** theory of cataclysms on it, but not even this was fertile ground for studying mimetic analogies. Generally speaking, the era of „national schools" of biological thought had already started in the second half of the 18th century, which coincided with the development of the modern state in European history, so they used their national languages for their publications instead of Latin, which was used up until then (in the case of the „German" school the language used was not really national, but a scientific-communication language with a wider range of use, which encompassed almost the whole Continent, not including "Latin" countries). The different language structures of these individual national schools alone led to different thought contents becoming more or less prominent. The total life span of the national schools of biology can be said to have begun in 1790 and to have ended in 1945, at which time the prestige of the German language as the language of science drastically fell and the „German" territory, which suffered large personal and economic losses, fell into insignificance, if not disdain (at the same time the importance of the French language was lessening, and so the only predominant language - and perspective - in biology became the English language, though at this time coming more from the U.S.A. than from Great Britain). The particularities of the different concepts of these schools will be dealt with later on, but at this point it is necessary to state that the idea of some supra-national, „objective" science, independent of language, cultural context, and the influence of the so-called greater history and its intellectual impact, is utterly fictional for everyone, who has ever, even if only superficially, dealt with the history of any scientific discipline. Every cultural environment is sensitized for certain perceptions of aspects of living nature and for a certain type of thought processes associated with them. Today, after the fall of the national schools of science, it is again possible to loudly proclaim the unity of the Sciences and that it represents a cumulative process of acquiring knowledge, during which nothing, or almost nothing, is lost. This standpoint is completely misguided, the more so thanks to the fact that libraries (primarily central European ones) as still full of traces left behind from the previous „schools", which are of a completely different style and which are quickly sinking beyond the horizon, including factographic details and even complete intellectuals conceptions. It is certainly true (as was stated in the introduction) that for the following generation of scientists to be able to „major" in their specialization it is necessary to, in some way, rid ourselves of the burden of accumulated traditions and particularities and to create a wide open space for new studies and concepts. Nevertheless, this process should not be unconscious and we should retain at least an idea of what was „swept under the carpet", how it was different from our concepts, and where we could possibly find it, if the need arose.

The rather archaic situation in British biology, which with its interest in forms and their description and bionomy rather reminds us of the biology of Linne's era [the most important forum for this type of biology was in any case the *Linnean Society* and their printed debates (*Transactions of the L. S.* - we can find a short mention of the camouflage techniques of the crabs using brown algae as early as 1801 on page 389)], in conjure with the study of imported foreign forms led to an eventual awakening of interest in mimetic analogies. In the 21st chapter (which was written by W. Kirby alone) of the second volume (1817) of the well-known entomology textbook written by **W. Kirby** and **W. Spence** (volume I., 1815, volume II. 1817) we can find various observations on the defensive abilities of insects against their natural enemies. W.Kirby describes various cryptic and phytomimetic phenomena (it is specifically for this phenomena that he firstly uses the term *mimicry*) found in beetles, moths and their caterpillars, bugs, mantids, and stick insects. He also describes the masking of the larvae of the leaf beetles *Lema merdigera* and *Cassida* by way of its own excrements. His conclusions concerning certain extreme phytomimetic phenomena are also very interesting - the South African bladder grasshopper of the genus *Pneumora* (all names have been preserved in their original form, which is quite different from today's nomenclature) who's pink elythra imitate a flower, the Brazilian leaf beetle *Chlamys bacca*'s imitation of a red berry, the histerid beetle *Hister sulcatus* reminds us of the seeds of umbelliferous plants, etc. Specifically the astonishing similarity of the Brazilian stick insect of the genus *Phasmia* to a dry twig led to the first use of the term „mimicry". They were also the first authors to mention an instance of true mimicry, in today's sense of the word, which was the similarity between the hoverflies of the genus *Volucella* and *Pterocera* to bees and bumblebees - in this way Providence made sure that they could enter bees' nests and lay eggs undetected, which under different circumstances could cost them their lives (he mentioned the species of *Pterocera bombylans*: *„... a different kind of imitation, affords a beautiful instance of the wisdom of Providence in adapting mean to their ends*" - page 223; surprisingly the author completely neglects to mention the clearwing moth *Sesia oestriformis*, pictured at the end of volume I.). Another interesting aspect of their work is their anticipation of future „conventions" concerning pseudo-aposemantic coloration (not established until 1907 by **Prochnow**), this can be seen in their description of the Brazilian swallowtail butterfly *Papilio Menelaus*, which allegedly blinds and confuses birds, which would like to eat it, with its very bright luster. The ruby-tailed wasps (*Chrysis*) also blind other Hymenoptera (bees, wasps, *Bembex*), whose nests they parasitically use, with their glossy metallic colors (here the author defers to the expert **P.-A. de Latreille**, 1802, a museum entomologist in Paris, who wrote of this and many other defense mechanisms of insects used against their enemies). They also concentrated in detail on chemical defenses based on discharges of toxic blood and other repugnant secretions - they anticipated the later idea of the sequestration of insect toxins from their feeding plants in a very interesting manner, except that the example of the oil beetle *Meloe proscarabaeus* and the crowfoot, *Ranunculus* is very poorly chosen (the situation where the idea precedes concrete examples, which would prove it, is quite common in science and was discussed in more detail in the preceding chapter). The same category of phenomena includes the description of the osmeteries in the swallowtail butterfly *Papilio machaon* caterpillar and the explanation of their repugnant functions as „fennel odor". From the rest of the diverse descriptive repertoire (exempting stories of stiffening posture, defensive displays, luminescence, stridulation, etc.), especially the account of false heads in butterflies are of importance. The false heads of the butterfly called *Hesperia jarbas* are caused by the projection of the hind wings, which look like antennae (at their base they even have an eye-spot). When the hindwings move (which obviously causes the „antennae" to move as well) the impression of the false head is even strengthened. The authors conclude that this phenomena works to confuse and frighten the butterfly's enemies. The paragraph concerned with the mandibles of certain beetles (*Lucanus cervus, Prionus cervicornis*) and the dark and foreboding appearance of others (*Scarabaeus, Cicindela, Carabus*) and the deterrent effects on children, which then (sometimes) protects the insects from sadistic manipulations is in itself especially pleasing. This paragraph is interesting for another reason as well - it is one of the oldest text in which such activities of children are condemned - in times past these activities where considered to be quite legitimate. Kirby and Spence also marginally mention the great reproductive power of insects (besides which, the book came out after the publication of **Malthus'** *Essay on the Principles of Population* - 1798) as a method of resistance to their enemies, but they do not mention any of the possibilities of natural selection which arise from this theory (the large overproduction of offspring was almost generally ignored in the pre-Darwinian era and it is not a simple coincidence that it was first noticed in humans by Malthus, and only later „discovered" in nature - this theme will be discussed in detail in the chapter about Darwin). Both authors were absolute believers in creationism (in another work Kirby uses the term „Creative Wisdom") and saw the potential similarity between insects of the type *Volucella* and *Bombus* as being the result of a decision of Providence, bright coloration was almost always seen as being decorative. In the first volume of their book (page 12) Kirby undertakes an „exegesis" of the external appearance of insects in general - insects carry on their exteriors geometric patterns, maps, numbers and letters, heraldic symbols, they have fins like fish, beaks like birds, horns like quadrupeds, and other imitations. Not only do they imitate all sorts of things in nature, but „*may be regarded as symbolical of beings out of and above the nature*", as emblems or ideas pointing to supernatural beings („*blessed inhabitants of other worlds*", „*evil demons*", „*impure spirits*"). **Linné** and **Fabricius** are cited here as authorities on the subject, using on occasion generic names from demonic terminology (*Belial, Beelzebub*, etc.). Of course the authors did not believe that insects themselves were manifestations of demons, but their strong symbolic significance, given to them by the Creator, was not denied (they judged the portrayal of a skull on the thorax of the deaths-head hawkmoth in a similar way: vol. I., page 35, vol. II., page 241 „*symbol of death*"). Both were enthusiastic „*insect friends*", and regretted that the general public considered entomology to be a childish pursuit and a narrow-minded pedantic study. Besides numerous entomological discourses W. Kirby also wrote one piece from a natural-theological series (The *Bridgewater Treatises*), which was sponsored by the foundation of the Earl of Bridgewater (**Kirby**, 1833). Kirby's curriculum vitae as one of the leading British entomologists and from the year 1833 as the chairman for life of the *Entomological Society* can be found in the work of **R. B. Freeman** (1852). Kirby's son continued (**Kirby**, 1883), in the tradition of natural-theological works, including works on the problems of mimicry, in his father's work. In 1819 and 1821 two volumes of the work „*Horae Entomologicae*" by **W. S. MacLeay** were published in London, which is a detailed taxonomic account by a very professional and thoughtful author with deeper theoretical knowledge than that of the strait-forward natural-historical enthusiasm of Kirby and Spence. In volume II. (page 365) he describes the similarities between certain flies (hoverflies - Syrphidae) and hymenopterans, further he extensively analyzes the question of differentiating between **affinity** and **analogy** in nature. He returns to this question in an article in the *Transactions of the Linnean Society* read in the year 1822 (**MacLeay**, 1823), which is a debate concerning the newly published mycological work of **E. Fries** (1821). In the world of organisms he divides similarities into two parts: essential similarities, which is basically a similarity of important features (in plants this is for example the number and configuration of stamina, in insects the structure of the mouth apparatus and its details) and secondly superficial similarities, which are similarities in less important features, especially external conditions like appearance, form, color, or patterns. The first case, which denotes kinship, is called an affinity, the second an analogy. Talking about one organism being related to another was a problem in this prevalently Creationist era (Lamarck's opinions on descendence were not even taken seriously in France at that time, in England they were more or less unknown). This is because this kinship did not signify a common ancestry in the sense of affiliation, but the definition pertained to a sort of inner kinship similar to the spiritual closeness of two very good friends. It was, of course, possible to group various species into a linear series according to their corresponding features, or even to group them cyclically, where these cycles would in places touch. Species connecting various branches or cycles that contain the essential features of one branch and the accidental features of the other, were are of primary interest for MacLeay. Possible gaps in the series or the cycle are explained as belonging to species not yet discovered (at that time quite a probable possibility, or as belonging to species which were destroyed by cataclysms of the geological past). MacLeay had no doubt about the existence of missing species, because nature does not „jump ahead" or leave gaps - earlier Enlightened biology denied even the possibility of extinct species, much in the same way as Ohms law cannot „die". Cases, which today are considered to fall under the category of true mimicry and cases of external similarities (which today are grouped under the category of convergence or „coincidental" similarities) at that time belonged under the category of analogies, or, in other words, the category of accidental similarities. And it is this category which interested Kirby in his study of three non-European beetles and one dragonfly, which constituted the content matter of a piece published in the same year by the same magazine (**Kirby**, 1823), which was a reaction to MacLeay's article and a practical application of his principles. At the same time nobody expected that the „model" and the „mimic" live sympatrically in the same area (for the powers of Creation as causes of similarities it was not necessary). From Linné's era such „out of bounds" (unexplainable) species were often labeled with the suffix *-formis*, before which was placed the fore-label of the given „model" (*Sesia apiformis*), but these cases were never commented or explained in detail - the Creationist God is free in His decisions and such extravagances are fully within His powers - the goal of an entomologist is only to assess the „essential" attributes of the given organism and to correctly taxonomically categorize them. MacLeay saw very extensive analogies and correspondences even between quite distant groups (for example between mushrooms and echinoderms) and that the whole system has, as is the case with certain German natural philosophers and biologists influenced by natural philosophy, certain mystical aspects concerning geometry, especially concerning symmetry and cyclicity. A number of other British taxonomic studies published in the thirties and forties of the 19th century (**Shuckard**, 1836, **Strickland**, 1840, 1841, 1846, **Swainson and Shuckard**, 1840) also studied the theme of affinities and analogies in (especially insect) systems. Usually the goal of these studies was to circumvent the „erroneous" grouping of species into taxonomic categories based on „analogies". Similar opinions occasionally appeared in the second half of that century, especially in the United States, which were at the time going through a kind of late „natural philosophy period". This applies the most to **L. Agassiz** (1807-1873), originally a French Swiss who later emigrated to the United States and founded his biological school of thought. According to him (**Agassiz**, 1858), the specific features of a species were those, which were essential and which did not change in the course of the geological evolution of the species (even though he accepted this principle). From this point of view, for example, the hoverfly is a real wasp, which abandoned its „waspness" and basically moved through the course of eras into the dipteran category. These aberrant cases of specific features (in this case freed from their „hymenopter-ness", on which they would in their original state depend) are easier grasped. The American paleontologist and vertebratologist **E. D. Cope** had similar views, he also repeatedly pointed out the taxonomic heterogeneity of the so-called coral snakes complex in American snakes (this is a complex of various species with similar red-black-white coloration, which belong to different families, Elapidae and Colubridae, which are numerous in warmer climates of both of the Americas). In his view the attributes of organisms including form, coloration, etc. are not infinite in number and at the same time are more or less freely combinable, in much the same way as chemical elements are, for example (**Cope**, 1887). He interpreted the before mentioned phenomena of coral snakes (**Cope**, 1860) and many more of his paleontological discoveries by this method (many combinations of basic „elements" of the living world, in today's time unknown, existed in the past). He admitted, like Agassiz, that one species can be part of various families in various geological eras and in the course of its evolution keep its most constant attributes, size, and general appearance. Cope called „parallel" evolutionary branches (marsupials and placentals, Diptera and Hymenoptera) *homologous series*, and the corresponding species within the series are called *heterologous*. Similar opinions, based on the assumption that species can suddenly undergo „essential" changes without a noticeable change in appearance, were held by the before mentioned **Brunner von Wattenwyl** and the Viennese phytopaleontologists **Ettingshausen** and **Krašan** (1890). The British entomologist **J. O. Westwood** followed up on MacLeay's arguments with a piece read in the year 1837, which again appeared in the *Trans. Linn. Soc.* (**Westwood**, 1840b). His preliminary piece was published in the

Magazine of Natural History (**Westwood**, 1840a). In the introduction he again discusses and brings into context the terms affinity and analogy (The nightjar and the swallow are analogous in the bird class, the relation between them and bats is again analogous, but in this context their similar appearance is in fact a true affinity, or in other words kinship. On the other hand, in the relation with dragonflies, birds and bats are analogous, but in the same situation, taken from the view of vertebrates, the relation between the two groups is a true affinity.). In his work he then presents us with a number of non-European insects, which today would be classified as distantly convergent in form to members of different families (not even the Darwinian view differentiates perfectly between convergence and mimicry - if convergence has been caused by „similar selective pressure“, and if the selective pressure is caused by predators and not abiotic factors or food types, then such cases fall under the classification of „true“ mimicry as well). What was most interesting for future developments was Westwood's description and illustration of Java's bush-crickets *Condylodera tricondyloides*, which is virtually indistinguishable from the tiger beetle of the genus *Tricondyla* (for some time Westwood even had it placed in his collection under a series of this insects). As an extra to this remarkable analogy Westwood adds that both forms come from the same region, that is Java (let us add something, which is not present in the piece, namely that both insects in their entirety compellingly remind us of large ants). The entire phenomenon is not commented any further.

In a similar way the French entomologist **Boisduval** (1836) mentions the external similarity of three butterflies from the region of western Africa, which are not closely related (*Euploea Naivius, Diadema dubia, Papilio Westermanni* - the original names). The mention, which appears in his book on butterfly taxonomy (page 372-373), is also without further comments. In 1839 **G. R. Waterhouse**, the curator of the London *Zoological Society*, published a taxonomic study of South American and other exotic insects, which were collected during the expedition on the *Beagle*. He also diligently differentiated between analogies and affinities and pointed out mimetic species, which copied the external appearance of other species – a weevil imitates a beetle of the same family (genus *Lixus*) and the ruby-tail wasp imitates beetles of the genus *Mordella*. We can also find a number of examples of mimicry in the unpublished journal books and collections of the British traveller and collector **W. J. Burchell** (**Poulton**, 1909). The long-horn beetle *Promeces viridis* (Cerambycidae), which he brought back from his South African expedition, imitates the digger wasp of the genus *Sphex*, and even though it was labeled *Sphex totus purpureas*, it was classified correctly and placed in the correct slot (this trip also gave birth to the wholly natural theological explanation for the cryptic „stone“ coloration of a desert grasshopper, *„Gryllus“*, which appears in his book of travels from the year 1822, page 311. The same book also contains the oldest description of cryptic and mimetic phenomena in plants - this will be discussed in a different chapter). One of Burchell's handwritten accounts from his South American expedition was preserved, and in it we find a record on bugs which imitate different orders (the nymph of the genus *Alydus* imitates an ant, another species *Luteva macrophthalma* imitates the digger wasps not only in appearance but also in movement of its body and antennae) and another record concerning spiders from the family *Salticidae*, which imitate ants, again both in appearance and movement. Because Burchell never published these finds, they were lost and were only much later found and put to paper as a historical curiosity by Poulton.

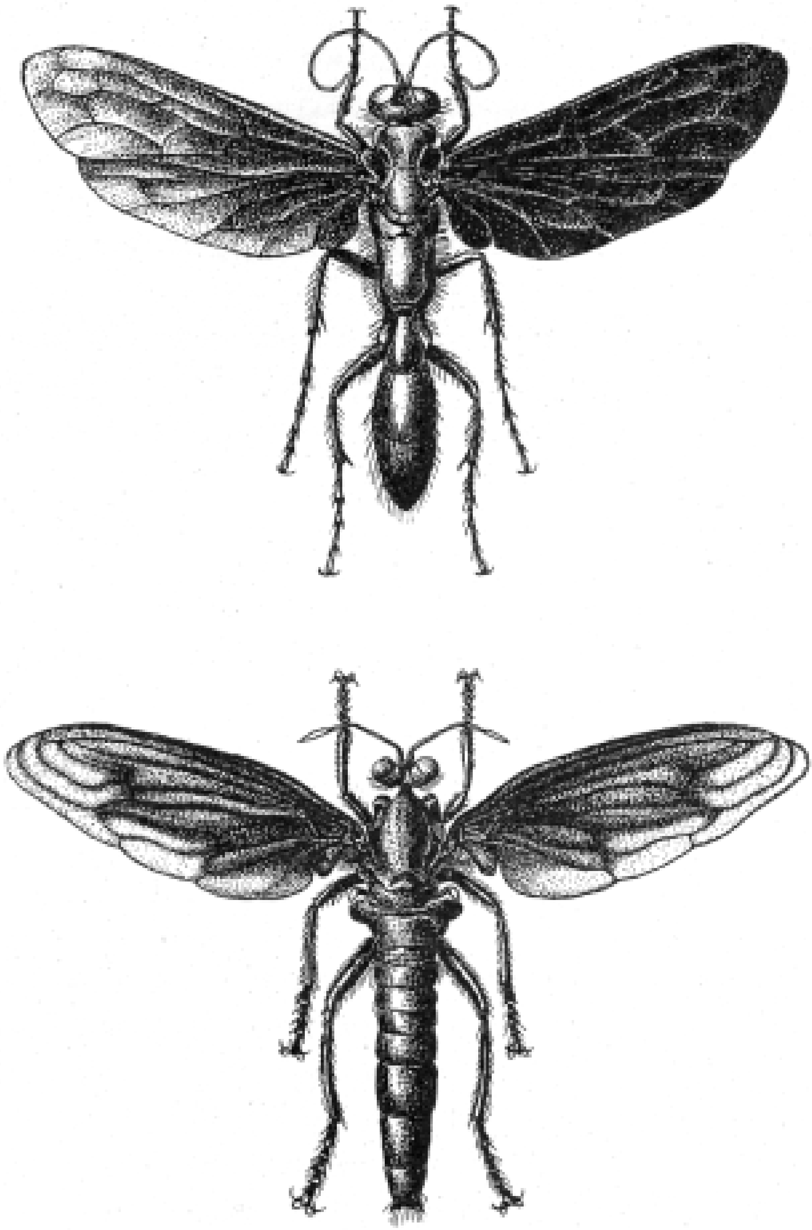
The work of the Berlinian entomologist **A. Gerstäcker** (1863), which was published in the *Stettiner Entomologische Zeitung* definitely belongs to this era, even though the work was made public only after the publication of Bates' breakthrough article (Gerstäcker knew of this piece and even cited it, even if only in connection with the mimicry of bush-crickets from the genus *Scaphura*, which mimick sand wasps, but not in the main section). In his work, which later almost disappeared, he does not even use the term „*Mimikry*“, but instead „**formal analogy**“ (*Formanalogie*) and these similarities are not interpreted through selection, he doesn't even contemplate the advantages this could bring to the bearer. Their functional explanation is left for a later time when their biology and their interactions with predators will be known in detail - until then the interpretations will be only speculative. Gerstäcker calls special attention to the „sensible“ meaning of similarities between three specific species of flies (which are parasites of bumblebees) and their hosts (*Volucella, Mallota,* and *Criorrhina* x *Bombus*) and further on the analogy of form between prey and predator (bush-crickets *Scaphura Vigorsii, S. nitida* and *S. ferruginea* x spider-hunting wasps of the genus *Pompilus* and *Pepsis*). He describes in great detail the analogy of form between the Brazilian bush-crickets of the genus *Phylloscirtus* and the tiger beetles of the genus *Odontocheila* (Cicindelidae) and additionally between the Philippinean bush-cricket *Scepastus pachyrrhynchoides* and the weevil *Pachyrrhynchus venustus* (Curculionidae), which is imitated by the prior species perfectly not only in shape, but more importantly in its metallic luster. He also calls attention to the fact that analogies of form often occur in the same country, even in the same locality, but he does not deduce the cause as arising from selective pressures of predators. He also mentions the analogy of form of various stages of larvae, in which the end result is quite diverse, for example the great similarity between the hairy caterpillars of the moth *Acronycta* (Noctuidae) and the tiger moth *Arctia* (Arctiidae). He considers the external appearance of the swallowtail, *Papilio* /this can be seen not only in butterflies, but also in the moth families Uraniidae (the genus *Urania*, *Nyctalemon*) or Geometridae (*Ourapteryx sambucaria*)/ or the appearance of the beetles of the genus *Lycus* (the similarity of the family Lycidae will later be considered a typical example of Bates' mimicry) to be exceptionally common. His work mentions a large number of species pairs, which were later interpreted as Bates' mimicry, including the example mentioned by Westwood (*Condylodera* x *Tricondyla*) or later the famous case of the species *Papilio dardanus* (*P. Hippocoon* x *Danais Niavius*), described by **Boisduval** (1836). He also mentions a number of apparent similarities /*Drepanopteryx phalaenoides* (Neuroptera) x *Drepana lacertinaria* (Lepidoptera)/, which were later classified as incidental. **Gerstäcker** also published another work, in which he voiced quite a reserved opinion of Darwin's concept of mimicry (1874) - the study of formal analogies in butterflies by the before mentioned **A. Rössler** (1880) was written in a similar tone, and although it was published very late, it reverted the intellectual atmosphere back to the years before 1860, just like the work of **Thieme** (1884).

The time-period between 1859 and 1900

This co-called „classical" era of research of mimetic phenomena is enclosed by two dates. The more important of the two is the year 1859, which is the year of publication of the most important of Darwin's books *On the origin of species...* (**Darwin**, 1859). The era ends with growth of importance of **E. B. Poulton** a short time before his gaining the title of professor of zoology at the Hope museum of Oxford University (1893). After the fading of the first wave of interest and discussion in the sixties and seventies of the 19th century came the fading of interest in the eighties in mimetic phenomena and publications about them, this had been revived when Poulton became an established specialist.

The first Darwinian oriented works on mimetic phenomena

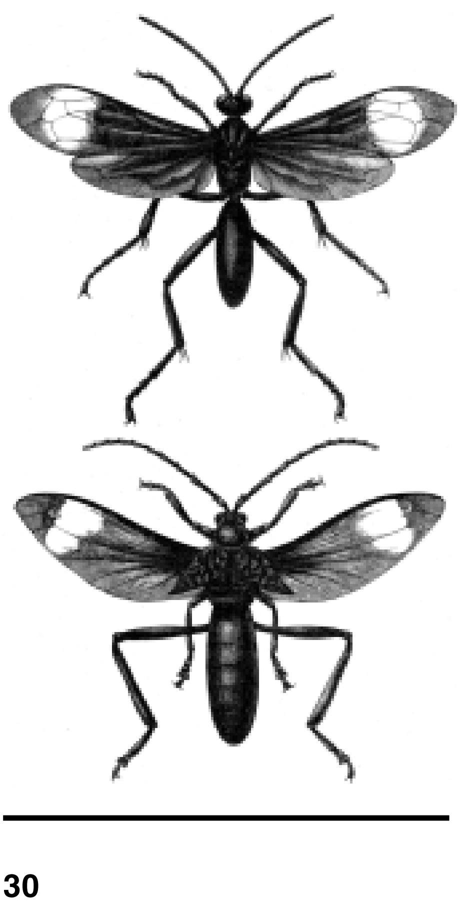
This entire era is in the context of the research of mimetic phenomena dominated by British authors, Continental publications make up only a small fraction of the whole. Practically all specimens of study, on which research rested, are tropical butterflies, which continue to be a dominant theme for the research of mimetic phenomena for all later eras. Long before Darwin's book was published a small relatively unnoticed event had a unusually strong impact on the research of mimetic phenomena, it was the departure of the enthusiastic amateur entomologists (and biologists in general) **A. R. Wallace** (1823-1913) and **H. W. Bates** (1825-1892) for Amazonia (in 1848), where they intended to search for the „origin of species" on the spot (besides other factors, they were also influenced by reading a popular evolutionary essay published anonymously by **R. Chambers**: *Vestiges of the natural history of creation*, 1844). Neither one had a university education - Bates was originally a store clerk and amateur entomologist, Wallace worked before their departure as a geodesist and teacher and both of their finances were quite limited. It is good to remember that such an expedition, especially in view of the length of their stay (Bates 11 years, Wallace 4 years), was at that time practically suicidal. In today's world there is not any place as remote and dangerous as the Amazonian basin was back then. Both protagonists were at that time a bit over twenty years of age and the few people that knew them did not count on their return. Bates' and Wallace's unusually strong friendship was the cause of much gossip in Victorian England and from a psychological point of view it would be quite interesting to study to what extent can personal experiences motivate the sublimation of types of research such as the study of „deceit and imitation" in the living world by use of the sciences. After a number of years of traveling together both of the researchers departed and started working alone. Wallace returned to England in 1852 and lost all his painstakingly acquired collections during a fire onboard ship. Endowed only with his experience as a biologist in the tropics and a bit of money, which he collected from the insurance



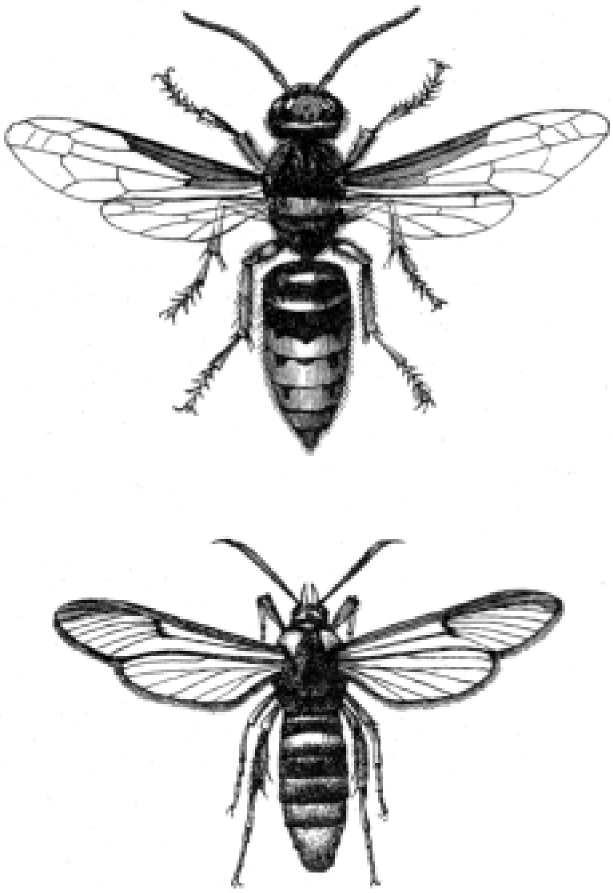
An example of Batesian mimicry: at the top the spider-hunting wasp *Pepsis ruficornis*, at the bottom the imitating fly *Mydas praegrandis* from South America (according to Jacobi).

company, he left for British and Dutch holdings in south-eastern Asia, into Malaysia and today's Indonesia, where he stayed until 1862. On the basis of his two essays, which he sent to the Linnean Society, **Wallace**, 1855, 1858, in which he independently of Darwin formulated the theory of organic evolution based on natural selection, he caused Darwin to „prematurely" publish his book (excerpts from this book were published at the same time as Wallace's second article from 1858), which happened in 1859. In the same year **Bates** returned with a large collection of South American insects and immediately he became acquainted with the new book, which was the subject of interest and many discussions for not only biologists, but for the general public as well. During the preparation of caught butterflies of the genus *Ithomia* (family Ithomiidae, in the sense of that era Heliconiidae) he discovered that amongst these specimens there are always a number of almost indiscernible butterflies, which belong to the family Pieridae and the genus *Leptalis*. On the 21st of November, 1861 at the meeting of the Linnean Society he read a lecture on the theme of butterfly fauna from the Amazonian basin (the family Heliconiidae in the sense of that era) and in the following year this extensive, detailed, thorough, and in its approach to the problem of analogies in insects wholly new work was published in the *Transactions Linn. Soc.* (**Bates**, 1862a). Even before Bates' lecture, mimetic analogies in insects were presented and discussed in London's entomological society, in the years 1833-61 eleven times - the last six were concerned with material sent by Bates and in the year 1860 he carried on the discussions and presentations himself. Unfortunately no extensive work came of these social events. Mentions of the strange genus *Leptalis* and its analogical capabilities can be found also in Bates' letter, published in the magazine *Zoologist* (**Bates**, 1858) and of the strange group of families „Heliconiidae", which are difficult to identify in the field, probably newly created (*modern creation*), not fixated very much, and perceptive of the effects of their surroundings, nonetheless they do not copulate between themselves and they probably do not interbreed. This appears in Bates' letter published in the *Transactions Ent. Soc. Lond.* (**Bates**, 1859). This theme (*mimetic analogies, mimicry*) is discussed on pages 502-515 of the above-mentioned journal. In the extensive table Bates calculates all mimetic analogies between South American butterflies which he noticed (there are a great many of them and include the families Papilionidae, Pieridae, Danaidae, Heliconiidae, Ithomiidae, Erycinidae, Nymphalidae, Castniidae, and Pericopeidae in today's sense of the terms). From this large amount he was the most interested in and documented the best the analogies between the before mentioned genus *Ithomia* and the genus *Leptalis*. These similarities between local varieties in external appearance (*dress*), already known at that time by his colleagues and later generations of entomologists as „local coloration" or „*genius loci*", a sort of „locally dominant fashion", is reinterpreted by him on the basis of newly created Darwinian concepts - Bates in his article still speaks of affinity and analogy in the **MacLeay** sense, but he also speaks of adaptation and selection. That era was above all concerned specifically with the species transmutation, the creation and transformation of species, not higher taxa (the Enlightenment idea of constant species was still very much in effect, **Darwin's** principle work was not entitled for example *On evolution*, but *On the origin of species ...*). Bates establishes a similarity, or even a sameness between this phenomena and cryptic adaptations and imitations of nonliving objects (which was then known as *mimicry* in **Kirby's** sense of the word - this custom endured for a very long time and even today the general public associates the term mimicry with „defensive coloration"). By way of this analogy he then begins an account of the possible ways in which the strange adaptation of the genus *Leptalis* can be advantageous, or using Darwinian terms, which selective advantages result from the adaptation. He comes to the conclusion that the genus *Ithomia* (and actually the entire family Heliconiidae by that era's definition) are in some way unpleasant, unpalatable (this was probably derived from some unpleasant smell) for their predators (mostly birds and dragonflies). He comes to this conclusion because butterflies belonging to this group, in spite of their slow flight and abundance, are rarely hunted by birds, while the Pieridae (he did not analyze the genus *Leptalis* on purpose), which fly much faster, are hunted (later he also inquires into the possibility of repellant glands in the Heliconiidae). Because the whole problem arose only from imported specimens and under the influence of Darwin's new publication, these claims are based only on a combination of speculation and experience in zoological fieldwork and not on experiments with various birds' butterfly diets, which were carried out later (a precise observer like Bates would never have passed over similar experiments, but after their return it was too late and the possibility of returning to Amazonia to carry out these experiments did not even cross their minds; even though this was, from a scientific point of view, the weakest part of the entire publication, it was not criticized - the elegance of thought of the entire work and the enthusiasm over a new, unexpected application of Darwin's theory by far overwhelmed even the voices of would-be critics).

An example of Batesian mimicry: the spider-hunting wasp *Mygnimia aviculus* (top) and its imitator, the longhorn beetle *Coloborhombus fasciatipennis* (bottom) from Borneo (according to Wallace).



Bates saw the usefulness of this application of mimetic adaptation in the fact that the „tasty" *Leptalis* hides in the company of „uneatable" butterflies of the genus *Ithomia*, which protects it from predators (such a species must be less numerous than its „model" and has to be less similar to relative species, it has to „stand out" more, and on the other hand, its model has the typical exterior appearance for its group). Bates explains the perfection of the similarity of the exterior appearance to the „model" by the selective activities of predators, especially birds, who through long term hunting choose those individuals, which are the farthest in their variations from the „model" (Bates, in the same way as Darwin, presumes small continual deviations), and so the similarity between both species increases in time. Bates understands that the starting similarity between both species must be relatively large, so that the insect-eating birds are deceived in the first place. Bates does not discuss the way that this starting similarity is achieved, and he leaves the question open (in later works - **Bates**, 1867 - he uncovers certain more or less intermediary forms of the genus *Leptalis* in butterflies imported by **T. Belt** from Brazil, these constitute „missing links"). It was especially the similarities between mimics and their models in the early phases of selection, which gave way to future selection, that was the subject of misgivings for many critics of the theory of mimicry in general - **Mivart**, 1871; **Cunningham**, 1900; **Kellog**, 1907; **Dean**, 1902, 1908; **McAtee**, 1912, 1932; **Shull**, 1937; **Urquhart**, 1957; etc.

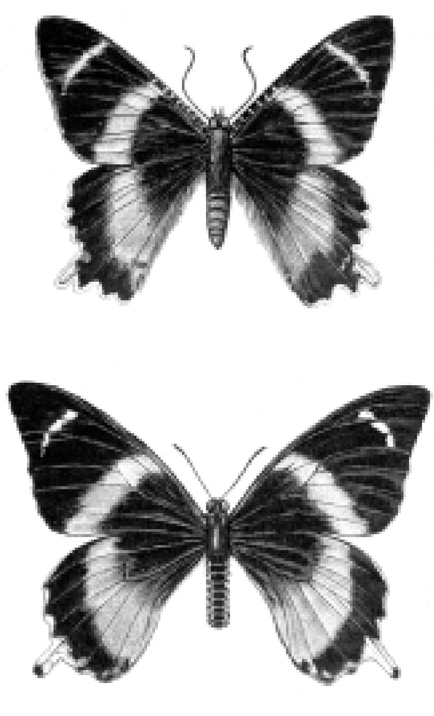


An example of Batesian, or perhaps even Müllerian, mimicry: at the top the hornet *Vespa crabro*, at the bottom the imitating moth, poplar hornet clearwing, *Sesia apiformis,* (according to Jacobi).

Two things are quite surprising - Bates was well acquainted with the phenomena of Müllerian mimicry, which of course was not yet at that time described, meaning the mimetic analogy of external appearance between „defended" species, for example of the families Heliconiidae and Danaidae . Even though this phenomeon is remarkably similar to the situation with the genus *Leptalis* and *Ithomia*, the difference being only in the interpretation and not in the phenomenon itself (two or more similar but unrelated species sharing the same habitat), he writes that the explanation for this type of similarity does not lie in the mechanism they proposed, but the root of the similarity can be found in the adaptation to abiotic factors of the given locality, which have influence maybe even as early as the caterpillar stage of the given species. He also disregards the loud yellow-black, or orange-black coloration of the „Heliconiidae" as warnings, primarily so that predators easily remember which species are inedible - this was interpreted first time by **Wallace** (*warning colouration*). Bates considered the coloration of the model to be also a form of adaptation or reaction to abiotic influences of the locality. In his work he quotes from the recently published book by **R. Trimen** on African butterflies (**Trimen**, 1861) and his examples of mimetic similarities between butterflies from southern Africa (*Papilio Cenea* - today's *P. dardanus*, where the female reminds us of the species *Danais Chrysippus* and the alleged male reminds us of the *Danias Echeria* - the names are according to the era's nomenclature). Further on he describes a number of other examples: parasitical bees and flies in bee nests from South America, which imitate their hosts; *Trochilium* clearwing moths, which imitate wasps; the South American caterpillar (probably a hawkmoth) which through eye spots and its overall appearance imitates a snake; the South American bush-cricket of the genus *Scaphura*, which imitates a "*Sand Wasp*" (which actually feeds them to its larvae - in this situation the prey imitates its predator!); another local bush-cricket, which imitates the

Odontocheila tiger beetle (here Bates cites an older work by **Westwood** - Bates was one of the only British authors who knew not only British studies but Continental works as well, he cites **Rössler's** article on cryptic phenomena in butterflies as well and Bates' own work starts with a quote from one of **K. E. von Baer's** speeches), and further some extreme examples of cryptic phenomena (he does not use this term) - the Amazonian beetle *Chlamys pilula*, which imitates the excrement of caterpillars, the local tortoise beetles, "Cassidae", which imitate dew drops on their shiny exteriors, etc. On the basis of **Wallace's** studies he cites the first ever published example of mimetic similarity between birds, in this case from today Indonesia - the oriole *Mimeta* (family Oriolidae) and the honeyeater *Tropidorhynchus* (family Meliphagidae): from the island Buru the *M. Bouroensis* x *T.*sp.n., from the island Ceram the *M. Forstini* x *T. subcarinatus* (the names are given in their original form). These examples of „sympatric" mimicry are sharply differentiated from similarities of species which occupy different localities, where the similarity is either accidental or caused by kinship between the two forms (*by blood-relationship or affinity*). He does not consider this type of similarity to be mimetic in nature. This caused a more or less arbitrary restriction on what could and what could not be considered a relevant similarity - a relevant similarity is either one which is caused by true kinship (not only Owen's homology, but his analogy as well, which are not fundamentally connected to the basic building plan, but only loosely tied in with it, are still very „essential" attributes - **Owen** /1843, 1848/ himself used both terms with meanings opposite to those, which were later established), or is caused by external, „accidental" attributes, with the difference that these attributes are loosely, like a mask, fitted onto the building plan (without causing any change in the organs or in the organism as a whole) according to the biotic and abiotic surroundings (the selective profit, from which the similarity arose, should be apparent in every typical example, and there should be less „imitations" than „models" in a given biotop) - in this case we are dealing with „mimicry" or a „true mimetic analogy". All other cases of similarities, spreading like bush-rope throughout the entire spectrum of animal and plant kingdom, do not deserve consideration, as they are „coincidental", maybe excepting similarities of **convergence**, caused (selectively, as we would say now) by the influence of the environment or the type of food supply in the sense of the "Tasmanian tiger" (*Thylacinus*) and the wolf (the term „ecological niche" was not to be found at that time). Besides the differentiation between „relevant" and „irrelevant" similarities, Bates' work was also an absolutely fundamental turning-point in the history of the research of mimetic phenomena in the sense that it was „grafted onto" classical Darwinism (we can say that the study of similarities in nature carries out a sort of „metamimicry", it always latches on to the prevalent explanation of the living world and it optically merges with it - before classical Darwinism it „merged" with natural theology, later it acted similarly with neo-Darwinism, and eventually even with sociobiology, eventually becoming its successor). Bates' work was the first to include the thought of selection and optically oriented predators (primarily birds) as the agents who directly perform the selection into the field of mimetic similarities. His work also joined the hitherto more or less separately treated concept of „*mimicry*", in other words phytomimesis and cryptic coloration and the concept of „analogies" of appearance of various groups of insects between themselves. His work was also the first to specify a term for the whole complex of these phenomena, which all have in common some kind of deception and some advantage gained by it, which manifests itself in the Darwinian method as a selective advantage. It can be said that it was this connection which gave birth to the view on mimetic phenomena and the basis of research as we know it today. Bates' work, so often cited in textbooks, but much less often actually read, is generally considered to be the starting point of the research of mimetic phenomena (that this is not entirely true and in the last chapter we can clearly see that Bates' work represents a milestone more in interpretation than in fact). New

At the top the day-flying moth *Alcides agathyrsus* (Uraniidae), underneath its mimic, the swallowtail butterfly *Papilio laglaizei* (Papilionidae) both from New Guinea and the Aru islands (according to Jacobi).



viewpoints actually always arise from the joining of two categories of phenomena generally thought to be disparate (**Ampere**: electricity x magnetism, **Mendel**: statistics x heredity, **Lamarck**: the concept of development and progress x biology, **Darwin**: Malthusianism and political economy x „Natural History"). Bates implemented this operation not once but twice - he combined the world of „mimicry" (in the older sense of the word) and the world of insect „analogies" into one phenomenon and the outcome of this was then combined with Darwinian doctrine. An accompanying phenomena of such grandiose scientific operations is that on the one hand they open massive cognitive room for expansion, and on the other hand they close and forbid certain areas which were earlier open. After such connections have been established, it is very hard to think outside of the design set by them, attempting to think outside of them and again to open the individual theories they assimilated can be as difficult as the establishment of the connecting theory itself. Bates' work is also a good example of the fact that a theory which conforms to the „spirit of the times" does not have to have a thorough foundation in empirical experimentation - in a typical situation it needs none at all (see the above mentioned absence of experiments with birds feeding on butterflies) and "mental" experimentation only is enough. The work is accompanied by two hand colored tables displaying mimetic butterflies. Bates was not, in spite of his obvious talent and **Hooker's** and **Darwin's** recommendations, accepted (much like **Wallace**) as an entomologist by the British Museum (priority was given to a downright incapable rival candidate, who had his connections help him, **R. Owen's** disapproval also played a part) and so he became the second secretary to the Geographical Society, where he proved himself thanks to his extensive linguistic and geographical knowledge. Bates did not write any other major work in the area of mimetic phenomena, even though he was a very energetic entomological taxonomist his whole life and published many more high quality works - mentions of mimicry in beetles can also be found in his work on Amazonian longhorn beetles (**Bates**, 1862b, 1870) and on the imitation of ants by South American tiger beetles (**Bates**, 1868). Even Bates' South American travelogue (**Bates**, 1863) does not mention mimicry. In the year 1863 Bates, together with Wallace, became members of the London Entomological Society, where both occupied for many years various head positions. He lived, in spite of many difficult voyages, to quite a high age (68 years, and his co-traveller Wallace amazingly lived to 90), which seems to be typical for travellers to South America in that century (**Alexander von Humbolt** also lived to 90 years). The question is whether to interpret this through Lamarck, meaning that they were hardened by the constant obstacles, or through Darwin - many aspiring young scientists left for the American tropics, but those with a weaker constitution succumbed to selective pressure and the mists of time have covered even the memory of their existence. Bates' detailed biography, compiled by **E. Clodd**, can be found in the preface to the second edition (1892) of his Amazonian travelogue, and a shorter biography from more recent times was written by **H. P. Moon** (1976). **Darwin** was enthusiastic about Bates' views, as can be seen in his review of Bates' main article (*Nat. Hist. Rev.* 1863, p. 219) and from the extensive correspondence between the two thinkers, which was compiled and published by **Stecher** (1969). Amongst others, a review of Bates' publications written by the American botanist **Asa Gray** (**Gray**, 1863) appeared in 1863, who, although he was an evolutionist, did not believe in complete variability as Darwin did, but in a evolutionary „goal", or some kind of regulatory law, possibly stemming from God. In 1866, an extensive discussion on mimicry took place in the Entomological Society of London (**Westwood**, **Wallace**, **Bates** et al., 1866), where Bates and Wallace sided with the „Darwinist" point of view, while mainly the museum entomologist **D. Sharp** and **Westwood** (who believed that mimetic similarities indeed do exist, but that they were already created in the form in which we find them) argued against.

The nature of the observed events forces us to somewhat abandon our chronological ordering and immediately cover two more fundamental works concerning mimicry in tropical butterflies, which were published in the sixties of the 19th century again in the *Trans. Linn. Soc. London.* The author of the first of these is **A. R. Wallace** (1865), whom we have already mentioned (and in the following text will mention even more often) - this work was read in the Linnean Society on the 17th of March, 1864. The treatise deals with faunistics, variability, and zoogeography of the swallowtail butterflies (Papilionidae) from the „Malay" region, meaning today's Malaysia, Indonesia, the Philippines, and New Guinea, the work has 71 pages and seven colored tables. Relevant information on mimicry can be found between pages 6 and 22. In contrast with most earlier describers of exotic butterflies, Wallace actually visited the vast majority of the islands and abundantly collected the butterflies, he knew most of the species he dealt with from direct field research. In this treatise he also describes, for the first time in literature, the phenomenon of mimetic polymorphism. In this case he primarily deals with the species *Papilio polytes* (in the text *P. Pammon*) and *Papilio memnon* (*P. Memnon*), where the female appears in two very distinct forms (without a transitory stage). One of these forms is similar to the male and lacks tails, while the other has tails and imitates members from the same genus, which are not direct relatives and are today classified separately in the genus or subgenus *Pharmacophagus*. He describes another similar polymorphism, which appears in the North American swallowtail *Papilio glaucus* (*P. Turnus*), even though he was not aware that this dark female form imitates the toxic swallowtail *Battus philenor*. Regardless of how much Wallace believed that bright colors and excessive forms found in many insects are caused by sexual selection, he did not accept such an explanation for mimetic polymorphism and he considered the acting agent to be natural selection, where natural enemies „direct" the originally broad variability in directions which cause similarities to related „protected" species. This reduction in variability to two or three types is later hereditarily fixed and does not allow further continual variability. He considered the female gender in butterflies as needing additional protection because they generally fly slower and are exposed to greater danger when laying eggs. He compares the situation of discontinued mimetic polymorphism to a model situation, where a human population, composed only of Nordic type males and African and Indian type women, is established on some island - their descendents, however, would not be mulattos, as would be expected, but the male children would be of the Nordic type and the female children of the African and Indian type, while both being born of the same mother. Wallace also shortly discusses the suitability of **Bates'** use of the word „*mimicry*" for describing „external" analogies between butterflies, and he finds that the use of the term, including its derivative forms (*mimic, mimickers, mimicked*) is correct, mainly because of its established usage. But other English words, which make up approximate synonyms (*resemblance, similarity, likeness*), do not seem to him to be applicable to the whole scale of phenomena and to every situation. Besides mimetic polymorphism Wallace also describes a large number of other mimetic similarities of the swallowtails of the genus *Papilio*, either in relation to each other (with members of the „*Polydorus - group*", in some way protected), or in relation to members of the family Danaidae, which serves as the model (in one case the model is even New Guinea's morphine butterfly *Drusilla ocellata*), he even describes a similarity between the day-flying moth of the genus *Epicopeia* (family Epicopeidae) and the „protected" species of swallowtail butterflies. As an interesting note Wallace adds a description of the imitation of both genders of the model *Euploea midamus* by the respective genders of the mimic *Papilio paradoxus*. The „protection" of a model is judged according to their low speed and altitude of flying and especially according to their abundant population, which is *eo ipso* a confirmation of their "immunity" and easy way of life. Wallace, just like **Bates**, did not conduct practical experiments with insectivorous birds and his entire account is for the most part speculative. Wallace, who possessed an extremely fine-tuned observational talent and many years of experience with the habitats of the various islands, placed much value in considering „local" factors which affect the external appearance of individual butterfly species. In his work he notes and in detail analyzes certain prominent observable tendencies: swallowtails of the same or closely related species are smaller in size in the Greater Sund (Java, Borneo, Sumatra) and again in New Guinea than they are in the Moluccas and Celebes, and at the same time the Amboina and Celebes islands hold the first place in size. Species, which in Lower India (Vietnam, Cambodia, etc.) have a well developed wing tails, slowly loose them the farther east one travels until they disappear altogether. On the islands of Amboina and Ceram female butterflies of certain species have a dull coloration, while on surrounding islands the same species are colored brightly (he mentions a large number of other „local mode" colorations). He then in detail analyzes the different shapes of the fore-wings of most of the species of swallowtails from Celebes, which in comparison with related forms from the surrounding island are not only larger, but the front edge (*costa*) of their wings is more curved and the apex of the wing ends in a longer sickle-like projection (which is similar to the related genus *Ornithoptera*). A similar phenomenon can be found, although it is not as apparent and not as often, on Celebes with the families Pieridae and Nymphalidae. Wallace believed that these adaptations serve to increase flight speed and the ability to maneuver in the air, similarly to the overall „design" of falcons and swifts. This is why he assumes that the island is, or was in the past, inhabited by an important predator, which feeds or fed on butterflies (even though he did not find any significant example among the island's birds). He therefore concludes that the protected species - „*Polydorus*-group" and the family Danaidae are not affected in this way. Wallace's reference to the geological past is very interesting in this situation, it is *de facto* like referring to the underworld for information - it does not require evidence and can support any hypothesis. Later **Trimen** (1885) used this method to deduce the reason for the noticeable similarity between the large African swallowtail *Papilio antima-*

chus and the much smaller butterfly of the genus *Acraea* by stipulating that the model for this butterfly was a now-extinct larger species of *Acraea* (this whole argument was again disproved by **Poulton**, 1903b, where he cited **Dixey**). [This last example is just an exceptionally powerful one of how classical and even modern Darwinism can serve as an inexhaustible resource of „ethiological myths“ about animals. An ethiological myth explains why things - nations, traditions, animals, etc. - are the way they are. If we must mention a classical myth instead of a modern one, then the myth about the dark face, hands, and feet of the hanuman langur we mentioned in the first chapter would be a good example.] Traditional peoples often saw traces of the past as rudiments and atavisms: according to bushmen, the baboon and the quagga have a belly similar to humans because they were „human“ in the past - **Holm**, 1965. The attraction of ethiological myths also lies in the fact that each is different - in their Darwinian form they only have to refer to the principle of usefulness in some way, or later to the principle of the propagation of one's own genome - with different species the myths are narrated afresh and quite differently.

Wallace mentions a number of other „local colorations“ of the Papilionidae, especially according to reports from South America from his friend **Bates**. This aspect of Wallace's work, even though it was quite extensive, was never worked on again or cited because the problem of „local modes“ cannot be inserted into modern science, which silently bases itself on the concept of isotropic space (and time - moving into past geological eras). A number of these are easily explained adaptations (the common white coloration found in polar species or the ochre coloration of desert species), but for a number of other species a causal interpretation is quite complicated and jagged, for example **Mertens'** (1956) explanation of the „local mode“ of coral snakes in the American tropics, where part of the explanation just evokes resigned shrugs. Another example of this type of explanation concerns the occurrence of „slanted“ almond shaped eyes in Asia, not only in humans (on occasion this was explained as an adaptation to sand storms in Asian deserts, *sic*!), but also in orangutans, langurs, Asian black bears, and Vietnamese domestic pigs (the last case may be caused by artificial selection preferring specimens closer to „my own image“). The lack of bright colors in the original Hawaiian butterflies and birds is also a similar case. These phenomena are sometimes discussed or mentioned in literature, but in the end, in the framework of our paradigm, there are no conclusions to be deduced from them, even though every observant field botanist or zoologist with experience in more than one region knows about them. In connection with the theory of mimicry, the British entomologists **Kaye** (1903, 1906) and **Dixey** (1913a, b, c) studied this phenomena, mostly using examples of South American butterflies. Connecting organic mimesis with mode trends, which in human society spread like a mysterious plague, like the meaningless acceptance of a certain model, propagating certain tendencies and engulfing various aspects of human life, can only be attempted in modern times by liberal intellectuals similar to **R. Callois** (1960, 1963).

R. Trimen (whose work was read on the 5th of March, 1868) was the next to follow in the tradition of **Bates** and **Wallace**. He was a first-rate expert on butterflies from South Africa, where he also spent much of his life (1840-1916, the last 25 years of his life were spent in Oxford, which he mostly spent working on the collections of the Hope Museum, he was also friends with **Darwin**, who entertained him in Down during his visits to England and with whom he exchanged professional correspondence, which was later published by **Poulton**, 1909, pp. 213-241). /The first mention of mimetic similarities of African butterflies is even older than this (**D'Urban**, 1865), not to mention the before described passage in **Boisduval's** book/. In his work Trimen calls attention to the unusual toughness of protected „models“ (in the case of African butterflies this refers to the families Danaidae and Acraeidae) and on the elasticity of their bodies, which protects them from physical damage caused by predators and allows them to survive attack and being „tasted“ by the predator (he notes the same characteristic in the moth families Hypsidae and Zygaenidae). He also writes about their pungent and repulsive secretions, which is similar to the shedding of blood by the ladybird (Coccinellidae), and the extruding organs which serve to spread repugnant odors (Trimen, like **Bates** and **Wallace**, does not in essence doubt that it is smell which causes birds to shun „protected“ species). He also writes of their slow flight, their carelessness, and the absolute lack of cryptic coloration in these species. He is also the first to summarize a number of examples of birds hunting butterflies, which starts off a series of studies and notes on this theme, which prevail with astonishing regularity and in an amazing number the whole of literature on mimicry up until the 50's of the twentieth century. [The discussion on whether birds do or do not hunt butterflies and in what amount, was a very important aspect of mimicry theory, and was discussed by both sides with an unbelievable determination and was based on a large number of cases. The whole problem is made more complicated by the fact that it is possible to find examples supporting both extreme viewpoints - most insectivorous birds do in fact eat butterflies, but irregularly and in small quantities, only a few groups are specialized for hunting larger insects, even /or especially/ butterflies - the bee-eaters, Meropidae, the todis, Galbulidae, certain trogons, Trogonidae, or flycatchers, Muscicapidae. This reason alone casts the question of whether and how birds eat butterflies (generally) into an unfavorable light - it does not seem to be formulated correctly - locally, the answers to this question are quite varied and a summarized answer „sometimes and only some species“ seems to be more of a provocation than a scientifically sufficient statement. As it is with all incorrectly formulated questions, this one also caused widespread discussions and exciting argumentative exercises, which for a long time after filled the pages of zoological journals. A more explicitly formulated question, that is whether (local) selective pressure on butterfly eating birds can cause a shift in the form of the mimic in the sense of imitating the „protected“ species, would quite rapidly lead to an answer more in the style of a declaration of religious belief, because practical verification in such a limited time would be impossible.]

Trimen also mentions his observations of the butterflies from the family Nymphalidae being hunted by lizards and of the Pieridae being hunted by dragonflies, which completely ignore the „protected“ species of the genus *Acraea*. He did not even find the remains of members of the families Danaidae or Acraeidae mixed in with the feedings of the mantis, which catches insects which indiscriminately *en mass* gather around the sap of the acacia. The two mentioned families serve as models in the described mimetic analogies, the Nymphalidae and Papilionidae families serve as mimics (in modern nomenclature the *Danaus*, *Amauris*, and *Acraea* on one side, and the *Hypolimnas*, *Pseudacraea*, and *Papilio* on the other). Trimen especially concentrates on the species *Papilio dardanus* (Trimen's *P. Merope*), who's similarity to the Danaidae is also mentioned in his book from 1861 on South African butterflies. He notes, just like another article from that time (**Trimen**, 1868), that the habitually completely different and individually categorized species (*Papilio Merope*, *P. Hippocoon*, *P. Cenea*, *P. Trophonius*, and *P. Dionysos*) all actually belong to one species - the first is the male, and the rest mimetic polymorphic versions of the female. At the same time he writes about the Madagascarian population, where both sexes are colored the same, and in the same way as continental males, including the presence of tails on the wings of the females (these were not present on the then known mimetic forms of the females). This piece of knowledge was quite shocking for the scientific community (the form *cenea*, which imitates the species *Amauris echeria, f. hippocoon* the species *Amauris niavius*, *f. trophonius* the species *Danaus chrysippus*, all from the family Danaidae - the names are according to modern nomenclature) and there was no lack of critical voices, which doubted the con-specific nature of these forms. Trimen kept working on this problem and in his treatise from 1874 (**Trimen**, 1874) he confirms the new connection between these forms, which stems from the raising of caterpillars and eggs. This work laid the foundation for an unusually large amount of studies, which dealt with and still deal with this curious case, in later times especially from the genetic side of the whole issue, as will be seen further on. After **Wallace's** discoveries in Malaysia and after **Darwin** destroyed the old concept of species as something necessarily, „essentially“, morphologically unchangeable, the concept of mimetic polymorphism without continual variability was not wholly foreign, the same also applied to the concept of mimicry occurring in only one sex, that being the female sex (the species *Hypolimnas dubia*, which Trimen called *Diaema*). Trimen concludes his treatise with an declamatory expression of his own views, which is contained in the following phrase: *„Natura non facit saltum“*, from which he induces that the evolution of nature, organic and inorganic, is a slow process and concepts of cataclysmic changes or other rapid turnarounds will eventually be filled in and changed into a continuum. Trimen later published a large number of smaller studies concerning mimicry in insects generally and in South African butterflies specifically (especially **Trimen**, 1885, 1897), which were published in journals right up to the WW I. In the years 1887 to 1889 he also published an extensive trilogy of monographs on South African butterflies (**Trimen & Bowkers**, 1887-1897). The first collective study of mimicry of North American butterflies (**Walsh & Riley**, 1869) was published in the same year as Trimen's main work, and it is a continuation of **B. D. Walsh's** first letter, published in 1864 by the *Proc. Ent. Soc. London* and is the first to mention the now famous mimetic similarity of the butterfly *Limenitis archippus* (viceroy) to the species *Danaus plexippus* (monarch). The British botanist **Alfred W. Bennett** was an important opponent of the theory of mimicry, and he published two articles on this theme (1870, 1872), the first even included a mathematical model explaining why natural selection cannot work. He enthusiastically welcomed in his review (*Nature* 3: 270-273, 1871) **Mivart's** (1871) anti-Darwinian book (Mivart, who among other things was a converted catholic, tried to combine the effectiveness of selection with the concept of the „government of law“ in nature in the spirit of Darwin's opponents). Bennett also published one of the first studies on plant mimicry (**Bennett**, 1877), in which the concepts of mimicry blend with ecological convergence.

Darwinism and sociomorphic modeling

After briefly outlining the basic concepts, put forward in the first three „pioneer“ works concerning the Darwinian concept of mimicry, it would not be without interest to analyze the basic underlying thought, in other words Darwin's basic teachings, in more detail. Darwinism is a classical example of so called sociomorphic modeling, meaning the tendency to explain nature through the prism of the social structure of the given human society. This concept is dealt with in more detail in older works by this author (**Komárek**, 1989a, 1992) and in a some instances it draws upon certain ideas of **E. Topitsch** (1958) and **H. M. Peters** (1961). On the whole it is possible to say that every human society has a tendency to understand itself so to speak „cosmically“, meaning the community, the *polis*, represents a *microcosmos* which is in some way analogical to the *macrocosmos*. This tendency is in an open way apparent in each and every society whose traditions are not derived from a Greco-Roman heritage, which includes either relatively archaic civilizations (old Mesopotamia), or relatively late civilizations (the Chinese empire). In such civilizations the ruler is directly responsible not only for the workings of human affairs, but also for the continued working of nature, the cosmos, including the regular movement of celestial bodies, and for natural catastrophes as well. If this tendency was suppressed in the Greco-Roman heritage, it does not mean that it was driven out completely - although it is accepted that the government is supposed to care only for human things (the category „*nomoi*“), especially during totalitarian rule, reminiscent of archaic societies, the government feels competent to, for example, intervene in human reproduction and sex, „conquering space“, „molding nature“, and on the other hand concealing epidemics and catastrophes much in the same sense as the archaic view of the *polis* as a mirror to the cosmos. In all countries with a European tradition the „feeling of cosmicity“, the feeling that the social system is legitimate because it is in harmony with the order of nature, has at least become a part of our consciousness (it would be possible to find an analogy in the fact that centralized societies view the constitutive principles of the world primarily through the motives „centralization“ and „planning“ in the sense of the Sun - King of the solar system, God the Creator as the „Great Planner“ - for example during the Baroque era, or, on the other hand, the emphasis on stochastic processes in nature in societies where this is a constitutive factor, for example in democratic mechanisms - in Anglo-Saxon countries). But this legitimacy is not achieved by adapting the functions of society to the functions of nature (certain basic elements are shared by both anyway, but if both were identical, it would be impossible to single out society as being society, it would become an un-reflected part of the natural process and the question of eventual harmony between the two could not even be formulated). For this reason harmony between the two is achieved by projecting social structures onto nature, in this case onto the biotic aspect of nature, and from the infinite amount of phenomena which nature offers we choose those which seem to validate and legitimize social processes („Butterflies do it like that as well“). Examples of such projections can be found everywhere. Even hunter-gatherer societies projected kinship relations, which were constitutively important in the framework of family structures, onto the animal world (for example the sparrow hawk is the younger brother of the eagle). The European Middle Ages saw animals not only as a manifestation of Christianity's vices and virtues, but even in roles equivalent to a feudal hierarchy (the eagle - king of birds, the lion - king of animals, these views were not taken only metaphorically). In the same way pre-Linnean classifications of organisms were a direct projection of the table of ranks for officials in absolutist states or the hierarchy of angels or devils, according to the era's inclination. Even the thought of progress appeared first in society (at the beginning of the 18th century, for example **Ch. Perrault**) and only after a hundred years did **Lamarck** project this idea onto nature as a gradual developing towards perfection, where lower life forms, basically through their immanent effort to become perfect, developed into higher life forms (the growing interest in paleontology at the turn of the 18th and the beginning of the 19th century also went hand in hand with the increased interest in archeology and human history generally). A nice example of this type of projection can be found in **Cuvier's** work (1815), where geological cataclysms are portrayed as „revolutions“ (*révolution*) of the Earth's crust. Cuvier, a child of the revolution and its successful exploiter, projects contemporary experience onto the external world as a creative principle and mover of (geological) history (it is not a coincidence that many cataclysmic notions arose in paleontology in the eighties and nineties of the 20th century). Taken from this point of view, **Darwin's** and **Wallace's** appearance calls for exceptional attention. It is definitely not a coincidence that both authors, both of which practically independent on one another came up with the thought of natural selection (as we will see in more detail later on), lived in the most industrialized country in the world and saw the functioning of selection, struggle, and competition between people, so to say, on a day to day basis - in **Wallace's** case it was at least a fresh memory (it is impossible to imagine **Darwin** as an ancient Greek philosopher, an Indian sage, or a Middle Ages monk - very few views on nature and the world are as based and dependent on the era and situation in which they arose as Darwin's are). The projection of social phenomena onto nature is even more apparent in literature. While animals in **Tolstoi's** stories have typical attributes of the Russians and their lives progress in terms of service, suffering, and occasionally passion, **E. T. Seton's** animal heroes are furry incarnations of American self-made men, complete with their toughness, endurance, and sense of fair play. It is without doubt that nature is always viewed through eyes made by that era's society and their way of thinking, and at the same time certain phenomena are chosen from nature and certain other phenomena are implanted into nature, depending on which phenomena reflect and validate the „social climate" of the given era. The „unwanted" phenomena escape, in spite of their conspicuousness, the attention of the scientific community (a good example of this is the well-known story about **Bernard from Clairvaux**, who overlooked Lake Geneva in his meditations, even though he traveled around it for two days). As **A. Koestler** writes (1978), there are always enough arguments supporting a given theory, once we have, for any reason, accepted it. If thoughts, which are foreign to the „social climate", nevertheless appear, they are considered to be mad or in the best of cases uninteresting and the person behind the thought or theory is dealt with accordingly. Only shortly before a change of social atmosphere do these unorthodox views become more common and eventually they themselves become accepted as the only truth.

Although the natural world surrounding us has in the last five thousand years changed only imperceptibly, it is surprising how many diverse aspects are searched for and eventually found. For example the social life of bees, a phenomenon known to mankind from times immemorial, was earlier understood in a diametrically different way. Tribal societies, if they even paid attention to the bees, probably saw them as something like a family or a tribe, which collects supplies and protects them (an interesting relic of this view is the German word for a bee hive - *Bienenvolk*). The significance of the central position of the queen, or according to the era's conceptions, the king, was realized only after the differentiation of social hierarchy, markedly for example in Antiquity. It is also typical that **Pliny** considered the drones to be the bee's slaves. The Middle Ages considered bees to be a representation of the ideal state or a monastic society. An enticing work, which is a testament to this belief, was written by the Dominican **Thomas from Cantimpré**, entitled *Bonum universale de apibus*, in which he put to paper mainly fictitious stories from the lives of bees as moral teachings for his brothers in the order (this type of literature was not at that time considered only poetic license, but it was taken as a real expression of the author's view on the world). Only after industrialization was it possible to develop a view of a hive as an ingenious organization which ensures a material advantage in the competition with other solitary bees for nectar and pollen.

It is probably impossible to completely secede from the above mentioned way of understanding natural phenomena, and it probably is not even desirable - but it is imperative to recognize this tendency and not allow momentary results of the aim to see ourselves in Nature to be attributed absolute and final validity. It is no coincidence that the „new biology" of the Stalinist USSR specifically refused to accept natural selection and competition. **Lysenko**, **Lepešinskaja**, and other protagonists of this movement replaced natural selection with the concept of active „adaptation to the environment" and they saw species as being unlimitedly transmutable. This is a nice self-projection of a society which eliminated every vestige of economic competition, but where „active adaptation" was, due to the rapid day to day changes in orders from the Party, a basic ability necessary for survival. This doctrine was an exception in the history of biology, because it carried the mark of forced introduction of the state's power and in places the biological doctrine was intentionally doctored and modified in order to be in accordance with the political doctrine (see also **Komárek**, 1989a). In most other cases, this process is carried out as well, but unintentionally - discoverers of new biological concepts (with a strong sociomorphic context) always have a subjective impression that they have discovered the true order of nature and they don't usually feel the need to point out the social implications of their discoveries. Somewhere deep in their understanding lies a certain satisfaction, stemming from the discovery that the workings of nature are basically identical to the processes of society, but this thought is rarely articulated and it is never said that this is actually a projection and a form of support of the specific social doctrine of that society instead of being a true unveiling of nature itself (this phenomenon is quite apparent in the study of ethics, which in trying to find the „natural“ moral codex turn to biological studies, which are in turn disclose information based on sociomorphic projections - in this way the current ethical system of the society is uncovered as being „natural“ and the self-verifiable circle is closed). Even postwar neo-Darwinian and sociobiological movements, which grew around the world after the victory of Allied weapons, more or less monoculturally undaunted by „continental“ thought (the concepts of Soviet Russia were not considered worthy competitors), in a way which interestingly mirrors the changes in society (for example the emphasis on collectivism of the sixties in the concept of „*kin-selection*“, also from the sixties). The notion of a selfish gene (**Dawkins**, 1976) using whatever means available to spread itself in as many as possible, mirrors in an important way the attempt of the isolated individual trying to assert himself, as can be seen on thousands of television screens, in illustrated magazines, or quoted by scientific publications, in a postindustrial world (others serve only as a substrate, at the most they can join in a cartel which serves as a „vehicle“ through which each member attempts a certain goal - the aim again is to expand and enlarge one's own standing, not the standing of the others). In accordance with this view of the world, it is obviously necessary in some way to „explain“ for example any acts of altruism and re-form them into some cunning form of egoism, in the last instance on a genetic level. It is basically the same process that allowed pre-Darwinian natural theology to view nature's cruel and horrible moments, for example predatorial or parasitical behavior, through their own „eye pieces“ and „explain“ them as they saw fit, the only difference being that they viewed the events from an opposite perspective - the uncomfortable is today considered unselfish (in any case early theoreticians of the bourgeois society, for example **T. Hobbes**, saw the joining element of society, the element which in effect allows the society to function, in individual egoism - now that the much sought harmony had been achieved - like nature, like society). In any case it is apparent that the Darwinian and neo-Darwinian concepts are in some way existentially linked to the „open“ type of society, where competition and selection make up a substantial part of day to day life and the battle for self-presentation on any level is a relevant and socially accepted and endorsed activity. This is the reason why societies, where the „arm of the market“ or „social selection“ were in some way weakened or eliminated entirely (Bismark's and Wilhelm's Germany, Soviet Russia), did not acknowledge the biological concepts of Darwinism or at least developed a strong counter-movement. Are Darwinian concepts linked to a certain social structure, to which they owe their origin and whose maxims legitimize them? Would the demise or a fundamental metamorphosis of the society lead to the demise of such a type of science as well? The enthusiastically accepted Darwinism and its quick projection into various individual branches of human activity (linguistics, pedagogy, law, literature, political and military doctrines) is an illuminating example of a teaching which came „at the right time“ and fell on fertile soil, only to eventually enter a „spiraling“ process of self-influencing social doctrines through biological ones and the other way around, which culminated in the vulgar socio-Darwinian theses that formed the basis for the First, and, in essence, the Second World War (for example the Austrian chief of staff **C. von Hötzendorf** was a passionate reader of „social Darwinian“ literature and **A. Hitler** (1942) was also influenced by degenerate brochures of this type - a wholly curious example of reverse projection of nation socialist thought back into biology can be found in **Netolitzky's** study on „blond“ insects in northern Germany). Of course these later „applications“ were never even considered by **Darwin** himself, as he was a serious private thinker with amazing observational skills of natural phenomena (at the same time he never reflected on the feasibility of the „applications“, which is generally typical for distinguished individuals with „idealistic“ goals, that have gotten out of hand). Darwinism also has much in common with other reductionist teachings, which were so common in the second half of the 19th century. One of the elementary experiences of this type was explaining the „higher“ by way of the „lower“, „nothing-but-ism“, discovering things which lead to the casting down of some up to then accepted idol, and then showing that the core of this idol is completely different from what would be expected, it is filled with something banally simple, or even directly by something repulsive and low. This archetype is present in each of the three main schools of thought of the second half of the 19th century, schools which fundamentally affected the 20th century and at the same time called for a universal, self-contained interpretation of the world: Marxism, Darwinism, Freudianism. The serenity changes to hell in the face of closer scrutiny. A clearing in a forest, where bees of various species fly from flower to flower to the tune of singing birds, suddenly gains a new dimension: male birds are competing for territory and in desperate fights for domination they mark their territory with song. Plants use various unfair tricks to lure pollinating insects, so that they loose the least and gain the most possible. Solitary bees are running a race against time for nectar and pollen, competing pressures in the population and in inter-specific struggles let a seemingly charming activity change into a life-or-death fight for survival. Different scenes end up in the same way: the exotic scenery of harbor workers in Batavia, loading packages of strange spices onto the waiting ship, suddenly acquires a bitter taste when we realize that the colonial exploiters attentively removed from their workers every commodity above the basic necessities needed to regenerate the worker's ability to function, and that when capitalism reaches its highest phase of imperialism, the colonies will be even worse off than before, when they were a source of raw material and outlet for industrial production - they will experience a direct outflow of capital from their home country. The Freudian interpretation of an idyllic picture of a young mother playing with her year old boy on a park bench are provocative in the extreme (Freudianism is in any case the only reductionism which reduces its subject to something very thrilling).

It is, of course, possible to object that this short sketch is more a caricature than a detailed portrayal of these diligently thought out and respected teachings. Nevertheless, the example shows a fundamental aspect of these teachings - the feeling of ripping off the mask of the world and showing that underneath is something primitive, even a bit repulsive. Contrary to other reductionist teachings, the above mentioned branches contain not only explanations, but in the way of „investigative journalism“ also a strong emotive element, and that may well be one of the causes of their exceptional historical success.

The fact that certain aspects of the living world are sociomorphic projections which have been highlighted and sent to the front does not actually mean that they do not really exist in nature (every projection in the end has to hold on to some „hook“, they must have some hold), they are just „under a shadow“ until their discovery. Fundamental principles must be first understood on the social level (for example a hierarchy or evolution due to progress), so that later they can be seen on the level of nature. The same applied to the principle of overproduction of offspring as a necessity for natural selection (which chooses from the surplus). However much the phenomenon itself is evident on many plants, insects, and actually on all species, **Malthus´** perception was necessary for (**Malthus**, 1798) to mention the geometrical growth of the human population so that both **Darwin** (he mentions in his biography that it was in the year 1838 - **Darwin F.**, 1887) and **Wallace** gained independently of each other the necessary inspiration (Already certain natural theologians before Malthus, for example **Linné**, 1749, 1750, mentioned the large fertility and proliferation of certain species, but they interpreted this in the framework of the basic tripod of „natural economy“ - reproduction - preservation - destruction. It is certainly not a coincidence that specifically Malthus came from the theologian camp.). The necessity for the reduction of the natural population by predators was seen by more authors as well - for example the British ichthyologist **J. M'Clelland** (1839) wrote of the meaning of the colors and luster found in Indian fish, stating that it served to make the fish more conspicuous for the kingfishers, terns, and other birds, which serve to reduce the fish population. **Darwin** drew the idea of necessity and the „creative role“ of competition in conjunction with the egoism of individuals not only from the general social conscious, but also from the writings of **A. Smith** (1776). Alongside this idea comes another concept, which is labeled „semisociomorphic“ - meaning the selection necessary for the cultivation of various breeds of domestic animals, Darwin was friends with many such breeders and he himself breed many species as well, especially pigeons (Darwin's England was very strongly marked with a taste for breeding ornamental species of birds and horses in the elite class, even cultivating useful breeds of pig, cattle, and sheep and managing artificial selection was considered a basic skill in this class). Domestic animals make up a kind of transitory zone between the natural and human worlds - as living things their roots can be found in the natural world, but their incorporation into human society and the notable influence on their exterior appearance and attributes by man make them something like living artifacts (On some of them we can find phenomena which are analogous to mimetic phenomena found in nature - petit dogs can be sincerely considered to be something like parasitical and at the same time mimetic midget forms of the wolf, which even in adulthood imitate childlike behavior and de facto parasite on the emotional aspect of their „parents“, without having any other requirements concerning „usefulness“ /how strong this relation is and how perfect the substitution of childlike behavior can be seen in **Ceausescu's** Romania, where the mentioned dictator, in an attempt to destroy the last authentic relation between living creatures, gave orders to eliminate all dogs because they needed to be fed, and food was scarce even without them - but the Romanian villagers always, in spite of the great danger of such an act, managed to hide some dog and later resumed their breeding./ The moment of mimicry can be seen especially well in /for example/ the Mexican naked lapdog, which have a fur covering only on their heads and usually have no teeth - Mexican villagers often breast-feed them and pamper them as if they were human babies. Even the blond bristles and blue eyes of the German domestic pig in contrast with the dark skin and almond eyes of South Asian pigs show certain „mimetic" similarities. The question is whether in this case the selection was intentional or subconscious, only certain specific pigs are in some way considered more „cute" than others. The Finnish „fox" dog also deserves mention, it is selected to resemble a fox and its job is to attract the attention of birds during a hunt so that they do not notice the hunters. Another worthwhile mention goes to many breeds of sheep dogs /e.g. Pyrenean and Carpathian/, which resemble sheep in size, color, and fur type.).

Darwin made artificial selection, for which he knew the effects very well and which he described in detail (Darwin's contribution to determining the origin of domesticated animals, which is quite fundamental, is generally not appreciated), the model for natural selection (he declared both processes to be essentially equal), which he could verify in its direct consequences only so to say *ex post*. It is interesting that Wallace, in his earlier essays (**Wallace**, 1855, 1858), never used the word „*selection*", instead he used „*surviving*" - this is because Wallace did not share Darwin's appreciation of domesticated animals and he considered both processes as being completely different, domesticants according to Wallace were unnatural freaks, possible only under the protecting arm of man (even these moments give insight into the differences between the two thinkers, **Wallace** alone in the rainforests, surrounded by wild forms, real danger, and the „battle for survival", while Darwin was surrounded at his families estate by many relatives and domesticated animals).

The notion of the struggle for life was also viewed more subtly by **Darwin** than by Wallace, who viewed more through the later „popular" concept of the „law of the jungle" (Darwin always stressed the quieter and inconspicuous forms as well, for example the shading and overgrowing of slow-growing trees by trees which grow faster). This notion was diametrically opposite to all earlier views of nature, which always emphasized harmony, mutual interlacing, and a functional connection between organisms, not uncommonly even mutual support (flowers take care of food for bees, they in turn make honey for humans, forest and field crops provide for humans, while the oak with its acorns feeds wild boars, etc.). **Darwin** (1859) *expressis verbis* stresses that no organism in nature ever does anything for the good of others, but only for its own good (even cases where neither participating side suffers losses, for example the pollinating of plants by insects or the spreading of seeds by fruit-eating birds, are understood as being at best an equal „business exchange"), which of course is a considerable sociomorphic projection and even a type of faith (cases of extreme egoism in nature are of course numerous and arguments of the type that the oak would better and more energy-efficiently spread with flying seeds of the dandelion or birch type can be easily tossed aside by the tautology statement that if the creation of acorns survived the selection process, then it must be the most effective). It is interesting that the occasional post-Darwinian works, which attempt to stress the altruistic component of the relation between organisms (for example **Kropotkin**, 1902), are also strongly under the influence of sociomorphic projections, but this time in the sense of politics which emphasize social solidarity (a suggestion of this type of thinking can also be found in biological literature of Lysenko's era). The idea of the survival of the fittest is of course a tautology and it could be in caricature imagined in this way: A discussion in A.D. 1400: Why are swans white? I don't know, but the Creator in His wisdom certainly knew why He made them white. The same discussion after 1859: Why are swans white? Swans are white because this color came out on top in the selection process. Why this happened, I don't know, but because the swan has this color, it must have had some selective value (from the above the unstoppable progress of science is apparent, as well as the quick end to various forms of obscurantism). The concept of the „struggle to survive" was projected in an interesting manner even into illustrations of biological works. **A. Portmann** (1966) points out quite well that illustrations of apes, for example orangutans, during the Enlightenment (for example **Buffon's** work) were typologically closer to humans, mainly by being drawn in a standing position with a „mild" expression, and with a stick or other simple instrument in their hands. The orangutan pictured in **Wallace's** (1869) book „The Malay Archipelago" is a furious wild animal with massive bared canine teeth.

If the Cartesian revolution indeed created a radical division between religion and nature in its actual state (the belief in the occupation of nature by various spirits and elementals with anthropomorphic features was present not only in traditional societies, but this belief lasted up until Paracelsus' era), then Darwin separated religion from Nature in its creation. (This in no way implies that Darwin and Wallace were radical atheists. Darwin, himself a successful graduate of Anglican theology at Cambridge, did not doubt the godly origin of life and he joined in formal religious events within the framework of his conservative-patriotic-petty bourgeois work way of life /certain aspects of his arguments continue in the manner of scholastic disputations, which he learned during his Cambridge studies, and the influence of natural theology was very strong during his youth – in his autobiography Darwin - **Darwin, F.,** 1887 - mentions mainly **Paley**, 1802./. Wallace, on the other hand, was an active member of certain spiritualist groups and he saw the origin of man as directly caused by spiritual entities which wander the Cosmos. Most of all this concerned human attributes which have a neutral or negative selective value, such as mathematical or musical abilities, ethics, loyal friendship, etc. (see also **Wallace**, 1870). Wallace, if only because of his long life, was a many-sided and from today's perspective contradictory individual. Near the end of his life he returned to the concept of the Divine hand, guiding all evolution (**Wallace**, 1911). His own detailed life story (**Wallace**, 1905) and **Marchant's** (1916) published correspondence reveal much more than could fit into this book.

This deep, though not yet completely secularized world, carries with it a great many problems of interpretation, which did not occur in this manner before. Besides others, the problem of the external appearance of organisms arose. While the "reason" that a specific organism looks as it does and in no other way could earlier be explained away by introducing a hidden and for us incomprehensible reason of the Creator, in the post-Darwin era the "reason" or "goal" became one with its function. In some cases such a reinterpretation was quite easy, in other cases very difficult. As was said in the prior chapter, no problems arose with cryptic phenomena, which are also in detail described by Darwin in the *Origin of species...* (**Darwin**, 1859 – the book did not contain a single reference to mimicry in the narrow sense and they were introduced only in the fourth edition on 1866). Even though Darwin was later concerned with mimicry and followed all publications written about them – he did not see the theory of mimetic imitations as a pillar of his own theory and he viewed the theory more as a "marginal improvement" – his extensive book on the origin of man and sexual selection (**Darwin**, 1871) contained only three pages out of more than eight hundred concerning the theory of mimicry. Darwin himself left two mentions of his own original observations concerning mimicry in his correspondence – both cases deal with similarities of turbellarians to slugs, the first case is from Monte Video (in the letter to **Henslow**, from the 15th of September, 1833, **Darwin F.**, **Steward A. C.**, 1903, I. p. 9) and in the second case from Britain (in the letter to **F. Müller** from 1867, **F. Darwin**, 1887, III., p. 71). Darwin was interested in the reinterpretation of all types of coloration in living nature, including plant coloration. In his book on the origin of species (**Darwin**, 1859) he extensively deals with the color of flowers as a means of luring pollinating insects, he also adds that the majority of plants with colorful flowers are pollinated by insects, whereas plants with inconspicuous or green flowers are usually pollinated by the wind (this rule of course works, but as with all rules governing the coloration of living organisms there are exceptions – the more or less green flower of the grapevine, or the currant and, on the other hand, the bright flowers of the violet which, in contrast with the inconspicuous, ground-level, and cleistogamic flowers of the same plant, do not produce seeds). In this manner Darwin smoothly reinterpreted the observations of **Ch. Sprengel** (1793), who understood the relation between insects and plants in terms of natural theology - Sprengel was a Protestant minister. Immediately afterwards **H. Müller** (1879) continued in Darwin's footsteps. He was a teacher in Lippstadt in Germany and the brother of **Fritz Müller**, the discoverer of Müllerian mimicry - in his work he dramatically broadens and expands the Darwinian interpretation of flower coloration and flower biology concerning the interaction between plant and pollinator, by which he initiated an unbelievable series of works on this theme /the pollination of plants, but more from the mechanical aspect than from the role of the colors was later also explored by Darwin, his subjects of study were orchids (**Darwin**, 1862) and sages (**Darwin**, 1880)/. The work from 1862, which includes a large quantity of detailed observations, also incorporates data from the English botanist **Smith**, which he compiled in 1829. In Kent he observed male solitary bees of the genus *Andrena* flying themselves quite forcefully at the flowers of the *Ophrys* orchid (he considered these actions to be attacks), and the conscientious gatherer of information, Darwin, cites these data and attaches a note, in which he states that it is quite difficult to come up with any reasonable explanation for this particular phenomenon - later it was allegedly shown that this is one of the most spectacular examples of mimicry in plants, which imitate the female of the pollinating bee in olfactory attributes and in shape (it is sometimes called after its discoverer - Pouyanne's mimicry) - the attacks are in fact attempts at copulation. Darwin's concept of flower coloration also provoked many critical comments, for example the French botanist **G. Bonnier** (1879) (who's own viewpoint arose from the concept that the purpose and goal of an organisms' form lies within that organism, and never outside of it) contests Darwin's claim that there is a relation between the color and form of a flower and the activities of the pollinating insects, especially the possibility of long term selection from the side of the insects (one of the attractions of biological study is that it is always possible to collect a number of particular examples to support any given theory that the biologist happens to believe, as can be in detail seen in **A. Koestler's** /1978/ work, and, of course, Bonnier does the same). Darwin in his book on the origin of species (**Darwin**, 1859) also mentions the coloration of fruits of many plants as being an adaptive mark focused on fruit eating birds, or even mammals, which then spread the seeds (of course, not even this was wholly new, because this is literally completely evident, the only new thing was an interpretation which was not in accordance with the natural theological viewpoint). Wallace also summarized, more or less in the same way as Darwin (chap. 11), the theme of the coloration of plants in his compendium of Darwinism (**Wallace**, 1889) - he also pointed out for example the lack of bright colors on nuts and acorns in contrast with juicy fruits. In the same chapter he included an extensive disputation with **G. Allen** (1879, 1882), an American author who was concerned with esthetics in nature and „comparative" esthetics of natural and human phenomena. Grant Allen emphasized that animals which have some contact with flowers and colorful fruits (something akin to the principle of synchronicity, or even better, syntopicity) are themselves quite colorful (butterflies, flower-feeding beetles and other insects, hummingbirds, parrots, etc.), while species which operate underground, at night, or are predators, carcass eaters, or saprophagous, usually have dark colors (as with many other biological observations, like **Haeckel's** law of ontogeny as a shorter version of phylogeny, it seems to be a nice global metaphor, but under closer examination one finds that it is too global and has more of a poetic character - but it is important to realize that basically all scientific statements are metaphors, although sometimes they are less apparent and so to speak „rigid" in their use - „the level of sugar in your blood has gone down" - knowledge that is not mediated through metaphors and analogies more or less does not exist). But G. Allen thought that animals are inspired by the colors that surround them and that they favor them in sexual selection (Allen was inspired by Darwin's intellectual legacy in other particularities in his book as well - for example colorful and at the same time toxic berries are interpreted as a lure for fruit eating birds, which then die and their dead bodies provide fertilizer for the sprouting seed). Wallace considered it necessary to extensively discuss every example because of his many travel experiences of these concepts, which, of course, were not quite supported by evidence.

Concerning animals, Darwin was of course aware that the originally seamless spectrum of colors and external appearance must be, due to his interpretation, divided into two disparate categories - those types which can be explained by natural selection, that is **cryptic** colorations, about which he wrote in his most famous book (**Darwin**,1859) and those which cannot, which are called **semantic** by the later nomenclature, which are caused, according to Darwin, by sexual selection. The category of sexual selection was already introduced by Darwin in his work on the origin of species (**Darwin**,1859), but a more detailed account can be found in his later work on the origin of man (**Darwin**,1871), in the second section from three in the book. The discourse is unusually long (over 300 pages) and it points out the entirely central position of sexual selection in Darwin's works (out of the remaining British authors of the 19th century, **Cunningham**, 1900, and **Beddard**, 1892 for example concerned themselves with this theme). Already essays published together with Wallace in 1858 („*Joint Essays*") for the *Journ. Proc. Linn. Soc. London* mention sexual selection, even though the concept is Darwin's and Wallace was never reconciled with the idea /Parallelism in the thought of these two thinkers otherwise is amazing - in an essay sent to the Linnean Society in 1858 written on the island Ternate in February of the same year, which was also inspired by **Malthus'** thoughts, Wallace independently of Darwin wrote of exactly the same opinions, except that he didn't use the term „*selection*", which was taken from breeding terminology, as was stated earlier. In an earlier essay (**Wallace**, 1855), written in February of that year in Borneo, he anticipates on a zoogeographical basis biological descendence and affiliation, but at that time without the concept of the survival of the best adapted and of selection generally. While some thoughts voiced in this essay were later correlated with Darwin's own (Wallace for example considered the rudimentary limbs of certain lizards or male boa snakes to be nascent and not reduced), he never accepted the concept of sexual selection, even though he held great esteem and had a good relation with Darwin (Wallace especially propagated the term „Darwinism" for the new selective-evolution teaching, even though his name could have been used as well - this term was at the time already used in English literary theory as a derisive term for didactic poems in the style of **Darwin's** grandfather **Erasmus**). Darwin's inclination to the above mentioned concept is not surprising, considering that his own experience with sexual selection (although opposite of what he usually spoke of) guaranteed for him by means of a wealthy marriage a calm lifelong career as a private thinker and as the father of a family. In the same way Wallace, after returning in a more or less unemployable state from his many-year stay in the tropics and being without money or property, was hustled around various „livable" posts (he was for a time the director of the botanical gardens in Kew), and through Darwin's assistance and eventually from 1880 thanks to his state pension, he could then turn his interest in natural phenomena (as was pointed out earlier) to concepts of various deceptions, mimicry, and protective colorations, which in comparison with his great biological erudition are for Darwin quite short./.

Sexual dimorphism and selection, exaggerated structures

Darwin's concept of sexual selection lies in the idea that females of higher animals (in some rare cases the males as well) conduct active selection of their partners on the basis of esthetic criteria. This concept is of course anthropomorphic, even though in this case it is intentional and not very strong. As **Callois** (1960) correctly notes, there are two basic types of anthropomorphism in understanding the natural world - positive and negative. The first, to which naivete is traditionally ascribed in modern society, interprets non-human phenomena as completely or roughly analogous to human phenomena (in extreme cases for example the childish interpretation of a parked car as being „asleep", in weaker cases for example **Pasteur's** (1857) observation that crystals with a damaged surface „heal" in a saturated solution). The second type, which was in the same era considered especially „scientific", intentionally interprets non-human phenomena as being completely different from human phenomena in every case (in extreme cases for example an injured cat does emit certain sounds, but there is no reason to come to the anthropomorphic conclusion that he feels pain, in lesser cases we can say that a hen perceives grain through the eyes only after experimenting with blinding the hen). If we take the last view to the extreme, we come to the conclusion that we cannot even come to a certain conclusion about our human neighbors *per analogiam* with ourselves (a well known Chinese narrative tells of two sages, one of which is watching fish jump up from a mountain stream and he comes to the conclusion that they are rejoicing. The second answers, how can you know anything definite about the fish if you are not one of them? The first answers, how can you know anything about me, if you are not me yourself?). Not only non-human organisms, but even people (this is best seen with people belonging to different ethnical and cultural groups) can only be described from the outside, where empathy cannot play a part. That empathy has its limits and can be a source of error is, of course, another matter, but the longing for scientific „infallibility" which resigns empathy, cuts us off from one of the most powerful sources for understanding living beings, which we are as well. Of course, the distance between a given organism and ourselves plays a very important role [a tiger „angrily" wrinkles his forehead in a way which is in analogy undoubtedly closer to a similarly tempered person than a „frowning" storm cloud above a mountain - the word cloud incidentally has a nice residuum of archaic interpretations of abiotic phenomena which are analogous to humans and their bodies - for example the earth as an organism with hair (grass) and skin (the surface layer of soil), which was called biomorphic modeling by **Topitsch** (1958), as compared with the later, modern, name - mechanomorphic modeling]. In criticisms of various views on the coloration of organisms and their purpose (in the post-Darwinian times this was identified with function) - for example **Heikertinger** (1954) - we often find criticisms of hidden anthropomorphic conceptions, which at the least assume that optically oriented animals (e.g. birds) view the world similarly to us. It's possible to criticize Darwin's concept of sexual selection even more because of this, because it assumes a generally spread esthetic sense in the natural world, which is analogous to the human esthetic sense. The criticism though is pretty absurd if we realize that the structure of an animal is much closer to our own structure than to the structure of some machine, regardless of whether mechanical or based on relays, or integrated circuits. For the post-Descartes world, a machine is, of course, an exemplary phenomenon and the standard gauge of „science" in its applications and its projections into the natural world (the argument against anthropomorphism - „it's nice, but it's not science" can be countered be the aphorism „it's science, but it's not nice"). The bias of the mechanomorphic world view has the same „hidden" anthropomorphism as the idea that the world is the most economical (if not the best) of all possible worlds (the regular geometry of echinoderms, coelenterates, or flowers can be interpreted in this way as well) - the obvious luxury and reveling in the natural world does not fit into these systems and is therefore explained away or denied - in any case it can be easily seen that this idea, the idea of nature as being sober and economical is a strong projection of early modern Calvinist thought about the correct functioning of the world, which was supported by the bourgeoisie, as compared to the reveling of baroque nobles, or even villagers.

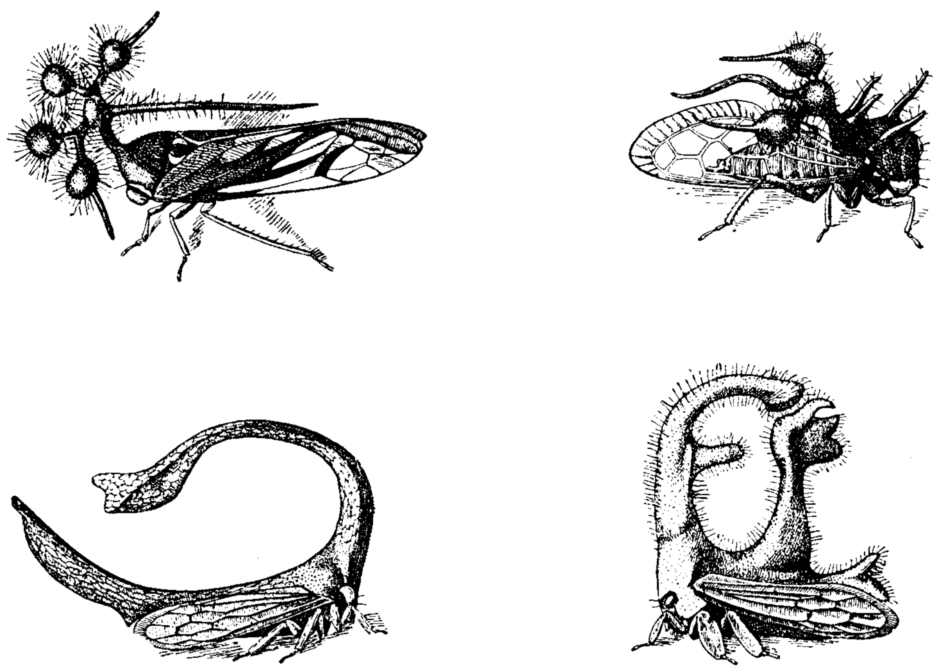
That which was written earlier about sociomorphic projections, especially within the Darwinian framework (competition, survival of the fittest, evolution and progress within it), applies to the above mentioned as well. Darwin was an ingenious and very honest observer with an uncanny sense of detail. His work on sexual selection is literally overfilled with an unusually large number of particularities and quotes of literary and even oral messages, while at the same time he thoroughly examines not only phenomena which support his theories, but also those which refute it (he gathered these with the same honesty as those which were „appropriate" for his theories, which is a virtue not often seen in scientific practice). Darwin was one of the most outstanding personalities representing a phenomenon, which was at its height in European culture in the middle of the 19th century, even though its beginning can be traced back to the Renaissance (**Leonardo da Vinci** is a nice example of this), and which can still be felt today - the sense for particularities and observational talent, in other words faithfulness to the observed object and their correct and complete portrayal (that this cannot be completely done „*sine ira et studio*" was already established in the last chapter, and it is not possible to dispute the fact that certain eras have developed this ability to a greater, or lesser, degree). The faithfulness to the observed object can be read from the amount of prestige that the descriptional branches of study (geography, taxonomy, but even travelogues or realistic painting) have in the society. Some eras on the other hand completely conformed all observations to some abstract model or view and had basically no interest in particularities (the European Middle Ages, also the 20th century in a progressively growing measure). The absence of realism in the arts of both eras clearly shows that the world was viewed as a world of „hidden essence", and not as a world of changing surfaces (we can even say of biology, especially in the second half of the 20th century, that it contains „neoscholastic" features - this phenomenon will be examined later). Darwin had a very fine sense not only of observation and detail, but also of analogy (Analogies are without a doubt, in the same way as the before-mentioned metaphors, one of the most basic ways of understanding the world, they are fundamental for understanding itself - a spiral as a mathematical entity, as the shape of cosmic nebula, and as a snail shell, or the radial symmetry of organisms, crystals, etc., even radiolaries which conform to the Platonic ideal bodies are a good example of this. Right - left asymmetries occur in stereochemistry as well as in snail shells or humans - not only physically, but also in the intellect - for example in feeling the anisotropy of space in the most widespread religions. These analogies can be labeled „transverse", while the others can be labeled „co-ordinated", as, for example, the similarities of the legs on individual segments of a centipede or the similarity of certain legal clauses to each other.). Darwin's ideas arose from the deep-seated analogy between humans and animals /he was a very sensitive observer of animal mentality, as can be seen for example in his work on the expression of animal and human emotions (**Darwin**, 1872) and even if he had not become famous for his selectionistic theory, then just his zoopsychological views and his study of the origin of domesticated animals would have ensured his general fame/. His concept of analogy (which in his case is backed by the acceptance of a common heritage and direct historical affiliation between humans and animals, that is primates) allows the same human emotions and feelings to arise in animals. A sense for beauty and for enjoying beauty necessarily belongs to this. For Darwin this is, of course, a subjective thing, which is inherent as a pleasant feeling in the observer or listener, not an attribute of the object itself. This „esthetical" sense is fundamentally different from the good feeling felt when seeing food, one's offspring, etc., or the bad feeling aroused by unpleasant factors such as bad weather or enemies. Especially the choice of mate from the point of view of the female is also or mainly affected by the following criteria: an attraction to contrasting colors, unusual forms, combinations of various tones, which the male must, if possible, wholly fulfill. Darwin's esthetics actually equal conspicuousness - but Darwin also stresses that the taste of non-human organisms or even remote or „primitive" human societies is very often very distant from the „good" (at that time English) taste of his society - the „disgusting Mexican idols" or bizarre Indian temples are placed right next to the dorsal crests of male iguanas or the inflatable red throat sacs of the frigate bird. Specifically Victorian England, whose female population was careful in forging intimate bonds, choosing their future husbands according to their orderly exterior and other attributes of their broader self-presentation (a nicely ordered accommodation, a secure position and its exterior attributes, like a uniform for example, certainly belong in this category - in any case self-presentation is not limited to exterior appearance even in the animal realm - Darwin mentions, for example, the courtship bowers of the bowerbirds, *Chlamydera,* or the dance floor of the lyrebird, *Menura*, also the nest decorations of hummingbirds), gave Darwin an excellent starting position and observational basis for this type of projection. Not only Darwin, but his adversary in this question Wallace, were both utterly convinced of the pleasure displayed by the female upon seeing a male with the right esthetic qualities for her (we must not forget that even human fashion was more or less uniform at that time) and also of the self-consciousness of own beauty seen in birds and other animals which self-present themselves in courtship dances and postures. Both Darwin and Wallace point out, for example, the evident satisfaction of male birds of paradise kept in captivity, when they are admired by people. Female animals, after many generations, practice a selection of males to find one which looks the best to the female and most conforms to her esthetic canon (Darwin admits selection by the male in only a few cases where the female is more colorful than the male - a few species of butterflies and certain groups of birds, for example the phalarope, *Phalaropus*, where at the same time the role of „mother" is reversed). This possible form of selection would be greatly more probable if there were more males in a group than females - Darwin analyzes this problem using a great amount of material, but he finds the prevalence of males, if their is one, to be very weak, only 10% to 15%. He sees the esthetic preferences of males as a very complex issue (size, form, color, luster, sound effects, in some cases even smell), the ideal male as pictured by the female is something akin to Platonic ideas (Darwin did not of course use this expression) - something like an attractor, or a point of the horizon, to which „real" males get closer and closer as time and selection do their work, and which is „not of this world" and basically does not succumb to selection. Darwin otherwise allows for changes in the „taste" in the evolution of the species, but this process is very slow (certain species of heron have an inconspicuous first plumage, others a white one, in maturity the first become white, the second either white or some other more colorful luster - Darwin assumes that their predecessors gained a white color through sexual selection and that the older, inconspicuous gray was preserved only in the young - afterwards the taste changed and the preference moved to gayer colors, which in adulthood drove out the white variety, which was at the time firmly fixated and which was then retained only in the juvenile plumage). Darwin does not further address the problem of where, how, and why these various types of taste and ideals of beauty arose - he considers them to be completely analogous to human tastes, only they change slower (he points out for example the relatively slow evolution of male clothing in European culture). The establishment of a certain type of taste in females is directly connected with Darwin's concept of the formation of instinct - a certain type of behavior, originally only a gained habit (in this case fashion), is through constant repetition fixated and becomes hereditary, in the same way as in humans, on an individual level, the subconscious ability to drive a car or write on a typewriter has become fixated (Darwin would see even this as becoming hereditarily fixated after many generations, passing so to say into our „hardware"). Darwin was not less than **Lamarck** convinced of for example the reduction in size of organs which are not used (for example eyes in cave fish), and others, today called „Lamarckian", incidents. Darwin knew that these decorations and colors are not directly useful for their owners and in certain extreme cases (the tail covers of the peacock, the flight feathers of the great argus pheasant, the deer's antlers) they can even be hindrances or actually dangerous for the owner. /He often stresses the energy expense associated with creating such decorations or „weapons" and he voices the conviction that beauty and feasibility are often not directly proportional - especially the „most beautiful" (meaning the most bizarre) breeds of domesticated animals and birds are usually the most delicate (Darwin directly compares the feather decorations of various naturally occurring birds with the decorations of excessive breeds of pigeon, which he himself bred/. This reason alone made it necessary for him to postulate a different type of selection from the natural one he postulated earlier. From the fact that some conspicuous structure or color exists on an organism he elicits *eo ipso* its importance for the organism in the sense of „purpose" or „function". From the fact, that some occur within the framework of sexual dimorphism as secondary sexual marks only in the male, he concludes that their cause certainly lay in sexual selection. The conspicuous disparity between morphological and ethological observations of sexual dimorphisms and courtship displays from the whole animal kingdom (one of the most detailed compendiums on this theme ever) is extremely interesting, considering also that the sexual selection is demonstrated on such a poor set of evidence (basically only a small number of casuistic material from the environs of domestic animals, mainly dogs and pigeons, where the females refused one male while longing for another). Considering the fact that Darwin in his diligence does not mask casuistic material which gives the opposite evidence (for example the indiscriminant nature of female moths, the quick replacement of a shot partner with another in various bird species, the choosy nature of male pheasants, etc.), we can say that the whole business at the time of the writing of the book lay solely on Darwin's intuition and his rich experiences with the natural world. Darwin emphasizes, in a weaker way than later Wallace, that when possible courtship ceremonies or self-presentations occur rather than mutual fights between males. He even considers the form of the antlers of various recent and even extinct deer and antelopes as having been influenced by the taste of the female, he also does not consider proved that the horns on the head and thorax of some lamellicorn beetles or the mandibles of stag beetles actually serve for fighting between the males, but that they are mostly decorations produced by selection from the females. It is interesting that he never mentions the males of the same species as being the recipients of the bright colors and other structures of a male member of the species, meaning that in this way this member seems dominant and causes sexual selection himself (as with for example the birds of paradise, **Beehler**, 1987), but Darwin never even hypothetically considers this (later observations confirmed that this type of selection is indeed very important). Darwin interprets bird song as being not only used to lure females, but also as a battle of song between males (in this context he quotes the older ornithological report by **Daines Barrington** in the *Philosophical Transactions* from 1773, who anticipated this concept, including the observation that females do not sing and are inconspicuous in their coloration because they are more vulnerable to predators during the incubation of their eggs). The fact that many birds sing even in times when they are not reproductively active is interpreted by Darwin as the animals' general love for games and letting their instinctive behavior „use itself up" (the games a cat plays with a mouse, a cormorant with caught fish, the courtship ceremonials of the black grouse in the fall, the playful flight of birds, etc.). He puts instrumental „music making", such as the drumming of woodpeckers or the swishing sound produced by the tail feathers of snipes and other birds (examples of duets by African shrikes of the genus *Laniarius*, which are adjusted to each other are also very interesting - **Thorpe**, 1973), into the same category as classical song. He interprets in a similar way imitations of voices of other species, a very widespread phenomenon, and even the imitation of the human voice by captive birds (even in species where it is unexpected, for example pheasants - **Ruplinger**, 1975) /both of these phenomena have been sporadically described concerning mammals as well - seals (**Ralls**, **Fiorelli**, and **Gish**, 1985), dolphins (**Richards**, 1986) and others (**Nikolskij**, 1984) - and the phenomenon of imitation was later often discussed in literature from the neo-Darwinian standpoint - for example **Dobkin**, 1979 - interpretations which suggest some increase in fitness in this way are all so absurd, that they only confirm Darwin's zoopsychological genius./. Darwin also notes a relation between the size of birds and the elaborateness of melody which they sing (most species are small, the largest being the genus *Menura* - the lyrabird) and in them a negative correlation between the song quality and the level of bright coloration, which fits most cases. Besides bird song Darwin also mentioned epigamic stridulation of cicadas and orthopterans, and even duet „singing" by gibbons.

Considering the fact that the majority of conspicuously colored organisms are brightly colored in both sexes (marked dimorphisms constitute only a minority of cases), a problem obviously surfaces: how to interpret the bright colorations of the females? For Darwin these species, where both sexes are conspicuous and at the same time similar, constituted a major problem. He used sexual selection to explain even such structures as for example the excessive beaks of toucans - which is the same for both sexes and which needed a whole scale of other adaptations, e.g. an upturned tail to allow them to fit into tree cavities or a very sophisticated lightening of their huge beak, which for their type of food is unnecessary - he doesn't even mention some others, such as the bizarre shapes of the pronotum of South American treehoppers of the family Membracidae, which is the same for both sexes, and which was interpreted with much difficulty by later authors (e.g. **Fairmaire**, 1846, **Poulton**, 1903a, 1913, **Funkhouser**, 1950, **Haupt**, 1953, **Ekkens**, 1972, **Boulard**, 1973, **Suchantke**, 1976b, **Hinton**, 1977a, b), even though he must have known of them as an experienced biologist with direct experiences of the South American coast in Brazil. The problems of these exaggerated or „luxurious" structures, either sexually dimorphic or monomorphic, was later pointed out a number of times (**Rensch**, 1947, **Gould**, 1974) but basically no progress was made on the theoretical level. What is „excessive" and what is not, is of course anthropomorphic and arbitrary, but even so certain cases literally shout out, as if a certain organ „gained dominance" and „had" the animal, and not the other way around. In the orthodox Darwinian or neo-Darwinian view, the problem actually doesn't exist - every structure is exactly as big as natural and sexual selection allowed it to be, and the latter can, through selection against the entire fitness, dig a grave for a whole species.

Darwin saw the whole problem as a gradual transfer of attributes, mainly through sexual selection, onto the female as well. Whether this process occurs in full (both sexes are semantic and the same - e.g. the hoopoe), only in part (female peacocks have lustrous feathers on their necks, but lack the other decorations), or not at all (the male is wholly semantic, the female wholly cryptic - e.g. the capercaillie), depends according to Darwin on some hidden factor, which influences heredity (Darwin imagined heredity quite differently from Mendel's understanding of this phenomenon - for Darwin it was continual and in the framework of his understanding of „*pangenesis*" each and every organ creates small bodies, „*gemmules*", which then travel to the sexual organs and in this way pass on to the next generation - for this reason he was also convinced of the heredity of certain acquired attributes - as long as the altered gemmules arrive at the gonads). He saw inconspicuous coloration as generally being more archaic and evolutionarily earlier (retained for example in bird females and juvenile plumage, or even in the basic plumage of ducks), and lively and vivid colors as being derived (the whole theory can be, in spite of its evident reasonability, interpreted as a fancy projection of the idea of progress onto nature - the path of the inconspicuous to the beautiful). Wallace's well known theory, that brightly colored female birds always nested in hidden nests (hollows, burrows, "row" above the nest), while cryptically colored birds nested in the open (**Wallace**, 1870) is explained by Darwin as being caused by a change in nesting biology in the females that acquired the vivid coloration (Wallace, as will be shown later, understood the whole thing in an opposite way - cryptic coloration in females was forced by natural selection). Darwin saw a substantial role of sexual selection in cryptically colored birds, e.g. woodcocks, which are at the same time inconspicuous and beautiful. Darwin surprisingly considers the spotted or banded coloration of juvenile deer, tapirs, and pigs as being originally caused by sexual selection. He did not doubt that they conserve the archaic state of their ancestors, but he could not explain why this disappears in adulthood. In various places of his work he discusses the so-called principle of compensation, first expressed by **Cuvier** and **Goethe**, where a certain morphological change in an organism provokes some compensation, „saving material" elsewhere (various deer have either evolved thick strong canines or large antlers, no recent mammal in general has evolved strong enlarged teeth and at the same time larger outgrowths in the form of horns or antlers, the lamellicorn beetle *Onitis furcifer* does not have in the male form chitine horns on its head, but on its coxae or on other parts of the lower side of the body).

The principle of compensation is also the most important explanatory principle in newer trends of Goethean biology, it is used for interpreting striking colorations and sexual dimorphisms in birds (**Kipp**, 1942, **Suchantke**, 1964). Both authors deny the existence of sexual selection from the female side (for example many cases of interspecies hybrids of birds of paradise) and consider species with great sexual dimorphism, in which the „absorption" of

Exaggerated structures formed by projecting pronotum in four treehoppers, members of the family Membracidae (according to Heikertinger).



males by courtship rituals, and in which decorative morphological structures are „shown off" as being more or less in a degenerative process, which excludes males from the reproductive process and gives them certain attributes which can be found in mechanical toys: certain morphological and ethological externalities devoid of any inner attributes (females of these species are on the opposite end of this spectrum, they are completely absorbed in breeding and are completely cryptic in appearance). The principle of compensation can be seen for example in the bowerbird *Amblyornis* (Ptilonorhynchidae), which build courtship „buildings" from twigs - the more complicated the structure the more inconspicuous appearance of the species (Conspicuous, Portmannian species really do have something feebly unreal and at the same time artificial about them, and the idea that the black grouse was just wound up with a key just before its courtship display does not seem too absurd. The neo-Goethean interpretation of organisms, if only because it picks up the tradition of German romantic biology and is quite different from all branches influenced by Darwin /and Creationism as well/, is incredibly interesting, if just because it is an example of a completely different way of thought and perception of the organisms. Because of this the study of its basic compendiums /**Schad**, 1971, 1982, 1983/ is quite beneficial, for example for realizing that common interpretations are not self-evident and for realizing some of the problems of alternate conceptions.). Compared to all other authors (e.g. Wallace, but also **R. Meldola**) Darwin believed in the concept of sexual selection for bright colors in insects as well (which later led to the formation of the concept of warning coloration, as will be shown further). He was especially concerned with (not counting for example dragonflies) butterflies, an essay about their sexual selection was published in *Nature* in 1880 (almost nothing was at that time known about the ethology of butterflies). The coloration of moths and the underside of butterfly wings was interpreted as camouflage (the orange color of the hindwing of moths of the genus *Noctua* - Darwin's *Triphaena* - was according to Darwin a false target for attacking birds, which damage a less important part of the body. Darwin interprets the coloration of the upperside of the butterfly wing as the result of sexual selection from the side of the female, and only rarely from the males). Surprisingly, much later experiments confirmed the meaning of sight orientation in the courtship behavior of butterflies (**Magnus**, 1958) and the meaning of the mutual interaction of males for the fastening and contrasting of the color patterns (**Smith**, 1984), and also selective behavior from the female (**Wiernasz**, 1989). Darwin saw the only other source of butterfly coloration in mimetic imitations and he cites a short passage from **Bates'**, **Wallace's**, and **Trimen's** work and appends comments. The question of the origin of mimetic imitation, further strengthened by selection by bird predators, is solved by the thesis, that the beginning of the mimetic similarities lies far in the past, when both species looked much more similar than they do today. The „model" then through its own sexual selection grew farther apart from its original state and „took" its mimic with it, because they were linked from the beginning. Quite interesting are his comments concerning the mimicry in females of certain butterfly species, while the male has coloring which is typical for the family (*Papilio dardanus*, *Perrhybris pyrrha*), which is explained by conservatism of the females during sexual selection, which in this case is stronger than natural selection by the predators. He enthusiastically describes the observations from Nicaragua of the engineer and amateur biologist **Thomas Belt** (1874), who observed that male mimetic butterflies of the genus *Leptalis* have a white spot on their hindwings (the wings are otherwise orange and black) on a place which is usually covered by the fore-wings. This spot is the last remainder of the „traditional garb" of the females and at the same time a result of their untiring sexual selection.

Darwin also meditates upon the eyespots on the wings of butterflies and moths and even in them he sees a result of sexual selection, even though he is aware that the whole hypothesis has a weak spot, namely that the spots are not more vivid in the males than on the females in any species. He studies in greater detail and longer the eyespots on the feathers of pheasants and peacocks, where they are without doubt secondary sexual marks of various localities (on peacocks on their tail coverts, on the peacock pheasants of the genus *Polyplectron* and in addition on the second wing coverts, on the great argus pheasants on their flight feathers). Darwin describes the complicated and elaborate nature of these arrangements and their deployment and presentation with special attention given to the argus pheasant, where he demonstrates various stages of the metamorphosis of the shadowy spots on the flight feathers into eyespots, which give the impression of semispherical bulges, which are simulated by the shading. He mentions the especial extraordinary fact, that when the wings are spread into a form which roughly copies a segment of a spherical mirror, the formation gives the impression of being lighted from the top, which is caused by the shading on the individual feathers according to their position (Darwin considers this phenomena to be the most cunning that sexual selection can achieve). For Darwin and his view of the world, sexual selection was such a key component because, besides other reasons, he saw historical evolution of humans through it and he saw (partially correctly) its enormous import especially on human society. He explains for example the lack of fur, as an expansion of the originally bald areas of the face and buttocks of primates, often vividly colored (e.g. mandrills), through sexual selection. On the other hand he sees in it the cause for the existence of facial hair in the white race as a continuance of similar structures found in certain primates (e.g. many guenons), or other fur decorations like manes found in male mammals (even the striking coloration of many mammals, for example tigers, zebras, or antelopes, and in the same way for example the penetrating odors of male goats and male deer, were all interpreted by Darwin as examples of sexual selection). He saw sexual selection as also being the agens behind the evolution of „higher" attributes (ethics, friendship, musical ability, intelligence generally, and also carefulness and prudence), which **Wallace** (1870) considered to be caused by the intervention of numinous forces (Darwin's interpretation really requires a great conviction in sexual selection, Wallace knew enough about the minor selective power of these phenomena from his long and agitated life). His pronouncements concerning feeling race specific external attributes by individual races to be beautiful (and their strengthening in this way) were more plausible. Considering the fact that polygamous species have in proportion to the level of polygamy a greater difference in size between the males and females, it can be said that humans, due to the larger size of the male in generally accepted measurements, are „slightly polygamous". Sexual selection in the Darwinian sense of course necessarily requires the existence of differentiated sensorial input and to an extent mature mental abilities. Darwin finds these in crustaceans and insects (inclusive) and higher, and he sees bright coloration in lower species not as an attempt at communication or crypsis (even as a warning they are very rare), but as a coincidence (explaining something as a coincidence is always very bad - if it's not an admission of incompetence and a resignation on the attempted explanation, then it is certainly that that which we consider a coincidence is *eo ipso* meaningless). He calls attention to „coloration without intention" in the world - the bright red color of arterial blood, the vivid colors of gems, derivatives of aniline, the blue of the sky and sea, the green of plants, the vivid colors of leaves in the fall, etc. This understanding of coloration in nature as a coincidental byproduct of the exchange of matter (e.g. the later interpretation of the white color of Pieridae butterflies as a deposit of the otherwise unpassable urinal acid) or as a byproduct of something functional (hemoglobin can cause the attractive blushing of girl´s cheeks, but its own function is quite different) was repeated many times in later literature. Basically until this passage in Darwin's book this opinion was never so *expressis verbis* delivered. The complicated designs on the shells of certain sea snails are still „coincidentally" formed by their growth according to Darwin, and in the same way the elegant shape of shells of certain bivalves (he also notices the coloration of nudibranchian snails without shells caused by light shining through their hepatopancreas). The translucence of medusae, pelagic snails, crustaceans, and many fish were interpreted as being cryptic, by which the organisms are effectively invisible for predators. He was unsure about the vivid, shell-less, sea gastropods from the group Nudibranchia, which evidently do not in most cases display cryptic coloration, but Darwin was in any case unsure as to whether hermaphrodite organisms can undergo sexual selection according to esthetic criteria - in the end he did not wholly discard this thought. Darwin also noticed the phenomenon which in the end came to be called **Oudemans'** principle, which is that the vivid coloration of mollusk shells do not continue in places which are hidden by the palium. The interpretation of secondary sexual attributes through sexual selection has not been significantly innovated since Darwin's time. One addition concerns the aspect of the effect of coloration and exaggerated structures on males between themselves and the selective significance of such ritualized „battles", the whole concept was in detail developed (e.g. **R. A. Fisher**, 1930), but nothing completely significant was added. Hypotheses about the advantages of selected males with such „handicaps", either because he survived in spite of them (**Zahavi**, 1975), or because it was an indicator of good condition (**Hamilton & Zuk**, 1982) are so full of convulsive attempts at explanation of an uncomfortable residual phenomenon in the sense of a sociomorphic definition of „advantage" that it isn't even necessary to comment on them (Zahavi's concept is more interesting as a distinct sociomorphic projection, which reflects the experiences of his ancestors, who were handicapped and ostracized in ghettos).

Wallace's concept of adaptive coloration

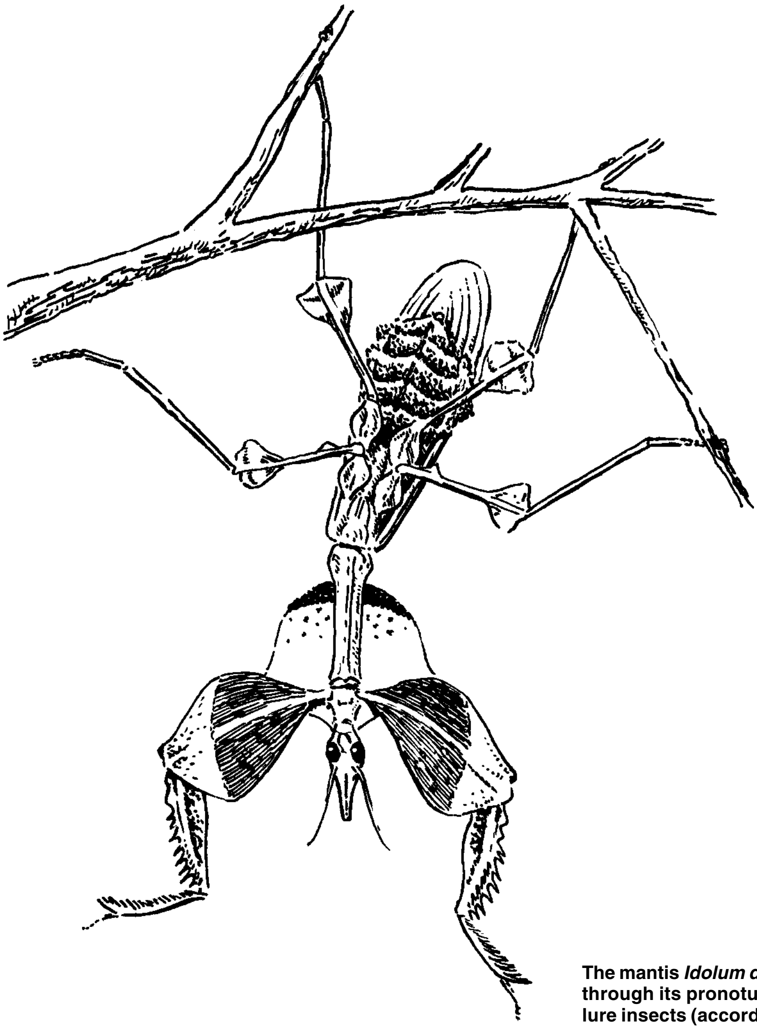
In contrast with Darwin, Wallace did not believe in the influence of sexual selection on the appearance of animals. Surprisingly though this was not because he was not convinced of the female „fascination“ for strong and nicely decorated males which could on occasion lead to selection based on esthetic criteria, but because these excesses are quickly exterminated by natural selection, where only the strongest survive (Wallace understood these as being the strongest, with the highest level of health, energy, possibly aggressivity, more or less in the style of top athletes - Darwin in contrast widened this term to include all those who are well adapted to their environment - in human terms we could include even those who are physically weak, but in a company environment ideal office workers) - these can survive only as domesticated animals, where the selecting factor is a human, who in any case artificially keeps these monstrosities alive (he argued here using human fashion, saying that it isn't just the taste of women which influenced all the fluctuations in fashion from the Elizabethan era up to the present). The vivid colors, excessive shapes and sounds in animals are, according to Wallace, caused by the necessity to distinguish individuals as members of a specific species (this concept was anticipated by **Roesel von Rosenhof** in 1749, as was mentioned in the first chapter, but his message was lost and Wallace, who did not know German, most probably did not know of it). The category of so called *typical colouration* was founded in Wallace's work from 1878 (1878a) and it was further analyzed in his compendium on Darwinism (**Wallace**, 1889), it includes all optic, shape, sound, olfactory, etc. phenomena which serve for intraspecific communication and the mutual distinguishing between species which live socially (antelopes, many birds, coral fish, etc.), or at least not completely individually (this concept was appreciated only much later with the development of ethology, for example by **Portmann**, 1953). Even here Wallace, like Darwin, argues for the existence of color (in a typical case in both sexes the same) for its functionality (in this case as a species specific identifying mark), and the ability of animals to optically distinguish members of their own species according to these marks points to natural selection as the cause.

While, for Darwin, striking features in both sexes was a problem, for Wallace the opposite was true. That is why he considered species with sexual dimorphism to be derivative, and that because of the pressure of natural selection on the female in the sense of inconspicuousness, especially in the time of breeding young. In his work on the correlation between the coloration of birds and their nest type from 1868 (*A theory of bird nests, J. Travel Nat. Hist. 2* in **Wallace**, 1870), which was already mentioned, he considers the method of the nesting of birds (in closed and open nests) to be primary and the inconspicuous coloration of females from species which nest freely to be secondary, caused by natural selection by predators /He also analyzes the question of the coloration of bird eggs, where in fact a correlation exists between white coloration in nests in various hollows and colored eggs in open nests, but only statistically, not in all groups. He mentions for the first time the question of color adaptation of cuckoo eggs to the eggs of host species, which was later analyzed many times, and he comes to the conclusion that this occurred due to selective pressure from predators, which noticed nests with vivid or conspicuous eggs, and not from the pressure of the adopted parents. At the same time he cites the curious work of an Australian author (**A. H. S. Lucas**, *Proc. Roy. Soc. Victoria* 1887: 52-60) about the influence of colorful items, which the female often sees during the maturing of the eggs in her body, on the coloration of eggs - this work noticeably suggests old archetypal beliefs about being influenced by certain articles by human mothers and female animals during pregnancy, as is written for example in the **Old Testament** (*Gen.* 30: 37-43)./. Wallace also considers bird song in females to have disappeared through natural selection, and not primarily just missing. The switching of roles in certain species of birds, where the male is inconspicuously colored, is interpreted in the same manner. He considers various colors, lusters, and decorations as signs of vitality and a way to get rid of extra energy and nervous tension in the males, the same goes for their song, which they produce in abundance, and their courtship ceremonies, which he compares to human ways of getting rid of extra energy, by song, dance, and social events. The battles between males are not considered by Wallace to be ritual tournaments, but direct and bloody battles „teeth and claw“, which would correspond to the popular Darwinian concept of the „law of the jungle“ (it is interesting to note in how much detail e.g. **A. Hitler** /1942/ bases his own actions on a vulgarized version of the battle for the female in nature and society and on such „sexual selection“ generally). Wallace sees in these battles a form of natural selection, even if only within members of one species, about the same as the battle for power within one group. He adds that courtship ceremonials can also be found in birds colored wholly inconspicuously, which have no meaning besides demonstrating vitality and ventilating tension (in this way he comes much closer to the newer authors cited at the end of this chapter, where ornamental structures are also only an epiphenomenon of vitality). But this does not solve the problem of excessive secondary sexual characters, especially not those which have a very sophisticated structure and necessarily need a whole scale of other adaptations (e.g. the extendable crowns and neck collars, the peacock's tail, etc.). Wallace already in his work from 1867 mentions between the lines and later analyzes in detail (**Wallace**, 1878a, 1889) his theory, which states that live organisms, if left to themselves and under the influence of light and air (here he is alluding to colorless or inconspicuous species, such as cave animals, internal parasites, endophagous larvae, etc.) gain contrasting colors and patterns, and even metallic lusters, if these phenomena are not removed through natural selection in the sense of cryptic phenomena (in the first of the works he mentions the bright colors and lack of cryptic coloration in „protected" families of butterflies - Danaidae, Heliconiidae, and other insects - wasps, ladybirds). Conspicuous coloration and structure can then arise wherever the species can „afford it", and is not really selected away through natural selection. As he concludes in his last Darwinian book (**Wallace**, 1889), conspicuous structures and colors do not arise on the organism's body by coincidence, but on "liking" or predilected places, which in some way observe anatomical givens (e.g. prominent bones directly under the skin, on the head, spinal prominence, leg joints, ribs, shoulder-blades, the pelvis, further in places where large veins and nerves reside, the attachment of massive muscles to the tip of the ears, tail, legs, nose, around the eyes, etc.). These thoughts are taken from the then recently published book by **A. Tylor** (1886). Spots can form primarily at these locations, and can eventually become bands or eye-spots (this process is especially used to explain for example the bands or spots in many large mammal juveniles), or even places with elongated fur or feathers. The thought that animal patterns in some way follow the anatomical design was not new at that time (the connection between veins on butterfly wings and the wing pattern was noted as early as 1861 by **Rössler**) and Wallace uses medical arguments as well, e.g. following certain nerves through certain herpetic rashes (that the dependence of patterns and decorations on anatomical features is only half of the truth and that a whole series of phenomena are independent of anatomy, was shown much later). Every group has different predilectic places - butterflies have wing venation, birds have the tops of their heads, their throats, around their eyes, on their coccyx, on their furcula, and on their tail covers, butterfly caterpillars on each segment, beetles on their scutum and elytra, or even on their margins and corners. Conspicuous colorations are especially strong on protrusions of the skin - fur, feathers, scales, and also scales on butterflies and on their wide wings in general (Wallace understands this in part as „advertisement space" for coloration which serves for intraspecific recognition, in part as a component of their defense strategy - bird predators will damage the large and bright part, which isn't vital, rather than the small body). Wallace considers birds with unusual feather decorations especially successful in the struggle for survival, with a large surplus of vitality and strength, which can „afford" their decorations and excesses (He understands birds of paradise in this way as well, while Darwin considered them unusually fragile and endangered by their own sexual selection - from the male side unable to contribute to the nesting and breeding process - newer studies, e.g. **Beehler**, 1987, show the extreme concentration of all life interest of the males on the courtship ceremonies, in many species collectively. The males consider the female as something marginal and are in a large way concerned only with themselves.). /For this reason Wallace was later taken with **Weismann's** idea of *Germinal-Selection*, which channels variability in only one direction (basically orthogenesis) and natural selection can then only affect that one direction. This concept allowed for the explanation of ornamentation and vivid coloration without resorting to sexual selection, which was from the beginning an eyesore for Wallace (in any case Wallace himself did not have good experiences with it, as compared with Darwin, who through sexual selection produced an idyllic family and good standing - personal experiences of scientists often find their way in a transformed and impersonal form into their scientific opinions - those principles which we understand to be constructive or destructive for us personally tend to be projected onto the world)./.

Wallace demonstrates the importance of semantic coloration for intraspecific recognition and communication on many more examples, e.g. on the coloration and patterns of bird flight and tail feathers, which in many species form a continuous and meaningful color pattern or ornament only when the wings are spread during flight, or the phenomena where color patterns of many species become more intense at the borders of their geographical areas or in places where many related species live together, or even the deterioration of these patterns in species which appear individually on secluded islands (e.g. certain ducks). He also mentions global laws which define the degree of occurrence of vividly colored species of birds, mammals, insects, etc. in relation to geographical conditions - generally speaking inland species are more vivid than coastline and island species, further from north to south and with the increasing humidity of the air (Wallace paraphrases so-called **Allen's law** - **Allen**, 1874) - he explains this phenomenon as being caused by the increase in hiding places in the rich vegetation, the abundance of food, and the stable conditions of the tropics, which suggests conditions in Europe's tertiary and which enables a whole scale of semantic colorations and mimetic phenomena (the aspect of long time-periods of stability in tropical biotopes and the large number of generations of insects during the year, which allows a much quicker selection process, which Wallace didn't mention, was added later). Wallace mentions in his essays on tropical nature (1878b, also 1891) his observation of the common occurrence of white spots and bands in butterflies and birds on tropical islands and concludes that this is caused by the small quantity of predators and the large quantity of hiding places in the vegetation (see also the mention about „local factors“ in his work on Malayan butterflies from 1865).

Wallace interpreted a whole scale of coloration in large mammals, e.g. the striped zebra, as being used for interspecific communication and differentiation. /In connection with this it would not be amiss to mention some theories concerning this striking phenomenon, which expanded on every imaginable thought (details in **Cloudsley-Thompson**, 1984). Explanations range from ones which consider it a nonfunctional byproduct of irregular growth of skin zones during embryonic development to „cryptic“ functions in the night (the animal does not appear to be either a dark or a light mass), an optical approximation to the predator, making it incorrectly calculate its jump, a provocation of the predator, making it attack prematurely and therefore unsuccessfully, a cryptic function in high grass and bushes, a repellant for bloodsucking insects, especially flies of the genus *Glossina*, to the role of intraspecific communication according to Wallace. It is quite symptomatic, that each and every one of these theories can be at some point verified by direct experiences of the observers, but they are exactly proven less often. At the same time we can observe the lessening or even disappearing of the stripes as we progress from the north to the south, from the many thin and contrasted stripes of the Grévy´s zebra (*Equus grevyi*) to the few but broad strips of Böhm's zebra (*Equus quagga boehmi*) and lastly to the now extinct quagga from the Cape region (*Equus quagga quagga*), which had stripes only on its front and legs. The rest of the species of the genus *Equus*, wild asses, kulans, and other semi-asses, and horses are striped in the best of cases only on their legs and they survive anyway. This case shows so to say *in nuce* the problems of interpreting animal patterns and colors in general, even though it is a case well known since the 19th century and which has been well documented./. Wallace deduced the left-right symmetry of animals' exterior color patterns from the necessity of intraspecific recognition, which can also be seen in the work of the Yale zoology professor **W. H. Brewer** (*Proc. Am. Assoc. Advans. Sci.* 30), which dealt with the left-right symmetry of zebras, tigers, and other feline species, where the optical symmetry is always more or less present, but where small differences in the number and configuration of stripes is present as well - Wallace deduces from this that the symmetry, which is often flawed in domestic animals (Wallace does not mention the few examples of this from the wild, in the harp seal, *Pagophoca groenlandica* ant the Cape hunting, *Lycaon pictus*), is maintained in nature by the functionality of the patterns for intraspecific communication. So called *recognition marks*, found in many mammals and birds (**Wallace**, 1878a, 1889), were a matter of great interest for Wallace. In mammals these marks are generally white and can be found on the anal end of the body, or in certain cases on the head or on different parts of the body, including the shape of the horns and antlers (gazelles and antelopes, hares, rabbits, etc.). In birds these would be semantically colored spots (on the throat, chest, coccyx, etc.) in otherwise cryptically colored feathers. Any coloration in the world can be, of course, explained using a combination of hypotheses on cryptic and identifying marks, but it seems that Wallace's interpretation isn't as absurd as it appears at first and a number of species really display either cryptic or semantic traits, depending on the situation (even though it is sometimes necessary to strongly believe Wallace's theory to see this). In connection with this he also cites the American author **Todd** (1888), who in his work discusses these „*directive colourations*“, to which he surprisingly also attributes the countershading of mammals, which was later described by **Thayer** (1896) - the light color of the inner sides of the legs and belly as compared to the darker back. Wallace also contemplated whether the coloration of mollusks can function in intraspecific communication, he absolutely refuses to apply this concept to lower marine organisms, where he considers all coloration to be cryptic (a very bold standpoint).

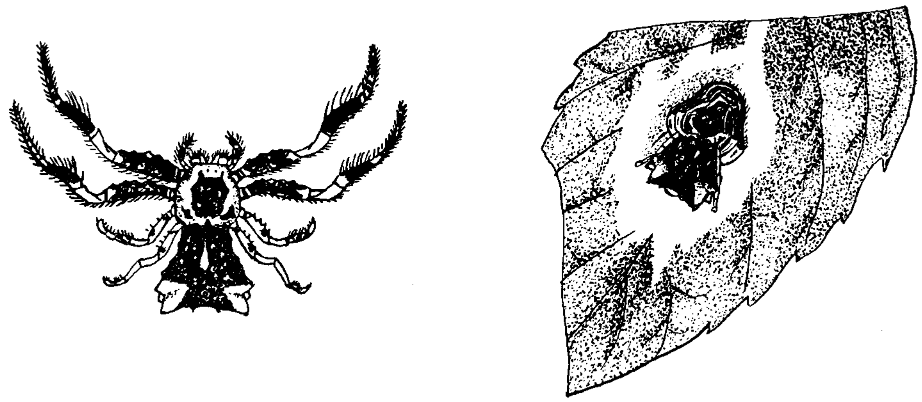
Cryptic coloration were in all Wallace's favorite theme and he often saw them in phenomena, which Darwin considered to be the result of sexual selection (e.g. the coloration of tigers, as can be found in his correspondence, **F. Darwin**, 1887). In the work from 1867 he describes, amongst numerous other examples, Asian butterflies (the family Nymphalidae, genus *Kallima*, especially *K. paralecta* and *K. inachis*) as typical examples of leaf mimicry and extreme cryptic adaptations (it was this „hypertelic“ crypsis which gave rise to doubts about its origin in natu-



The mantis *Idolum diabolicum* from western Africa imitates through its pronotum and fore femora an orchid flower to lure insects (according to Wickler).

ral selection, e.g. **Mivart**, 1871, **Beddard**, 1892, or **Morgan**, 1903). These butterflies, which Wallace observed during his trip to Malaysia, pervade not only all of Wallace's subsequent work, but all literature on mimetic phenomena, including the most popular pamphlets which promote classical Darwinism to people whose iconography necessarily includes not only pictures of *Archaeopteryx*, the evolutionary line of larger and larger ancient horses, and of primates climbing down trees and slowly straightening their posture and becoming more human, but also pictures of Darwin as a wise elder with a long, gray beard.

Wallace (1878a, 1889) separates the category of „*alluring colourations*", even though they basically represent extreme cases of crypsis which serve to deceive prey, from the main body of cryptic colorations - e.g. Asian mantids of the genus *Hymenopus* and *Gongylus* which imitate flowers (**Wood-Mason**, 1878) or a Borneo spider which evokes the impression of bird excrement, which is achieved not only by his own body but also by the web on the leaf, which serves to ensnare butterflies and flies that land on it (**Forbes**, 1885). These phenomena were later subsumed under so-called **Peckhamian mimicry**. Wallace also marginally mentions a number of insects, which assume various threatening postures or which present bizarre displays or colors when disturbed, even though they are more or less edible rather than dangerous for the predator. This is on one hand a continuation in the naive tradition of **Kirby** and **Spence** (1817), and on the other an anticipation of the later doctrine of **pseudaposematism** (**Prochnow**, 1907). These threatening and warning postures of various organisms, which attempt to scare or at least cause uncertainty in the predator with unusual appearance or behavior, are in detail analyzed by **Callois** (1960), who observes their similarity to war dances, which are connected to body paint on warriors, ornaments or horns on their shields and helmets, and fearful battle cries, which are all part of the „ethology" of masculine rituals in many societies, or on the other hand their similarity to ritual dances of shamans and masked dancers, which are also



The spider *Ornithoscatoides rothschildi* from Borneo imitates bird excrements on leaves (according to Pocock)

made up of ecstatic and spasmodic gestures, or even frenetic and wild gestures. This behavior, which is supposed to mediate feelings of the numinous and the dangerous at once [basically these two are the same thing - **Otto's** (1907) *mysterium tremendum et fascinans*], has a surprising number of parallel features with the indicated trends of organism behavior and self-presentation with the goal of intimidating, or scaring away, the observer.

Aposematism

Wallace also deserves credit for the formulation of the theory of **aposematic coloration** (*warning colouration*, the term *aposematic* was already used by **Poulton** in 1890), whose genesis cannot be properly understood without a broader understanding of Darwin's and Wallace's concept of animal coloration. Darwin, while collecting material for his book (**Darwin**, 1871), came upon an unsurpassable problem in his interpretation of brightly colored insects, which he *en bloc* considered to be products of sexual selection. The problem was in many butterfly caterpillars, often loudly and vividly colored and often having many „ornaments" in the form of various hair arrangements and structures. In 1866 he wrote, based on advice given by **Bates** *„You had better ask Wallace*", a letter (**Darwin F.**, 1887, III, 92, 93) in which he turned to Wallace with this problem (because not even a very strong belief in sexual selection could convince him to apply it to larval stages). Wallace really very quickly fabricated a hypothesis, stating that the bright colors of caterpillars are not meant for members of their own species, but for predators with an optical orientation and the colors indicate inedibility or toxicity /Darwin was thrilled, as follows from his answer - **F. Darwin**, 1887, III., 94, 95 - *„Bates was quite right, you are the man to apply to in a difficulty. I never heard anything more ingenious ... That is a splendid fact .. It warms one's very blood to see a theory ...*" - and in the same way as in the book on the origin of man, **Darwin** (1871) adds to Wallace's contribution that he is one *„who has an innate genius for solving difficulties*"/. Because the relatively soft and fragile body of a caterpillar would not survive more than one „tasting" and probably wouldn't survive even the first, such a lesson for the predator is of great use only for the surviving members of the species, which are then easily recognized by the predator because of their vivid coloration, and subsequently left alone because the predator does not wish to repeat its unpleasant experience. /The idea that one (the first to be found) specimen would ‚sacrifice' itself in this way for the others, was not uncommon in that era - theories that this could happen only within *kin selection*, where the „sacrifice" would save its siblings, with which it lives if possible gregariously in a group, and in that way save at least part of its own genome, came much later (**Haldane**, 1932). It was finally supposed to be shown that even caterpillars, not to mention adults, can in a significant percentage survive the gastronomical assaults of birds (e.g. **Sillén-Tullberg**, 1988, 1992)/. In the same year Wallace organized a discussion about the problem of warning coloration under the *Entomological Society of London*, the *Proc. Ent. Soc. Lond.* contains a summary of the minutes /**Westwood, Wallace, Bates, et al.**, 1866/. In the following year /*Proc. Ent. Soc. Lond.* the 4^{th} of March, 1867/ he invited members of the Society to, in the following season, make observations of the feeding on caterpillars by various predators. The first results, concerning experiments on frogs, were published by **A. G. Butler** in 1868 and in the following years a whole range of additional works were published (**Butler**, 1869, 1889, 1890, 1910, **Weir**, 1869, 1870). This time Butler experimented with green lizards (*Lacerta viridis*), and Jenner Weir with various species of passerine birds. Wallace's assumptions were more or less confirmed - hairy or thorny caterpillars were for the most part dismissed, bare ones which had vivid, usually yellow-black coloration, were also ignored. Especially caterpillars and imagos of the magpie moth (*Abraxas grossulariata*), which was later a model example for aposematism study and even early genetics, were downright rejected, the same goes for caterpillars and imagos of burnet moths (*Zygaena*). These results were then referred to by Wallace in the second edition of his essays from 1867 in the collection of essays on natural selection (**Wallace**, 1870), along with a now complete theory of warning coloration (the first edition only emphasizes, as was mentioned above, the absence of cryptic coloration in well-armed and inedible insects and their vivid colors - wasps armed with a sting, ladybirds secrete blood with a repugnant taste, bugs with repugnant glands, the bombardier beetle *Brachynus* defends itself with explosions from its perianal glands, etc.). Wallace considered the lightening of glow-worms to be aposematical as well. He expanded on the theory of warning coloration in his works from 1878 (1878a) and 1889 (it is interesting to note that the only case of anticipation of Wallace's concept of warning coloration comes from **Roesel von Rosenhof's** book (IV.), cited in an earlier chapter in connection with the question, whether vivid colors of the tiger moth which was later named *Arctia hebe* are not intended for its predators, that is bats - in the end though Roesel abandoned this concept). In the last mentioned work Wallace mentions his typical example of the aposematic coloration of the skunk, whose repugnant glands with their disgusting stink guarantee complete protection and allow relatively slow movement and „bold behavior" and at the same time it has a contrasting black and white pattern (aposematism in Mustelidae is described later in the extensive work by **Pocock**, 1911). Wallace also summarizes works which were already published on this theme - experiments by **A. Weismann**, which will be discussed later, with caterpillars, especially interactions between hawkmoth caterpillars and green lizards, the extensive study by **E. B. Poulton** (1887), which organizes in tables all earlier research and adds his own experiments with various insects and lizards, geckos, and tree-frogs. Darwin himself more or less accepts Wallace's views, to which he refers in the chapter on butterfly and moth caterpillars in his book on sexual selection (**Darwin**, 1871). In the same book there are only two other mentions of aposematic coloration - one very brief mention in connection with lower sea organisms in the sense that certain species have coloration which could be easily interpreted in this way, and the second in connection with the contrasting (black - red) coloration of the La Plata frog *Phryniscus nigricans*, very prolific and conspicuous, therefore probably ignored by birds (a letter addressed to **Henslow**, sent from Monte Video on 11. 24. 1832, dealt with this species as well, **Darwin F., Seward** 1903 - *„it may be christened ‚diabolicus'* „). **Darwin** also cites **Belt's** (1874) observations from Nicaragua, where he fruitlessly offered an aposematic frog of the genus *Dendrobates* to a young duck.

In spite of his satisfaction that his problem with the theory of aposematism had been solved, Darwin never returned to it nor did he attempt to apply it to other cases, because it went against his theory of sexual selection (Darwin's debate with Wallace about sexual selection and dimorphism dragged on through personal correspondence and in printed publications for a long time - for more on this problem see **Kottler**, 1930, **Gould**, 1980, and **Ghiselin**, 1969 and 1974). Darwin's friend and neighbor **J. Lubbock** also dealt with the theory of the coloration of caterpillars in relation to their hair-cover and edibility, and also wrote speculatively about the archaic origin of human society, he was also an enthusiastic Darwinian - but only an amateur, he was in reality a wealthy businessman. Earlier works which tested the edibility of aposematics for various predators, especially birds, started an absolute flood of publications on this theme. For example Butler expressed his opinion in his work from 1910, **Prochnow** (1907) organized his own and others' results, **Heikertinger** (1922) summarized earlier results including a list of used predator and insect species and added extensive commentary, **Jones** (1932, 1934) conducted extensive experiments with wild North American birds and insects, **Süffert** (1935) summarized the results of investigations from between the two wars, and further **Cott** (1940), and **Przibram** and **Brecher** (1919-24) comment in detail on stomach analyses carried out on wild birds. Works on the edibility of the meat of vividly and cryptically colored birds by **H. B. Cott** (1946) are also very interesting - they were carried out in Egypt during the war using people, cats, and wasps as predators and he concludes that inconspicuous species (larks, quails) taste better than vividly colored species (bee-eaters, hoopoes, rollers). Of interest are also other works by Cott on the same theme (**Cott**, 1964, **Cott & Nelson**,

1970) and the first proved toxicity in an aposematical bird - the hooded pitohui, *Pitohui*, from New Guinea (**Dumbacher, Beehler et al.**, 1992). After the Second World War there was a drastic increase in works studying the toxicological aspect of aposematism (**M. Rothschild, L. P. Brower, M. D. Bowers** - for more information see the *Bibliography*). At the time one of the favorite subjects of study was the North American monarch butterfly *Danaus plexippus* and its African relative *Danaus chrysippus*, where, as a model organism, individuals were found to have differing levels of toxicity, which was formulated in the „*automimicry*“ hypothesis (e.g. **Brower**, 1968) - basically this theory is a play on words which indicates that less toxic or non-toxic individuals „hide“ in a way behind their toxic relatives (of the same species), so they mimic (in any case they look the same) and profit from their protection from predators, without actually contributing to that defense. Because the vast majority of works on aposematism do not contribute anything conceptually new, which would have to be *expressis verbis* included in this book, I would like to direct the interested reader to the *Bibliography*. And although it follows from the vast amount of work that organism with aposematic types of coloration are eaten less often and with less enthusiasm by predators than cryptic species, nonetheless „protection“ based on repellants or toxins (either *de novo* synthesized or sequestered from precursors found in their diet, usually toxic plants /sometimes, as in South American butterflies from the family Ithomiidae, the toxin is acquired only by the imago by sucking plant flowers [**Brown**, 1984, 1987] /) is not by far as perfect as the old authors believed it to be. It is obvious, from the huge amount of often contradictory evidence, that the preferences of not only certain predator species, but of individuals within that species can vary and even factors such as momentary hunger play a very important part (starving birds will of course eat even aposematics) in a way similar to receptions, where the tastiest food disappears from the table first - inedibility is always a category which is very relative to the given situation, and not something which functions mechanically, as was sometimes thought. Of course, certain species and groups of birds, which feed primarily on aposematics (in Europe for example bee-eaters and orioles), exist and even model aposematic species, such as the above mentioned *Danaus plexippus*, containing a large amount of cardenolides, are regularly eaten by birds and rodents in their Mexican winter retreat (e.g. **Brower & Calvert**, 1985, **Brower et al.**, 1985). It has already been mentioned that a whole scale of insects, not only in their adult stage, but in the larval stage as well, can survive the gastronomical interest of predators and even reproduce. A large number of aposematic species live in a markedly gregarious fashion in larger or smaller groups of individuals, which are surprisingly slow and bold in flight and on land, and at the same time very long-living and immune even to mechanical damage (e.g. the before mentioned butterflies and moths from the families Danaidae, Heliconiidae, Zygaenidae, etc.), for example imagos of the family Heliconiidae typically rest together at night, or the mass-wintering of the monarch, *Danaus plexippus*. Even the reproductive period of aposematics is usually, due to the long life of the imago, quite long and the number of laid eggs is relatively small. Red, orange, and yellow (and rarely white) with black (or less often dark brown or blue) are the most common aposematic color combinations used. These combinations can contain up to three or even four colors (e.g. red, yellow, and white with black). **Wallace** (1889) emphasized that a combination in itself without an esthetically pleasing pattern basically does not appear in nature and aposematic patterns also have, in his view, the function of intraspecific communication (for **Darwin** they are also an object of sexual selection). It is surprising that the concept of aposematic coloration did not come before **Bates'** Darwinian theory of mimicry, but on the contrary came 6 (the final publication came 9) years later, even though in essence it is the logical precursor (as was said before, **Bates** considered the vivid aposematic colorations of „models“ to be adaptations to abiotic factors of the habitat, and not as being caused by and intended for predators). Wallace and a large number of his followers (not including **J. Weir** and **Distant**) understandably considered young insectivorous birds naive, in the sense of a *tabula rasa* (as the 19th century almost without exception considered man - Darwin and Wallace also considered bird song to be primarily a learned thing - **Locke's** belief that apriori ideas do not exist, which in the 19th century was at its peak, pervaded very strongly into beliefs concerning the animal world, where the absurdity of this belief is even more apparent than in the human world). In certain experiments young birds really did act naively and attack aposematics, and only later did they learn to keep away, or in some cases a remarkable correlation between the time taken to leave the nest and the minimal occurrence of hoverflies which mimic wasps was observed in North America (**Waldbauer**, 1981). Different experiments on the other hand show that young birds (the family Tyrannidae) are born with an aversion to snakes with a „coral“ pattern (**S. M. Smith**, 1975, 1977, 1978, 1980) or the fact that newly hatched pheasant chicks refuse to eat mealworms which are colored with black and red ornaments (e.g. **Schuler & Roper**, 1992).

This seems to be an archetype which is very widespread among vertebrates and well known in mankind as well - the combination of red and black was traditionally connected to „diabolic“ powers or other threatening factors, incidentally it is this combination - red light with a black frame - functions as a warning on road crossings (even various warning signs have, without imitating natural aposematics, evolved in very analogous ways - the combination of orange and black, yellow and dark blue, etc.). A nice example of this analogous feeling are the uniforms of the papal guard, designed by **Michelangelo**, which have the same combination of colors as is typical for example for hornets (even here we are dealing with a creature which is better left in peace, untouched, if only for its excellent armaments). /This whole business points to a very interesting fact: the basic archetypal ideas are found not only in humans, but in vertebrates and sometimes in invertebrates as well - even a non-zoologist can instinctively distinguish between young and adults in other classes of vertebrates. Fear and stress can be discerned not only in the vocalizations of human infants, but also in lonely young chickens or goslings and even in an „agitated“ bumblebee, which is being held in a pair of tweezers – while when the bumble bee is in a flower the buzzing seems „happy“./

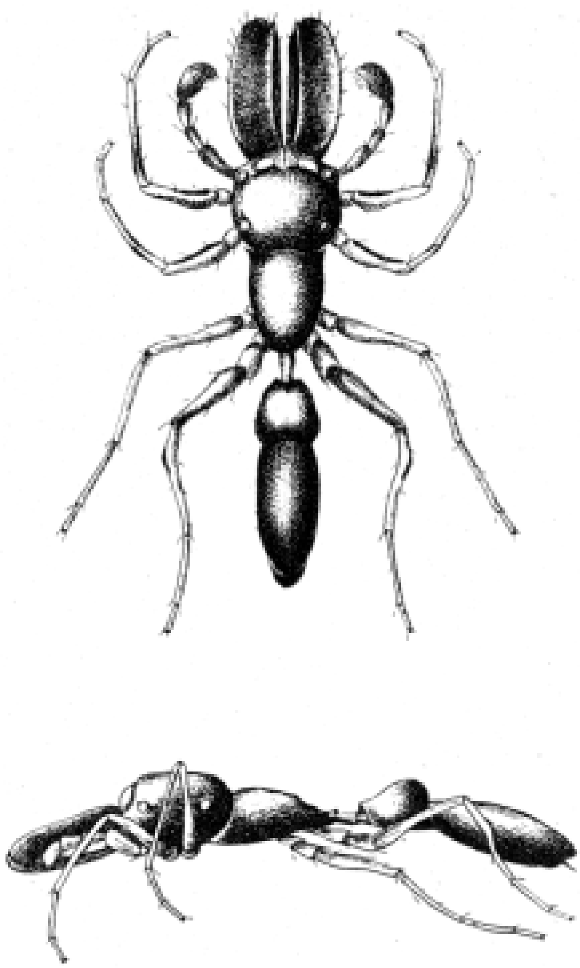
The theory of aposematic colorations is certainly statistically valid, but like many other theories about the many-faceted living world, it is just that - only statistical. A large number of groups, which are perfect textbook examples of aposematism and are frequent models for mimics of course exist. But then again a large group, where this theory falls short, exists as well - wasps which have a sting are generally aposematic, but bees with the same weapon are basically cryptic (even so they are the subject of mimicry, e.g. by the drone-flies of the genus *Eristalis*, which copy not only their form, but the frequency of their buzz as well). Many poisonous snakes (*Micrurus, Elaps*) are markedly aposematically colored, other just as poisonous snakes (Crotalidae, Viperidae) are mainly cryptic. Besides many aposematic and inedible butterflies and moths, a number of cryptic species, which are also avoided by predators, exist as well (from our own for example the buff-tip moth, *Phalera bucephala*). Those interested in a more detailed account of aposematism with many illustration can turn to **Wickler's** book (1968).

In spite of a certain vagueness of Wallace's interpretation and division of animal coloration, his concept in combination with Darwin's (both are to an extent complementary and emphasize that which the other disregarded or ignored - this is obviously applicable to the authors as well) still today serves as a basis for „evolutionary selectionist“ interpretations of the external appearance of living beings, which is why they were both dealt with in such detail (not even neo-Darwinism brought any significant innovation, only a more detailed and more „truthful“ analysis of the concept - a characteristic of both Darwin and Wallace was that they were too good at observation to be true „Darwinians“ - that was only to come later, when biologists no longer came into contact with indefinite and basically burdensome nature, but only with „models“ of it, either mathematical or in the sense of „model“ organisms). Not many alternative concepts were ever developed (**Hingston**, **Portmann**), not including newly revived creationist concepts, which are basically just an attempt to reestablish the diminished natural theology of the 18th and 19th centuries.

The aposematic coloration of the eastern African tree frog *Megalixalus fornasinii*, which is also an example of Oudemans' phenomenon concerning the formation of „holistic“ coloration, seems to be painted on the frog when in a calm position regardless of morphological particularities (according to Cott).

Wallace's concept of mimicry

In his works, **Wallace** (1867 and 1889) introduces a large scale of casuistic observations on various types of mimicry in organisms, which covers almost the whole range of easily observed instances of these phenomena and the observations in this work were later used as a basis for secondary literature. Especially the work from 1867 is rich in examples of Batesian mimicry in butterflies and beetles (including the imitation of aculeate Hymenoptera by longhorn beetles, Cerambycidae), he also mentions a tropical spider (probably from the genus *Myrmarachne*) which imitates an ant, which Wallace interprets as an aggressive mimicry because the spider should feed on the ants (cases of myrmecomorphic spiders, especially from the family Salticidae, are often in literature interpreted as either examples of mimicry aimed at predatory birds or as mimicry aimed at ants, which are actually eaten by some of the species - e.g. **Oliveira & Sazima**, 1984, 1985). Wallace also describes cases of mimicry in the „coral" group of snakes from tropical America (on the basis of data supplied by the curator of the reptile collection of the British Museum, **Günther**) and in his work from 1889 he also cites the work by **A. B. Meyer** (1870) on this theme (Wallace considered „coral" patterns to be aposematic) and in the same work he interprets the rattlesnake's rattle and the cobra's ability to spread its throat as being instruments of warning. In his work from 1867 he writes in more detail about the mimicry of Indonesian birds, which was mentioned earlier by **Bates** - a species from the oriole genus *Mimeta* (Oriolidae) imitates a species of honeyeaters genus *Tropidorhynchus* (Meliphagidae), which in a later study he extends to include other examples, the most spectacular being the imitation of the Bornean pheasant of the genus *Euplocamus* by the Bornean ground cuckoo *Carpococcyx radiatus*. From the subsequently described mimicry cases in birds, the imitation of turkey vultures of the genus *Cathartes* by the American zone-tailed hawk *Buteo albonotatus* in flight (e.g. **Willis**, 1963, **Mueller**, 1972, **Zimmerman**, 1976) deserves special mention because it appears to be used to deceive prey into believing the bird is a non-hunting carcass-eater. The imitation of the sparrowhawk by cuckoos is also interesting (e.g. **Kuroda**, 1966, **Hustler**, 1990). Certain parallelisms in the coloration and type of figure of owls and day birds of prey in certain regions is also quite curious (e.g. hawkowl, *Surnia ulula* and sparrow hawk, *Accipiter nisus* in northern forests, spectacled owl, *Pulsatrix perspicillata* and harpy eagle, *Harpia harpyja* in Amazonian jungles), not to mention species pairs of African bush shrikes of the genus *Malaconotus*, that have the same external appearance in certain regions, which is somewhat analogous to local Müllerian parallelism found in the butterflies *Heliconius melpomene* and *H.erato* in the Amazon basin (**Hall, Moreau & Galbraith**, 1966). A curious case of bird crypsis, which deals with the imitation of a bush after hiding the head seen in ostriches (**Saleh**, 1984) confirms the old „myth" about hiding the head in the sand. The work from 1867 also includes cases of mimicry in mammals, again from the Malayan area - the imitations concern various squirrels, which are imitated by tree shrews (from the genus *Tupaia*, Wallace uses the name *Cladobates*). The goal of this imitation is supposed to ease sneaking up to small birds and insects (subsequent literature knows of other cases between mammals, like the imitation of brown hyaena, *Hyaena brunnea*, by the aardwolf , *Proteles cristatus*, or the imitation of the ratel /*Melivora capensis*/ by young cheetahs /*Acinonyx jubatus*/). From the wide range of later described mimicry cases in



The myrmecoid spider *Myrmarachne formosana* from southeastern Asia lives nearby ant-hills on plants which are visited by ants (according to Jacobi).

vertebrates, some of the most interesting are the imitations of invertebrates, as is the case with both of the following young lizards - Kalahari racerunner lizards of the genus *Eremias* mimic ground beetles of the genus *Anthia* (**Huey & Pianka**, 1977) and the Turkestan geckos of the genus *Teratoscincus* imitate scorpions (**Autumn & Batur**, 1989). The imitation of vertebrates by invertebrates is more common, for example the numerous cases of mimicry of snakes by hawkmoth caterpillars (Sphingidae) - see the *Bibliography*, the imitation of the shrew by the Malaysian eggar moth *Suana concolor* (**Mortensen**, 1922) is also quite curious.

Wallace also writes (1889) of certain cases of flower deception aimed at pollinators, e.g. the bog star, *Parnassia palustris*, which imitates nectar in its flower using transparent projections, which are in turn licked by flies, which effectively „without cost" pollinate the flower. In his first work, Wallace also in detail defends the theory of mimicry from various objections - the most serious is generally considered to originate with professor **Westwood** (1805-1893, the author of one of the earliest works on mimetic similarities /**Westwood**, 1840/ and from 1863 a professor at Hope Museum in Oxford - this placement was later taken over by the famous **E. P. Poulton**), who on one hand acknowledged the existence and practical use of mimetic similarities, but he considered species to have been created separately already with the similarities. Wallace denies, in a similar manner as Darwin, the separate creation of species and he especially emphasizes the occurrence of mimetic phenomena only in the females of certain species, that is in more important half of the reproductive process, while the male retains the original ancient appearance of the species. In a different place Wallace cites **Westwood's** book *Oriental Entomology*, which includes illustrations of Indian clearwing moths (Sesiidae), which not only perfectly imitate the external appearance of „basket" bees (Scaphulipedes), but also use fluffs of lengthened hairs on their hindlegs to imitate collected pollen.

Similar cases serve as the strongest indication that mimicry is not an artifact of our interpretation of animal appearances, which only seems to us to be similar to each other, but that at least in certain cases it is in some way „intentional" from the side of the imitating creature (even though of course it is not on a conscious level), which has the nature of deception, causing error, imitation (even if usually using different material), or just optical illusion. For example the purely optical "contraction" of the abdomen in many ants or wasp imitating beetles, moths of the family Syntomidae, certain spiders, etc. all belong to this category. The trim wasp-like waist is caused by „repainting" the sides of the abdomen (or opisthosoma in spiders) with a light pigment, which causes its optical contraction (nicely illustrated e.g. by **Cott**, 1940). A wholly spectacular adaptation in this sense can be found in members of the South American moths of the family Syntomidae, which imitate aculeate Hymenoptera, and besides many imitations of the „optical wasp waist," certain genera (*Sphecosoma, Myrmecopsis*) have an abdomen which is contracted at the base, and which is unlike any other moth - the genus *Trichura* adds an elongation of the abdomen, ending in a protrusion which resembles an extended sting, the genus *Macrocneme* also imitates pollen-laden legs using yellow or orange hairs on their tibiae (many of these cases were already described by **Gerstäcker**, 1863). When facing such cases it is difficult to support the opinion that all accounts and literature about mimicry belong in the sphere of cultural history and have nothing to do with biological processes (e.g. **Heikertinger**). But this does not mean that the many cases described in the vast series of literature are not actually examples of such an interpretative aim.

Wallace also formulates in his works laws, which dictate how to correctly ascribe true mimicry to an organism. In his first work (**Wallace**, 1867) he proposes three:

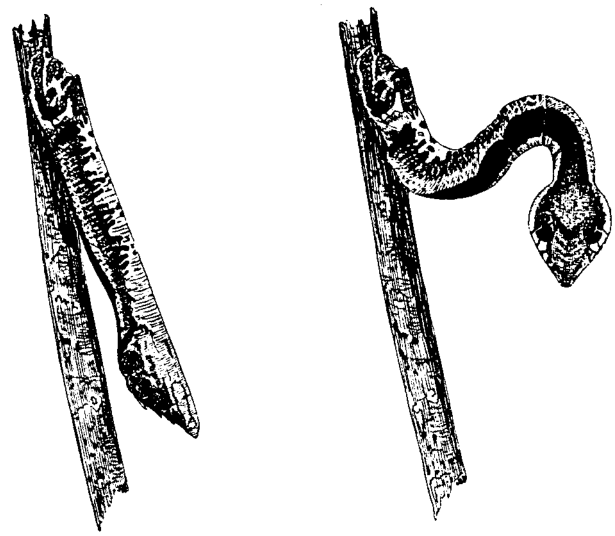
1) the occurrence of both species in the same locality
2) only certain species, which have a large population, serve as models
3) there are less mimics than models

In his later book (**Wallace**, 1889) he constricts these criteria:

1) the occurrence of both species in the same locality
2) the mimic is always more vulnerable
3) there are always less mimics than models
4) the mimic is markedly different from related non-mimetic species
5) the imitation is always only external, calculated optically and not aimed at hidden attributes

These formulations found an unusually broad audience and are cited by many later authors - not only for example **Poulton** (1890), but say **Wickler** (1968) as well, even if with certain reservations. Of course it is possible to find a large number of counter-examples – in rule 1) it is a matter of definition, what is to be called mimicry. We know, for example about a whole range of moth species from various families which occur in places far apart from each other but nonetheless are so similar in external appearance that if they were to occur in the same

The caterpillar of the South American hawkmoth *Hemeroplanes ornatus* imitates a snake – on the left in a calm posture, on the right in a threatening position (according to Cott).



locality they would definitely be labeled mimetic /e.g. the *Attatha regalis* (Arctiidae, Philippines) and *Fadonia attathoides* (Noctuidae, East Africa), or *Semnia auritalis* (Pyralidae, Brazil) and *Carpostalagma viridis* (Noctuidae, Western Africa)/ (**Hering**, 1926). A spectacular example of this phenomenon is the New Guinea pheasant pigeon *Otidiphaps nobilis*, which imitates in appearance and in movement in every detail the pheasant of the genus *Lophura*, which does not occur in New Guinea (which is why this case was considered a „convergence"). Law 2) also has many exceptions - besides the so-called Mertensian mimicry (**Mertens**, 1956) in snakes with „coral" coloration, which is probably just speculation without a true correspondence to the live world (we will return to this later), many imitations of relatively non-toxic butterflies (e.g. *Delias*) by relatively toxic moth species (in this case the genus *Psaphis* - the subfamily Chalcosiinae of the family Zygaenidae), which occur in Indonesia, are known (**Poulton, Sanderson & Dixey**, 1920, **Poulton, Sanderson & Harvey**, 1921, **Hampson**, 1898), (Extremely toxic South Asian species of the subfamily Chalcosiinae are usually very rare /up to 1:100 in favor of the model/ and more than 50% mimetic - certain imitated species are not very toxic - the genus *Dysphania*, Geometridae /mimic - the genus *Pshapis*/, others are more toxic - the genus *Nycthemera* ; Arctiidae /mimic - the genus *Pseudonycthemera*/; the genus *Cyclosia* imitates various butterflies, *C.eucharia* in the male gender imitate the family Hesperidae, the female imitates the genus *Therias* - Pieridae, from an oral account of **G. Tarmann**, Museum of Innsbruck). Not even the third rule must apply in all situations, especially if the model is especially toxic or inedible, as we can see in **Dixey** (1908) and later, for example, **Wickler** (1968). The last two rules must be satisfied in order to distinguish between mimicry and true kinship and to establish mimicry as pure external imitation.

A. R. Wallace's influence was probably most felt in the area of animal coloration in general, and specifically in the area of mimicry, which was a result not only of his theoretical analyses, but also of his untiring propaganda, his never-ending gathering of cases, and his discussions on this theme within the scientific community and outside of it. From the mid-sixties of the 19th century the *Entomological Society of London* became the main center for the study of mimicry and the Society's press became the main tribunal for discussions and publications. These journals were the *Transactions of the (Royal) Entomological Society of London*, which published longer contributions, and the *Proceedings of the (Royal) Entomol. Soc. Lond.*, which published minutes of their meetings, the discussions led there, extracts from materials presented to the assembly, which were later published in the *Transactions*, and later even short contributions on their own (the *Proceedinsg* were paginated, in contrast with the *Transactions*, using Roman numerals, the annual editions of both publications were not numbered). Especially contributions in the *Proceedings*, which often included unique information or opinions, were never published elsewhere or repeated in the *Transactions*, and are to an extent quite valuable, but for the bibliographer they are, thanks to the confusing layout of the journal, literally a nightmare. The *Proceedings* also retain the singular atmosphere of the learned society of Victorian and post-Victorian England with the unusual mixture of aristocracy and elitism in combination with enthusiastic amateurism, extensive knowledge and professional qualification, thanks to many colonies with almost limitless geographical possibilities, and even the particular flavor of sincerity and naiveté combined with severity and a lack of self-reflection, which was so typical of the 19th century, especially in England. Letters from colonial reporters (officers, civil servants, parsons) took up an important part of the magazine, especially if they came from India, Malaysia, or Eastern and Southern Africa, which was strengthened later when **E. B. Poulton** became the central figure of the Society. He spread an ingenious net of observers and collectors of biological material across the whole British Empire, their reports, besides their scientific interest, still reflect the now lost romance of the colonial, which we see for example in **Kipling's** style. Both of the mentioned periodicals became the main forum for English works on mimicry up until the 50s of the 20th century, that is for almost 100 years (the significance of the *Transactions of the Linnean Society of London* basically ended with **Trimen's** work from 1869).

This work covers almost all works which in any way concern mimetic phenomena up until 1865. After **Bates'** appearance a landslide of publications commenced and individual works, which do not bring anything significant, will no longer be mentioned and interested readers can peruse the *Bibliography*, where it is possible to view the publication activity and the prevalent themes year by year. The history of the research of mimetic phenomena and the external appearance of organisms cannot be described by a list of publications (which were often quite short anyway) and their abbreviated contents. A part of these publications is certainly very interesting and beneficial, but a significant number of published works, based on either cases or discussions, are painfully monotonous and endlessly harp on one or two basic thoughts. Some of the main debaters on the problems of mimicry in the Entomological Society were: **Wallace**, **Bates**, (sometimes even **Darwin**), **Weir**, **Butler**, and further **Raphael Meldola** (1849 - 1915), a professor of chemistry and amateur entomologist, who was very interested in the problem of mimicry and aposematism and published a number of works on these themes (see the *Bibliography*).

Müllerian mimicry

Thanks to his profession, **Meldola** was the only member of the Society who knew how to speak German well, and so established contact with Continental biology. In 1879 Meldola translated for the *Proceedings* (Pp. 20-29) an article by the German physician **Fritz Müller** (1822-1897), published in the journal *Kosmos* (**Müller, F**., 1879), which immediately caused a sensation and was pleasurably received. **Fritz Müller**, the brother of the before mentioned **Herrmann Müller**, emigrated for political reasons to Brazil, where for the majority of his life he worked as a landowner, teacher, and professional collector in the towns Desterro and Blumenau. As his brother, he had a deep interest in biology and published over 200 works, in the beginning mainly concerning the biology of flowering and interactions between insects and flowers, later he concentrated on butterflies (even **H. Müller** was interested in the defensive mechanisms of insects, e.g. his work from 1879). He corresponded extensively about his research with many biologists in Germany and England, especially with his brother and R. Meldola (Müller's biography, correspondence, and other material was published by **A. Möller**, 1915- 21, more works by Müller about adaptive colorations can be found in the *Bibliography*). The journal *Kosmos*, published since 1876, was a tribunal to German Darwinians and over more than ten years published a whole range of articles on evolution, including many small observations on mimicry, aposematism, flower biology (H. Müller was a regular correspondent), and even some translations of foreign language publications (e.g. **Wallace**, 1878a, reprinted in the same year). The journal included a large number of applications of evolutionary theory on other branches of study, for example on linguistics or history and it is still a very interesting documentation of the era's thoughts and the enthusiastic atmosphere, invention, and profound and at the same time blind views of reality in Germany at the time. Müller's work tries, with an unusual formal elegance, to resolve the problem, already known to **Bates** (1862a) and **Wallace** (1867), of the striking similarity between pairs of species which belong to the „protected" type /as is apparent from correspondence with **Darwin** (**Darwin, F.,** 1887, III., the letter from 1.12.1872) Müller was originally convinced that the appearance of „his" type of mimicry was caused either by sexual selection or by directly copying vividly colored butterflies from the area, **Darwin** took this view seriously and even passed it on to **Weismann** in a letter from 4.5.1872 (ibid., p. 157)/ . As was stated above, **Bates** was well aware of these analogies, but he explained them through adaptations to abiotic factors of the environment, which probably affect even the caterpillars. **Wallace** also observed this similarity and came to the conclusion that certain members of the

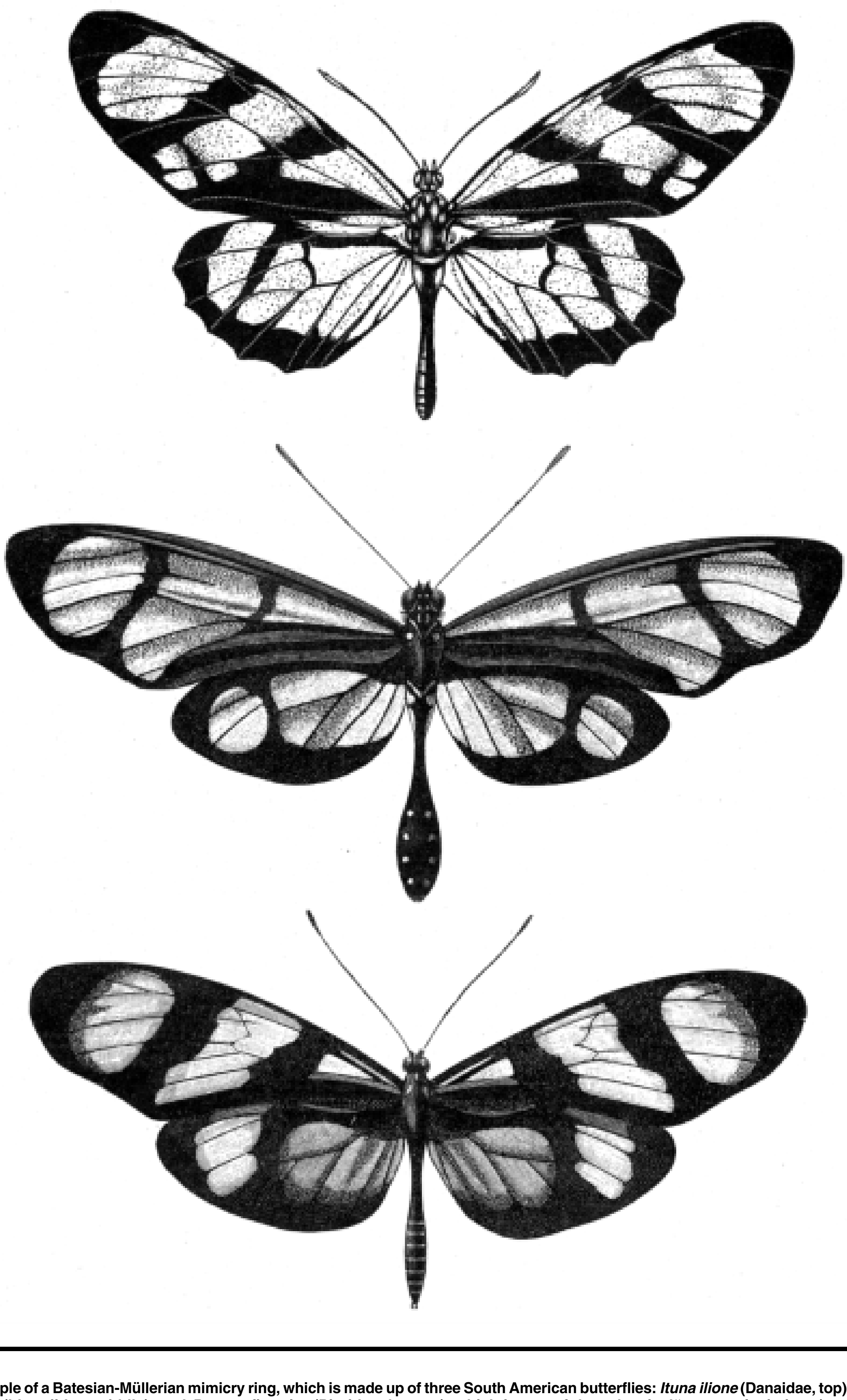
„protected“ group have a lower or even missing level of toxicity, which causes the initiation of (basically) Bates' selective mechanism. He noticed the unusual typological similarity, but at the same time the striking pattern variety in Heliconiidae, which he explained as being caused by the fact that any marked deviation from this appearance was immediately spotted by predators and removed, regardless of the level of inedibility. There wasn't a long distance to go from this point to the formulation of Müller's standpoint. Müller understandably assumes that naive predators, which need to experience and learn of the inedibility of „protected“ prey, consume at least one specimen in their youth, which is an opinion generally accepted in the 19th century - in his work he puts forward an opposite position as well, but he rejects it. Afterwards it is more profitable for two species to retain one joint appearance, so that the damage caused by the „tasting“ each year is not inflicted on only one species, but is divided in half, because the losses are basically constant (there is a constant population of predators). Müller's example shows that such a „cartel“ would be especially advantageous for inedible, low population species - if in a certain area there are 2000 members of one species and 10000 members of the second and 1200 young naive predators, then if the first two had a different appearance, the predators would eat 1200 members of the first species (only 800 will remain, which is catastrophic) and 1200 members of the second species (8800 will remain, which is an acceptable loss). If their external appearance was the same, then from 12000 members of both species, only 1200 would be lost and statistically these losses would be divided in proportion, that is 200 lost for the rare species and 1000 lost for the abundant species. This proportion is especially advantageous for the rarer species, whose survival can be secured in this way in certain cases, but it is not without advantage statistically for the abundant species. If both species have the same population, this brings a tangible benefit, because they cut their losses in half (Müller supports his speculation with an elegant mathematical model - the first ever used in the history of the research of mimetic phenomena). Müller used the South American species *Thyridia megisto* (Ithomiidae) and *Ituna ilione* (Danaidae) as the models for this theory. In cases of the coexistence of a rarer species with an abundant species, selective pressure from the predator should move the appearance of the rare species in the direction of the abundant „model“, while in cases where both species have similar populations, their appearance should converge so that it becomes impossible to tell which is the mimic and which the model. As was mentioned, Müller's clear and convincing formulations were immediately accepted and they became generally known and established (not even Müller experimented with predators, everything was based on speculation and observation, even if based on a mathematical foundation - basically we can see in mathematical modeling a belated remainder of Pythagorean numerical mysticism - it is only after this procedure is applied that a phenomenon seems „realer“; few of those that in modern times consider mathematical objects to be the basis of the world actually realize this). Besides **R. Meldola**, from the next generation of biologists the ones most infatuated with Müller's theories and their application were **F. A. Dixey** (1894) and **E. B. Poulton** (on the other hand, **Bates** and especially **Weir** and **Distant** did not accept this solution, mainly because of their belief in the innate idea of inappropriate prey in predators, who therefore are not „naive“ and don't need to learn). **Poulton** (1890) proposed the term **synaposematism** to describe Müller's findings, which corresponds to the phenomenon much more than the term **Müllerian mimicry**, which is commonly used (the phenomenon is basically an „aposematic cartel“ of two or more species). This expression did not catch on, just like another term **Poulton** (1898) proposed: „*common warning colours*“ and his later term (**Poulton**, 1908) „*diaposematism*“, while **Dixey** (1894) uses the term „*reciprocal mimicry*“. Certain later authors refused Müller's concept (**Marshall**, 1908), and others defended it from attack (**Dixey**, 1908), or expand its formal aspects (**Fisher**, 1930). Already in the first half of the 20th century it began to be clear that Batesian and Müllerian mimicry only represent two extreme examples of a continual Batesian-Müllerian spectrum of mimicry (**Carpenter** and **Ford**, 1933, further for example **Wickler**, 1968). Especially in the tropics whole *mimicry rings* (germ. *Mimikry-Ring*) were found, which often included a large number (sometimes tens and tens) of in appearance very similar butterflies from various families, from very edible types to lightly toxic and more protected to inedible types (e.g. **Winhard**, 1996). Similarities in appearance between unrelated species where the mimic and model are both very edible, of course occur quite frequently. Certain authors, e.g. **Marden**, 1992, consider this phenomenon an imitation of species that fly quickly by those that don't. Certain authors (**Poulton**, 1908) also thought they had found a Batesian-Müllerian mimicry of the second and third degree (the North American swallowtail *Battus philenor* is imitated by the mutually mimetic triad of species *Papilio troilus, P. asterius,* and *P. glaucus*, which are again the models for the red spotted purple, *Limenitis astynax,* and this last one is imitated by the species *Argynnis diana*). At the turn of the century certain authors believed that the majority of mimetisms are the Müllerian type, although they did not contest Batesian mimicry (**Poulton**, 1908). In recent times it has actually been shown that a whole scale of cases considered for more than a hundred years to be examples of Batesian mimicry are actually Müllerian mimicry - e.g. the clearwing moth (Sesiidae), a family which imitate wasps (**Rothschild**, 1985) or the North American viceroy butterfly *Limenitis archippus*, which imitates the textbook aposematic monarch *Danaus plexippus* (**Ritland**, 1991, **Ritland & Brower**, 1991).

This is indicated namely by the fact that mimicry and aposematism occur only in certain groups of organisms (on the family, or even genus level), while they are entirely lacking in other groups, and the same family can produce not only prolific mimics, but prolific models as well (e.g. Pieridae, Papilionidae, and Syntomidae). Why certain groups (e.g. Cerambycidae) are markedly more „prepared" to create mimetic forms (even though rarely certain members are models for mimics) than other groups (or they complement this tendency with a tendency for aposematism) is in the end a difficult question (also different groups are almost completely aposematical without mimetism - Danaidae, Coccinellidae). Certain forced theories have of course surfaced, but the bare fact that mimetism is limited to a very small group (aposematism as well, but this can be more comfortably explained by the toxicity of the whole group or their common ancestor) is a fact worthy of notice, which indicates something like a generically defined „tendency" towards a certain phenomenon, even though in its final form it appears differently in each case (see also, for example, **Komárek**, 1989b, on the tendency of eye spots to appear in certain lepidopteran families, or in other animals in „predilected places" and their independent occurrence in related groups in the course of evolution). So not only local „fashions", but kinship-defined fashions also exist, and at the same time the external appearance does not have to be typical for the given group, but something quite variable, which has the only common denominator for mimicry.

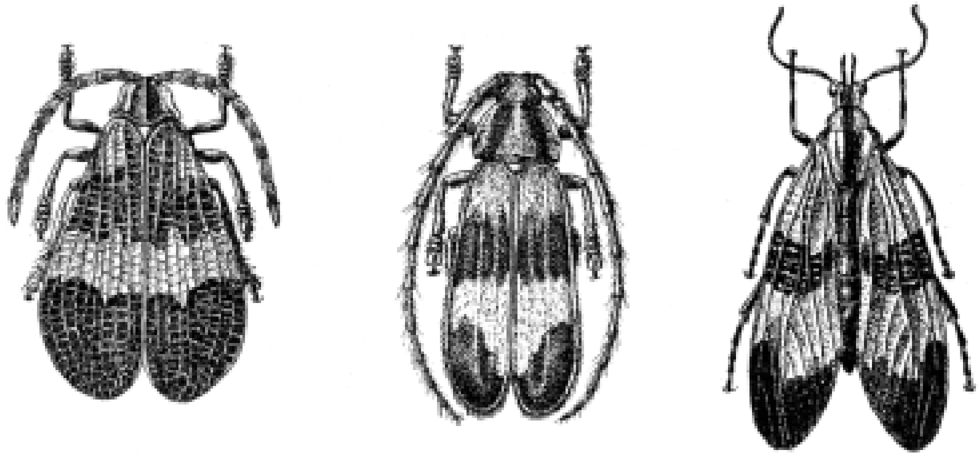
Mimicry rings

The fact that usually a number of groups of species of butterflies or other insects, all with a very different types of coloration and color pattern, live in one biotop, is not very good for the concept of Müllerian mimicry rings (Müller's mathematics requires a maximum of one type). This question of a number of mimicry rings found in one biotop is resolved by **Papageorgis** (1975), for example, by his theory that various mimicry rings can exist in various storeys of the rainforest and therefore have different bird predators (this solution is very elegant and a certain connection between the dominant color pattern on butterflies and the storey on which they live exists, but this author, based on his experiences in Peru, does not think that the relation is as strong as Papageorgis' theory would require). Various experiments (e.g. **Brower, J. V. Z.**, 1958) indicated that birds can mistake the mimic and the „model" when the similarity is at a certain level, but that these cases oscillate - sometimes the similarity could be quite crude, in other cases even fine nuances in external appearance were spotted.

The existence of mimicry rings (this term originated with the well known geneticist **A. Weismann** - in his version *Mimicry-Ring*) has occupied many authors, from which some came to pretty startling conclusions. The proposition supported by **Eimer** (1897) and **Heikertinger** (1954) for example consists of a „coincidental" similar stage of transformation of the patterns in various species of butterflies, will be discussed later when dealing with these authors. **A. Suchantke** (1974, 1976a, 2000), on the basis of field experience with African and South American butterflies, came to a conclusion similar to **Papageorgis'**, with the difference that the more or less same appearance of butterflies from different habitats is caused by a correlation or harmony with the dominant optical effects of the given environment (the common occurrence of rusty colors similar to dried grass in savanna butterflies, the combination of a black or dark substrate and white or yellow spots of various sizes in species living in bushes or in various forest levels - the design of sunspots shinning through holes in the forest cover, and then the prevalence of blue and green iridescent colors as derivatives from the original black in species which live in bright sunny green treetops, or a transparency with a number of black spots in species which live on the floor of the same forest). Even though these designs and shades have, according to Suchantke, a certain cryptic function, he does not see their origin in selection from the side of predators, but in a „harmonizing" development of a certain biotop and its fauna (Suchantke was influenced primarily by neo-Goethean concepts in biology). / The fact that the occurrence of mimicry is more common in woody areas, concretely in Africa, in contrast with open areas was mentioned already in 1933 by **Carpenter** and **Ford**. In open terrain the occurrence of „*mud drinker's aposeme*" - contrasting yellow-black coloration of the lower side of mud drinking butterflies (e.g. the genus *Mylothris* - Pieridae, imitated by *Phylaria*



An example of a Batesian-Müllerian mimicry ring, which is made up of three South American butterflies: *Ituna ilione* (Danaidae, top), *Methona confusa* (Ithomiidae, middle), and *Dysmorfia orise* (Pieridae, bottom), which is one of the „classical“ cases of mimicry (according to Wallace).



An example of a mimicry ring made up of two beetles *Calopteron limbatum* (Lycidae, left) and *Pteroplatus lyciformis* (Cerambycidae, a mimic, middle) and one moth (Syntomidae, a mimic, right) from Brazil (according to Jacobi).

cyara - Lycaenidae) is more common./. Suchantke sees butterfly fauna of the tropics as more influenced by and more derived from the environment than from its given group, especially in the case of sunshine, while in the central latitudes most species have their „typical“ appearance and in polar locations darker colors prevail (this last fact is explained by Darwinian biology by the importance of dark colors for the quick accumulation of solar heat, which is necessary for functioning in the otherwise cold country). Thought of „prestabilized harmony“ between the color of an organism and its environment was, of course, to be found earlier as well - **Bates** (1862a) mentions the work of the reverend **J. Greene** (*Zoologist*, 1856, p. 5073) about the harmony between the colors of British autumn moths and the colors of nature in that season, which he reinterprets from the Darwinian standpoint. Suchantke's book about insect metamorphoses (**Suchantke**, 1965) and his work on exaggerated structures of treehoppers (Membracidae) (**Suchantke,** 1976b) are both very interesting and intellectually innovative, his work on sexual dimorphism in birds was mentioned earlier.

The time period from 1890 to 1953 (with a note on later development trends up to the nineties of the 20th century)

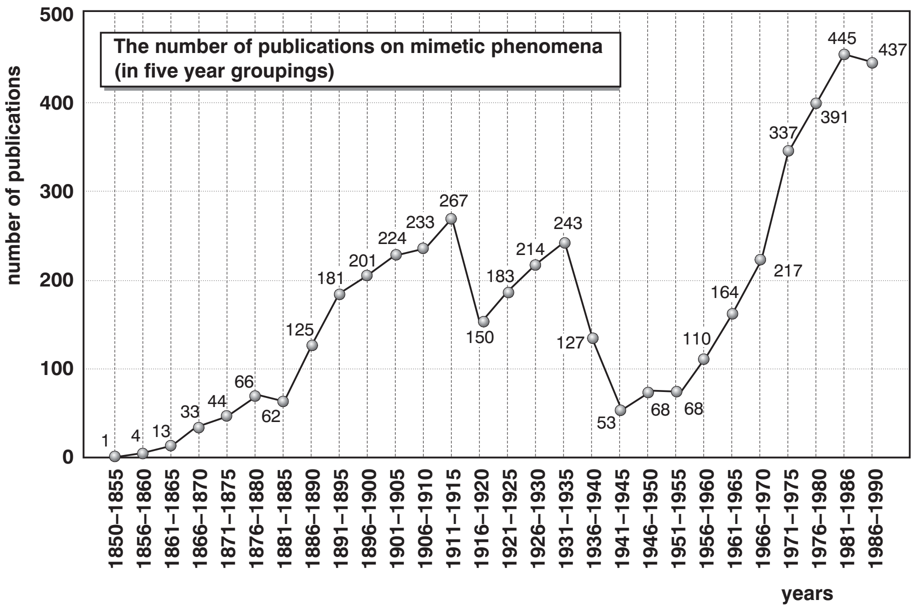
At the end of the eighties of the 19^{th} century the preliminary enthusiasm for the Darwinian interpretation of mimetic phenomena was slowly ebbing and works on this theme, especially innovative or breakthrough ones, were less and less common (it was a time when Darwin was already dead and the other protagonists /**Wallace**, **Bates**, and **Trimen**/ were getting old, and the Continent showed only marginal interest in mimetic phenomena, even though the enthusiasm for Darwin's work was still great in the „German" cultural sphere /**Rádl**, 1908/ - Continental biology at the time was interested more in embryology and marine biology, even if from a Darwinian perspective /**Haeckel** and his students/, which in combination with bad access to the tropics caused „German" biology to become isolated from the problem of mimicry.

Teachings on mimicry and interpretations of the external appearance of organisms in England

The first publication of **E. B. Poulton** appeared at the end of the eighties, and this marked the beginning (more or less from 1890, when his first and only book on the problems of adaptive coloration in organisms came out) of a more or less 50 year career in which he dramatically influenced the way English biology viewed mimicry and revived interest in it. Poulton was one of the few people who professionally dealt with mimicry his whole life (besides him to an extent this applies to **G. D. H. Carpenter and L. P. Brower**, and as an amateur, **F. Heikertinger** as well).

Basic biographical information: **Edward Bagnall Poulton** (1856-1943) was born in the family of an architect from Reading, he studied biology at Oxford and from the beginning worked in geology and later in comparative anatomy of mammals (in 1888 he discovered teeth in the jaws of a juvenile platypus, which was a fundamental discovery). He was strongly influenced by Wallace, with whom he was later personally acquainted and he was also acquainted with **Meldola**, whose translation of **Weismann's** work on descendence theory into English (1883) inspired Poulton to carry out a number of experiments which tested the adaptations of caterpillars and chrysalises to various surfaces and their optical adaptations in view of predators (**Poulton**, 1884-1888 in the *Bibliography*, from Poulton's 276 works, published during 55 years, we can cite only a fraction here, for further information see the data in the *Bibliography*). For these contributions he was in 1889 elected as a member of the prestigious *Royal Society*. In 1890 he published his well known book „*The colours of animals*", a very elaborate and well-arranged work (all of Poulton's works are characteristically very precise and formally well-arranged, while containing an abundance of facts, as compared to the difficult, syntactically complicated, and detail-overloaded books by Darwin or the readable and essay-like observations written by Wallace, where imagination outweighed the particularites). In 1893 Poulton was chosen to fill the vacant place of professor of zoology with the *Hope Museum* at Oxford. His predecessor and teacher **Westwood**, whom we have mentioned above twice, was on one hand interested in mimetic phenomena, but he explained them through the Creationist standpoint and many times warned Poulton against accepting the ominous new evolutionary doctrine (Westwood was an unusually experienced insect taxonomist and knowledgeable of their forms, but already in his time he represented something akin to a living fossil - up until his death in the 88^{th} year of his life he directed the museum and lectured). Westwood's wish concerning the orientation of his follower was of course not fulfilled - already in 1875 Poulton was reading **Darwin's** book „*On the Origin of species ...*", which literally became his Bible and life message (in 1878 he was also introduced to **Wallace's** essays and later to Wallace himself, but his standpoint was closer to Darwin, whom he did not know personally). Poulton became one of the most passionate advocates and protectors of Darwin's legacy and a extensive commentator of his works (**Poulton**, 1896, 1909), something like the high priest of the Darwinian cult and the caretaker of his heritage (in the atmosphere of the turn of the century, when classical Darwinism got into a crisis and clashed with Mendel's genetics, he was but one of a few). Poulton's placement in a university position and his long activity there (40 years) for the first time gave the research of mimetic phenomena an outstanding organizational base and an enthusiastic coordinator (for Poulton's biography see **Carpenter**, 1942-44). Poulton not only attended to the pronounced completing of collections and lecturing, but he also cared for the scientific education of the young (**Perkins**, **Cott**, and other important laborers in the field of mimicry were his students). His organizational activities were irreplaceable, he managed to gain, partially from his students sent into the world, in part from various enthusiastic, often professionally very adept, amateurs from the whole of the British Empire a large number of coworkers and correspondents, who sent him their observations and material for the museum (this whole unusual group was first described in connection with the *Entomological Society of London* and its periodicals, the *Transactions* and the *Proceedings of the Entomological Society of London*, which published the fruits of their labors and discussions on their findings). Among these coworker were **G. D. H. Carpenter, F. A. Dixey, H. Eltringham,** and **G. A. K. Marshall** (which will be mentioned later**), H. St. J. K. Donisthorpe, Ch. J. Gahan, W. L. Distant, F. Finn, E. F. Green, W. J. Kaye, G. B. Longstaff, N. Manders, J. C. Moulton, S. A. Naeve, R. I. Pocock, H. J. S. Pryer, K. St. A. Rogers, R. Shelford, V. G. L. van Someren, C. Swinhoe,** and **C. F. M. Swynnerton** (the list of their publications, which surpasses the aims of this book, can be found in the *Bibliography*).

Carpenter, Eltringham, Naeve, Rogers, Someren and **Swynnerton** distinguished themselves through their research in tropical Africa, **Finn, Green, Longstaff, Manders, Pryer, Swinhoe,** and **Shelford** in India and Indonesia, and **Gahan, Kaye,** and **Moulton** in tropical America. Besides the above mentioned periodicals, their contributions were also published especially in the *Journ. Bombay Nat. Hist. Soc.*, *Spolia Zeylanica*, *Journ. As. Soc. Bengal*, *Proc. Zool. Soc. London*, *Journ. Linn. Soc. London* and others. Poulton's works were reprinted with the already published works of his colleagues (usually in the *Trans. Entomol. Soc. London*) in the form of collected essays under the name „*The Hope Reports*", from 1897 to 1913 thirteen volumes were published (Poulton widely popularized the theme of mimicry in British society, as can be for instance seen in the humorous article on this theme in the magazine *Punch* from the 2nd of May, 1906 - **F. A.**: *Moral reflections at the Natural History Museum*). Organizational, research, and publication activities of Poulton and his associates deserve a more detailed study, but that is above this book, if only because of the enormous amount of collected facts and exhaustively recorded particularities. Those interested can find more detailed information in the *Bibliography*, the study of source texts (especially the *Proc. Entomol. Soc. London* and the *Trans. Entomol. Soc. London*) is in this case, as in all other cases mentioned in this book, absolutely mandatory. From „faithful" Darwinism Poulton took not only the belief in the continual variability of organisms and the belief in the omnipotence of natural selection on the basis of this material (natural selection for Poulton, always written with uppercase letters - "*Natural Selection*" - took up the place of the Creator, in a de-personified and diffuse way), but also a deep inclination to observing particularities. (Even though this method was often criticized, in combination with a good intuition they are the source of something like a „direct" overview, not dissimilar to the ancient Greek method of understanding geometrical „truths". It is true that the Nicaraguan observations of **Belt** /1874/, often cited in the classical Darwinian era, were based on observations of particularities in the rainforests and his experiments with the edibility of aposematics, which mainly consisted of throwing them to a tame ape and some domestic ducks, elicits a grin from experimenters, nonetheless the future showed that all of his speculations were basically true. In a circular fashion we have returned to a theme from the first chapter, whether the „deeper" truth is found in what we see and observe, or in that which is hidden and must be „flushed out" through complicated experiments and if possible supported by a mathematical model.) Poulton was gifted with an unusual, today very rarely seen in such a scale, knowledge of forms and an excellent memory, which in connection with his wide-spread net of observers allowed him to orient himself in an unbelievable amount of particularities, including basically a systematics, ecology, and ethology in one integrated whole. Knowledge of this „*natural history*" eventually (**E. B. Ford**, **R. A. Fisher**) began to fade in preference to the abstract concepts of classical genetics (Poulton in essence represented, even in his own time and primarily because of his long and continual activity, an apparent archaism, even if a very sympathetic one). It cannot be said that he did not know or was biased against classical genetics, which was contradictory to his ideas of Nature as a gradually changing entity (instead of genetics, he was more interested in eugenics, as were many biologists at the turn of the century). His small talent for mathematics and his disinterest in it caused that his relation to the application of genetics on mimicry was reserved, as is apparent from his criticism of **Punnett's** book (1915) - **Poulton**, 1916 and as will be seen later. Poulton was socially very successful and had a chair in many boards and elite scientific societies (*Royal Society, Entomological Society, Linnean Society*) and was the bearer of many decorations. This social involvement together with his extensive correspondence constantly distracted him from writing another, amended, and extended version of his book on adaptive coloration in animals, which was true even after his retirement in 1933, when his „*opus magnum*" was generally



expected (a number of thorough preliminary works preceded this planned book, e.g. **Poulton**, 1898, 1908). Even though Poulton practically until death published and corresponded, his strength was dramatically ebbing and his obsession with detail and his geriatric one-sidedness kept him from completing this goal. This caused his intellectual legacy to be disseminated in hundreds of publications, from short articles to works hundreds of pages long. His is the largest number of articles that any one person ever wrote on the problem of mimicry. Many other articles, which do not appear in the *Bibliography*, deal with the theory of Darwinism or are celebrations of various Darwinian anniversaries. Poulton's generous leadership of his institutions can also be seen in the fact that he supplied even his „intellectual rivals" from the area of mimicry research (e.g. **F. Heikertinger** from Vienna) with literature and supported their work /Poulton's successor was his longtime friend and younger coworker, **G. D. H. Carpenter**, who represented, as is often the case, a loyal, yet pale and inconspicuous copy of his teacher. Carpenter directed the museum and was the museum's resident professor of zoology until 1948, he died in 1953, coincidentally in the same year as **F. Heikertinger**, with whom he conducted a literary disputation even during the WW II (**Heikertinger**, 1940, 1942). The mentioned year was not only the definite end of another era of the research of mimetic phenomena, but also a time of absolute disinterest in mimicry, the number of publications during this time, in comparison with the time between the wars or the new boom in the sixties, was almost nil. It is interesting to note that the events during the WW I barely affected the research of mimetic phenomena, whether in England, or in Germany and surrounding countries, while the WW II destroyed „German" biology, as will be seen later, more or less completely (even though some individuals were still active after the war) and badly wounded classical biology in Britain. The number of works on mimetic phenomena, cited in the *Bibliography*, grouped in five year intervals, can be seen in the graph on the top of this page – the depression caused by WWII, which began even before the war and dragged on at least ten years after its end, represented the strongest blow to the research of mimetic phenomena ever (after the rapid recovery from 1960 to 1980 a certain type of stagnation is now settling in).

Poulton, in his attempt to be terminologically accurate and formally unambiguous, created a completely new nomenclature and new classifications dividing animal colorations, which was initially published in his only book on this matter (**Poulton**, 1890) and later appended in an extensive essay about the relation between mimicry and defensive coloration (**Poulton**, 1908). The nomenclature for individual colorations was carefully chosen by Poulton, who consulted it with his friend **A. Sidgwick**, an expert on classical Greek. He thoroughly differentiated in each category between colorations, which were constant and those which were variable (by color change), in the same way he differentiated between colors which were inherent in the organism and those which were in some way gained (these were designated the prefix *allo* - *allocryptic* - the larvae of the caddisflies and their cases, *allosematic* - hermit crabs covered with a sea anemone - *allepigamic* - the colored bowers and ornamental display objects in bower-birds of the genus *Ptilonorhynchus*). Furthermore he always distinguished between colorations meant from the organism's protection and colorations meant to serve for aggression against others (*procryptic* - *anticryptic*), he not only used the term „*aposematic*" in today's meaning, but also „*episematic*" (in the sense of *recognition marks*), he also used both in the deceptive variant as well (*pseudaposematic* - Batesian mimicry, *pseudepisematic* - aggressive mimicry /e.g. *Volucella*/, or *alluring coloration* in **Wallace's** sense). In spite of the great sophistication of this categorization and its strictly logical system, only a few of Poulton's terms were generally accepted (*aposematic, aggressive mimicry*), others were accepted, but with a modified definition (*pseudaposematic*). It is useless to reproduce here the whole complex system of his interpretation of animal coloration, in which certain categories remain virtually empty, because it is not in use (those interested can view pp- 336 - 341 of the above mentioned book from 1890 or chap. X /pp. 283 - 381/ of Poulton's book from 1908).

Poulton, a classic of Darwinian interpretation

Poulton (the following text will mainly refer to both of Poulton's main publications on animal colorations, **Poulton**, 1890, 1908) in detail studied not only the development of colors from a physical point of view, but also their direct physiological function, for example for thermoregulation (later this was a favorite theme, for example in butterflies - e.g. **Chai & Srygley**, 1990). Poulton called the imitation of other objects by animals *resemblance* (the imitation of nonliving or plant objects) or *mimicry* (the imitation of animals). Poulton also gave much attention to crypsis, especially in butterfly larvae, which was a theme that he was devoted to in his youth.

He extensively covers color change in fish, chameleons, and other lizards, frogs, the mouts of summer and winter coats in polar birds and mammals, etc. He was especially interested in the optical regulation of color change in fish, amphibians, and reptiles and the lack of this in blind animals. Furthermore, he describes in detail the color adjustation of butterfly chrysalises (Pieridae, Papilionidae), or in better words their adaptation to the surface on which they are (which happens only once during the pupation process). This theme was discussed in an uncountable amount of studies, from **T. W. Wood** (1867), who discovered this phenomenon on the chrysalises of *Pieris brassicae, P. rapae,* and *Papilio machaon*, to very recent authors. Poulton was also concerned with the adjustment of colors to the environment in various moth cocoons, the reduction of cast shadows, the selection of appropriate surfaces by resting butterflies, the correlation between seasonal dimorphism in butterflies in tropical areas, the adjustment of their colors to match the changes in substrate in moist and dry periods, etc. In his work from 1908 Poulton also called attention to the problem of **industrial melanism** and he cites a work in which this phenomenon was explained through selection on the basis of the extinction of lightly colored individuals (especially the species *Biston betularia*, but others as well) by insectivorous birds in industrial regions empty of lichen (**J. W. Tutt**, *Entomologist's Record 1*, 1890-1891). **J. O. Westwood** was also concerned with moth melanism (*Trans. Ent. Soc. Lond.*, 1877), where he also mentions the dark specimens of *B. betularia*, which occur in Scotland and England. This theme later became one of the basic building stones of neo-Darwinism and was dealt with in an innumerable amount of professional and popular works, starting from the fifties of the last century (in summary, for example **Kettlewel**, 1975). Light and melanic specimens of the peppered moth *Biston betularia* on bark with lichens and without them with an insectivorous bird watching became the iconographical symbol of neo-Darwinism after WWII, much as the evolution of man, horses, or the *Archaeopteryx* were the symbols of classical Darwinism.

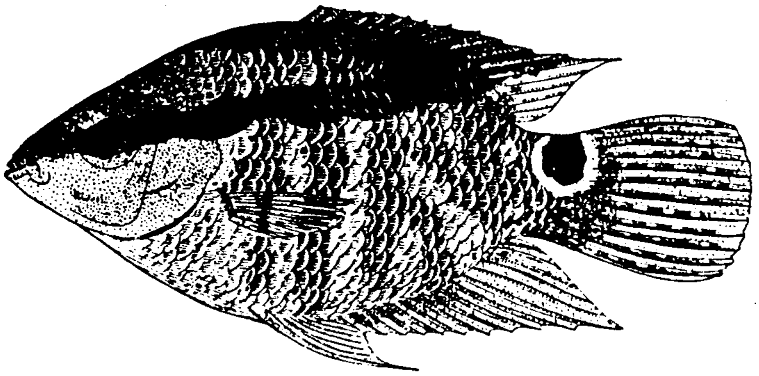
This theme is so well known in scientific community and in the public, that it will not be discussed in greater detail here (even though critical views, denying the selectionist model applies to the prevalence of melanic individuals in a population, were not lacking - **Harrison**, 1919, 20, 26, 28, 35, 56; **Harrison & Garrett**, 1926; **Lambert, Millar & Huges**, 1986a, b; **Sermonti & Catusini**, 1984), because the goal of this book is to describe concepts and events, which are in danger of being forgotten, and not those, which are generally known and give the impression of being obvious truths, which do not seem to have a complex and ambiguous developmental history and lack alternative variants, which have „sunk beyond the horizon" but in any case exist and are to a large extent different.

The problem of crypsis in the living world was in detail examined in the excellent book *Adaptive colouration in animals* (1940), which was written by Poulton's student and an employee of the Oxford Museum, **Hugh B. Cott**. This publication is on the whole the best and most detailed compendium ever published dealing with crypsis and all details associated with it. He also in detail analyses various cases of aposematism and describes experiments with feeding aposematics to various predators. He also devoted much space to mimetic phenomena and redefined Poulton's term „*pseudaposematic*" for a whole range of different phenomena, including the combination of conspicuous, basically „aposematic" coloration (e.g. black-red) and the edibility of the organism for predators. At the same time it is typical that the colored surfaces are often hidden when the organism is resting and are seen only during an escape reaction. This pertains mainly to the vividly colored hind-wings of underwing moths from the genus *Catocala* and *Noctua*, or grasshoppers, for example from the genus *Oedipoda*, further to the vivid coloration of the sides of the legs of certain tropical frogs from the families Hylidae and Leptodactylidae, and even the black-red skin flaps of the South Asian lizard *Draco volitans*, which cover the extensions of the ribs and serveas a flight membrane to assist in gliding. All of these colorations have the typical trait that they suddenly appear only during take off or during a jump (*startle display, flash colouration*), and then disappear after landing (this phenomenon is sometimes called **fulguration**, from the Latin *fulgor* - lightning). It is generally accepted that their function is to surprise, shock, and confuse the predator, which is either so scared that it stops its chase, or it cannot actually located the organism after its rapid change back to cryptic colors upon landing. A number of authors have mentioned this phenomenon in their works, starting from **J. Weir** (1869), and later in more detail lord **Walsingham** (1890), their concept was later also adopted by **Poulton** (1890, 1908), who thought that the hind-wings with vivid colors are also a target for attack on a less vital part of the body. These phenomena were also studied by **A. Weismann** (1902) and **M. C. Piepers** (1903), who created a new term - „*Misoneismus*" - the aversion to new things - to describe not only this phenomenon, but for all unusual colorations, respectively for their effect on predators. **O. Prochnow** (1907) puts these phenomena under the term „*Kontrastfarben*", which is a subcategory of the category „*Schreckfärbungen*", which also includes eye-spots and the imitation of snakes by caterpillars. **Heikertinger** (1954) labels these phenomena „*Ungewohnheitstrachten*" or "*Schrecktrachten*". Bestowing pseudaposematic colorations their own category enables us to easily classify all semantically colored species (for the moment we will not include epigamic colorations and those intended for intraspecific communication) into four categories:

- semantic, inedible, dissimilar to other species - **aposematic**
- semantic, inedible, similar to other species - **Müllerian mimic**
- semantic, edible, similar to other species - **Batesian mimic**
- semantic, edible, dissimilar to other species - **pseudaposematic**

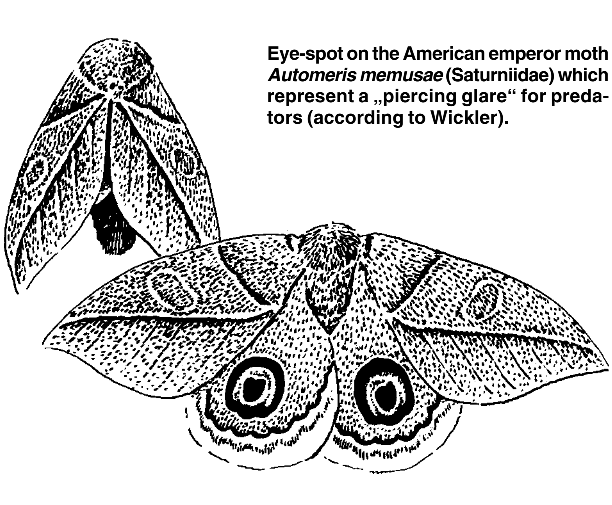
Because of the fact that these four categories cover all possible combinations and therefore *eo ipso* must „explain" every single case, which can occur, it is possible for the interpretation of semantic colors in these categories, thanks to their design, to become a self-validating farce. Nevertheless it seems that the category of pseudaposematic colorations have a certain correspondence in nature and are in fact effective against predators. The results of a series of studies by **D. Sargent** (1969c, 1970-82, 1976, 1978, 1980, 1990, **Sargent & Owen**, 1975) from the university in Amherst (Massachusetts), which were made on the basis of the underwing moths of the genus *Catocala* from the eastern United States using light traps, excepting that it is difficult to unambiguously interpret them, are very interesting. **Sargent's** works proved the close numerical correlation (which lasts for years) between pairs of species of the above mentioned genus, which both have similar cryptic external marks on their fore-wings, while only one has the typical aposematic pattern on the hind-wings. The second has single-colored, black hind-wings, so called **achromatic** coloration. Considering that even these „achromatic" species have a similar amount of *beak marks* caused by attacking birds, which they managed to escape from, as do „chromatic" species, Sargent concludes that the occurrence of these „achromatic" species guarantees that predatorial birds do not get used to pseudaposematic defense systems and are confused by the variations on it. In this way both types actually make up one pseudaposematic defense group, even if based on a complementary principle, and not on the basis of similarity in the sense of Müllerian mimicry (**synaposematism**).

In his main works **Poulton** (1890, 1908) also dealt with the problem of eye-spots, which was first analyzed and experimentally tested by **A. Weismann** (1876, he goes into more detail in 1902) on hawkmoth caterpillars with similar color patterns (the "elaphant hawk", *Deilephila*, Weismann's *Chaerocampa*), and also certain tropical species, which evidently imitate snakes (one of the few examples of the imitation of vertebrates by invertebrates). Weimann also noticed the tendency in caterpillars of the genus *Smerinthus* to produce two red spots on each segment, he calls this type of pattern, which possibly has an aposematic function, „*Schrec-*



The cichlid fish *Cichlasoma festivum* has an eye-spot near the beginning of the tail fin - the real eye is masked by a transverse band (according to Cott).

ktracht", but he doesn't consider it a result of selection - for originally cryptic organisms these can hardly have any use in its first stages, but can only be an inner predisposition, which was labeled "germinal selection" in his later works. **Seitz** (1887) noticed eye-spots in the imagines of the hawkmoths (e.g.the eyed hawk, *Smerinthus ocellata*), and he voiced the opinion that the symmetrical exposure and presentation of these patterns remind birds of the eyes of their own natural enemies, for example owls or martens. (It is very difficult to either prove or disprove this theory, but in any case the sight of these marks drives fear into small birds and scares them away - **Standfuss**, 1906, **Tinbergen**, 1958, the intimidating self-display of this species was described by **Japha**, 1909. This example, which made its way even into ethological textbooks, admirably demonstrates one fact - problems, which are not controversial, do not require many experiments to be accepted - a detailed revision of relevant literature showed that the number of specimens of *Smerinthus ocellata* presented to insectivorous birds in the experiments was not greater than ten. This does not mean that the mentioned pattern does not actually function as is believed, but only that textbook truths, which lie within the general pattern of scientific disposition, do not require very extensive proofs, while theories well outside of the prevalent scientific outlook do not have a chance even after collecting a large quantity of material.) The effect of eye-spots in other species, for example the effect of the peacock butterfly (*Inachis io*) on insectivorous birds was tested by **Steiniger** (1938a, b) and the effect of eye-spots generally was examined using lighted dummies by **Blest** (1957) (it was shown that the eye-spot is more effective when larger and closer to a real eye, with more concentric circles, with a reflection on the „iris", with an implied „squint", etc.; realistic eyes on butterfly and moth wings really do show all of these optical deceptions). Not all large eyes on butterfly wing are interpreted in this way - the large eyes on the underside of owl butterflies of the genus *Caligo* are interpreted by **Stradling** (1976) in a surprising, but probably correct way, according to him they are a part of the imitation of the profile of small lizards (geckos) or frogs by the resting butterfly, where the side spot imitates the lizard's or frog's eardrum. Poulton showed a tendency to interpret eye-spots, especially smaller ones (e.g. in the family Satyridae) as „*directive marks*", which guides the bird's attack to a peripheral part of the wing, thereby leading the bird away from vitally important parts of the body. It really does seem that the eye-spot serves as an „eye catcher" (germ. „*Blickfänger*") in the sense of catching the predator's attention, as **Darwin** noted

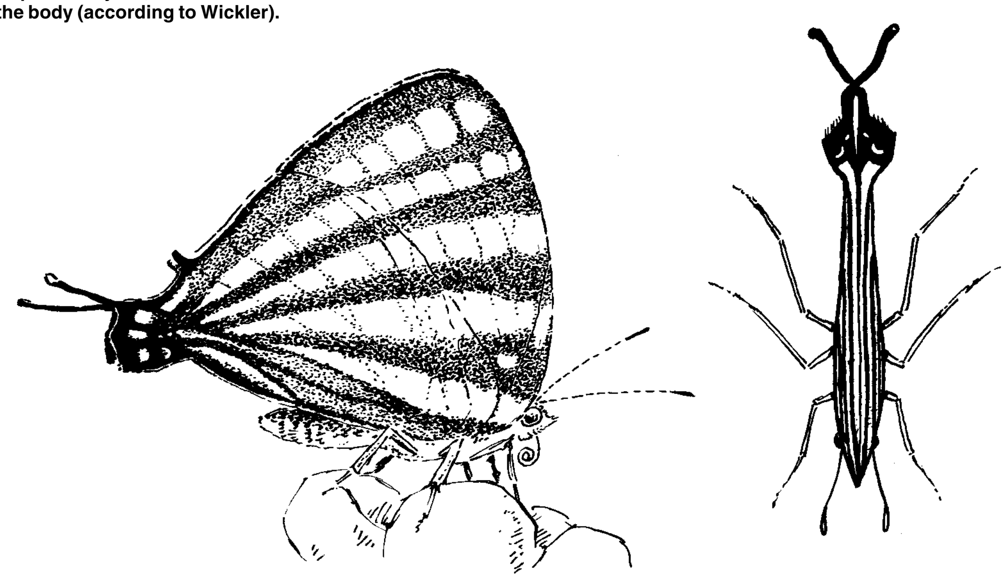


Eye-spot on the American emperor moth *Automeris memusae* (Saturniidae) which represent a „piercing glare" for predators (according to Wickler).

concerning pheasants and peacocks, in many fish it also serves to impress rivals during combat. Large and faithful eye imitations cause fright in birds, and smaller spots attract attention and attack. The eye and its depiction have incidentally always been among the most powerful of archetypal shapes, as can be seen in its thorough camouflage in many fish, birds, mammals, chameleons, etc., where the masking of the eye in a fundamental way protects the animal from revealing itself. The reader can turn to **O. Koenig's** extensive book *Urmotiv Auge* for more information on the basic meaning of the eye and its depiction in human society and traditions - the idea of the „evil eye" is more or less prevalent everywhere, the myth of Medusa or of Gorgons and the many depictions of eyes on the noses of cars, boats, and shields are good examples of this, incidentally concentric circles are the first visual objects which attract the attention of newborns, only days after birth. Eye-spots do not of course occur only in butterflies and birds, but also in certain species of mantids, beetles, peanut-head bug (genus *Fulgora*), or lantern fly (genus *Laternaria*), also in fish, lizards, and crustaceans. An extensive overview of these phenomena was compiled by **Wickler** (1968), more detailed information on the function, origin, and evolution of eye-spots in moths, especially in the genus *Smerinthus* (Sphingidae) can be found in this author's other works (**Komárek**, 1989b, 1991). Insects with evident eye-spots on their wings have been found in carboniferous sediments (genus *Protodiamphipnoa*, **F. M. Carpenter**, 1970) and from the upper Jurassic level (genus *Kalligramma*, **Walther**, 1904). If the hypothesis that vertebrate eyes are the models for some of these spots is relevant, then in the first case it would have to be the eye of an amphibian (works on mimetic phenomena in fossils are generally uncommon - **Lamont**, 1969, **Thulborn**, 1994, **Kácha & Petr**, 1996). The problem of eye-spots is directly related to the problem of false heads, which **Poulton** also mentioned (false heads on butterflies had already been described by **Kirby** and **Spence**, 1817, but in Poulton's time this had already been forgotten). This phenomenon can be described as an imitation of the head on the distant end of the body, the real head is if possible inconspicuous and masked. This phenomenon occurs in fish (the main part is played by the eye-spot at the end of the body, in some cases a slow backwards movement „at rest" accompanies this, with a quick „run" in the opposite direction if attacked - for more information see **Cott**, 1940), snakes (also in ancylosaurid dinosaurs - **Thulborn**, 1994), cicadas, and especially in butterflies (mainly the family Lycaenidae, occasionally in others as well), where the wing tails simulate antennae (including their movement when the wings rub against each other) and the wing angle carries an eye or similar spot, while the deflective strips on the upper side of the wings concentrate the attention of the bird predator on the false head, and not on the real one (the case of the South American weevils of the sub-family Zygopinae, which imitate flies, is also connected to this phenomenon, even if only distantly - but the polarity of the „fly" body is opposite in comparison to the beetle´s one - **Hespenheide**, 1973). An overview of the problem of false heads in butterflies can be found in **Robbins'** (1980, 1981) and **Tonner's** /et al./ (1993) works, in the animal kingdom in general in **Wickler's** works (1968). The question of so called occipital faces on the back of the head of many owls (e.g. the pygmy owl, *Glaucidium*) and some day birds of prey from the family Falconidae is also interesting. These false faces are more or less realistic eye imitations on the back of the head, whose purpose is not clearly known (maybe they serve to deter small birds from *mobbing* from behind by simulating a „second face" - a similar trick is used by Indian honey-collectors - they paint eyes on the backs of their shaved heads to deter tiger attacks). **Scherzinger**, 1986, **Schutz**, 1957, and others cover the occipital faces of owls in greater detail - see the *Bibliography* under the key *Glaucidium* (the article by **Mysterud & Dunker**, 1979, about owl „ears" serving as imitations of mammal ears is also interesting).

Poulton also noticed certain cases of **partial mimicry**, where the other animal is not imitated completely, but only a part or an aspect, which is especially relevant to predators, is imitated. He cites in this context the talented Russian entomologist **J. Portschinsky** (or **Porčinskij**) (1891), who observed in ermine moths from the family Arctiidae (*Spilosoma urticae* and *S. mendica*), which is whitely colored and rejected by predators, a „stinging" movement of their yellow-black „wasp-like" abdomen in stressful moments (Portschinsky, the longtime chairman of the Russian Entomological Society, is the author of many excellent works on mimicry and aposematism in insects, but because he published in Russian, he is almost completely unknown - **Poulton** and **Heikertinger** were nearly the only ones to know about him - see also **Portschinsky** - (1891-1897). This type of mimicry, which also includes the above mentioned eye-spots, is much more extensive than is generally thought - **M. Rothschild** (1984) proposed the term „*aide mémoire mimicry*" to name them. „Partial" mimicry affects possible predators more or less the same as a complete mimicry, with the difference that a partial imitation usually isn't presented all the time, but only when the organism is in danger - the predator's

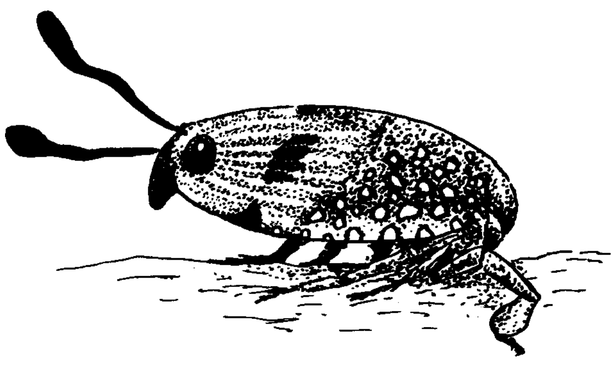
A false head on the caudal end of the hairstreak butterfly from the genus *Thecla* - the tail-like projections form „pseudo-antennae“, and at the base „pseudo-eyes“, and the dark bands call attention to this part of the body (according to Wickler).

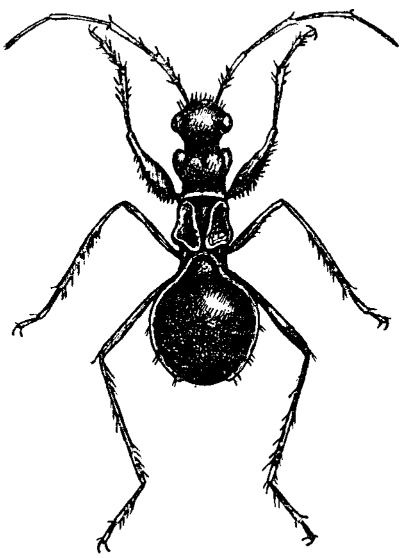


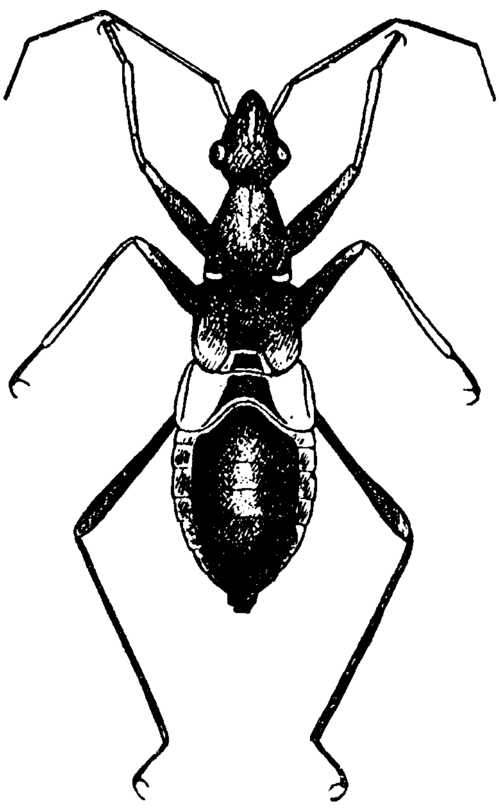
reaction is usually the same as if he saw the imitated organism as a whole, because the „important“ parts are imitated. This category of phenomena on the one hand leads directly to the formation of dummies (this concept was only formulated after the development of ethology in the forties) and on the other hand it leads to adaptive patterns of a non-mimetic type. South American members of the family Saturniidae, which also flash their „wasp-like“ abdomens but are otherwise non-mimetic, are another typical example (**Blest**, 1963).

Poulton, following up **Wallace's** observations, also emphasizes the meaning of stiff, threatening, and self-presenting postures assumed by aposematic animals. Poulton also introduces a new category of animal mimicry, called „*aggressive mimicry*“, in later times usually called **Peckhamian mimicry** instead. The name comes from the work of **Elizabeth G. Peckham** (1889), an employee of the museum in Wisconsin, who described the jumping spider *Synageles picata* (today *Peckhamia,* Salticidae, for Peckham Attidae), whose body imitates an ant, including a simulation of antennae using its second pair of legs and a conspicuous imitation of the body „waist“ (for more works by E. G. Peckham and her husband, see the *Bibliography*). It is typical that Peckham was convinced that the spider uses this disguise (in the sense of a wolf in a sheep's garb) to hunt beetles which live associated with ants easier (which almost certainly is not the case). The thought of mimicry as an aggressive function had at the time already emerged and was becoming established (the German term used by **Heikertinger**, 1954, is *aggressive Zoomimese*, **Wickler**, 1968, used *Angriffs-Mimikry*). Myrmecomorphic spiders were described not only by **Wallace**, but also by **Belt** (1874) in Nicaragua, who thought that the adaptation serves to help the spider mix with the ants and then take them as food. Literature about myrmecomorphic spiders (especially the jumping spider genus *Myrmarachne*) has, since then, been abundant (see the *Bibliography*). **Poulton's** opinion that this is basically a form of Batesian mimicry, whereby the spiders, which move around on

A false head on an unspecified cicada from Thailand - the „antennae“, „eyes“, and „beak“ are false and on the wrong end of the body, the real head is completely inconspicuous (according to Wickler).



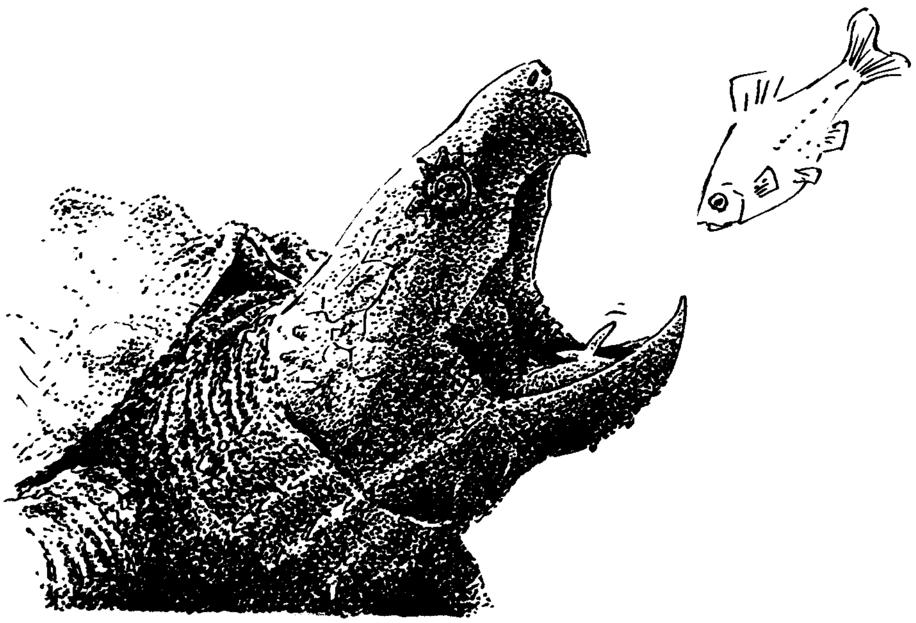




plants in the company of ants (never in the ant nest though), are actually hiding behind them to escape notice from birds, which usually do not eat ants, is today often accepted, even though direct observations of such spiders eating ants actually do exist (**Oliveira & Sazima**, 1984, 1985). The problem of the imitation of ants represents a phenomenon *sui generis*, very widespread in nature, where the next most common imitators are Heteroptera and their nymphae, and the nymphae of bush-crickets and even mantids (e.g. **McIver & Stonedahl**, 1993, many other citations can be found in the *Bibliography*). Besides this the ants are imitated by a number of beetles, especially rove beetles (or "devil´s coach horses), family Staphylinidae, which live, in contrast to all of the before mentioned species, inside ant nest (this problem will be addressed in connection with **E. Wasmann**, the biggest expert on this phenomenon). **Poulton** also discusses the question of whether the well known imitation of bumblebees by hoverflies of the genus *Volucella*, whose larvae live in bumblebee nests, is not also a case of Batesian mimicry, because the nest can also be infiltrated by parasitic flies (but basically they are all more or less innocent inhabitants, including the *Volucella*) which are dissimilar (this concept was later accepted by **Carpenter & Ford**, 1933, and many others). In spite of this it is difficult to wholly refuse to accept certain cases of similarity between organisms which are in some way connected, usually not only by their occurrence in the same locality, but also through parasitism or predation. Besides the already mentioned myrmecomorphic spiders and insects, which live among or close to ants, partially as predators or „guests" (basically something between symbiosis and parasitism) and the notoriously well known cases of the bumblebee and the *Volucella* or the cuckoo bumblebees of the genus *Psithyrus* and the bumblebees, *Bombus* (as well a parasite and host), the range of similar examples is very broad. The robberflies of the genus *Hyperechia* (Asilidae) not only hunt carpenter bees of the genus *Xylocopa*, which they imitate, as adults, but their larvae are also parasites in their nests (**Poulton**, 1904b, 1924a, b, 1925a, **Shelford**, 1902, **Green**, 1904, **Marshall & Poulton**, 1902, **Tsacas et al.**, 1970, and many more smaller reports /*Proc. Ent. Soc. Lond.* 1925: 12-15, 1926: 1-2, 44-47/), and this phenomenon also occurs independently in Borneo and in South and East Africa. Poulton also discovered a very important correlation of appearance between other members of the family Asili-

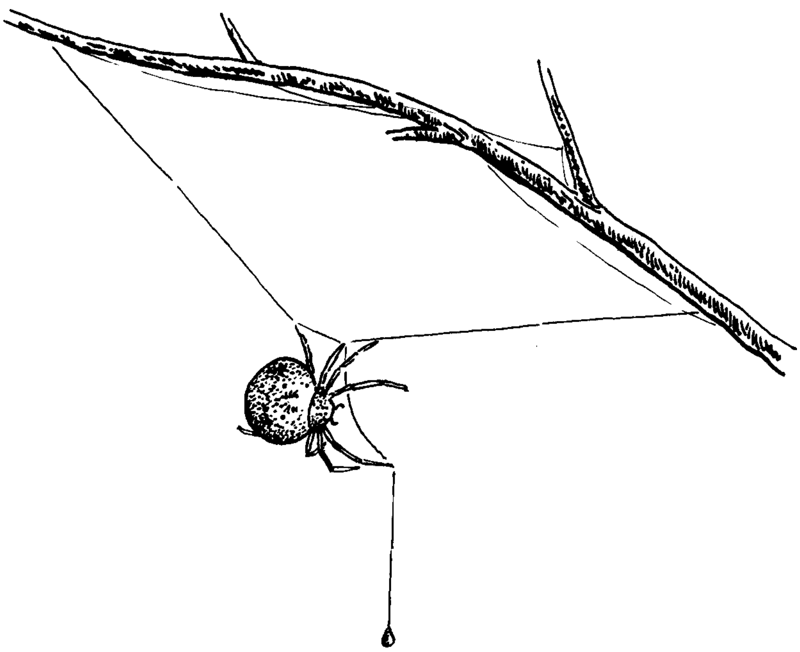
Top: The myrmecoid bug *Myrmoplasta mira* (Pyrrhocoridae, eastern Africa) imitates in form ants from the genus *Polyrhachis* in quite impressive detail (according to Gerstäcker).

Bottom: The myrmecoid nymph of the bug *Nabis lativentris* (Nabidae). The form of the body is imitated only optically, without a real narrowing of the body (according to Heikertingger).



An example of Peckhamian mimicry: The North American alligator-snapping turtle, *Macroclemys temmincki* lures small fish directly into its mouth using moving worm-like appendages on the tongue (according to Wickler).

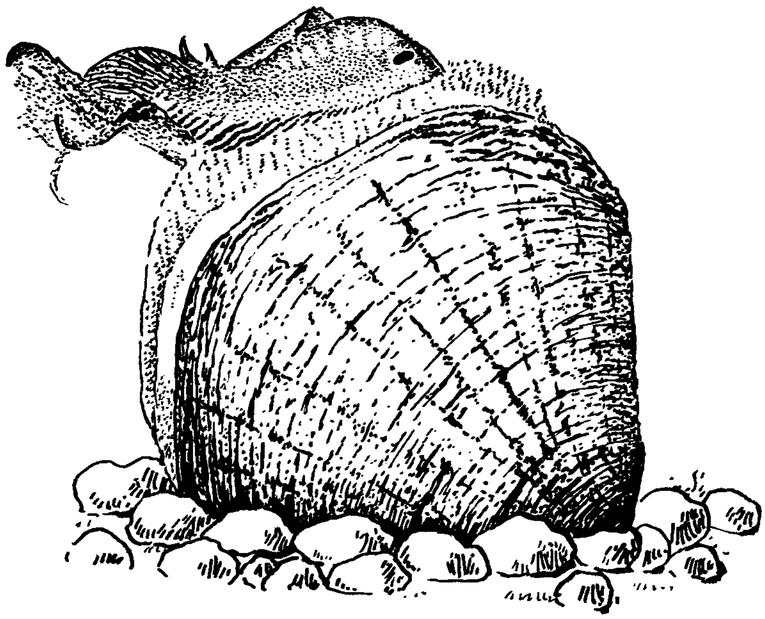
An example of Peckhamian mimicry: An American bolas spider from the genus *Mastophora* hunts male moths using a sticky ball hanging from one thread, which contains an analogy of sexual pheromones (according to Wickler).



dae (robberflies) and their hymenopteran prey - that is the larger the specialization on one specific prey, the greater the imitation (**Poulton**, 1904a, and **Study**, 1926). Cases of the prey imitating the predator have also been recorded, for example Bates' description of the bush-cricket of the genus *Scaphura* which imitates the wasps which hunt it and many other cases, which were already described by **Gerstäcker** (1863), as mentioned above. **Poulton & Seitz** (1913) also noticed that bush-crickets of the genus *Scaphura* imitate their wasp predators in the shape of antennae, which are wider at the base and circled with a yellow „end", even though the antennae continues further. Further this concerns the imitation of spiders from the family Salticidae by flies from the family Tephritidae (**Fernandez**, 1974, **Monteith**, 1972, **Eisner**, 1985, **Mather & Roitberg**, 1987, **Greene et al.,** 1987, **Greene**, 1988, **Whitman et al.**, 1988, imitations the other way around were observed by **Morrison**, 1981), and possibly the imitation of predators by the pacock bass (or "eyespot cichlid") *Cichla ocellaris* (**Zaret**, 1977), and even the imitation of parasites by the host /the New Zealand ichneumon wasp *Zanthocryptus novozealandicus* (Ichneumonidae) is imitated by the longhorn beetle *Neocalliprason elegans* (Cerambycidae)/ - **Harris**, 1978 (other similar cases were mentioned earlier in connection with Peckhamian mimicry). Arizona's longhorn beetle of the genus *Elytroleptus*, which acts as a predator or brutal external parasite for the net-winged beetles, the genus *Lycus*, mimic their prey, which surprisingly does not defend itself at all (**Eisner, Kalafatos & Linsley**, 1962). Of course neither predation or parasitism necessarily do require such a relationship of external appearance, which in any case sometimes does exist. Every case can in some way be explained „functionally", but at the cost of substantial intellectual strain, strong belief, and the uncertainty factor that most predations and parasitisms do actually work without such similarities. Folk traditions outside of modern science speak of an organism growing similar to those it eats or lives with (in folklore it is usually an extreme case of convergence between man and his dog, a teacher and his student, old couples, etc.). A nice example of this phenomenon are the semi-parasitical shrubs from the family Loranthaceae, especially in Australia, which imitate the shape and type of leaves of trees on which they parasite (**Wiens**, 1978). Explaining this very complex phenomenon by way of selection from the side of a few small herbivorous marsupials (**Barlow & Wiens**, 1977, **Wiens**, 1978) requires a real belief in the omnipotence of selection. This spectrum of phenomena also includes the adaptation of birds to nest parasitism, for example the African whydahs (Viduidae) are similar to their hosts, firefinches (Estrididae) not only between hatching and their juvenile plumage, but in voice as well, including the fact that they „adopt" the song of their host species (adult male whydahs on the other hand are quite different in appearance from their hosts, especially in their conspicuous tail feathers) /e.g. **Nicolai**, 1974/. Parasitical species of cuckoos in the Old World and Australia not only imitate the egg color and pattern of their hosts, but sometimes the appearance of their young as well (e.g. the genus *Clamator* imitates magpies and crows). The problem of our cuckoo's (*Cuculus canorus*) egg imitating the eggs of its hosts (there is a large number with various egg coloration) in various cuckoo „clans" (*gentes*) was not in detail examined by Poulton, which can be explained by his indifference to classical genetics (as will be shown later).

Poulton further writes of another case of aggressive mimicry, which concerns various deceptive lures in the animal kingdom, for example the worm-like movement of the tongue of the alligator-snapping turtle (*Macroclemys temminckii*) from the United States, the angle-like lures of the monkfish *Lophius piscatorius* (first described by **Aristotle** in the *Historia animalium*) and similar glowing structures in the seadevil species *Ceratias bispinosus* and *C. uranoscopus*. He also interpreted the pink formations in the corners of the mouth of the Central Asian agamid lizard *Phrynocephalus mystaceus* as being a flower dummy used to attract insects, which would bring this group of mimicry very close to the group labeled „*alluring colourations*" in **Wallace's** sense (mantids imitating flowers, etc.).

This category also includes phenomena which were recorded later, for example the imitation of light signals of related species by the female North American firefly of the genus *Photuris*, which serves to lure the male, who is consequently eaten (**Lloyd**, 1965, for more authors see the *Bibliography*) or the American „bola-spiders" of the genus *Mastophora*, which hunt using only a sticky bead attached to the end of one single thread, which the spider swings with its front legs - the bead contains a substance analogous to the sexual pheromones of certain moths, which lures the males, causing them to get stuck on the bead (**Gertsch**, 1940, 1947, and a number of other works). A large number of very interesting cases of this type were analyzed by **Wickler** (1968), for example the imitation of mosquito larvae by the cercaria of the flatworm *Azygia lucii* (meant for the fish for which the flatworm is a parasite), the imitation of a caterpillar or worm by the sporocyst of the flatworm *Leucochloridium macrostomum*, which lives in amber snails from the genus *Succinea*, and which in daytime extends onto the snail's



An example of Peckhamian mimicry: The North American freshwater clam pocketbook, *Lampsilis ovata,* imitates through its edge of the palium a small fish. The clam injects larvae, glochidia, into the mouth of predatory fish, which attack the „fish". The larvae then parasite on the gills (according to Wickler).

antennae in hope of being eaten by an insectivorous bird, which it parasites. He also mentions the case of the North American clam *Lampsilis ovata*, which has a false fish pattern on its side, which attracts predatorial fish which are then infected through the mouth with parasitical larvae, glochidia, by the clam during the attack. **Wickler** himself described a very interesting case of Peckhamian mimicry, specifically the imitation of the marine cleanerfish (or cleaner wrasse), *Labroides dimidiatus* (family Labridae) by the blenniid fish, cleaner mimic (or "false cleanerfish") *Aspidontus taeniatus* (family Blenniidae). While the first species gets food by cleaning the surfaces of grateful larger fish, to which it attaches after a typical „dance" ritual, the second species, which is similar in appearance and movement, attaches in a similar way and then rips off the fins, which serve as food, of the larger fish (**Eibl-Eibesfeldt**, 1959, **Wickler**, 1960, 1961, 1963, 1966a, b, 1968).

Poulton was also interested in aposematic coloration and emphasized their smooth transition from cryptic coloration (e.g. the caterpillar of the mullein moth *Cucullia verbasci*). Poulton also considered the metallic luster of many chrysalises from the family Nymphalidae to be aposematic. Besides these golden hues, many insects also sport blue or green metallic hues. Because these hues are in fact interference colors created on a complicated chitine structure made of a combination of thin layers, often built in quite a sophisticated manner, it is apparent that this is not an „accidental by-product" of something else. Studies on the function of these colors (in contrast with work on the physical aspects) were quite rare (practically none exist - more or less relevant mentions or works include **Cockerell**, 1891, **Newbigin**, 1898, **Biedermann**, 1904, **Schuster von Forstner**, 1925, **Neville**, 1977, **Young**, 1971, **Schultz**, 1986a, b, **Selman**, 1985, **Schultz & Bernard**, 1989) and in comparison to pigments based aposematically, these conspicuous phenomena never achieved a high popularity. In certain cases (in birds, butterflies) the colors obviously play a part in epigamic interactions, but what function do they have in cases where the colors are apparent in both sexes in the same amount, such as in blow-flies from the genus *Lucilia* or in many beetles (e.g. the genus *Chrysomella, Geotrupes*, etc.)?

During his study of mimicry Poulton gathered an unimaginable collection of cases, many of which are very bizarre. These mainly concern the lantern fly (or alligator bug), *Laternaria*, a large South American homopteran insect (**Poulton**, 1924c, 1932, also **Monte**, 1932, **Hogue**, 1984, **Ridout**, 1987). The head of this insect extends into a massive snout which does not serve any evident purpose (in older works we can often find the opinion of the Dutch illustrator and biologist of the 17th century **M. S. de Merian**, 1705, who said that this extension glows, which gave the organism its name, but nonetheless it is untrue). The mentioned extension surprisingly in many details resembles the head of an alligator, excepting its 5 cm length. Poulton resolved this by means of selection, in the sense that even the small dummy of a dangerous adversary can confuse and repel predators (in this case monkeys) in the rainforest environment, where judging size is quite difficult. As an example of similar phenomena Poulton mentions a poodle, which was driven quite mad by a small figure of a different dog. This case was later published with various bewildered commentaries many times in various publications, and the only really interesting remark was made by **Callois** (1960), who believed that in the case of the lantern fly the extension is a frightening mask implemented in a different order of magnitude, and not an imitation of an alligator. Darwinian explanations were used even for such absurd cases as the Japanese crab with a picture of a samurai on its carapace - **Fisher** (1930) believed that this picture developed and was perfected because of selective conservation of the most perfect individuals by Japanese fishermen, who traditionally do not eat this species because of this design. There are many more cases of dramatical size differences between the model and its alleged imitator - the chrysalis of many South Asian and African butterflies from the family Lycaenidae resemble a human or primate skull shrunk to about 1 cm or less (**Sevastopulo**, 1977, **Hinton**, 1958, 1974, **Aitken**, 1894, **Holland**, 1892, **Anonymous**, 1896) - even here we can find a selectionist explanation with primates as the agents of selection. A work interpreting a South American looper, which has a pattern typical for coral snakes, as an example of mimicry, also exists (**Fassl**, 1910).

Poulton interprets the black and shiny eggs of various parasitic Ichmeumonidae (e.g. the genus *Paniscus*), which are laid on the skin of certain caterpillars, as being a sign of „occupation“ and basically a „recognition mark“ for members of their own species. He also believed that the small dark depressed surfaces on the sides of the caterpillar of the lobster moth *Stauropus fagi* are a mimicry of the eggs of such parasites. Many similar phenomena were described – certain plants mimic eggs, or even the caterpillars of some butterflies, which feed on the plant, which serves similarly to give the impression of „occupation“ – the simulation of caterpillars and eggs of the family Heliconiidae in passion flowers, *Passiflora,* was described by **Gilbert** (1971, for other works see the *Bibliography*) and **Rothschild** (1974), dummies of eggs from the family Pieridae on cruciferous plants were described by **Shapiro** (1981) A large number of organisms, for yet not completely known reasons, mimic infestation (by parasites) or injury – a great amount of references to butterfly cocoons, onto which the caterpillar sews imitations of the cocoons of their parasites from the family Braconidae (braconid wasps), have been written (**Lamborn**, 1911, 1913, 1930, **Poulton**, 1931, **Kirkpatrick**, 1957). **Portschinsky** (1891) had good reason to believe that the cocoon of the European butterfly *Limenitis populi* (poplar admiral) simulates on its back an injury which bleeds haemolymph fluid, as cited by **Poulton**, 1910. Also the Luzon bleeding heart (*Gallicolumba luzonica*) evidently simulates a bloody injury on its light colored chest feathers. (**Portschinsky**, 1897, thought that the caterpillar of the lobster moth, *Stauropus fagi,* uses its folded caudal shield with antennae-like extensions to imitate a sting bug from the family Pentatomidae, which attacks caterpillars and sucks out their bodily fluids). Plants often simulate leaves which have been chewed up by caterpillars, for example the family Moraceae – *Broussonetia* (papper mulberry), to an extent *Morus* (mulberry), and even the fig tree, *Ficus carica* (**Niemelae & Tuomi**, 1987). This is interesting because the „chewed off“ structures appear only on leavesonly about to a meter and half above ground, which led to the conclusion that this provision could be intended for larger phytophagous mammals, which cannot reach any higher. Unambiguous „functional“ explanations of the above mentioned mimicry cases are simple only in certain cases, in others the explanation seems forced. Understandably many types of injury and fungal infestations of plant leafs are imitated by cryptic leaf imitating insects (certain weevils, for example *Cionus hortulanus*, imitate seeds of the vetch, *Vicia*, including the etrance openings of the seed weevils from the family Bruchidae, which live in these seeds). The imitation of galls on plants, which are made by gall midges of the family Cecidomyidae, by butterfly eggs was described by **Trotter**, 1903. From the strange mimicry cases described by **Poulton** (1891), we should also mention the nymph of a treehopper species from the family Membracidae (Homeptera), which imitates leaf-cutting ants from the genus *Atta* carrying a cut off portion of a leaf (the corresponding surfaces of the organism are colored green and brown), or the example mentioned by **W. W. Fowler** (1918) of members of the same family (*Heteronotus trinodosus*), which imitate ants with an extremely enlarged pronotum (**Poulton**, 1908). Both illustrations were republished many times in various entomological compendiums and publications on mimicry. Imitations in nature and culture were also studied by a contemporary of Poulton's, **Steel** (1900).

The largest group of cases collected by Poulton obviously concerned butterflies and moths. He didn't even disregard cases where the mimic and its model lived in different environments or geographically distant localities (the *Abraxas etridoides* /Geometridae/, which lives in India's mountains, imitates the *Teracolus etrida* /Pieridae/, which lives in the lowlands, or the area of western China, where the *Athyma puntata* and the *Limenitis albomaculata* live - these imitate the male of the species *Hypolimnas misippus* (all from the family Nymphalidae), which lives in the region from southeastern Asia all the way to Kashmir – **Poulton** considered this species to fall under Müllerian mimicry, therefore being a protected species). Poulton's explanation of this phenomenon is precisely on the border between „positive teachings" and a fable – the whole phenomenon is explained by introducing a selective agent in the form of a migratory insectivorous bird, which moves between these regions and transfers the image of the „model" from its mind even to areas, where it does not occur. Poulton also noticed the fact that non-mimetic relatives of mimetic species often occur on islands. Poulton generally considered most mimetisms as Müllerian, instead of Batesian. For Poulton the criterion for distinguishing between the two was the cryptic coloration of the underside of the wings in Batesian mimicry in comparison with the aposematic coloration found in Müllerian mimicry. Besides well known cases concerning the mimetic polymorphism of the females of certain butterfly species (Poulton was especially interested in the swallowtail species *Papilio dardanus*, and he described a large number of new forms, for example the mimetic females from the Abyssinian subspecies *P. d. antinorii*, which have tails), and also other cases of species where males and females which mimic other species – the Indian species *Elymnias leucocyma* (Satyridae), whose males always imitate the species *Euploea harrisi* and the female imitates the *Euploea mulciber* (Danaidae) – or where both sexes imitate the same model species– the Indian moth *Epicopeia philenora* (Epicopeidae) imitates in both sexes the respective sex of their model, the *Papilio protenor*. Cases where non-mimetic females are accompanied by mimetic males are extremely rare – for example the South Asian laceving genus *Cethosia* (Nymphalidae), where the males are not very sophisticated mimics of certain brownish Danaidae (similar cases can be found in some spiders, where only the males imitate ants and the females are non-mimetic).

W. L. McAtee, who was a well known and influential applied ornithologist from the *Biological Survey Division* of the *U.S. Department of Agriculture*, often discussed the problem of mimicry and aposematism with Poulton. McAtee conducted extensive researches concerning the nutritional habits of many birds in view of their economic usefulness for American agriculture. The contents of the birds' stomachs showed a more or less equal representational ratio of aposematic and mimetic insects, as they appear in nature, from which McAtee concluded that these precautions are not effective on predatory birds, which painfully touched on a theme that Poulton considered especially important and which he extensively researched, mainly using so called *beak marks*. McAtee published the first work of this type in 1912 and a whole series soon followed (**McAtee**, 1912, 1932, 1933, and others in the *Bibliography*), which Poulton and others responded to accordingly. McAtee's basically anti-Darwinian view is not surprising for American biology at that time. It is good to remember that the founder of American biology **Agassiz** (1858) and his followers, such as **Cope** (1887) or **Osborn** (1917), **Hyatt** (1880), and **Scott** (1894) were more or less Lamarckians and that America at the turn of the century also had its **Mičurin** in **Luther Burbank**. Neodarwinism in America surprisingly became accepted only much later thanks to immigrants (especially **Feodosij Dobžanskij**, an important population geneticist from Russia, from 1929 in the USA, later known as **Theodosius Dobzhansky**, or the German **R. B. Goldschmidt**). Only after WWII did neo-Darwinism, later in its sociobiological modification, become monoculturally accepted and exceptions are very rare – e.g. **Bateson** (1973).

Concerning ***epigamic colorations***, **Poulton** (1890, 1908) rigorously held to the **Darwinian** standpoint of sexual selection from the side of the female, rejecting **Wallace's** concepts. He emphasized for example the fact that conspicuous colors do not appear on those parts of the body which move too quickly for the coloration to be perceived /the wings of hummingbirds, or even the wings of many insects which move quickly – Diptera, Hymenoptera (here there are of course exceptions, e.g. the family Tephritidae or the genus *Xylocopa*, but there aren't many, on the contrary, species with slow wing movements – butterflies, dragonflies, certain Neuroptera – Ascalaphidae, Nemopteridae, Myrmeleonidae – often or regularly have wing patterns)/.

Hingston and his original conception of animal coloration

A much more interesting and uncommon approach to the exegesis of animal coloration and external appearance appeared during Poulton's life in **R. W. G. Hingston's** book *The meaning of animal colour and adorment* from 1933. A major of the medical service in the British army, Hingston was a perfect example of a natural historian officer with many experiences with the nature and culture of India, Ceylon, and Burma, and later Guyana as well (his later books were entitled for example *Problems of instinct and intelligence, A naturalist in the Guiana forest*, some other articles concerning mimicry are included in the *Bibliography*). Even though Hingston was close to **Wallace** and basically even **Darwin** in his enthusiasm, considerable autodidaxis, originality, and scope of interest, he not only stayed in their shadow, but also was not very important in his era, which was quite different from the 19th century (he is cited quite sparsely – he is mentioned by **Heikertinger**, 1954, for example). In spite of this, his book is one of the most remarkable ever written about the explanation of the external appearance of organisms, even though it has the fault, which is common to all authors who have formed some interesting viewpoint, that his rigorous application of this view on all phenomena in the world clearly shows that the world is not wholly homogeneous and certain applications require an indecent amount of violence on particularities (this is also true for Darwinism, as well as others). Hingston preceded the development of ethology by many years and his book is through its exceptionally original observations very interesting for anyone interested in the appearance of the living world. Characteristically, the book lacks a list of literature – it is apparent from the text that the author knew **Darwin** and **Weismann**, and some few published or orally transmitted observations from field biologists, mostly from Hingston's colleagues – colonial officers. Otherwise the book is the product of his own thoughts and observations and has all the positives and negatives of works, whose authors have individually worked out a world view and were not assisted by a formal education in the field. Hingston's observational talent was equal to Darwin's and in some respects surpassed his, both had a deep interest in the connection between animal psychology and the animal's external appearance (**Darwin**, 1872) and the expression of emotions in animals and humans alike. Hingston also represents a perfect textbook example of the projection of observation from society onto the external world and the interpretation of the world through these eyes. Hingston's military profession and detailed knowledge of the military traditions of past eras (the British army contained in Hingston's time many archaisms, which had long been removed on the Continent) led to the interpretation of nature through the principle of battle – he literally speaks of the "battle of life". The external appearance of animals and humans serves according to Hingston to adequately express emotions, the basic emotion being anger. All semantic coloration serve to express threat (Hingston of course did not in the least doubt that the male, which is more or less ornamentally richer, represents the evolutionarily more advanced half of a species). A fundamental concept for Hingston in the explanation of external appearance of organisms is the tension between cryptically colored portions of the body and the semantically colored parts, called "color conflict" (generally speaking, Hingston's explanations, which emphasize the importance of polarity and binary opposites, are very similar to structuralism in linguistics or **Lévi-Strauss'** method of exegesis of myths, but it is almost certain that Hingston developed this concept separately, without any knowledge of structural linguistics at all). This conflict of colors is parallel to the basic emotional conflict between anxiety and anger and is its external correlation – this is why most organisms have in some proportion both types of coloration, nonetheless some have only one, according to the prevalent side. In the frame of semantic coloration the contrast between light and dark surfaces is again important, as are various complementary colors, feather or fur ornaments and manes, horns and antlers, protruding teeth, butterfly tails, etc. On the whole, Hingston was closer to **Wallace** than **Darwin** because of his disbelief in sexual selection, even though he deeply respected Darwin and often cited him. The difference between him and Wallace lies mainly in the fact that he considered intraspecific communication to be mostly derived from aggressive or threatening gestures (he saw these components, with just cause, also in the mating rituals and dances of birds, in copulation behavior, etc.), which is also a noteworthy anticipation long before the general acceptance of Lorenz's works on the mutual homology of various types of behavior in animals and the key role of aggression as an inborn phenomenon. (Hingston definitely did not know **Lorenz**, and the importance of the latter in this area is necessary to emphasize. But it is also important to remember that both grew up in the atmosphere between the wars, and before the first, and saw unbound creativity, directly related to the living source of existence, in the battles and wildness /as compared to the satisfied, indolent, and wasteful world of domesticants or cityfolk, who slowed the development of natural expression with its spontaneity and cruel tragic beauty/. It is interesting to note that one of the first ascribers to this way of viewing the world included not only **Nietzsche**, but to a degree Wallace as well, and as Hingston they scorned all domestic forms – these moments can also be found in Lorenz's works from the WWII years, which dealt with the „autodomestication" of man. A similar intellectual substrate stood at the birth of the intellectual basis of German nazism and Italian fascism, and was widespread in Great Britain as well, especially in army circles, and in many other groups in Europe.).

Unlike **Wallace**, Hingston believed that battles did not depend solely on teeth and claws, but he emphasized the importance of imposing, threatening, and frightening postures assumed, without the need for a direct assessment of strength, in a wholly ritualized form. He also stressed the importance of this interaction in all conspicuous groups of organisms, especially in birds and butterflies. (Hingston directed his attention to higher vertebrates, mammals and birds, but he also knew invertebrates well. He was best acquainted with birds from India and the surrounding areas and his book includes a schematic, but very faithful, sketch of various ethological situations in animals.)

The precise nature of Hingston's unconventional perceptions and ethological observations, which came about before the formation of ethology as we know it today, is fascinating and is an expressive testimony of how interesting yet atypical books are „forgotten". Hingston was nevertheless convinced of the existence of natural selection, but only as a negative selective mechanism which discards the weak and ineffectively adjusted individuals, and not as something with a creative aspect – the further evolution of the external appearance of an animal depends, according to Hingston, on their internal efforts at self-expression (the self-expression of aggressive emotions – this is the main difference between Hingston and **Portmann**, who in any case did not know Hingston), which can either be supported by natural selection, or be hindered and slowed by it, but it cannot be influenced by it. Hingston believed that the evolution of an individual and the evolution of a species are guided by the same principles, which in this case are dependent on immanent factors, not external ones. Forms with luxurious or exaggerated structures, for example the „Irish elk" from the genus *Megaceros*, sabertooths, or mammoths and other fossil elephants with large tusks, were considered to be the "final" or target form by Hingston – these animals attained the final consequence of the self-expression of their aggressive emotions and then so to say died of "old age", for the life of not only an individual, but a whole evolutionary line is not infinite, but has its natural span, after which it ends. Hingston believed various forms of domesticated animals to have been allowed, by humans and their protection, to evolve, through the hypertrophy of certain parts of their bodies, the ability to better express their emotions (breeds of domesticated pigeons with enlarged crop, tail feathers, beaks, eye circles, changed voices, way of flight, etc. are good examples of this) - considering that every body part is in some way connected to a specific emotional self-expression, it is possible to apply this theory everywhere - but the fact still remains that breeders do not have an infinite amount of possibilities in choosing variations, the original wild form has many crossroad branches of possible paths to follow, but the number is not infinite - the nature of the body and living forms themselves allow only certain morphological and ethological changes in domesticated species and the guided possibilities of emotional self-expression.

Aposematism for Hingston becomes just another subset of threatening and fighting appearances, where the inedibility or repugnance is one of many possible „weapons". He would have probably interpreted mimicry in the same way - he considered a great many threatening and defensive strategies to be based on deception, fraud, or deceit - but he was not interested in this field of study, which was due to the fact that their interpretation would exceed the already wide spectrum of his book (411 pages). Like **Wallace**, Hingston understood conspicuous species as being those which through their aggressiveness, speed, or other „weapons" gained ground, and cryptic species were those which were most exposed to the pressure of natural selection in the direction of inconspicuousness and optical fusion with the substrate. Many times Hingston emphasized (he was generally the master of fitting analogies) the analogy between animal patterns and ornaments and war paint on bodies, colorful and vivid uniforms, ceremonial weapons, etc. /Considering that in the last decade of the 19^{th} century the armed forces underwent a significant change from „semantic" to „cryptic" uniforms (this applies to army vehicles and ships as well), it is difficult to imagine according to today's analogies the fundamental role of ornamented dress and weapons, musical and other artistic productions in military endeavors of the past - even the Turkish siege of Vienna in 1683 seems, according to documents from the time, to be more like a monstrous fashion show than a military conflict of life and death (even today's more or less cryptic uniforms have their „semantic" parts, exactly in the sense of Hingston's „*colour conflict*"). The theme of the evolution of military uniforms and the changes from full functionality to signs of importance of the wearer (their epaulet, hat), rudiments, and other biological analogies were researched by the Austrian ethologist **O. Koenig** (1970), who did not actually know of Hingston's book; Koenig was interested in the comparison between the evolution of human artifacts and biological evolution in general/. Hingston compared numerous threatening postures and mimics with war masks (his interpretation of the grooves on the face of the mandrill and the small lines of feathers on macaw parrots from the genus *Ara* as being constant masks of an angrily wrinkled face, which serves to make the animal seem formidable, are very interesting and probably true). He understood the display of „flowering" mantids of the genus *Idolum* to be threatening postures as well, even though they are usually considered flower dummies, which is in an interesting fashion later adopted in studies of the order Mantodea (**Edmunds**, 1972, 1976, also 1974). Hingston even considered bird song, in spite of its musical complexity, to be mainly a way of gaining dominance over males of the same species (this explained why birds sing outside of their mating period) and the imitation of other songs was explained as an attempt to gain dominance over another species and drive them out of the imitator's territory. Like **Wallace** and **Tylor**, but in much greater detail, he worked on the theory of predilection places for color spots, or feather or fur ornaments in birds, mammals and insects, but this time not only in relation to morphological givens, but also in view of the maximal effectiveness of emotional expression - Hingston often uses the term „machinery" to describe the whole system of patterns and ornaments on the body of an animal. He also, in great detail, analyses the external appearance of humans and the role of hair, beards, pubic and other hair - axillar hair, in man this is the only one without an analogy in the primate world, he interprets these hairs as being meaningful conveyers of threat, shown when raising a weapon or fist (because man stands upright the hairs in axilla can be seen). His numerous perceptions on human ethology and the meanings of gestures and countenances were picked up again (and again without direct knowledge of his work) much later - **Eibl-Eibesfeldt** (1984), **D. Morris** (1977). Within the framework of threats and „psychological warfare" he noticed the amazing detail not only of bird feathers, but also of the colorations of the bird's iris, legs, the insides of their beaks (even the vivid colorations of the insides of the beaks of young songbirds were a combination of begging the parents for food and a threat to smaller predators, according to Hingston), „beak dummies" found in hornbills, and other phenomena. In great detail he analyzed the differences between the young and adult form of mammals and birds, the differences in external appearance in periods of non-reproduction and periods of reproduction, or the differences between appearance during various seasons / These cyclic changes include the casting down of antlers of deer - Hington considered them to be primarily instruments of intimidation for competitors - they are not so effective in actual battle; but also the seasonal dimorphism in butterflies, which, even though the realization comes to pass only in later generations, is counted in this category of phenomena (this phenomenon was already studied by **Weismann**, 1875). Hingston considered the external appearance of these butterflies during the wet seasons in the tropics, which is usually more semantic with larger eye spots, to be more „aggressive" than the mostly cryptic coloration in dry seasons/. Hingston explains butterfly coloration as „aggressive", to an extent meant for members of the butterfly's own species (he knew very well the flying showdowns and „fights" between males and their territoriality), and to an extent meant for predators - in this way he explains the contrasting coloration in females and the common only slight dimorphism (the rhythmical opening and closing of the wings towards the observer, which is found in many species, was later described by **Portmann**, and Hingston understood it as a threat, which goes for eye-spots as well). Hingston's interpretation of tails on the hind-wings of many butterflies is also interesting (These filiform and often flat spoon-like formations, usually appearing singly, but sometimes in pairs and even threesomes, on the hind-wings of certain species and are very difficult to explain in terms of functionality - the occasionally presented explanation that they serve to balance flight is an illusion, especially if we realize that many tailless species fly quite well. In some cases they appear in various different stages of development in very closely related species or in various sexes or local forms of the same species - this last case applies for example to the well known swallowtail *Papilio dardanus*). Hingston also noticed the frequent existence of a vivid spot or ocellus at the base of the tail, which in these cases he considers to be an extension (in the sense of the frequent existence of a colorful spot and bundle of hair or feathers, which serves as an extension into space, on the predilection places on birds and mammals /threat - marks/. Moving the tail by rubbing the hind-wings in species with „false heads" (Hingston does not use this term) was interpreted as an act of ethologically emphasizing threatening colors, which is strengthened by the tail (the problem of butterfly tails was also addressed by **Piepers**, 1904, **Röber**, 1905, and **Wohlfahrt**, 1989). Hingston also noticed the positive correlation in butterflies between bright contrasting colors and quick, strong, and very versatile flying ability, and oppositely the correlation between dull colors and weaker flying abilities (the contrast between a cryptic coloration of the underside and a semantic coloration of the upperside, much the same as the contrast between the cryptic fore-wings and semantic hind-wings of the underwing moths, *Catocala*, is interpreted by Hingston as a typical example of his principle of „colour conflict"). Excessive „weapons" like the beak of the toucans and hornbills, the canines of the babirussa (*Babirussa*), the massive claws of male fiddler-crabs from the genus *Uca*, excessive antlers, etc. are interpreted by Hingston as being only „psychological weapons" used in intraspecies conflicts, and only occasionally used in conflicts with different species. He interprets the luminescence of fireflies and some South American click beetles of the family Elateridae (who can actually be collectively synchronous - e.g. **Buck & Buck**, 1976) in the same way, which also applies to many deep sea organisms (Kirby and Spence, 1817, and Wallace, 1889, also interpreted the luminescence of fireflies as a way to drive off enemies or as an aposematism, and not as a method of intraspecific communication - for Hingston this was confirmed by the fact that not only adults, but larvae and eggs as well, have this ability - in the same year **Carpenter & Ford** (1933) come to the conclusion that fireflies and luminescent insects general have to be *eo ipso* inedible, because otherwise their luminescence would drive them right into a predator's open mouth).

Hingston's book is very good for the unbiased reader, its weaker sides are balanced by a noteworthy view of the world, but still it lay isolated and unnoticed and later, authors who had similar ideas never even mentioned it (not even **Poulton's** reaction is known, but we can imagine that it was very negative). The book is an interesting example of how to reinterpret the external appearance of organisms in such a different way from the classical Darwinian view with a similar level of believability, if you start from a different angle. In addition the principle of Occam's razor is applied even more severely in terms of the minimalism of principles put forward (which does not necessarily lead to the truth, but definitely gives a more „elegant" and understandable work). Besides this, the book is an excellent example of an open sociomorphic interpretation of Nature, as compared to the unconscious sociomorphic interpretations by **Darwin** and **Wallace**. Hingston was so convinced that the microcosm of the army provides a true picture of life in the macrocosm that he didn't even try to hide his sociomorphic interpretation and he wasn't in fact so to say explicitly even aware of it (for example, his comparison of the collective movements of aposematic insects, for example larvae of the sawflies from the genus *Croesus*, to collective exercises in the army, is quite charming, another good example of this is his analogy between many types of intimidating movements of many animals and the army's „parade" march). Even so he remains one of the most original observers and interpreters of the external appearance of organism ever.

Poulton's coworkers and followers

One of **E. B. Poulton's** closest friends was also the doctor (histologist) **Frederick A. Dixey** from Oxford (1861-1935), who is known primarily for his work on the phylogenetic meaning of the wing patterns of butterflies from the families Nymphalidae and Pieridae (**Dixey**, 1890, 1894). In his later works (**Dixey**, 1896, 1897) he studied the transformation of color patterns in mimetic butterflies, especially from the family Pieridae, and compared them to their non-mimetic relatives, from which he concluded that the „starting" structure of the patterns can undergo metamorphosis in a number of directions into various types of mimetic patterns, but on the other hand the individual color patterns of the mimic and the model do not have to correspond in their origin and often come from morphologically different parts of the pattern (for more details about this theme see the chapter on the research of butterfly patterns in German biology, for more works by Dixey, see the *Bibliography*). **Harry Eltringham** and **Guy A. K. Marshall** were also Poulton's close friends. **H. Eltringham** (1873-1942), a rich shipwright, left his occupation at 35 and turned, as a private student, to the study of mimetic butterflies with Poulton at Oxford. The product of this study was a beautiful and even today very instructive book entitled *African mimetic butterflies* from 1910 with rich illustrations, which display the mimicry rings of sub-Saharan butterflies, which are based on imitations of the families Danaidae and Acraeidae (this is still today the last complete monograph on this theme which includes all of Africa). The book also in detail deals with the edibility of the butterflies by birds and the question of whether and in what quantities they are hunted. Eltringham also published a monograph about the South American genus *Heliconius* (1916) and a number of other publications, where he also deals with chemical communication between butterflies, their sight and hearing, etc.

G. A. K. Marshall (1871-1960), a colonial office worker and specialist in applied entomology, published in 1902 with **E. B. Poulton** in the *Trans. Ent. Soc. Lond* (**Marshall & Poulton**, 1902) the results of 5 years of observation and experimentation on cryptic, aposematic, and mimetic insects in South Africa (1896-1901). Even though the work is basically a magazine article, it represents one of the largest monographs on mimetism that was ever published (almost 300 pages) with a massive collection of factographic material, both descriptional and experimental, which if unknown would seriously inhibit any earnest attempt at the study of mimetism and aposematism (the method of interpretation is always in accordance with Poulton's own, as Marshall was something like Poulton's „extended self" in the tropics - Poulton himself had only limited experience with the tropics and was usually tied down by his position at Oxford).

The work, which also contains short inserts of observations by other authors, includes amongst others experiments of offering aposematic, mimetic, and cryptic insects to various predators - mantids, lizards, frogs, birds (kestrels, hornbills, etc.), mammals (mongooses, baboons), offering aposematically colored birds to the mongoose, and human olfactory and taste impressions of insect aposematics. Other parts of the work concern the season-based dimorphism of the buckeye butterflies, *Precis,* and the differences in the formation of eye-spots in various seasons, further on the work deals with aposematic and mimetic butterflies and beetles (especially the family Lycidae) from South Africa, the imitation of various Hymenoptera by other insects, including for example by the mantisflies, family Mantispidae (Neuroptera) and lastly about the mutually convergent groups of bugs (Hemiptera) in the South African region. This incredible amount of information dealing with the problem of aposematism and mimicry was never outdone, especially not for this specific region. Marshall's study has not lost its value even today and is still astonishing in its extent. (see also **Marshall**, 1909). Similar studies, although in a smaller scope, and other observations of mimicry in butterflies from the South African region were made by **C. F. Swynnerton** (1919, see the *Bibliography* for more works) around the first half of the last century.

Poulton's favorite, his follower and successor **Geoffrey Douglas Hale Carpenter** (1882-1953), the son of a university professor from Oxford, himself studied medicine at Oxford and afterwards entered the Colonial Medical Service, where from 1910 he studied the African trypanosomiasis ("sleeping sickness") and its carriers (tsetse flies, *Glossina*) in Uganda. He regularly sent reports about African mimetic and aposematic insects to his fatherly friend Poulton, and later he specialized specifically in butterflies (Carpenter wrote 125 articles on mimicry in insects, see the *Bibliography*). He did not leave Africa even as an ambulatory officer during the First World War, when, on the other hand, his research on mimicry was dominant over all his other activities. After the war he continued his service in Uganda, which lasted until 1930. He wrote two books about his activities as a naturalist in eastern Africa (**Carpenter**, 1920, 1925) and of course many medical-entomological articles, which are not mentioned in the *Bibliography.* After 1930 he settled down in Oxford, where he was unanimously voted in to be Poulton's successor in 1933. He kept the directorship until 1948 and he continued publishing until his death in 1953. His successor **G. C. Varley** was concerned with different themes and so the continuity of the institute, which almost 60 years dealt practically exclusively with mimetic phenomena, ended. During WWII Carpenter, and his younger colleague **Cott** (who served in the British army in Egypt) were hired to advise and train British troops to correctly mask themselves and their vehicles, which included writing an instruction manual (**Cott**, 1938). Carpenter shared Poulton's views in all respects almost exactly and his book, written together with **E. B. Ford**, later a professor of genetics at Oxford, was published in 1933 to commemorate Poulton's retirement. The book itself is more or less a condensed version of Poulton's views that he did not have time to put into writing. The book is not very long (134 pages, from which Carpenter wrote 100), but is very informative and content-wise very full. Carpenter put into the book his many experiences as a field zoologist and his brilliant stylistic ability, even today the book has instructional value. Carpenter, unlike Poulton, completely rejects the idea of aggressive mimicry and considers all examples of it, especially the imitation of the host or prey by the parasite or predator, to be Batesian mimicry, as was stated before. Besides numerous examples, the most taken from East African insects, he also includes cases of mimicry in plants - the imitation of size and form of the seed of the flax plant by the seeds of the weed *Camelina linicola*, which evolved from the species *Camelina glabra* because of human intervention, that is the constant pressure of selection while cleaning the seeds and the surface (the plant suggests flax much more than the original species and even has an elongated shape and a more similar external appearance) - this is one of the few cases of mimicry which is evidently caused by mankind, who is at the same time the selective agent, and above all according to a well known criteria (mimicry in plants will be discussed in a separate chapter due to its different nature from animal mimicry).

Carpenter devotes much attention to nest parasitism of the cuckoo and the color and color pattern adaptations of its eggs, which make it similar to the host's eggs. In the twenties this problem became very popular (**Lucanus**, 1921, **Baker**, 1923, **Rensch**, 1924, **Jourdain**, 1925, **Poulton**, 1925b, **Berg**, 1926, **Punnett**, 1933, and others). The problem wasn't really in the adaptation in species which use only one host, but in species which have multiple hosts and adaptations of individual cuckoo clans, „*gentes*", to the color and pattern of „their" eggs, as is the case for example for our cuckoo *Cuculus canorus*. Even though nest parasitism by cuckoos has been known since **Aristotle's** time, dealing with this problem came only much later (see also **Wickler**, 1968). Because the „gentes" are not reproductionally isolated groups (of course, the cuckoo as a polyandric promiscuous bird doesn't even form pairs), it was later deduced that the genes which influence the coloration of the eggs have to be on the female heterochromosome (birds, which have the determination of sex of the type *Abraxas*, have heterogametic females, and not males, as is the case in mammals, including humans). In this way genes concerning the egg coloration are passed on from mother to daughter irrespective of the father, and so the individual „gentes" adjusted to particular host species, in whose nests they themselves grew up and where they will lay their eggs, and do not change (due to the immense difficulty of breeding captive cuckoos, this theory has yet to be verified, but it seems plausible). A curious alternative concept was proposed by Lysenko's biology, which bitterly fought the „reactionist Mendelian-Morganian concepts". The appearance of the eggs from which the cuckoo is born is, of course, the same in appearance as the „host's" eggs - because they are in fact the host's own eggs. But in years which have an abundance of furry caterpillars a part of the young of smaller songbirds transform into cuckoos, which are in a way derived from what bourgeois science called the „host" species. This hypothesis illustrates that the criterion of simplicity and elegance is not the only factor determining whether a theory is considered to be true or not.

The second part of the book, written by the geneticist **E. B. Ford**, follows in the footsteps of the tradition started by the Cambridge professor of genetics **Reginald C. Punnett** (1875-1967). In his book on Mendelism (**Punnett**, 1905) he mentions and in his later book „*Mimicry in butterflies*" (**Punnet**, 1915) fully develops another revolutionary change in the field of mimicry, which was its interconnectivity with the then very quickly developing field of classical genetics (earlier we mentioned the unusual ability of the study of mimetic phenomena to lock onto new and revolutionary concepts in biology). Because this theme was thoroughly analyzed by **Kimler** (1983) and **Turner** (1983) and the results of the genetic research of mimetic butterflies were compiled in a very lucid way by **Nijhout** (1991) and the fact that theme is generally very popular at the moment, this passage will only deal with it in brief and with many references to the *Bibliography* (the goal of this book is not to emphasize well known facts, but the opposite - facts which are overlooked). Classical Darwinism with its concept of a more or less continual all-sided variability came into a crisis after 1900 because of the development of classical genetics, because it became apparent that changes in the appearance of organisms are basically gradual. This in conjunction with **Weismann's** idea of the impenetrable barrier between somatoplasm and idioplasm (in today's terminology between the phenotype and the genotype) shook up the belief in heritability of acquired attributes and the direct influence of the environment on the organism (in 1933 **Carpenter** still felt the need to stand against the belief that the direct cause of mimicry lies in the influence of the environment - it can generally be said that the atmosphere between 1890 and 1930 was more than just neo-Lamarckian - most biologists believed in a mixture of classical Darwinism, neo-Lamarckism, and autonomistic thoughts represented for example by **Eimer's** orthogenesis). This caused a deep crisis for classical Darwinism and in its original form it was supported only by its most loyal followers, such as **E. B. Poulton**. Punnett, who was experienced mainly in the area of vertebrate genetics (hen, rabbits, guinea pigs, mice), on the basis of **Fryer's** experiments with breeding the mimetic polymorphic swallowtail *Papilio polytes* on Ceylon, came to the conclusion that mimetic forms of the butterfly come into existence through saltation, through great leaps, without going through the whole scale of intermediary forms from the original appearance to the highly mimetic form (in the *Papilio polytes* the individual mimetic forms of the female are segregated without any intermediary forms). Even though Punnett did not dismiss the notion of natural selection having an effect on the survival or extinction of mimetic forms (in any case he was not very convinced by the selective pressure of birds and other optically oriented predators), he definitely refused to accept that natural selection has any influence on gradual selection. In addition he was convinced that (like with small rodents) butterflies have similar forms or similar patterns due to identical genes. Therefore mimetic species are similar in their genotype and natural selection in the best case preserves the appearance of mimetics, which have mutated from „internal reasons“ into the same genetic and external form as their „model“ (this concept is quite similar to concepts put forward by **Eimer, Heikertinger**, and other German authors, who considered the mimicry phenomenon only as randomly overlapping stages of the transformation series of patterns). Punnett therefore moved the general attention to „internal“ factors, which influence the formation of mimetic similarities, for which he was criticized by Poulton (**Poulton**, 1916) in the journal *Nature* (Poulton, of course, maintained support for „external“ factors, in the form of selection, but certainly not Lamarckian environmental influences). Poulton's criticism of Punnett's work (besides the attack on Poulton's beloved classical Darwinism, the rivalry between Oxford and Cambridge could have also played a role) also included numerous allusions to various mistakes in the text and the incorrect determination of certain species illustrated in the color tables. Poulton especially referred to cases of mimicry between various insect orders and even between animals and plants, where an explanation based on genetic similarities is more than absurd. In spite of this unfavorable welcome, Punnett's work marked the beginning of a new era in the history of the research of mimetic phenomena, whose boom and development continues even now. In 1927 an extensive work by the Australian agricultural entomologist **A. J. Nicholson** who during his study at Cambridge was also Punnett's student, was published (**Nicholson**, 1927). Nicholson connected the findings of the genetics of gradual mutations with the theory of natural selection (He considered mutations to be caused by environmental influences and he used the studies by **J. W. H. Harrison** /e.g. **Harrison**, 1919, 1920, 1926, 1927, **Harrison & Garrett**, 1926/, who wrote about hereditary melanism being caused in this way. Works on this theme were very popular up to the thirties even in respected journals - the German author **Prochnow** (1927) summarized quite many - and the whole phenomenon shines a light on the interesting influence that the „social atmosphere“ has on the nature articles accepted by the scientific community - according to later doctrines a direct influence of the environment on the genotype does not exist and cannot exist, while during the twenties, when the general atmosphere was inclined to believe these opinions, these works made up an integral part of the truth of scientific journals and textbooks - editorial staff and later agencies which control research represent something like an internal court, which decides in secret what is and what isn't true). More in-depth research of these sources would probably bring much new information - if not about the nature of heredity, than at least about the nature of the scientific community.

According to Nicholson's concept, natural selection works with mutation, with small ones and the large ones alike. Large mutations are necessary to bridge the gap between the dissimilar mimic and the model (at least roughly), small mutations then „fine-tune“ the similarity. This concept (of course without the external cause of the mutation) basically hasn't changed - even **Turner** (1984) explains the evolution of Batesian and Müllerian mimicry as the result of one mutation with a large effect and then successive small, gradual mutations which fine-tune the mimetism - in Müllerian mimicry it is a convergence of both species, in Batesian mimicry it is the process by which the mimic gets closer to the model, whose goal is (it is threatened by the great number of edible mimics) to evolve as divergently from the mimic as possible (this last solution was proposed already in 1930 by **Fisher**). Even though the first breeding of and observation of the genetics of mimetic butterflies took place shortly after the turn of the century - *Hypolimnas misippus* (**Leigh**, **Rogers**), *Hypolimnas dubia* (**Lamborn**), *Papilio polytes* (**Fryer**), *Papilio dardanus* (**Lamborn, Carpenter, Swynnerton, Poulton**, those interested in precise details should look in the *Bibliography*), systematic interest in the genetics of mimetic butterflies came only with Oxford's population geneticist **E. B. Ford** (**Carpernter & Ford**, 1933, **Ford**, 1936, 1964, 1965, 1976, and many other works and books which are listed in the *Bibliography*), who maintained the continuity of interest in mimetic phenomena and their genetic background even during the fifties, when the older between-war generation died out and the field seemed to fall into disinterest and forgetfulness. Besides Ford, Cambridge's geneticist and evolutionary theoretician **R. A. Fisher** /1890-1962/ (**Fisher**, 1927, 1930) was also very interested in genetic-statistic matters concerning mimicry. The theme of mimicry and aposematism also did not pass by two other important biologists from Oxford - **J. B. S. Haldane** (1932) and **J. S. Huxley** (1938a, 1945) who was mainly concerned with the theory of sexual selection (1938b). **Provine** (1971) was very interested in the history of the rise of population genetics in the period between the wars. After WWII the medical geneticist **C. A. Clarke** and Ford's student from Oxford **P. M. Sheppard** studied at Liverpool the genetics of the mimetic swallowtails, Papilionidae, especially the *Papilio dardanus*, but also the *Papilio polytes* and *Papilio memnon* (occasionally the genetics of the genus *Heliconius* as well). They wrote quite many works, often together, from the fifties to the seventies - for a full list see the *Bibliography*. Especially the species *Papilio dardanus* was studied in great detail, the number of publications concerning it certainly is the highest of any mimetic species (this was caused by its relatively easy reproduction in England, including the possibility of feeding the larvae on the evergreen shrub, Mexican orange blossom, *Choisya ternata* from the family Rutaceae, which is often planted in parks). Just like in all other mimetic polymorphic species of the swallowtail genus *Papilio*, the basic mimetic appearance is governed by a single locus with a larger number of alleles, which are then in particular population supplemented by modificator genes for the precise „adjustment“ of the patterns in view of the model species. It is interesting that from the standpoint of the analysis of the origin of the color patterns, the mimetic color patterns of these species represent the archaic state close to some of their relatives, while the non-mimetic color patterns on the males (or even the females of the non-mimetic subspecies *P. d. meriones* from Madagascar) represent a much later and derived state - the mimetic patterns therefore represent something like an atavism (**Nijhout**, 1991). Research of the genetics of South American butterflies of the genus *Heliconius*, especially the duo of Müllerian mimics *Heliconius melpomene* and *H. erato*, was the theme of many works by **J. R. G. Turner**, a student of P. M. Sheppard from Liverpool, who later worked at the university in Leads (for the list of publications see the *Bibliography*). The relations in the genus *Heliconius* are considerably more complex than in the genus *Papilio*, the mimetic patterns are controlled by a large number of genes, but at least in species which form Müllerian duos or trios these appear to be the same, as once **Punnett** presumed, considering the close relation within the one genus. The species *Heliconius melpomene* and *H. erato* are made up of about twenty geographical races in the extensive area of the northern part of South America and the Amazonian basin, all of which are quite different in external appearance, but both species always appear the same in any given locality, which is one of the most amazing phenomena concerning mimicry in existence. Turner solves the problem of these „local fashions“ by assuming that during the last ice age, about 20 000 years ago, the Amazonian rainforest was fragmented into a number of “forest islands“ and during this isolation these Müllerian duos were formed, and then managed to survive even after the re-connection of the forest islands and the merging of the originally fragmented habitat. Further studies on the genetics of the genus *Heliconius* were carried out by **L. E. Gilbert** (1983), the genetics of mimics and the role of supergenes in their evolution was studied by **Charlesworth & Charlesworth**, 1975, and others (these last authors come from the USA). An important work in the field of the genetics of the aposematic and mimetic burnets, *Zygaena* (especially the species *Zygaena ephialtes*) was also conducted in the Czech lands (**Povolný & Gregor**, 1946, **Povolný & Pijáček**, 1949), other works by this author (**Povolný & Weyda**, 1981) dealt with other aspects of the defensive strategy of members of the genus *Zygaena*.

Considering that the genetics of mimetic butterflies is an especially difficult problem, which can be only lightly outlined here without the complicating particularities, it is necessary to lead the interested reader to original works or at least decent summaries (**Nijhout**, 1991, or even **Wickler**, 1968). The British school, mainly thanks to **Ford**, retained continual interest in mimetic phenomena even after the war. From the British scientists, who dwelt upon this problem, it is necessary to mention **D.F. Owen** (e.g. **Owen**, 1980) and **S. A. Smith**, who concentrated on the population genetics of African mimetic and aposematic butterflies (especially the lesser monarch or “plain tiger”, *Danaus chrysippus*). Further the baroness **M. Rothschild** was justly very popular due to her original concepts and systematic study of toxicology of various aposematic insects. Also see **M. Edmunds**, who studied various African mimetics, **J. R. Vane-Wright**, who studied the taxonomy of various mimetic species, **T. Guilford**, who worked on the theory of the genetics of mimicry, and many others (numerous works from these authors can be found in the *Bibliography*). After WWII the well known ethologist and later bearer of the Nobel prize, **Nicolaas Tinbergen** (1907-1991), who through his study of the epigamic behavior of butterflies and of the meaning of eye-spots on the wings of various species in Holland was actually quite close to the research of mimetic phenomena, also worked at Oxford. From his many students, for example **Lincoln P. Brower**, and his wife **Jane Van Zandt Brower** (who stayed at Oxford for two years from 1957 to 1958) established themselves at the university in Amherst (Massachusetts), where they founded a separate American school for the research of mimetic phenomena (their numerous works are also included in the *Bibliography*) and their students established themselves in many universities across the whole United States /The initial point which started the „new era“ of research of mimicry can be said to have been the seminar at the 16th International Zoological Congress in 1963 (**E. B. Ford, Ch. Remington, P. M. Sheppard, J. V. Z. Brower, L. P. Brower, G. Bernardi, C. S. Holling, D. Magnus**)/. The American influence was from the sixties to the nineties, not only because of the rich financial grants for their studies, the strongest in the world of mimicry research /This is definitely not a coincidence, but was caused by the decline of prestige of Germany after WWII (and in a more gradual manner England as well) and the rise of the USA (which culminated between the sixties and the eighties), which had to affect the field of research of mimicry as well/.

Research and interpretation of mimetic phenomena and external appearance of organisms on the Continent

Besides the mentioned works by **A. Seitz** and **A. Weismann** only a few works concerning the external appearance of organisms appeared before the nineties of the 19th century (the early works of **Th. Eimer** will be mentioned later). Such studies were considered to be inexact, and in comparison with the study of embryology or microscopic anatomy, not fitting for a university environment, which dominated over the German scientific community. For this reason it was the museum community which published the first two books to ever appear concerning exclusively mimetic phenomena. Both authors, unlike many university scientists, continued directly in the English tradition of the study of mimicry and both accepted as their own all the English interpretations in the classical Darwinian style, so that in thought they resembled Poulton.

The main book is *Untersuchungen über die Mimikry auf Grundlage eines natürlicher System der Papilioniden* (1893) by **Erich Haase** and especially the second part of the book, *Untersuchungen über die Mimikry*, which includes 161 pages and 14 color tables. Haase was a graduate and later assistant at the university in Königsberg and in 1892 he was chosen as the curator of the King's natural museum in Bangkok (Siam, today Thailand), which was being founded at the time. For the curious zoologist with an interest in mimetic phenomena in nature the chance of direct experience with field work in the tropics was impossible to refuse, but because of the severance from libraries and other sources of information from Europe, he only finished his book and gave it to the publisher with the last of his strength. Tropical sicknesses suddenly destroyed Haase's health and caused his death at an untimely age. The book itself, the first ever on mimicry, concentrates mainly on examples of butterflies and descriptions of their particular cases, other insects are only briefly mentioned and there are no mentions of all the other groups of organisms. Nevertheless the book has not lost its value even today, because certain cases concerning mimetic similarities described by Haase have not since his time been mentioned or depicted.

The director of the zoological museum in Dresden **Arnold Jacobi**, originally from a Russian German-Jewish family and later resident of Saxony, published in 1913 a book with the title *Mimikry und verwandte Erscheinungen*, which on one hand is only a perfect literary compilation of this theme from world literature, but on the other hand it offers 215 pages with many pictures and an excellent and logically perfect clarification of crypsis, aposematism, and mimicry in the animal kingdom (with the maximum amount of examples pertaining to classes of insects, especially butterflies, as can be expected from the theme, but the work also includes examples of vertebrates, spiders, and certain other invertebrates). The book still today, in spite of its understandable outmodedness, is in certain aspects very instructive, it contains almost the whole scale of mimetic phenomena and is a prime example of the depth and scientific seriousness even in compilations. For serious students of mimicry this is a fundamental book. An extensive summary of the ecological and ethological aspects of mimicry was written by **Handlirsch** (1927) as well.

A special trait of the „German" biological school was the extensive study of that which connects the functional aspect of the external appearance of organisms and their ontogenesis and phylogenesis - animal color patterns. A color pattern (*Zeichnung*) is that which either in color or more rarely in structure differs from the rest of the organisms' exterior, which forms a certain ornament and is capable of carrying some meaning, as for example **Darwin** or **Wallace** defined it. The term color pattern is occasionally in less precise works mistook for the term coloration (*Färbung*), but the latter generally describes the overall optical impression with emphasis on the color aspect of the whole organism, while the color pattern denotes the whole structure and configuration of this design. Animal designs basically follow the same rules as three-dimensional morphological structures, for example a skeleton, but because of their apparent flatness (two dimensional) and their *de facto* dispensability for the basic function of the organism, they have a much broader range of freedom in their „self-creation" than structures which are more „responsible" (*Bürde* in the sense of **Riedl**, 1975) for vital functions (an interesting „precursor" to these thoughts is **Froschammer's** book /1877/ about fantasy as a principle of world processes).

Color patterns can be analyzed basically from four different aspects. The first considers the practical, so-called eco-ethological function in the life of the organism, a view which was adopted mainly by English biology and which was discussed enough earlier. The second aspect concerns their creation during the ontogenesis of the organism, a theme which we will touch on only lightly. The third is the phylogenetic viewpoint, which studies the evolution and changes of these patterns during phylogenesis of the given group (considering the fact that fossils very rarely conserve their patterns, these debates always consist of comparisons and extrapolations on the basis of recent material; because **Haeckel's** law of ontogenesis as being a shortened phylogenesis is in the best case a poetic metaphor, it is impossible to meaningfully transfer finds from one branch of study to another - oppositely, in those cases where the ontogenesis and phylogenesis of a certain color pattern are known at least to an extent, the path leading to the pattern formation is always different - this is often the case for the ontogenesis of relatively similar patterns of closely related species as well, which often go through a very distinct developmental line). The last aspect from which we can analyze color patterns is through formal analysis, which does not take into consideration the history of the individual or the species, but only the present condition (This view is similar to **de Saussure's** structural analysis of language. With a certain amount of poetic license we could assign each of these aspects to the corresponding aspects of linguistics. The functional aspect would be analogous to the complete meaning of the finished sentence, the ontogenetic aspect would be the phonetic mechanism used in its creation, the phylogenetic would be the history of the roots of the words and grammatical forms in the sentence, and the formal aspect would be the structural analysis of the sentence.).

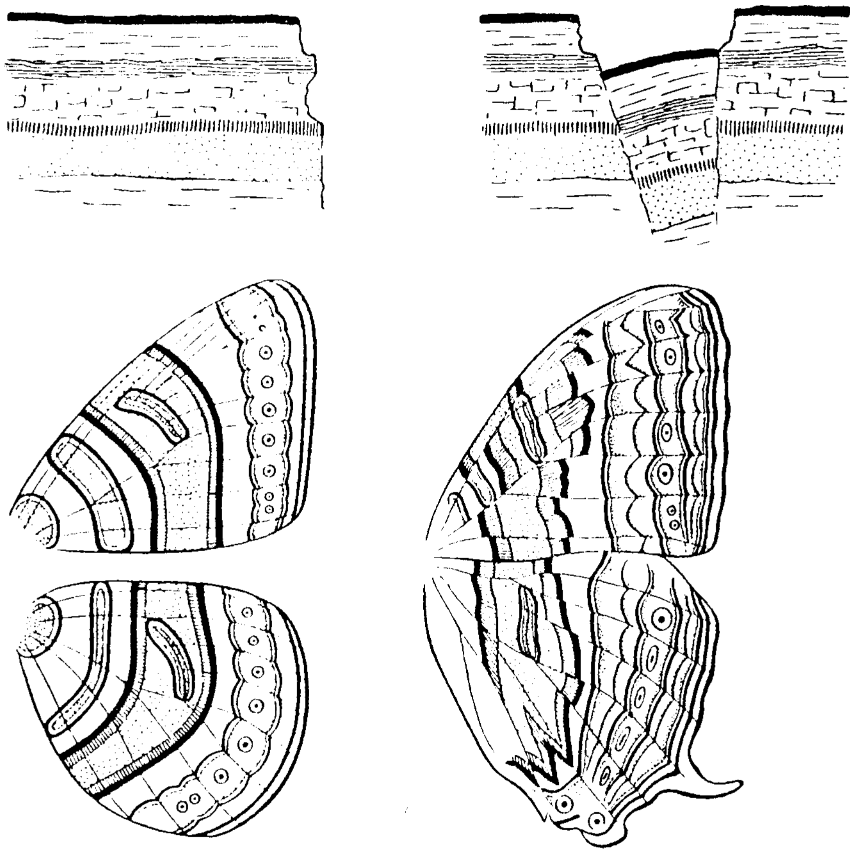
Eimer and the problem of animal color patterns

We can say that the father of the research of animal color patterns was the Tübingen professor of zoology **G. H. Theodor Eimer** (1843-1898), in his youth a coworker of **August Weismann** (1834-1914), professor of biology in Freiburg, with whom he parted later in anger. Eimer started his career with the study of the color pattern on the wall lizard, *Lacerta muralis*, which occurs on various Mediterranean islands (**Eimer**, 1874, 1881, 1882). He came to the conclusion that all existing types of color patterns can be ordered into one succession, which at the same time reflects the phylogenesis, in which the various individuals and various populations stayed put each time on a different level of this transformation (similar evolutionary lines can be reconstructed quite often, especially in the case of butterfly and snake color patterns - their linear development or uncommon branching are more or less unproblematic issues, but not so the meanings of their color patterns - which pattern is more archaic and which is more developed can be determined only rarely and most often it is more the subject of discussion than the fact of a continual and more or less gradual succession). Natural selection then maximally favors some type of color pattern and its concrete coloration, but it plays no part in this pattern's evolution. Later Eimer applied himself to the study of color patterns of mammal furs (**Eimer**, 1883, 1885, 1887, 1888b) and eventually he moved his attention to butterflies, a group which more than any other provides an innumerable amount of color patterns on its members' wings (**Eimer**, 1888a, 1889, 1895a, 1895b, 1897). Especially his last book, which has over 500 pages and which is Eimer's *opus magnum*, published only one year before his untimely death (for his biography see **Kluzinger**, 1899), his opinions about the nature of animal color patterns and mainly those of butterflies are formulated in detail. These opinions show a remarkable anticipation in this field, even though the individual deductions are for the most part incorrect. Eimer considered himself to be the legitimate heir and successor of **Darwin's** intellectual tradition, which was desecrated, ruined, and twisted by Weismann (Eimer's very strong expression, often used in the book, „*Weismannscher Afterdarwinismus*", nicely illustrates the tone of the discussion between German thinker, and has an /for us/ unimaginable vehemence - this pertained to other fields as well - **Marx's** and **Engels'** discussions are also evident examples of this style). The immovable conviction that there is only one truth and that truth is the one the author of the discussion believes in was mixed with personal touchiness, hurt vanity, the waging of a „holy war", the desire to destroy with an argument, and the unreflected projection of the „Jungian shadow" onto the opponent, who is severely despised. Eimer's works are a nice example of the world of emotions, which later served as fertile ground for the blind fury and wild spite of nazism and bolshevism. It is very symptomatic that in particular Weismann's opinions were in everything except for some details the closest to Eimer's own opinions at that time. Weismann's concept of germinal selection (*Germinalselektion*), which closely resembled Eimer's own concept of **orthogenesis** (*Orthogenesis*) was especially irritating for him. Eimer, unlike **Darwin**, refused all-sided variability in living nature, from which natural selection then chooses the best alternative, but believed that variability in a certain sense is always channeled in the dominant direction, without the assistance of natural selection (**Weismann** was convinced of basically the same thing, but so as to follow Darwin's principle of natural selection, he moved the channeling onto the zygotic level, where individual abilities, „*Determinanten*", compete between themselves on the basis of usefulness). Eimer even refused principle of functionality in the external design of organisms and in their structure, except for that small amount forced in by natural selection, which roughly disposes of individuals wholly incapable of living due to their excesses. Surprisingly Eimer's concept did not rely on the idea of „inner causes" (*innere Ursachen, innere Bildungsgesetze*) or on the principle of self-improvement (*Vervollkommnungsprinzip*) during the evolution of the organism, independent of external influences (he resented **Nägeli's** use of these principles and he associated them with **Lamarck** as well). Eimer imagined changes in organisms, independent of natural selection, as a direct consequence of external influences, especially temperature, humidity, sunshine, and available food, and not as a result of some inner direction. Generally speaking he did not see any difference between the inorganic and organic worlds and he imagined the development of organisms to be akin to crystallization, only a few orders higher up than the growth of lets say salt crystals (the idea of Weismann's barrier, which doesn't allow traits acquired from external influences to be passed down angered Eimer, as his relation with Weismann has numerous marks of negative limitations and a broken „scientific love affair"). Besides these (so to say) vulgarly physicalistic ideas, Eimer's work has another level to it, which directly builds upon **J. W. von Goethe's** work, whose quotes are used as introductions to each chapter in Eimer's last book. The whole book is infused with an untiring attempt at classifying and categorizing everything which can be, followed by an attempt at strictly differentiating between „higher" and „lower" in every imaginable context (besides the context of German at that time this is strongly reminiscent of the learned writings of old India - the question of whether this is the beginning of the radical „aryanization" of thought or some form of late cultural memory of our collectively Indo-European heritage must be left unanswered). The wide expanse dedicated to the „elements" is also interesting - the sun, warmth and cold, humidity and dryness, the earth and the plants which grow in it in their specific places, etc. directly influence, according to Eimer, the appearance of organisms, in this case butterflies (Eimer cites **Standfuss'** information on the change in color of butterflies of the same genus /*Colias,* yellow/ from the North to the South – the moorland clouded yellow, *C. palaeno lapponica* from Northern Scandinavia is the most pale, *C. regia* from Turkmenistan the most vividly colored /like fire/ - Eimer confidently attributes this to exposure to the Sun).

Eimer was the first to notice that wing color patterns of butterflies can be mutually homologized in the same way as any other morphologic structure and its derivatives, like the branchial apparatus of vertebrates or the mouth apparatus of arthropods /Not even this theory is completely original, because **Rössler** (1861) already noted that the wing color patterns of butterflies and moths represent variations on an archetype best seen in the family Noctuidae, and who also in the framework of the natural philosophy legacy categorized the tripartite wing patterns into outside, middle, and inside zones in accordance with the tripartite body sectioning of insects. He also noticed that certain color patterns copy morphological structures, others are independent of them, some „*in Richtung des idealisch schönen*" (*Habrosyne derasa, Geometra undulata*). Unfortunately Rössler does not expand on this thought and Eimer probably did not even know his work, in any case it was him who inferred the practical consequences of mutually homologous butterfly color patterns/. Individual components of the „archetypal" color pattern are made up of „material", from which the specific pattern is then created. Eimer believed that the original color pattern is made up of eleven crossed bands, which is preserved in certain Papilionidae, such as the Chinese yellow swallowtail, *Papilio xuthus*, and he decided correctly to homologize all other butterfly and moth color patterns with them (these deductions in their particularities turned out to be mostly false). These metamorphoses of color patterns, which according to Eimer occur without influence from natural or sexual selection or any kind of „functional" impulse, obey a relatively simple set of rules, which can easily be discovered, making it possible to order all individual color patterns into an evolutionary chart. The common occurrence of similar color patterns on non-related species is explained as independent evolution which happens to be on the same level, but in a different transformation line (*Homoeogenesis*). Eimer describes a number of transformations which pertain to butterfly wings and beetle elytra, which were confirmed in their particularities by later authors: the disintegration of bands into bands of spots, the transformation of longitudinal bands which intercept spotted lines into transversal stripes and vice versa, the reduction and even disappearance of individual stripes or spots, etc. On the whole Eimer believed that transformations can occur both ways, even if there is only one dominant direction - in butterflies the transformation went from the original 11 bands to the usual only single color black wing (many Papilionidae), or the one-colored white wing (many Pieridae). Mimetic butterflies are therefore for Eimer only members of a certain transformation level, which coincidentally find themselves on the same or at least similar level, independent on any type of selection by predators and of course independent of geographical distribution (for this reason butterflies belonging to different families and which are far removed from each other, but nonetheless have a very similar appearance, do not constitute a problem for Eimer). He strictly and negatively stood against **Bates'** theory of mimicry, in the same way he was against any theory which interpreted butterfly wing color patterns in the sense of adaptations. He also considered the „leaf" butterflies, for example the "dead leaf butterfly", *Kallima*, to be the product of a transformation of color pattern without any relation to predators or a functional imitation of a dry leaf. He sharply noted (even though his particular search of color pattern homology was misleading) that the leaf appearance of this genus and of others is built up from various parts of the basic pattern, which are cunningly set up to form a „middle rib" and side veins of the leaf. He also noticed that a large number of butterfly color patterns are evidently „on the way" to becoming various other types of pattern, which so far is only lightly hinted at, or on the other hand the pattern is strongly reduced and is slowly disappearing. Particularly leaf butterflies served him as the best argument against the adaptivity of the external appearance - certain color patterns were so weak that they could hardly fool a predator, other patterns were in the destructive phase, whereby the color pattern was receding and disappearing, with absolute disregard for the alleged usefulness for the butterfly. Surprisingly Eimer considered the main path of the transformations of the color patterns to go from the very complicated to the very simple and he also observed cases, where for example the mimetic female of the swallowtail *Papilio dardanus* represents an archaism in comparison to the simple yellow-black male. The white coloration of the top side of males of the mimetic genus *Perrhybris* (Pieridae), or even the hidden white spot at the inner portion of the hind-wings of males of the genus *Dysmorphia* from the same family, were all commented by **Darwin** as being the remnants of the original color pattern which has been preserved by the conservative taste of the females when choosing mates. Eimer sees these transformations as the result of moving to more „advanced" stages in evolution, in other words the one-colored pattern in the males is generally more advanced and carries progressive marks (*männliche Präponderanz*). Generally speaking Eimer's opinions on the sequence of colors during the transformations of the color pattern are also very interesting. It is a general archetypal notion that dull colors precede vivid ones. Eimer even agreed with **Darwin** in this matter, who also saw inconspicuous cryptic coloration as the original color and vivid and bright colors as being advanced and derived. But here the analogy ends - while Darwin, faithful to his linear view of progress, considered the most vivid organisms to be the most evolved (caused by sexual selection), Eimer saw the transformational order as being circular but closed by white and black, which are at both ends of the circle (even though in this initial state gray would fit better next to white). And so the whole cycle ends by returning to the „higher" state, from which the organism originally came, thereby going through all the stages of vivid transformation much in the way of **Anaximander's** sentence that that which is the creator of a thing is that thing's destroyer as well. Mythology concerning cyclic processes (which is a very fundamental theme) appears in Eimer's work in many various levels, another example is for instance the same coloration of the upper and under sides of wings in very archaic and very advanced forms, intermediate forms have a coloration configuration which follows precise rules and where both side are colored differently, and at the same time in the framework of the mythological anisotropy of space the forewings are considered to be more advanced than the hind-wings, and the upperside is more advanced than the underside (it would be interesting to analyze Eimer's work to determine if mythological themes worked their way into biology - it doesn't seem coincidental that fundamental mythological concepts appeared in Eimer's work in seemingly absurd contexts at the same time as similar concepts were voiced by his philosophically educated contemporary **Nietzsche**). Eimer's color sequences in a simplified version are as follows: white, gray, ochre, brown, red-brown, and black (the situation is much more complicated and much less evident than it seems, certain sequences also end in white). The theme of color sequences in butterflies was later also studied by **Piepers**, 1898, 1899, **Reuss**, 1918, **Tshirvinskij**, 1925, and **Giersberg**, 1929. /In this context it might be interesting to mention color sequences in **Hingston's** (1933) work as well, which he defined as following the natural sequence green-yellow-red, where green is the color of crypsis and represents fear, red is color of aggression and anger, and yellow is the intermediary between the other two (this intermediary also works from the wavelength standpoint). Even though Hingston does not call attention to it, this is the color sequence used later for most traffic signals, where green represents peace and freedom and red represents danger and caution - similar themes are analyzed by **Lévi-Strauss**. In more recent times, the Leiden thinker **Lucas H. Peterich** (1972, 1973) has written about the theme of colors in nature. His two articles are quite extraordinary and literally filled with very detailed observations about this theme, which cannot be reproduced here in full and nothing remains but to urge the reader to peruse the originals, which are supplemented with extensive color tables. Peterich's works are the result of many years of tiring comparisons of various color combinations, especially in butterflies, birds, and the flowers of higher plants. As was stated in the introduction, Peterich came to the conclusion that the „solid" warm spectral colors (red to yellow to neutral green) and cold colors (blue-green to blue and violet) are always separated from each other on the body by one of either black, gray, brown, or neutral green, and in rare cases white (this zone can be very thin). To a lesser extent this applies to fractal or weakened shades of these colors as well, for the bright spectrum colors it is always like this though. And the color model or pattern is never made up of more than one „solid" color, but usually only „half-colors" (By this term he means various shades of ochre, various degrees of woody and earthy browns, etc.). Black and white patterns are much less common and patterns with one of the „solid" colors and black, even less often with white, and least of all the combination of two „solid" colors, which are in every case separated by a neutral, usually black one. The affinity between „solid" colors and black or other close colors (dark brown, very dark purple) is interesting in any case - this effect was names the „jeweler effect" by **Portmann** in 1960, (because a jeweler always displays a bright gem on a dark background) who always proclaimed the many uses of this contrasting-esthetic principle in the living world. Peterich understood these principles as immanent for nature regardless of the concrete ability of an animal or even a human to differentiate between various colors. In reality, colors are mostly arranged in this way and not in any other, from which he concludes that the optimal manifestation of color is based on the principle of contrast (light /color/ x darkness /black or close color/). The term optimal manifestation does not mean in this case the biological function of colors - the optimal manifestation is „functionless", it just is. The opposite combination, a „solid" color on a white background, practically does not occur, and when it rarely does then it is usually weakened in shade in some way or framed in black. Peterich emphasizes that even color combinations which do not occur in nature would serve well as warning coloration or for intraspecific or interspecific communication (many color combinations are used in state flags for example), even so they do not appear in nature. Peterich's work is completely original in his specialization in modern biology and is worth to look. Similar transformational sequences, like those Eimer was looking for in butterflies, were developed for flowers by **A. de Candolle** (in **Rádl**, 1908): xanthic (white, yellow, orange, red) and cyanic (white, light blue, blue, purple). **I**nteresting is the fact, that no plant genus, whether in the garden or in the wild, is able to produce all usual flower colors, even though many display quite a variety - the „stumbing block" is either in the color blue (rose, dahlia, chrysanthemum) or in a strong orange (iris). Numerous works deal with the influence of colors on humans, a more biological one is for example **I. Eibl-Eibesfeldt's** work (1984). It is interesting to note his information that a „warm" color activates on an experimentally verified level the autonomous nerve system and increases blood pressure and pulse. Rooms painted in these colors are felt to be 3-4° warmer by experiment subjects than rooms painted in „cold" colors, even though the rooms have the same objective temperature. The color red is a favorite among children and uncultivated adults and at the same time (as the color of blood) is in some situations felt to be disturbing and frightening. Red-black color combinations and their effects were discussed in connection with aposematic coloration.

Eimer's work was slowly forgotten (not even **Nijhout**, 1991, mentions him), even though the whole field of research of animal color patterns is based on his teachings (with one notable exception - **Dixey** from England, who was „convergent" with Eimer in some aspects). Eimer is at most mentioned in connection with the term orthogenesis (like **Steinmann**, 1908), which later authors usually imagine to mean direct evolution without selection, which is based on some internal causes. Eimer represents in a certain sense German biology well, which characteristically understands the complexity and mutual interconnectivity of the biotic world, which therefore is difficult to squeeze into one explicit theory. Such a science is too complex to be easily and without problems spread and be understood by the „uninitiated" (the system of German universities with its network of more or less unbound professors, who for years „initiated" their assistants and created rival schools of thought, where science stood alongside a family and sometimes even religious cult-like atmosphere, played a large part in this opinion) Eimer's opinions later gave birth to the "**German Autonomistic School"** of biology (**Süffert, Henke, Švanvič, Portmann**), even though it followed and amplified only a part of his legacy, without the simplified physicalism and unconscious infiltration of archetypal myths. Eimer's work deserves a detailed analysis, not only because of his often brilliant biological insights and intuition, but also for the psychological aspect of the book, which shows how myths reemerged in middle-class reality in the eighties and nineties of the 19th century.

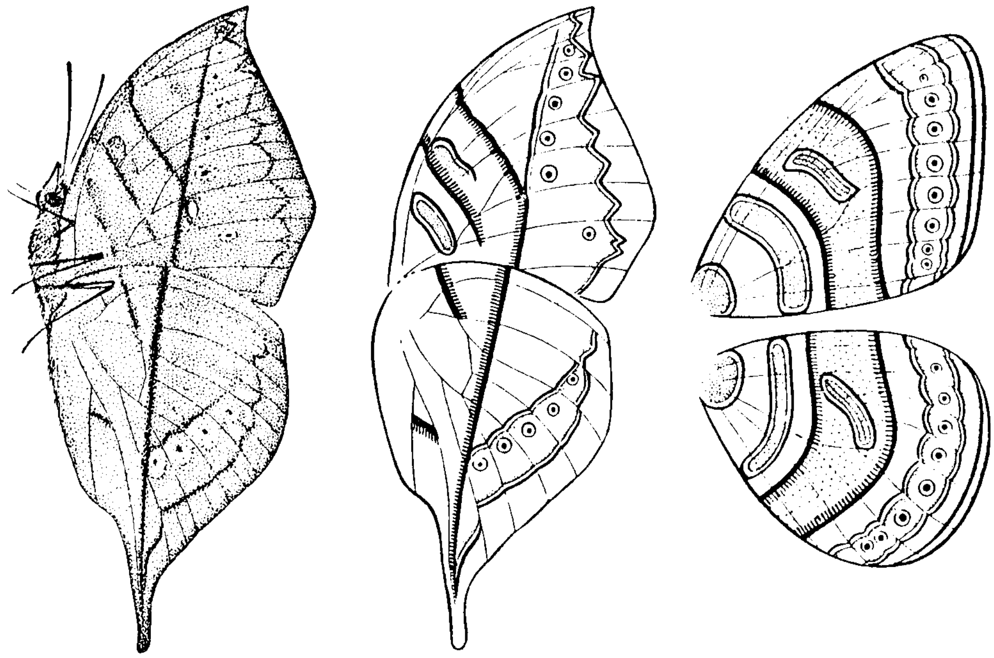
Research on color patterns on butterfly wings continued mainly in the work of Eimer's student, the baroness **Marie von Linden** (1898, 1901, 1902a, b, c, d, 1906) (due to the absence of mention in the *Bibliography*, all works on butterfly and other color patterns are given here in full). Around the turn of the century a few other authors were interested in this theme, mainly **A. R. Grote**, 1888 in Canada**, J. F. van Bemmelen** (1889, 1912, 1916a, b, 1917, 1918, 1919, 1921), **J. C. H. De Meijere** (1915, 1918) and **J. Botke** (1916a, b) in Holland, **A. G. Mayer** (1896, 1897, 1902) in the United States and **K. Fickert** (1889) and **F. A. Gebhardt** (1912) in Germany. The last mentioned compared the rhythmic distributions of pigments on the wings of certain butterflies (*Caligo, Brahmaea*) to the so-called Liesegangian figures in colloidal solutions and speculated on whether they could not be formed in the same way. **K. von Frisch** (1958) later returned to this thought. This type of fine wave pattern, called „*Reiselung*" (fogging) by Eimer and „ripple pattern" by **Nijhout** (1991), forms the basis or background of many butterfly color patterns, later **Süffert** (1929) included it into the category „*rhytmiche Flügelmusterung*" as an archaic type, independent of the morphological situation of the wings and of the anatomy of the butterfly. **J. F. van Bemmelen**, a professor of zoology in Groningen, pursued the study of comparative morphology of the color patterns of mimetic butterflies (**Bemmelen**, 1917) and came to the conclusion that in species with sexual dimorphism, especially the swallowtail *Papilio dardanus*, the males represent an evolutionarily advanced form, while the females represent an atavistic form, which is maintained only because of the advantages of mimetic similarity it brings (only a small number of authors, such as **E. Study**, 1919, 1930, considered the female to be more progressive). Up to the beginnings of the nineties the amount of information on the forms of butterfly color patterns was quite abundant, but their mutual homologization was still quite difficult, especially between various families. The worst problems were caused by the movement of the color pattern over the wing surface, which **Eimer** ascribed to differences in the growth of the wing (this explanation is more or less misguiding). The studies **by B. N. Švanvič, Fritz Süffert** (1891-1945), and **Karl Henke** (1895-1956) gave birth to a new phase concerning the understanding of butterfly and animal patterns. **B. N. Švanvič** (also **Schwanwitsch**, 1923-1956, 31 works cited) worked from the twenties to the sixties of the 20th century at the zoological institute in St. Petersburg (later Leningrad) and in spite of all the political problems of the time, he spent the greater part of his life researching the comparative morphology of wing color patterns in butterflies. At the start of the twenties together with Süffert he completely independently worked out the concept of a „basic plan" (**Schwanwitsch**, 1926) of wing color patterns for the family Nymphalidae. His completely revolutionary works in this field were left more or less unnoticed and under-appreciated in his own workplace (it is highly ironic that this man, one of the most important Russian biologists ever, gleaned more fame from the fact that his grandfather served **Puškin** as a model for the character of the captain in the novel „*The Captains Daughter*", than from his own scientific achievements), which only got worse after the increasing difficulties associated with publishing abroad from the forties onward. **F. Süffert**, who later became the professor of zoology in Freiburg i. Br., concentrated on the research of comparative morphology in butterfly color patterns for almost the whole 1920s (**Süffert**, 1924, 1925, 1927, 1929, 1937) and later also questions concerning aposematism (**Süffert**, 1935, this work mainly summarizes the results of research by **F. M. Jones** - 1932, 1934, which mainly consisted of offering variously colored insects to wild birds), and lastly he published an extensive and perfectly detailed study about the visual adaptations of butterfly caterpillars and larvae (**Süffert**, 1932). Coincidentally his research continued more or less in parallel with the disregarded research of his Russian colleague. Süffert died, symbolically closing the last chapter of German „autonomistic" biology, as a soldier in the national guard during an air raid on Berlin in 1945. **Karl Henke** was a professor of zoology at the university in Göttingen (for a short while he also worked in Berlin - Dahlem) and from the twenties he was concerned (**Henke**, 1924-1943, 10 works cited) with the study of not only butterfly color patterns (mainly the families Saturniidae, Geometridae, and Noctuidae), but color patterns of other insects as well (e.g. the fire bugs, *Pyrrhocoris apterus*), and also reptile, amphibian, and mammal skin and fur color patterns (felids, giraffes, etc.). Henke worked and published for the entire duration of the war, but afterwards he abandoned this study and devoted himself to classical developmental biology. In comparison to Süffert, Henke was a much



Bottom left an abstract depiction of the basic plan of the wing color pattern of the family Nymphalidae, bottom right the somewhat extreme concrete design of the genus *Cyrestes*, which is a phenomenon not too different from geological movements according to fault lines (above)- „Verwerfung“ (according to Süffert).

more productive author, but he lacked Süffert's ability to write coherent, understandable, and „panoramic“ formulations. In spite of a number of very interesting publications on the theme of the origin and evolution of color patterns, Henke is no longer cited quite so often, which is especially due to the fact that in his person „German biology“ reached its apex. In his attempt to put into word the unusually complicated genesis and transformation of butterfly color patterns he used such complicated formulations, accompanied by many new word formations, and such intricate syntax with a great number of subsidiary clauses, that his exceptionally interesting, deep, and multilateral view of matters, which is present in his works, is today quite difficult to understand even for scientists, for whom German is their mother-tongue. For those for whom German is only a second language the situation is nearly unbearable (Henke is something like the **Heidegger** of German developmental biology, which in a way cumulated its 150 year history in him and finally reached the end of its possibilities). The world of „German“ biology on the one hand understood the complexity, autonomy, and many interdependencies of the living world, but on the other it was limited by worries of excessive „scientivity“ (it is no coincidence that **Roux's** journal, which contained many of this science's fruits of labor, was called the *Archiv für Entwicklungsmechanik*). It is a world which today is for a large part filed away, much like the works and questions of later Antiquity or of the Middle Ages - the shift of accent and of the primary language of mainstream science towards the comprehensive and lucid Anglo-Saxon way of thinking after 1945 (even in Germany) leaves these studies to be buried in the depths of libraries, perhaps for future historians of biology. This shift of accent, among other things, shows that a new biological paradigm always appears on the shoulders of the winners (a similar shift took place in Japan), but it also shows that it is impossible to discard from a compact national intellectual heritage only those parts which directly gave rise to a historical catastrophe and humiliation and to keep intact the parts which did not play a part (After great catastrophes only basal attributes survive - in the case of Germany these were for example diligence, a sense for organization, social feelings, collectivism. Derivative attributes, even if those who represent them physically survive the catastrophe, are much more fragile and eventually dissolve, at the latest in the next generation.). In fact, the „German" way of understanding the world, at once complicated and cumbersome, and on the other hand deep and penetrating, understands man's nature and the nature of other organisms in such depth, that the possibility of misuse (even unconscious) is really great, therefore the conscious shift away at that time in history is quite understandable even in people with a profound ability of reflection and self-reflection (the Anglo-Saxon model of thinking, which only skims the surface of the object of study, on the one hand provides less information, but on the other hand it does less damage). It is no coincidence that after WWII the „German" tradition was strongest in countries which were most influenced by Germany, but did not directly participate in starting the war (Holland, Switzerland, the Czech lands, and the Baltic region, especially Estonia and St. Petersburg in Russia).

It is very difficult to describe in a concise and easily understandable way the majority of important conclusions to which **Süffert, Švanvič**, and **Henke** came to in their works. Because of the complexity and extraordinary appeal of the whole problem, it is necessary to refer the reader to the original works, because even the new compendium on the theme of butterfly color patterns (**Nijhout**, 1991) contains only brief extracts and the older works are not mentioned at all. The basic theory, which **Švanvič** and **Süffert** voiced quite independently and in parallel, was that it is possible to find something like a color pattern archetype, which is not dissimilar to what classical morphology called the „*Bauplan*", the basic scheme, which was sought in the world of „three-dimensional" morphology since **Cuvier's** time. From this basic plan it would be possible to derive through its transformation (although it would be much harder than the Cartesian transformations for fish, crustaceans, and mammal skulls, which were performed by **D'Arcy Thompson**, 1917) any now existing pattern of any given group (both authors worked with the family Nymphalidae, but their proposed basic plan is quite universal). This archetypal color pattern does not actually appear in its unaltered form and does not necessarily have to be the phylogenetic starting point in a given group. In the same way as three-dimensional morphological structures, a specific color pattern includes, on the one hand, a functional aspect (e.g. cryptic, aposematic, as an eyespot or false head, or for intraspecific communication) and on the other, a historical aspect, which uncovers the pattern's genesis in evolution, much the same as a bird's wing not only has the aspect of being an instrument for flight, but also the aspect of being a metamorphosed front limb (as was mentioned earlier, practically no fossil remains exist, so it is necessary to reconstruct the entire evolutionary progression from currently existing species, which in any case is the method used by other evolutionary studies as well; finding the direction of the changes constitutes a greater challenge). At the same time it is apparent that selective pressure can affect only the functional aspect of the color pattern, and not the concrete layout and the changes in the pattern's elements, whose development is guided by a more or less autonomous process, which follows its own, immanent rules. Individual components of the archetypal pattern form something like the „material", from which a concrete color pattern, usually in a complicated way, is constructed. Besides these „autonomous" components of the color pattern (*autonome Zeichnungen*), **Süffert** (1927) separately deals with „dependent" color patterns, which are given by the morphological structure of the wing - the veins, the margins, etc. - „*abhängige Zeichnungen*" (these were noticed already by **Rössler** (1861), even as the opposite to typical /autonomous/ patterns), and lastly he also deals with the before-mentioned „rhythmic" patterns of the „*Rieselung*" type. Like **Eimer**, **Süffert** also considered traverse lines, from which the transformation of the concrete color pattern emerged, to be the fundamental building blocks. These transformations can be very complicated and unexpected. **Süffert** (1927) was the first to describe the specific exegesis of the color pattern on the underside of the leaf butterflies of the genus *Kallima* in a way which is still accepted today - both the leaf's rib and main veins are in a complicated and „adventurous" way composed of various pattern elements with a heavy dose of „creative ingenuity and violence". It is quite common that one line is composed of two evolutionarily different components, which became joined in a secondary process and during their development became mutually „entangled" in a way which is similar to so-called „river-capturing" or to the differentiation of branchial apparatus in higher vertebrates, which is connected to fragmentation, a change in function, or on the other hand an integration of originally divided components of different origin (this joining or „entanglement" of two various lines was called „*pierellization*" by **Švanvič**, after the South American genus *Pierella* /Satyridae/, in which he observed this phenomenon). The analogy with geological processes does not end here: quite often a discontinuity of lines, caused by their movement, occurs. The discontinuity is often quite large along the wing's veins, and closely resembles geological slides along fault lines (Süffert uses the term *Verwerfung*). From a certain standpoint, as **Eimer** noted, each indivi-



Deducing various parts of the „leaf“ pattern on the underside of members of the leaf butterfly, genus *Kallima,* from the basic plan of wing patterns of the family Nymphalidae, from which so to say the „building material“ is taken (according to Süffert).

dual area between the wing's veins („*wing cell*“) seems to be a more or less autonomous part of the complete wing pattern. **Nijhout** (1991, and in all earlier works) was almost exclusively concerned only with species, where none of the color patterns extended beyond such areas (maybe for methodological reasons). Species, whose color pattern does not heed the veins and appears to be directly „painted“ on the wing, though are quite common, if not in the majority. The same pattern components can form in completely different groups - for example eye-spots can be formed by the fragmentation of traverse lines and the „condensation“ of pigments into a few eye models (this phenomenon was described by **Eimer**, who saw it as being an example of Goethe's law of compensation), or by the enlargement of one small eye by way of the so called ocellar lines (most butterflies), or they can even be formed by a regressive revolution and spiraling of an originally traverse line (many moth species from the family Noctuidae, e.g. the genus *Nyctipao*), or they can be formed by a joining of two secondary traverse lines and their derivatives (the peacock butterfly, *Inachis io*) - this author (**Komárek**, 1989b,1991) himself dealt with the method of formation of eye-spots in members of the eyed hawk moth, *Smerinthus* (Sphingidae) from the transversal lines of the hind-wing, with some stages in „autonomous“ evolution without the selective pressure of predators. Before him primarily **Süffert** worked on the evolution of eye-spots in other groups.

Süffert and **Henke** distinguished between so-called primary, secondary, and even tertiary symmetry systems on butterfly wings. This was the symmetry of the distribution of pigments of the same color on both sides of an axis on the wing (the primary is roughly in the center, the secondary to the right and left, and the tertiary is in a similar relation to the secondary). The symmetry in these cases does not have to be absolute, but only a very close match in the layout of pigments, which probably has its origin in the diffusion of substances which direct the later laying of pigments, the so called morphogens, on both sides from the region of the axis of the given system of symmetry. This, from a structuralist point of view, extremely complicated phenomenon can be best seen in the moth families Geometridae and Noctuidae, but is very difficult to discern in butterflies (the color pattern on upperside is very derivative and reduced, the underside is more archaic, as **Eimer** predicted, and very rich in particularities of form, which often serves to increase the overall cryptic appearance of the underside). Also, it is not possible to apply the schemes acquired by **Švanvič** and **Süffert** (1935, 1937) on members of the more primitive families (Hepialidae, Cossidae, Tineidae, etc.), **Lemche** (1935, 1937). As

Henke (1936) and **Henke** and **Kruse** (1941) showed, considerable portions of the original color pattern scheme can „pass beyond" the area of the wing and disappear, not only in the direction of the basis of the wing, but past its outer margin as well.

Therefore the color pattern is fluid basically over the entire area of the wing and its individual components can be considerably out of place (even after the shift of the components, they still usually appear on „predilection" areas of the wing, which **Henke** called „*Musterorte*"). In addition, color patterns on the upper- and underside of the wing evolved and developed wholly independent on one another. Butterfly patterns therefore are (in the same way as other animal color patterns, but with the difference that the „billboard-like" area of a butterfly's wings has an exceptional possibility of developing its specific traits) considerably autonomous structures, which are only weakly tied to morphological structures and are governed by selection only in so far as the overall „impression". In this way they are only a special and very apparent example of the overall autonomy of living organisms and their individual aspects, as was later emphasized primarily by **Portmann** (1960). Research of butterfly color patterns in the time between the World Wars was also conducted by **Švanvič's** colleague **G. N. Sokolov** (1936, 1947) and many other authors concerned with the development of the patterns through ontogenesis – in Germany **W. Köhler** and co-authors (1932, 1935), **A. Kühn** and co-authors (1926-1955, 10 works cited), **W. Braun** (1936, 1939), **W. Feldotto** (1933), **K. Magnusen** (1933), **R. Goldschmidt** (1920), in France **R. Catala** (1940), in the U.S.A. **E. Caspari** (1941), in England **Forbes** (1941), in the postwar years **V. Schwarz** (1962), **S. R. Bowden** (1988), **P. M. Brakefield** and **V. French** (1995, 2 works) and especially **H. Frederik Nijhout** and co-authors (1980-1991, 14 works cited). Nijhout, a Dutchman working as professor of zoology at Duke University in Durham, North Carolina, U.S.A., is one of the very few who at present is continuing in the study of the ontogenesis of butterfly color patterns. The physiological aspect of the origin of these patterns, which is still today not completely clear, is beyond the scope of this book, and so the only path possible is to refer the reader to the above mentioned works. Basically the theory is based on the idea of the diffusion of one or more morphogens, substances which evoke the formation of pigments in wing scales, from predilective locations, the so-called *focus*, or from their line very early after pupation. In this so-called sensible period of development the future color pattern can be influenced by external interference, especially the effects of cold weather or temperature rises (but also narcotization, injuries, intrapupal injections of various chemicals, radiation, etc.), in the sense that in slight cases the form which develops resemble some earlier phylogenetic stages (the eye-spot of the species *Inachis io* breaks up into the original two transversal lines), in the harsher cases the pattern can disintegrate completely. In the year 1864 the Austrian amateur entomologist **Dorfmeister** published his first article on this theme, and since then up to the beginning of the 20th century - **Merrifield** (1890, 1891, 1892), **Standfuss** (1896), **Fischer** (1895-1907, 5 works cited), **Prochnow** (1927, with a very rich bibliography) and others experimented with these thermal „aberrations". **Standfuss** (1896), cited by **Eimer** and also **Goldschmidt** (1936), and **Shapiro** (1980) repeatedly emphasized the similarity and on occasion the sameness of many forms caused by way of low temperatures to standard subarctic forms and of many forms created by way of high temperatures to southern races of the species *Papilio machaon, Nymphalis antiopa, Aglais urticae* and others /basically we are dealing with a phenomenon similar to a situation where a white European after being exposed to the sun for long periods of time starts to resemble a native of India/. This find strengthened the belief that the possibility of producing new species or subspecies was caused by the environmental conditions, and in the same way between the turn of the century and the end of the twenties many works that prove the hereditary nature of aberrant patterns due to temperature shocks across many generations in both moths and butterflies were written (**Prochnow**, 1927). After the change in atmosphere, to the disadvantage of Lamarckian tendencies (see also **Packard**, 1901), works of this nature stopped appearing /the influence of the „general atmosphere" on the nature of magazine type articles and the results expected from them has been discussed earlier in connection with **Nicholson** (1927) and **Harrison** (1919-1956, 7 works cited), this period in the history of science deserves closer inspection, including new repetitions of the original experiments and a comparison of the newly obtained results with the original ones/ and in 1938 **R. Goldschmidt**, in an extensive debate with followers of the Lamarckian tendency, argues and coins a new term for such phenomena, **phenocopy**, which denotes a phenomena of external appearance which does not influence the genome of the given species. A more detailed study of this problem was also published by **Kühn** (1926) and **Nijhout** (1984, summarized 1991).

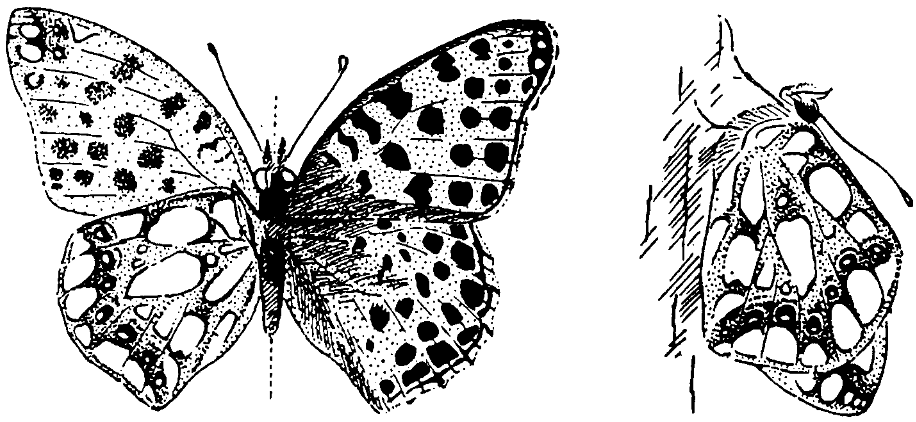
Eimer, like **Weismann** (1875), was concerned with the problem of seasonal dimorphism in butterflies, a phenomenon which is widely spread in temperate and tropical areas alike (in temperate climates the dimorphism concerns the spring-summer variation, in tropical climates it concerns differences in the wet and dry seasons). These considerable differences of external appearance (the Indo-Australian butterfly *Precis almana* /Nymphalidae/ goes as far as changing in the color pattern of the underside of the wings from a leaf mimicry in the dry season to a „typically“ nonmimetic pattern in the wet season) rely on the temperature or the photoperiod (or a combination of the two) in which the larvae develop and have little in common with the before mentioned phenomenon. Generally speaking, we can say that the external appearance of the underside of tropical seasonally dimorphic butterflies is more cryptic in the dry season than in the wet season, and a definite, functional, explanation for dimorphism in temperate regions is usually forced (see **Nijhout**, 1991). (**Weismann** was concerned with mimetic and similar phenomena until the end of his life and an extensive chapter about them, expanded for each new edition, can also be found in his collected lectures on evolutionary theory - **Weismann**, 1902). Color patterns of many other animal groups were also studied, and it was found that their organizational and transformational principles are basically the same. Color patterns on the beetle elytra were, for example, studied by **Tower**, 1906, **Filipov**, 1961, **Zajciw**, 1971, and **Kreslavskij**, 1977. The ontogenesis and phylogenesis of colorpatterns on bugs, especially from the family Pyrrhocoridae, including the cladistic analysis and study of mimetic complexes in the coton stainer, *Dysdercus,* was studied by Zrzavý and his colleagues in a number of works (**Tietz** and **Zrzavý**, 1996, **Zrzavý**, 1990, 1994, 1995, 1997, 1999, **Zrzavý** and **Nedvěd**, 1997, 1999, **Zrzavý**, **Nedvěd** and **Socha**, 1993).Mollusc patterns were studied by **M. von Linden** in his early work (1896). Additional authors interested in these patterns include **Becker** (1949), **Wrigley** (1948), **Raup** (1966), **Waddington & Cowe** (1969), **Oberling** (1978-87), and **Meinhardt** (1995b). **Portmann's** students, **Marianne von Harnack** (1953) and **Fioroni** (1961), studied snake patterns.

Many other classical works on patterns found on vertebrates also exist, for example **Werner**, 1890-1895, 5 works cited, **van Rynberk** (in **Harnack**, 1953), **Zenneck**, 1894, **Gadow**, 1903, 1911, and others. Even though **Werner** (1890) already put forward the theory that there exists a possibility of mutual homology of snake color patterns between themselves, quite often attempts were made at the deduction of vertebrate skin color patterns from the body's metamery, either of the vertebrae metamery, or of (**van Rynberk**) inervation zones in the skin of the zebra. It was specifically the work of **von Harnack** which showed that the skin color patterns of vertebrates, in particular snakes, are more or less autonomous, and have little connection with the rest of the given animal's anatomy. In addition certain species of snakes, in comparison with butterflies for example, undergo a gradual metamorphosis of their juvenile pattern to their adult pattern.

Animal color patterns and their ontogenesis are also quite suitable for mathematical modeling. The following authors have worked on the modeling of the genesis of mammal skin color patterns: **Bard** (1977, 1981), **Murray** (1981a, b, 1982, 1989). The modeling of the genesis of butterfly patterns was studied by **Bard & French** (1984), snake patterns were studied by **Murray & Myerscough** (1991), and the biological color patterns of predominantly fish and gastropods were studied by **Waddington & Cowe** (1969), **Meinhardt** (1982, 1995a, b), and lastly **French** (1984).

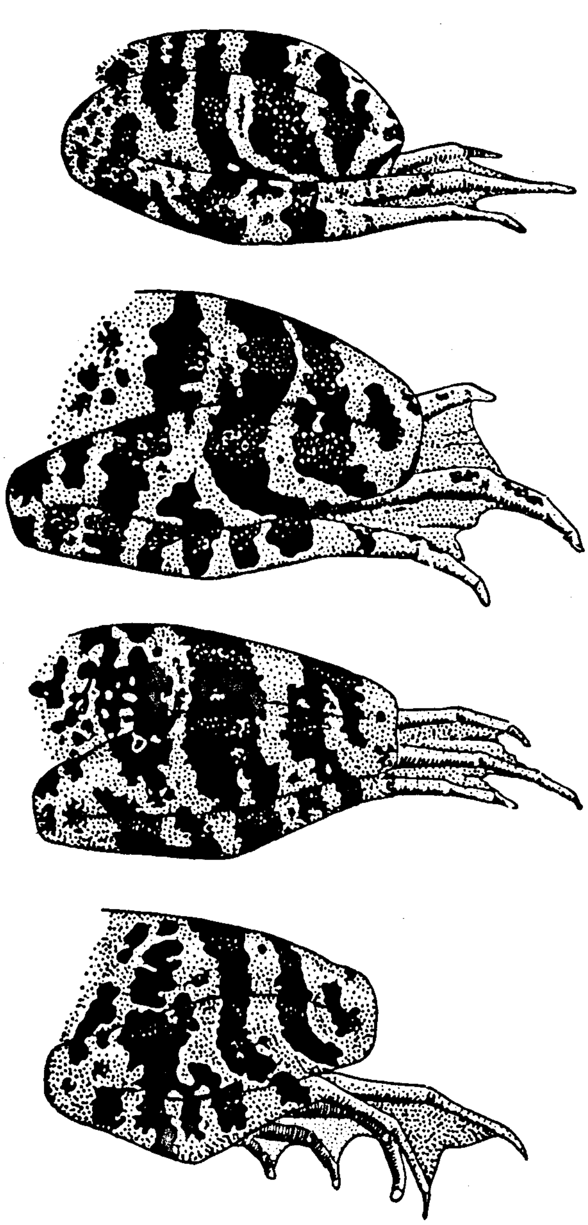
Linking color patterns and Portmann's concept

The first mention of so-called holistic patterns (*Totalzeichnung*), today usually known as examples of **Oudemans´ principle** (**Švanvič**, 1931), appeared in literature near the beginning of 20th century. The term arose more or less unjustly, coming from the Dutch entomologist **Oudemans** (1903), who, in his work, pointed out the agreement of color and pattern of the underside of the hindwings of the butterfly *Issoria lathonia* (qeen of Spain fritillary), (Nymphalidae) with the color and color pattern of the part of underside of the forewings, which in a resting position overhang the already mentioned hindwing. The covered portions are colored in a different way, basically an „x-ray“ of pattern on the top side (Oudemans' principle was already dealt with in the first chapter). The problem is that the phenomenon was not in fact discovered by **Oudemans** (who presented it at the international zoological congress in 1901, which gained him the prestigious award of the czar **Nicolai II.**) as is generally believed, but by the Swiss entomologist **M. I. Standfuss** (1894) when he described the cryptic color patterns of the family Notodontidae, which go beyond the forewings and are present on those portions of the hindwings which are not covered by the forewings (even **Darwin**, in 1871, noticed the plainness of those portions of bivalvian shells which are covered by the palium). /Even **F. Müller** (1878) mentioned this phenomenon in connection with the continuation of the color pattern from the upperside of the wing of the butterfly *Epicalia acontius* from the forewing to the hindwing. He considered this phenomenon to be the result of sexual selection by the females - because this



Oudemans' phenomenon – the shiny pattern on the underside of the wings of the queen of Spain fritillary, *Issoria lathonia,* is only found on parts which are visible when the butterfly is sitting calmly – the entire hindwing and the protruding apex of the forewing, the rest of the forewing has the same color pattern as the upperside of the wing (according to Oudemans).

is a species with a very high level of sexual dimorphism, he assumed that after establishing the „female" color pattern, the female taste changed and through selection established the male color pattern./ Additional work on this theme was then done by **C. Brunner von Wattenwyl** (1897, 1899) - in his quite pompous book on the beautiful coloration of insects he included, among other observations, one about „holotypical color patterns" (*holotypische Zeichnung*), where the color pattern seems to be painted onto morphological structures, which are not interconnected and are adjusted in such a way as to form a meaningful holistic pattern when in a certain position. (This includes not only the spread wings of butterflies, where the pattern continues from the forewing to the hindwing, /**Süffert**, 1927, who is incidentally the author of the term *Totalzeichnung*, proved that these patterns do not have to be homologous in terms of the material from which they arose/ but can also or example include the „linking" color pattern on the spread wings or tail feathers of many birds, as **Wallace** noted. The adjustment of two structures, which arose independently, to each other is on the other hand quite common with morphological structures - the teeth of the lower and upper jaw, which develop independently, typically „fit" each other.). Brunner, who in his later years changed position from being a „hesitant Darwinist" back to being a „hesitant Creationist", emphasized the „artistic" manner in which the holotypical pattern is painted without any respect for basic morphological properties (the Australian bug from the genus *Pirates* /Reduviidae/ has in the male form a yellow pattern on it folded forewings (or hemielytra), in the wingless female, one has the same on its abdomen, the Amazonian grasshopper *Mastax semicaecus* /Acridiidae/ has a band of color which crosses the lower portion of the compound eye). **Brunner von Wattenwyl**, whom we mentioned in connection with the term hypertely, was a specialist in the systematics of the Orthopteroid orders of insects (even his later work from 1906 deals with the genesis of color patterns in this group) and was a typical representative of the educated „scientific office clerk" in his era. The term **hypertely** (*Hypertelie*, **Brunner von Wattenwyl**, 1878) was not limited to describing cryptic phenomena, but could be applied to all types of coloration and configuration of the external appearance of animals, which seem to be „exaggerated", including those which **Darwin** considered being caused by sexual selection. Generally speaking, he thought that every living organism has in reserve a number of forms, which in usual circumstances are not realized (a certain anticipation of „sleeping" genes, which become active only in unusual situations or when the organism can „afford" to activate them). In the same work he pointed out the „closeness" of nature in creating animal color patterns as compared to creating those parts of an organism, in which any inaccuracy would be fatal - as an example he uses the inaccurate, that is only spiral eye-spot on the wings of the South African mantis *Pseudocreobotra ocellata* (later opinion classifies this as a pattern „in development" from a perpendicular band, but the observation is, as are all of Brunner's observations, true). There are very few works on Oudemans' principle in butterflies (**Graham**, 1950, **Sibatani**, 1987) and even fewer summaries - basically besides **Heikertinger** (1954), the best summary is **Portmann** (1960), where Portmann extends the principle to include vertebrates, especially those which have a divided surface (feathers, scales, etc.), which overlap in mutual superposition (a nice example of this is the wing „mirror" found in ducks or the scales of snakes of the viper genus *Bitis*, which appears to have a geometrical pattern „painted" onto its scales). Oudemans' principle is also connected to pseudaposematic phenomena (in the sense of **Cott's**, 1940, definition, as was mentioned earlier), where the pseudaposematic parts are hidden when the organism is in a resting position, e.g. covered by bent front and hind legs of many tropical frogs (frogs in general often have linking color patterns in resting positions, when the aposematic and cryptic patterns in the form of bands of color pass onto the frog's thighs and shins when in a seated position - **Cott**, 1940, **Portmann**, 1956). **Eimer** (1897) also noticed examples of Oudemans' principle in butterflies, but he explained other coloration of hidden parts of the forewings as being due to a lack of direct exposure to sunlight (!) and he was also convinced that the patterns on the underside of the wings was produced by a kind of „reflection" of the resting surface.

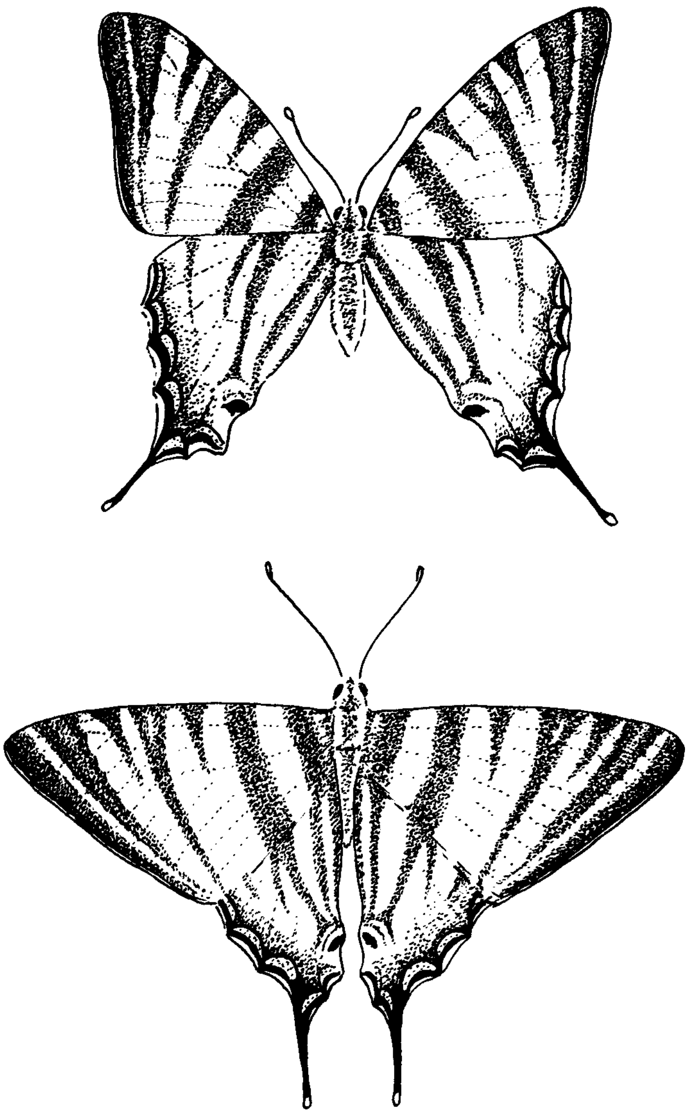


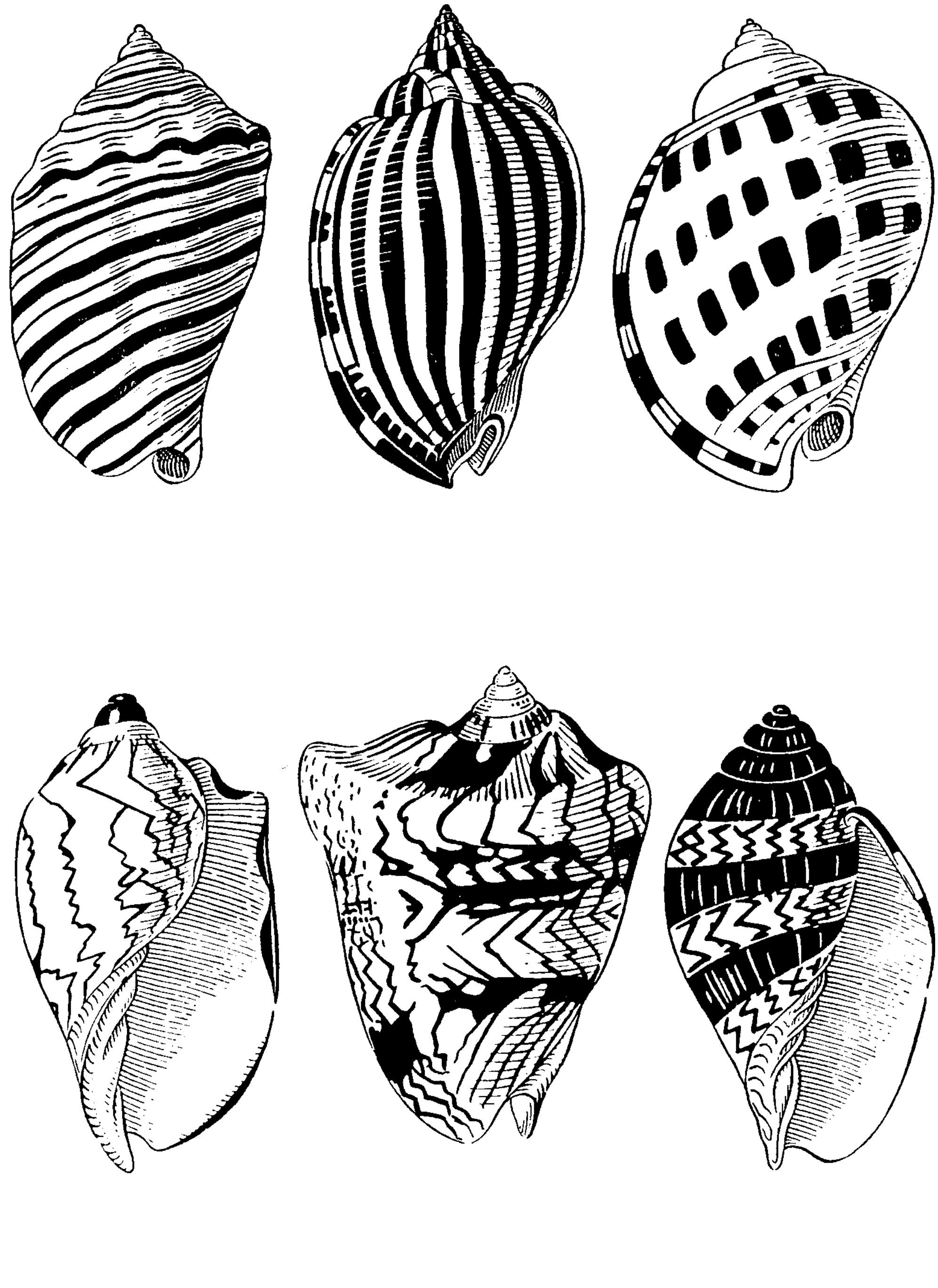
An example of Oudemans' phenomenon – the entire cryptic pattern of the hind legs of the common frog, *Rana temporaria*, which has bands on the various parts of the leg that connect when the leg is folded (according to Cott).

The German autonomistic school of thought culminated and was finalized by the works of **Adolf Portmann** (1897-1982), a professor of zoology at the university in Basel. Portmann, as was mentioned earlier, as a member of an undefeated nation in WWII, could continue after the war without (mainly inner) reservations in expanding the thought system of the „German" biological school, which in Germany itself was no longer practiced. Portmann was concerned with almost all aspects of zoology, but especially with higher vertebrates and opisthobranch sea gastropods (but for example his dissertation was on dragonflies appearing near Basel). Besides his many contacts with other biologists (e.g. **F. Süffert**), he also had an unusually broad scale of interests, especially in the humanities, philosophy, and analytical psychology (for a long time he was the chairman of he group *Eranos* and regularly contributed to their magazine - *Eranos-Jahrbücher*). Besides his contacts with **C. G. Jung** he was most influenced by the thoughts of the Dutch philosopher **F. J. J. Buytendijk** (1928, 1958), who dealt with biological phenomena, and also by the French thinker **R. Ruyer** (1962, 1964).

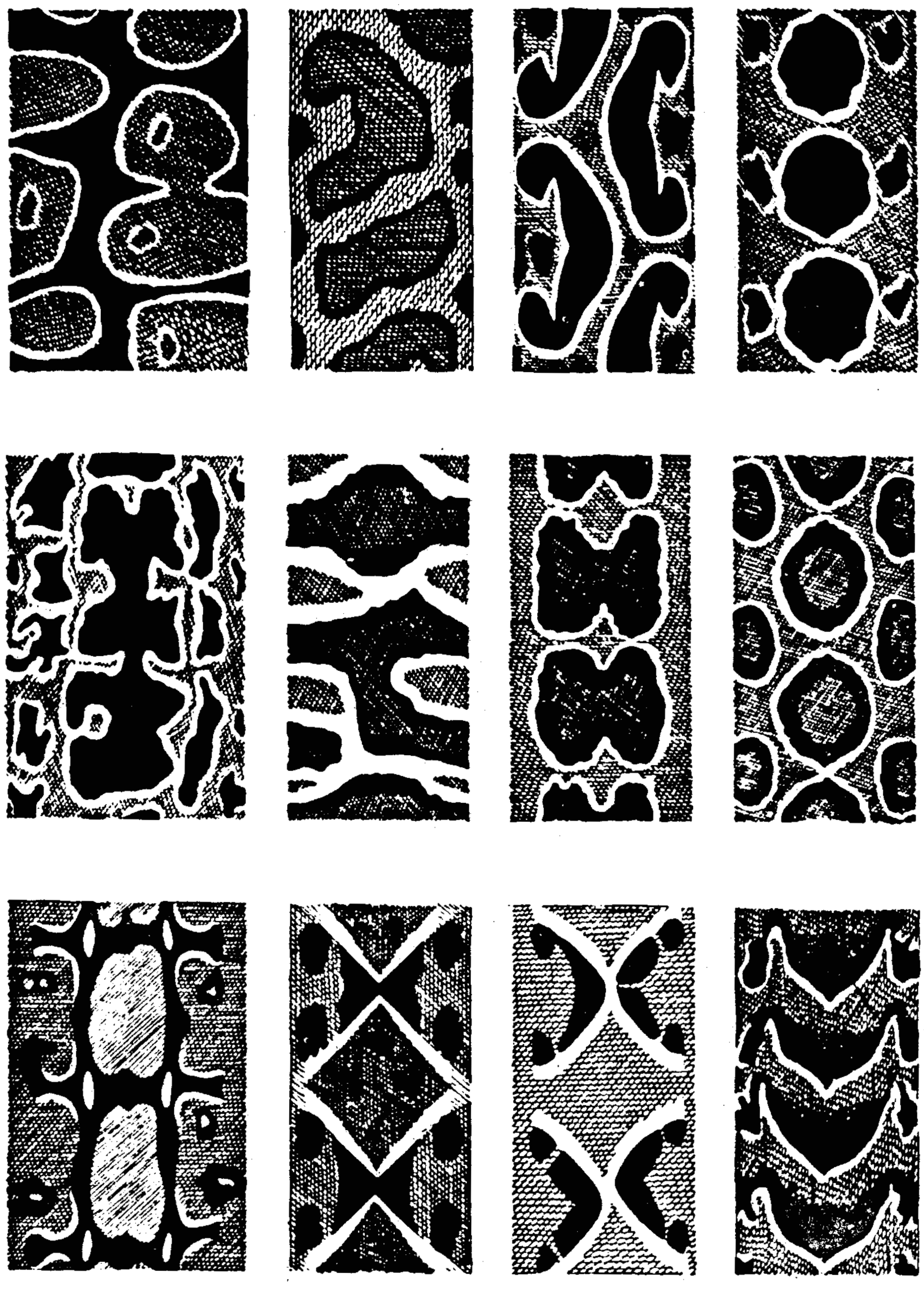
Besides many other specialized publications, the books which are the most relevant to our theme are as follows: *Die Tiergestalt* (1948), *Das Tier als soziales Wesen* (1953), *Tarnung im Tierreich* (1956),and *Neue Wege der Biologie* (1960). Because a summary of Portmann's interpretation of the external appearance of organisms has already been given in the first chapter (in order to give an easier understanding of the problem), the following lines contain only certain comments and elaborations. The concept of adaptive coloration, with is the subject of this book, is mainly discussed in **Portmann's** book *Tarnung im Tierreich* from 1956, where besides many examples of cryptic adaptations he also briefly deals with aposematic and mimetic phenomena. The book is exceptional especially because of the non-trivial way in which it presents the problem of visual adaptations and emphasizes the complexity of the entire phenomenon, which is an unusual approach in the world of „banal reductionist“ explanations of the living world. As far as the functional aspect of the external design of organisms is concerned, Portmann's interpretation, as was mentioned earlier, does not fundamentally differ from other post-Darwinian interpretations, but he does emphasize that the functional aspect is not the only factor in considering the external appearance of organisms. He always emphasized the unusually cunning „component“ system of the external appearance of organisms and he rejected the simple mutation-selection idea of the mechanisms of its genesis. Even though his concept is evolutionary and he considers selective processes (including mutations) as being very important, he does not give them a „monopoly“ on creative processes in nature (Portmann was obviously not a Creationist and he even openly reproached **Teilhard de Chardin** for his theistic concepts). He considered creativity in esthetic self-expression, which arises from the inside, to be an important aspect of organisms (including humans). /The basic difference between human creativity and creativity in other organisms is that the creative spontaneity of other organisms is for the most part limited to their own bodies and is unconscious, while human self-presentative creativity is usually projected externally in the creation of various artifacts, which can be either material - e.g. a vase, immaterial - e.g. a song, or living - e.g. a greyhound. Human creativity is on one side much more conscious than animal creativity, but it still always has its roots in the unconscious, in the hidden aspects of the mind. With humans, their „proper phenomena“ are attentively complemented by other improvements, like tattoos and make up, making up one's hair and beard, clothing, perfumes, etc. and this „extended self-display“ also includes the whole of our cultural structure, including buildings, the anthropic influence of the land, etc. (this „extended self-display“ also exists to a lesser degree in animals - spiders have their webs, a fox has its den, ants have their anthill and the system of paths which surround it, a colony of the South American viscacha, *Lagostomus viscaccia,* has all the objects that they found and collected, etc.). **O. Koenig** (1970), without a direct connection to Portmann, also studied the theme of the evolution of human artifacts and their role in human self-presentation/ . Portmann considered not only genetic and physiological givens, but also the inner aspects of life, especially in their relation to the external world (*Weltzuwendung, Weltbeziehung*), these being „hidden“, mostly psychological, aspects of organisms. Especially inner autonomy, the ability to modify oneself in embryo- and ontogenesis, was considered very important. Portmann's concept of „centricity“ (*Innerlichkeit*) can be considered synonymous to Antiquity's term *psýché* as a principle which guarantees integrity, individuality, and life processes, and which operates on the principle of self-construction (and in specific cases also regeneration) and which contains the goal and the idea in itself. From modern definitions this principle would contain in itself the „hidden“ aspects of the organism from the genome

Oudemans' phenomenon on the upperside of the wings of the scarce swallowtail, *Iphiclides podalirius.* In a normal position the bands on the fore- and hind-wings naturally complete each other (even though they often have a different origin), but in the position of pinned samples this effect is lost (according to Portmann).





At the top three basic types of color pattern on snail shells, at the bottom three concrete complicated patterns on volute snails, *Voluta*, which arose from a combination of the basic motives (according to Portmann).



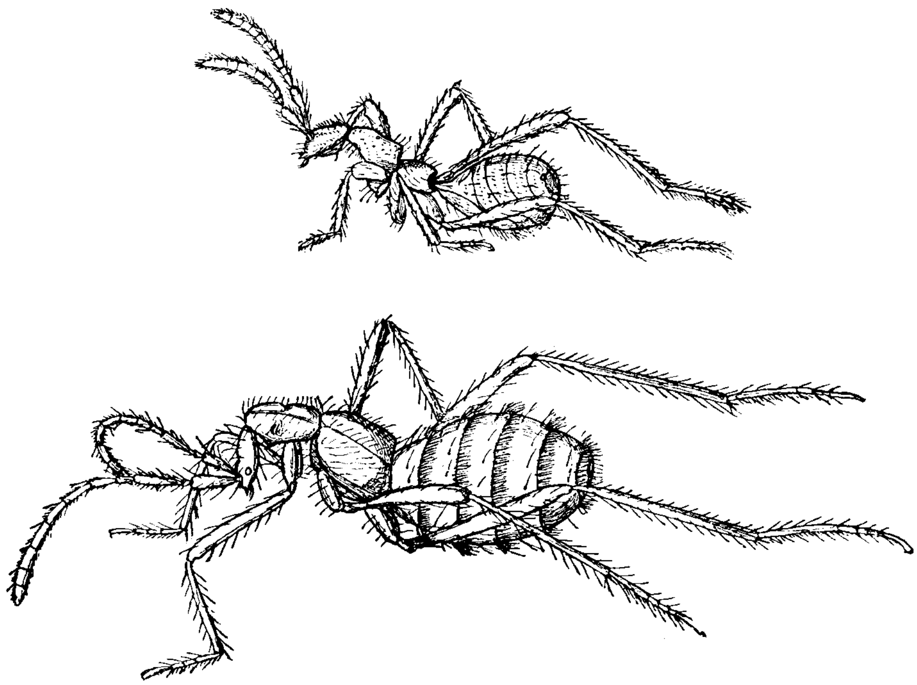
Skin patterns of various snake species in planar depiction - also a good example of disruptive coloration, the optical division of an organism into many parts (according to Cott).

to the Freudian-Jungian unconscious (and even the conscious - but Portmann obviously rejected identifying this centricity with consciousness). Portmann in depth dealt with the question of the so-called **rank** (*Rang*) of organisms: the concept of „high“ and „low“ aspects of human perceptions of the world, including the living world, which is one of the basic categories (a good example of this can be found in heraldic animal symbolism - lions or eagles are suitable on coats of arms, roundworms or tapeworms obviously are not, even though they are more numerous, more successful, and more important). Plants can be divided in a similar way, trees are „higher“ that herbs, striking flowers are „higher“ than inconspicuous ones - roses against nettles, in temperate climates plants which are green in the winter (mistletoe, ivy, holly) are considered „higher“, etc. It is symptomatic that the almost „religiously“ upheld distinction between the study of „higher“ and „lower“ plants and animals had a tendency to merge in the post-war years and this distinction - in literature as well - eventually weakened considerably). But it is relatively difficult to precisely determine what connects organisms which we consider „higher“ in comparison to those we consider „lower“ - it is not only the greater complexity of their structure, but more so in their relation to the world, especially in their perception through the senses and their relative autonomy on the environment in which they live, which can be seen for example in their mobility, as compared to a sedentary way of life, their ability to overcome the winter by being warm-blooded as compared to being in a lethargic stupor, their relative independence as compared to parasitism, etc. In comparison with this, „rank“ has no connection to the area of distribution, the number of individuals, the resistance to various factors, that is to the successfulness of a species (e.g. rodents versus primates). It is connected to the level of complexity of mental processes, sense impressions, and centricity in general. Living beings with a higher „rank“ are from a certain viewpoint more fragile and vulnerable, even though inside they are more complex and prolific, as higher and more valuable „estates“ tend to be. If it is at all possible to formally define the term „rank“, then it would be, in higher vertebrates, the weight ratio of the evolutionarily younger parts of the brain as compared to the brain stem. The higher this so-called **cephalic index** is, the higher „rank“ the organism has (invertebrates are similarly classified according to the degree in which originally separate ganglia have merged). Portmann asserts a direct proportion between the cunningness of the design of external appearance and the cephalic index level, but only within the framework of a systematic group, where the anatomical particularities are comparable. For mammals (but also for example fish) he emphasizes the importance of whole-body color patterns on the coat or skin in species with a low cephalic index level (if some color pattern even exists) as compared to color patterns which emphasize the head or anal areas in species with a high cephalic index level (ungulates, primates) - **Wallace** and **Hingston** noticed both phenomena, but interpreted them from a different standpoint: as being functional and used for intraspecific communication (for Hingston typical intraspecific communication was a threat). Portmann saw the increase in the cephalic index in the course of ontogenesis as the main reason for the transition from the „whole-body“ coloration of young deer, tapirs, pigs, etc. to the „polarized“ coloration of the adults (in Hingston's opinion the young undergo „fear“ and crypsis because of the threat from the adults). In a similar way Portmann sees a close connection between the cephalic index of birds and their coloration - species with a low index within the framework of a group are usually colored cryptically in both sexes, those species with a higher index have semantic males and cryptic females, and the highest have semantic coloration in both sexes (this more or less corresponds to Darwin's idea of the phylogenetic sequences of these coloration, but **Darwin** does not of course speak of a cephalic index - both concepts correspond in the idea of „progression“, or evolution from „lower“ to „higher“ levels). Portmann noticed a similar connection between the cephalic index level and the coloration in insects, but mainly in opisthobranch sea slugs. Portmann was one of the four authors who dealt with the exegesis of the external appearance of organisms in a new and original way (**Darwin, Wallace, Hingston,** and **Portmann**). While the first two, whose explanations were basically complementary within the framework of classical Darwinian doctrines, were more or less exclusively interested in the functional aspect of the external appearance and the possible selective pressures which led to it, Portmann and his students (e.g. **Sager**, 1955, **Brinckmann**, 1958, **Fioroni**, 1961, **Bürgin-Wyss**, 1961, **Durrer**, 1965, **Brun**, 1969) were mainly concerned with the genesis of the external appearance of organisms in individual ontogenesis and its morphological complexities, as follows from the traditions of the German „autonomistic“ school of thought (which does not imply a contradiction to **Darwin's** and **Wallace's** opinions). **Hingston**, who also considered „centricity“ (although he does not use this term) to be a basic source for the appearance of a organism (compared to Portmann, he almost entirely discarded the idea of selection), still concentrated his attention on the functional interpretation, although his version is somewhere between the Darwin-Wallace concept of total function and Portmann's ontological-structural concept (Portmann's view can be understood as an extension of Hingston's views on „German" developmental-morphological, philosophical, analytical-psychological aspects, but Portmann probably did not know Hingston, just as he didn't know **Peterich's** biochromatic studies). Portmann also shares with Hingston the favorite picture of a sitting butterfly, which opens its wings towards the observer. Portmann interprets this in a broader way, within the framework of general „self-presentation", which can of course in certain cases be considered a threat. Especially the communicational aspects of self-presentational activities are enlarged on by Portmann's exegesis of the peacock's tail fan from the point of view of ontogenesis and structure (**Portmann**, 1960, **Sager**, 1955) or of the external appearance of the African Sudan crowned crane, *Balearica pavonina*, where the overall impression is given by the red wattles, colored by hemoglobin, the white cheek areas, caused by the structure of the fibrous tissues (not based on pigment), further by the black forehead, which has deposit of melanine and special „velvet" feathers, and lastly by rays of feathers on the crown, which are strengthened by their own spiral structure (the coloration of birds was also interpreted as an expression of centricity by **Freiling**, 1938). Portmann also in quite some detail studied humans (**Portmann**, 1966, 1970) and the process of hominization in the course of human evolution, he especially supported the opinion that the humans represent (even in their exterior morphology) something like a neotenic form of higher primate which is analogous to their young children or advanced fetuses. Portmann's system made an impression more on philosophers (e.g. **Kugler**, 1967) than on neo-Darwinist oriented biologists, who on one hand could not refute Portmann's high level of formal and scientific competence in the field of biology and especially zoology, but on the other could not work with the world as Portmann presented it. Although during his life Portmann was a very well-known person and in Switzerland very famous as well (especially due to his many radio broadcasts) and taught a great many student-followers, it is typical that at the University in Basel his system was not accepted and some of his followers (**A. Suchantke**) had to switch to „alternative" activities, in this case to Waldorfian schooling. Portmann's general biological-psychological-philosophical reflections are mainly contained in the collection of essays *Biologie und Geist* (1955) and in his later book *An den Grenzen des Wissens* (1974). Portmann always formulated his thoughts with great reserve, they are so to say contained „holographically" in all his works at the same time. Especially his anthropological studies became popular with students of philosophical anthropology, but because of their lack of extensive knowledge of and a lack of interest in the factography of the external appearance of organisms, his works on this theme are usually ignored.

Piepers, Wasmann, Heikertinger, and other Continental authors

A large number of continental authors continued in **Eimer's** footsteps, which means the direct study of mimetic phenomena. One of the most interesting in this era was the Dutchman **Marinus Cornelis Piepers**, originally a lawyer, who spent over thirty years, from 1863, in the colonial government of Dutch India, today's Indonesia. Following in the footsteps of other colonial functionaries, especially the British, he started collecting butterflies and observing their bionomy (e.g. **Piepers**, 1897a, b), he was also interested in other organisms and spent his time thinking about evolutionary theory and other current biological questions. He recorded the results of these meditations in two books: *Mimikry, Selektion und Darwinismus* (1903) and *Noch einmal Mimicry, Selektion und Darwinism* (1907). The books are very distinctive, both having over 400 pages (the second is written in defense and is a supplement of the first, and it contain answers to criticisms of the first). The books contain an unusually large number of interesting observations and particularities, which are based on a thirty-year experience in the field in the tropics combined with amazing powers of observation and thought, but on the other hand it is extraordinarily difficult to read the books, firstly due to the strange and lawyer-like division of the chapters (the first book is divided into 42 „theses"), and secondly because of the untypical and cumbersome syntax used (the author was, after all, born a Dutchman, not a German). On the whole we can say that Piepers completely rejected both classical and neo - Darwinism, especially concerning the influence of selection on the appearance of organisms in general (selectionist and mechanist schools of thought were in general not accepted by Dutch, especially colonial, authors, for example the founder of holism **J. Smuts**). Mimetic similarities between organisms, e.g. between butterflies, was in his opinion (which was similar to **Eimer's**) caused by a similarity in the developmental stage, **homeogenesis** (bright coloration according to Piepers dissuade and frighten possible predators because the colors are new and unusual - he coins the term *Misoneismus* - to refuse what is new - to describe the tendency of /for example/ birds to conservatism in their feeding habits). According to Piepers, cryptic similarities, such as a similarity to the substrate background, were derived from the suggestive influence of the color and structure of the surrounding environment on the organism (the organism also in part actively seeks out a substrate similar to its own cryptic pattern - this behavior has been verified in butterflies and moths many times - **Longstaff**, 1906, 1912, **Sargent**, 1968, 1969a, b). As a true vitalist (Piepers considered all things, living and non-living, as possessing, in some way, at least the rudiments of a soul) the author saw in cryptic adaptations another (hereditary) level of color adaptations of the same type as color changes in fish, frogs, reptiles, color changes in butterfly pupae, etc. (this change can, but does not have to, occur through optical perception). In the same way as a person's face gains indelible marks of his profession or standing (clergy, army, intellectual sphere, mafia, etc.) after a few years, which represents a „stiff" expression of the prevalent mental state (even **Darwin** considered instinct to be a hereditarily „frozen" habit), the appearance of organisms is hereditarily modified after a few generations by the external environment, according to Piepers (this applies to humans as well, e.g. he judged that families of clergymen or financiers of many generations seem to have hereditarily fixed components concerning appearance and mentality). Piepers attributes the similarity between certain ants and their guests to suggestive influence and he utterly rejects **Wasmann's** explanation of „tactile mimicry". He surprisingly applied this suggestive influence only to animal, and left out plants - he angrily refuses such an explanation for the „snake-like" stem of the titan arum, *Amorphophallus*, which often have detailed „pictures" of lichens on the surface (**Beccari**, 1884 in **Piepers**, 1903). The book is also an extensive collection of mainly accurate, but also partially less successful anti-Darwinian arguments and in this sense follows the wave of repugnance towards classical Darwinism on the Continent at the end of the 19th century (e.g. **Schilde**, 1879, 1884, 1890). In spite of the sheer amount of facts and strong enthusiastically amateurish preconceived conceptions (which is a situation similar to the one which gave birth to classical Darwinism, except with a negative sign and a kind of prejudiced self-centeredness, even if quite educated and well read), the book contains many suggestions in the area of particularities concerning the world of mimetic phenomena. The „advocate-like" tendency to „outdo" one's opponent is another darker aspect of the basically page-wise most extensive book about mimicry and adaptive coloration ever published, even if the book is arranged very unwisely.

Erich Wasmann (1859-1931), a South Tyrol Jesuit who worked in Holland mainly on the research of special cases of mimicry, was quite a unique individual. His special field was the study of ant and termite guests, that is insects, or other organisms, which co-inhabit the ant or termite nests (see the *Bibliography* for details) with the ants or termites. For this research he ably made extensive use of the wide network of the Church, which (including missions) basically covered the entirety of the Earth's populated surface, including the most remote areas. Collected samples were amassed in the form of postal packages which arrived in his Dutch residence, and which allowed him to expand his collection in a completely unique way without even leaving Europe. He also kept guest species which occur in Europe and North Africa along with their hosts in artificial ant nests and he carefully and diligently observed their ethology. The phenomena of ant and termite guests is one of the most remarkable in the whole of nature. A large number of insect groups, especially beetles (from them the largest number comes from the family Staphylinidae), but other orders as well (Hymenoptera, Diptera, Orthoptera, Thysanura), further mites, spiders, and other organisms inhabit these anthills and termite mounds. Some species on a permanent basis, others only temporarily. Concerning the popularity of the guests among ants- it ranges from being hunted down (they can save themselves by running away or by having a smooth and tough exterior which the ants cannot bite with their mandibles - *„Trutztypus"*) to being accepted and even being spoilt and „pampered", the latter being fed as larvae and as adults, cleaned, and if circumstances require it even carried around, making them wholly reliant on the ants. All of these categories include some species which are in general appearance similar to ants, even though this represents a considerable „deformation" of the original type of body. **Wasmann** (1890) called this phenomenon „*Myrmecoidie*", in termite guests „*Termitoidie*" (later a similar term was coined for the imitation of wasps „*Sphecoidie*" and bees „*Apoidie*"). But basically only a small percentage of guests show signs of this type of adaptation. All groups also include species which eat either ants or their larvae, and at the same time some of these species are myrmecoid, and others aren't. **Myrmecoidy** isn't in fact limited to organisms which live in anthills (**Jacobi**, 1913, named this phenomenon „*synöke Myrmecoidie*"), but many other species, which live outside anthills, share this adaptation, even though they often live near anthills or on plants which ants frequent (**Jacobi** named this phenomenon „*metöke Myrmecoidie*"). This second category mainly concerns ant-mimicking spiders (as was discussed earlier), then many adult Heteroptera or their nymphs, and lastly many young nymphs of locusts and mantids. The functional meaning of these „external" ant-mimicry, which in certain cases does not lie in the perfect imitation of the body's shape, but in the excruciatingly detailed imitation of ant movement and behavior (the simulation of the movement of antennae by the first or second pair of legs of ant-mimicking spiders, etc.), is not, in spite of the eccentricity of the phenomena, completely clear. **Poulton** (1908), **Carpenter & Ford** (1933) and many other authors thought that these phenomena were for deceiving birds, **Wasmann** (1925) for deceiving the ants themselves, where he (often correctly) assumes that myrmecoid insects regularly prey on ants and find it easier to draw near as a „wolf in sheep's garb". The first case, according to criteria mentioned earlier, would fall under the category of Batesian mimicry, while the second would be Peckhamian mimicry. Many debates centered on the question whether, and to what extent, ants are consumed by birds (**McAtee**, 1912, 1932, **Heikertinger**, 1926-27, **Beal**, 1908, **Csiki**, 1905-15, etc.), and the results are not exactly conclusive - certain groups, such as woodpeckers, are specialized in ant consumption, while other insectivorous species consume them only infrequently. It certainly cannot be said that the external appearance of an ant provides universally better protection, more probable is the effect of being „lost in the crowd". Many „external" ant-mimicking spiders and Heteroptera in fact do eat ants (**Wasmann**, 1925, **Oliveira & Sazima**, 1984, 1985). „Internal" myrmecoids (living inside anthills) also have certain optical adaptations, e.g. imitations of light reflections on the bodies of ants using different resources (convex surfaces instead of concave ones), but an important part is played by plain mimicry of form, which serves for tactile recognition by antennae („*Tastmimikry*", **Wasmann**, 1890). Wasmann showed that for example the South American migrating army ants of the genus *Eciton*, which are unusually rich in intensely myrmecoid guests from the rove beetles, family Staphylinidae (the first were brought to Europe by **Bates**, but at the time not many were interested), have guests which have developed only tactile mimicry in ant species which are completely blind, those species which have developed ocelli have guests with a combination of both tactile and optical mimicry. Tactile mimicry, which includes not only form, but also the texture of the bristle surface and olfactory components, is sometimes also called **Wasmannian mimicry** (in a varied form this occurs in the orchid of the genus *Ophrys*, which imitates through its flower the female of solitary mining bees from the genus *Andrena* not so much optically, but more through the tactile impression and through bristles). **Wasmann** (1925) deduced that ants perceive a complex quality called „*die Geruchsform*", or an „olfactory-form perception" of their guests on the basis of a combination of tactile and olfactory sensations (from their antennae), an impression which we humans can hardly imagine because of our primary optical orientation (later works proved that a very important aspect of the guest's mimicry is the mimesis of the chemistry of the cuticle). /This does not imply that the imitation of the ant always has to be complete - beetles of the genus *Thorictus* (family Thorictidae), e.g. *Thorictus foreli*, which live as parasites on the heads of ants and tightly hold the antennae, for the most part are a complete imitation of the host ant's head. The reason for this is not entirely clear, but these insects secrete on their rear corners of the pronotum a secretion which is zealously consumed by other ants./. As much as Wasmann was convinced in his early works that this is a case of mimicry in the narrowest possible sense and that the ants care for and feed their guests because they believe them to be members of their own species (rove beetles, Staphylinidae, usually imitate that category of workers which is most similar in size to them), near the end of his life (**Wasmann**, 1925) he came to the conclusion that although the hosting ants are well aware of the fact that they are dealing with a different species, the similar shape, surface structure, and olfactory sensations are sympathetic for them and they tolerate them and care for them in a way that humans would care for a favorite toy (the importance of this aspect is further emphasized by the fact that many „pampered" guest species excrete on predilection places a special secretion, which the ants hungrily feed on - but in view of the minute quantity produced the secretion cannot constitute a vital part of their diet, but may be something more akin to a desert or drug). Although it is obviously impossible to verify the mental processes of an ant, there are a number of good reasons why Wasmann's opinion on this matter is correct. First of all, he spent more time than any other author studying the ethology of ants and their guests and he gained in this field experiences, which could not be attained by quick scientific „bustle" of later periods, secondly a very strong analogy between the domestication and process of adaptation of the guests exists (Wasmann, who always emphasized the diametric difference between animal instinct and human intelligence - **Wasmann**, 1899b - does not actually state this analogy, but it is very apparent anyway). Wasmann's psychological opinions were an application of Thomism onto the area of human and animal mentality and he was radically opposed to **Darwin's** concept of a purely quantitative difference between animals and hu-



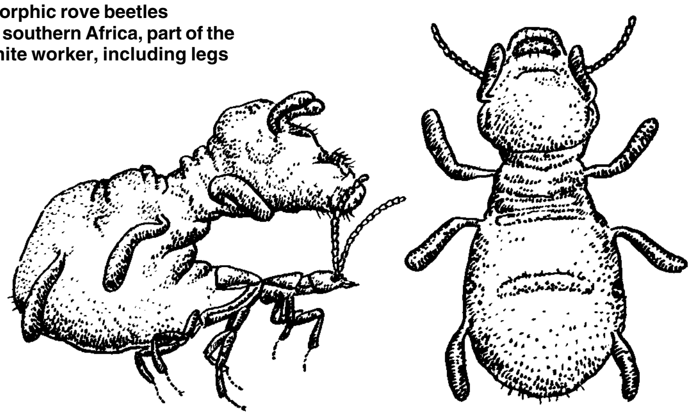
An example of Wasmannian mimicry: the rove beetles *Mimeciton pulex* (top) and *Ecitophyia simulans* (bottom), both guests of South American ants of the genus *Eciton* (according to Wasmann).

mans). A large number of human domesticants, as was shown earlier, have very pronounced „human“ attributes (although not in the sense of a whole body-shape imitation) - like one of many let us look at the example of the „monkey“ face of the Pekinese “lapdog”, combined with its child-like behavior. This adaptation lead to sympathy and a certain pampering, but resolutely not lead to mistakes in determining species. Besides natural selection, Wasmann introduces the term „friendly selection“ (*Amikalselektion*), which is based on caring for and preferring those guests who exude the desired secretion and which basically works against natural selection (Wasmann at this point also introduces the Freudian term *Lustprinzip*). This **amicable selection** can also be applied to the „cute“ appearance of myrmecoid guests, because the process is basically analogous to the usually unconscious human selection of those domestic animals which carry some of the human’s traits and so hit some „archetypal chord“ by their „cute“ appearance (as compared to the conscious selection, based on the desire to advance to some definite goal, such as with milk or meat production, hunting or racing abilities, etc.). Ant and termite guests represent the only analogy to domesticated animals which occurs in nature and the leaf-cutting ants of the genus *Atta* represent the only analogy to agriculture in nature - they cultivate the so-called ambrosia fungi in underground gardens on a substrate of chewed leafs. Wasmann, who dedicated more than 40 years of his life to his science, had a very persistent opponent in **F. Heikertinger** (1919a, 1923, 1926-27, 1954), who attempted with all possible vehemence and zest to prove that the phenomenon known as ant-mimicry basically does not exist (**Heikertinger** was even in general convinced, as will be seen below, that mimicry in general doesn’t exist). According to **Heikertinger’s** concept, the genesis of the similarity of the general external appearance of certain myrmecoid rove beetles, Staphylinidae, lies in a transformation of form which occurred in conjure with a lengthening and stretching of the body (excepting the abdomen), which would be analogous to the transformation of form of cave insects in general (the tunnels in an anthill are generally speaking underground areas, something like a system of very tiny caves). Certain details, like the fact that ant-like Staphylinidae have, in comparison with the large and broad one of an ant, a very small and thin head, supports this theory to a degree, or at least it should hint at the nature of transformations of form in the animal kingdom generally, which is that the individual dimensions of the body are mutually correlated and certain forms in certain groups just cannot be precisely perfect. The literary discussion between the two authors went on for many years in an unusually vehement tone, with many arguments and a well-hidden slight interpersonal disgust, hidden under a veil of objectivity and good-will. These discussions, which were with interest followed by the whole biological community at the time, eventually fizzled out, and the problem of the form of ant-like organisms has not undergone any significant change since Wasmann's death. The whole affair is unusually similar to the problem of which questions seem to be important at the moment in non-scientific structures, e.g. in the Church (in one period the problem of Christology, in another the regulation of childbirth, etc.). After all arguments have been discussed *ad absurum* under great emotional stress, a fall in attractiveness of the problem occurs, even though the originators of the problem, in this case ant guests, have certainly not „fizzled out". Wasmann, whose publications are characteristically concise, logical, and „condensed" in their style, was (partially also due to his theological and philosophical education) a great arguer and debater (his discussions with **E. Haeckel** in journals are well known). He was also concerned with the theory of evolution where, besides natural selection in the Darwinian sense, he saw the influence from the above mentioned amicable selection (similarly to **Kropotkin**, 1902, for example) and he saw God's influence (in spite of his theistic concept of the world this can be expected if only from his place in the Church) as being limited only to the creation of life and the creation of humankind, which he viewed from a Thomian perspective as a species on a completely different level from all other organisms (**Wasmann**, 1899a, b). The problem of myrmecophily and myrmecoidy, which Wasmann delved into very deeply in a number of articles (see the *Bibliography*) and in his very instructive 140 page book (**Wasmann**, 1925) (which includes many formal distinctions between several aspects of these phenomena), cannot be summarized on a few pages except in a very generalized way, and therefore it is necessary to point the interested reader in the direction of the original works.

After Wasmann a large number of other authors became interested in ant guests (**Hölldobler, Kistner, Jakobson, Klots, Seevers**, and others, see the *Bibliography*). For example, **Seevers** (1965) demonstrated various ways in which the myrmecoid rove beetles, Staphylinidae, imitate the body pedicel of the ant (for myrmecoids living inside the anthill this cannot be only an optical painting of the thinner body, but the actual thinning and stretching has to take place) and he distinguishes between twelve unrelated groups which have adapted in this way seemingly independent on each other (this „predestination" of certain taxa to a specific adaptation, which then repeatedly and seemingly easily occurs again and again in one group, but not another, also represents a very wide-spread, and again very interesting, phenomenon). **Kloft** (1959) came to the conclusion that ant communication with aphids (which don't exactly represent true guests in the anthill, but in **Wasmann's** nomenclature only so-called **trophobionts**) occurs on the basis of „mistaking" the abdomen with the hind legs and cornicles of the aphids for the head of another ant with antennae and mandibles and therefore relies on a „coincidental mimetism" of these two different parts. This explanation can be basically considered „fairytale-ish" because no other „special" adaptations for communication with ants ever developed on the end of the abdomen of any aphid. From the immense amount of myrmecoid and termitoid Staphylinidae that **Kistner** and **Jacobson** collected and described througout the years, the most unusual (termitoid) is the African species *Coatonachthodes ovambolandicus* (**Kistner**, 1968), which carries above the body a physogastric abdomen which serves as a dummy of a termite worker, which has cuticular appendages which simulate all six legs and a pair of antennae. This is one of the most monstrous insects that was ever described / **physogastry** is an enlargement of the abdomen, which often occurs in myrmecoid and termitoid rove beetles, Staphylinidae, and other guests (e.g. the fly family Termitoxeniidae) and which Wasmann considered a „side effect" of termitophily of no selective value, in the same way as the termite and ant queens have an enlarged abdomen/. The most interesting fact is that this strange adaptation of the above mentioned species is meant to be viewed from the top (the ethology of living specimens is unfortunately not known), which can occur with this species only when the termite-mound is destroyed or damaged, which this insect otherwise does not leave. Considering that their models, the termite workers, are not only edible, but are actually sought out by birds, the case becomes even more unusual. Every serious student interested in the research of mimetic phenomena should study its depiction very carefully.

Franz Heikertinger (1876-1953) is without doubt a special figure in the history of the research of mimicry. Among those who devoted most of their lives to this branch of study, Heikertinger was the only one who wasn't a professional biologist and who didn't even have a university diploma. He spent his life as a clerk in the postal bank in Vienna, in the end he advanced to

The strongly physogastric and termitomorphic rove beetles *Coatonachthodes ovambolandicus* from southern Africa, part of the abdomen above the body imitates a termite worker, including legs and antennae (according to Kistner).



the position of central inspector, who controlled the functioning of the whole bank. In his free time, which as an employ of the state he had quite enough of, he studied entomology and even more so mimetic phenomena, mainly in insects. This study was noteworthy for one special reason: Heikertinger did not actually believe in the „real“ existence of mimicry and he thought all hypotheses concerning them were misleading, unnecessary, and incorrect, projecting the prejudices of their creator onto nature. It is quite unusual to choose a life-long career in a branch of study, whose subject matter and even terminological validity is denied by the student (with the possible exception of some students of religious studies, which is to an extent analogous). And as is often the situation in the few analogous cases, Heikertinger's works are perfect examples of precise knowledge of particularities and extraordinary knowledge of pertinent literature. Heikertinger's works (**Heikertinger**, 1915-1954, see the *Bibliography*) are a model of not only diligence, but also of intimate knowledge of the subject and of bibliographical exactness, which can only rarely be found in other authors who wrote on this theme (Heikertinger's „archeology“ of original works concerning the external appearance of organisms, which appeared in the series „*Welchen Quellen entspringen die Trachtenhypothesen*“ from 1921-1927 is especially notable, even though the citations are pulled from context and serve his own purposes). These phenomena, as he himself emphasized, specifically the exaggerated scientific approach and exaggerated objectivity, are typical symptoms of talented and industrious amateurs, who compensate their lack of formal education by having a more „rigorous“ approach to the study. Heikertinger's concepts concerning the approach to the problem of mimicry barely evolved in the forty years of his work - right from the start he was convinced that the various forms of mimicry are nothing but the fixed ideas of their creators, which are hardly based, if at all, on correspondences with nature (we can see the full-blown skeptical-enlightened viewpoint of old Vienna, the distrust of various hypotheses later cumulates in a distrust of all hypotheses and finally in a concept of science as being composed of a number of partial tidbits of knowledge and particularities without any mutual connections). In Heikertinger's view, mimetic phenomena were only coincidental epiphenomena of the meeting of evolutionary transformational lines, regardless of whether he was dealing with butterfly wing color patterns or with ant guests evolving towards a cavernicole external appearance. Heikertinger's works on this theme appear, even for insiders, as reliable as „classical“ works on the theory of mimicry (in any case it is apparent that mimetic forms and patterns had to have been derived from similar non-mimetic structures and that the „causal“ connection between the model and the mimic through predatorial selection can easily be refuted, or at least it is difficult to clearly prove the connection or verify it through witnesses, as is always the case when dealing with evolution). Heikertinger basically refused any selective influence except for a negative one (and a negative influence occurred only in extreme cases, like for example in desert climates) on the external appearance of living organisms (he uses the term *Tracht* - meaning clothing, garb; in German the word *betrachten* shares the same root and it means ‚to watch‘, ‚to observe‘), which has its basis and its evolutionary dynamics in the „inner factors“ of the organism and species and selection can only rid the species of the extremities of such evolution, but it cannot itself influence this evolution. /In contrast to this **Heikertinger** (1933-41, 1953) acknowledges the influence of the „*genus loci*“ on living organisms, which not only causes „local modes“ of butterfly mimicry rings (these local „modes“ can cover a large area, e.g. the prevalence of yellow, ochre, and rusty colors in butterflies in sub-Saharan Africa or they can be restricted to relatively small areas, as is the case in some regions in South America). This influence of the „*genus loci*“ is not limited only to colors, but includes morphological structures, e.g. antennae (**Seitz**, *Ent. Rundschau* 43, 1926). For example the Sahel zone in Africa or inland Australia contain a number of groups of moths which have much larger antennae than their relatives in other zones (the Australian ghost moths, Hepialidae, *Porina fuscomaculata* and *Trictena labyrinthica,* from a family which in usual circumstances only has very slight antennae; in groups which usually have large antennae, e.g. the “tussock moths”, Lymantriidae - Australian members belonging to these groups usually have enormous antennae - e.g. *Pterolocera amplicornis*. The Australian carpenter-worm moths, Cossidae, also have antennae which in size resemble European emperors, Saturniidae; Seitz also mentions the superiority in size of the antennae of the North African population of the grass eggar, *Lasiocampa trifolii* over the same in Central Europe). In this context Heikertinger also quotes **Hering** (1926) and **Thieme** (1884). The latter describes many „analogies of appearance“ of beetles from around the whole world from various habitats, of which many of these examples would be considered mimetic in others circumstances. / Heikertinger considers the area which is not affected by selection to be quite vast and he basically does not acknowledge the adaptive explanation for mimetic, and even aposematic and cryptic, phenomena, which he considers a result of inner dynamics of living systems, and not a result of the selective pressure of predators (he especially criticized experiments concerning insectivorous birds, which he condemned as being methodologically weak and unscientific - predators which are endowed with optimal sight for their purposes, according to Heikertinger, would probably hunt various species in an equal and regular amount getting regular “tax”- „*Tribut*“ - and would not act as meticulous selective agents). Certain cryptic, and even some semantic, phenomena (in the sense of predators’ fear of new things - **Piepers’** misoneism) can have a kind of functional aspect in certain cases, according to Heikertinger, but the Darwin-Wallace division of various colorations and external appearances into many categories is not acceptable (Heikertinger especially disliked the category of epigamic colorations caused by sexual selection and also „*recognition marks*“ according to **Wallace’s** definition). Heikertinger only accepted one category - Wallace’s „*typical colourations*“, where the coloration and external appearance are only epiphenomena of the species with little or no functional or selective value, which serve in the end for recognition of individuals within the species but were not formed by selective pressure of this type. Basically Heikertinger was a supporter of selective and functional nihilism concerning the external appearance of organisms (as compared to **Portmann**, for example) and he did not attempt to elaborate on it as a means to express an organisms „centricity“ (Heikertinger did not even make use of this term and the external appearance of organisms did not interest him from this aspect). In his book (**Heikertinger**, 1954, and also **Heikertinger**, 1946, 1949) he quite thoroughly deals with **Oudemans’** phenomenon in butterflies, while at the same time completely rejects its functional aspect. He names the whole phenomenon (the model being **Süffert’s** dictionary) „*Totalzeichnung*“ and leaves the adjustment of two morphologically distant structures as an open-ended „mystery“. Heikertinger demanded (in truth, as an unattainable goal) something like a general theory of coloration, which would make use of one principle to explain the appearance, ontogenetic development, and evolution (and lastly the function as well) of all types of external appearance of any organism - something like the general and evolutionary crystalography of organisms (we can see **Eimer’s** influence here). Partial explanations did not satisfy him and he refused them as being only humorous ideas and drawing-room reflections, which do not adequately cover the topic (Heikertinger did not find, and in fact did not even search for a unified theory of all colorations and patterns; he spent all of his energy and intelligence on the refutation of „partial“ theories of mimicry and adaptive coloration). /**Heikertinger** (1919b, 1925, 1929, 1954) even invented a new strictly logical terminology for the types of external appearance and for mimetic phenomena, even though it is quite from a different angle than **Poulton’s**. Because the mentioned phenomena can be classified according to an infinite amount of criteria, it would be most advisable to consult the original work. It is quite important to mention the distinction between the term *Mimikry* (the imitation of aposematics) from the term *Mimese* - the imitation of objects which are not interesting for predators (*Zoo*-, *Phyto*-, and *Allomimese* - the last means the imitation of inanimate objects). He also invented the term „*Schrecktracht*“ and „*Ungewohnttracht*“ for pseudaposematic and generally bright and colorful external garbs of otherwise edible organisms - this was influenced by **O. Prochnow** (1907, 1927). / If we dismissing this prejudice, Heikertinger’s work is an absolute treasure-trove of information about mimetic phenomena, often taken from literature which today is for the most part forgotten and in any case very difficult to find (it is especially these publications, „lost beyond the horizon", that the *Bibliography*, which is an appendix to this book, is trying to save). Heikertinger's works are clearly the seriously „religious" undertaking of an erudite, hard-working, systematic, and brilliantly logical and concise thinker and violent atheist. Considering the fact that the interpretative aperture is the same in all of his works and that it is quite easy to ignore it if the need arises, the books are not only strongly recommended, but in fact intimate knowledge of them is basically required for a serious study of mimetic phenomena, not only for their factual content and bibliographical exactness. Heikertinger basically unveils all the weak spots in the Darwinian and post-Darwinian selectionist approach to mimetic phenomena and the appearance of organisms /and plants - **Heikertinger's** first works (1914, 1915) concerned the defense mechanisms of plants against phytophages/, his assault on the English school and **Wasmann** really partially expose the „nudity of the king" and also a certain subconscious deep-seated malice. Heikertinger's works combine a special blend of lucidity and torpidity and an ignoring of „obvious" facts with which he takes apart every aspect of the problem, and like every self-fulfilling system, and so confirms again and again his theory (reading Heikertinger is especially instructive for those who know of a similar system of thought, e.g. a sociobiological one, for the reason that the premises of both world-views are completely different). Heikertinger's authority and influence most probably deadened the interest in the problem of mimicry in the successor states of the Austro-Hungarian Empire and spread skepticism towards the whole problem on the Continent in general (of course the „reality" or „unreality" of mimetic phenomena is based on the interpretative aperture - the move Heikertinger caused leaves the „facts" intact, but does not allow them to be connected in any meaningful „system"; they carry importance only as coincidental and basically marginal epiphenomena of a different system - that which was earlier central and important now becomes peripheral and uninteresting). Actually Heikertinger represents only a different branch of the continental school of thought than **Süffert**, **Henke**, and **Portmann**, which is more „down to earth", moving from the elite university level to the level of amateur entomological groups (the German term *Vereinsmeierei* comes to mind), where the philosophical view is replaced by harsh clear-thinking empirism and steady hard-working attitude of those who were deeply involved in the matter and so to say fought in the front lines. After Heikertinger's death (1953), in the same way as **Carpenter's** death in the same year in England, the Continent almost completely lost interest in the study of mimicry - this was probably the worst era from the beginning of the research and lasted up until the sixties. It is not clear if or how much Heikertinger contributed to this decline, or possibly if it was caused by a lack of successors and a decline in the creative potential of the years between the wars. It is true that the post-mortem publication of Heikertinger's book *Das Rätsel der Mimikry und seine Lösung* (1954) was published in the Russian zone of Germany, in Jena, probably because it was considered an argument against the „Western" Mendelian-Morganian biology, which of course the author did not intend and was in fact not actually interested in this type of problem - he only made use of a lucrative offer, because in the years after the war it was quite difficult to publish a specialized volume of more that 200 pages and 7 color plates. The book, which is very extensive and yet concise, is the quintessence of Heikertinger's views on the external appearance of organisms with a very extensive array of facts and a large bibliography (at the end he compares the theory of mimicry to an old worn doll, which is well liked by a child but has to be taken away and finally thrown away). Even so, the study of this work cannot compensate for the study of his earlier works, which make up a very unique part in the history of the study of mimetic phenomena - after Poulton, Heikertinger's bibliography is the richest and with him, **Poulton**, and **Carpenter** the entire „world" of thought and research on this theme more or less entirely faded from sight.

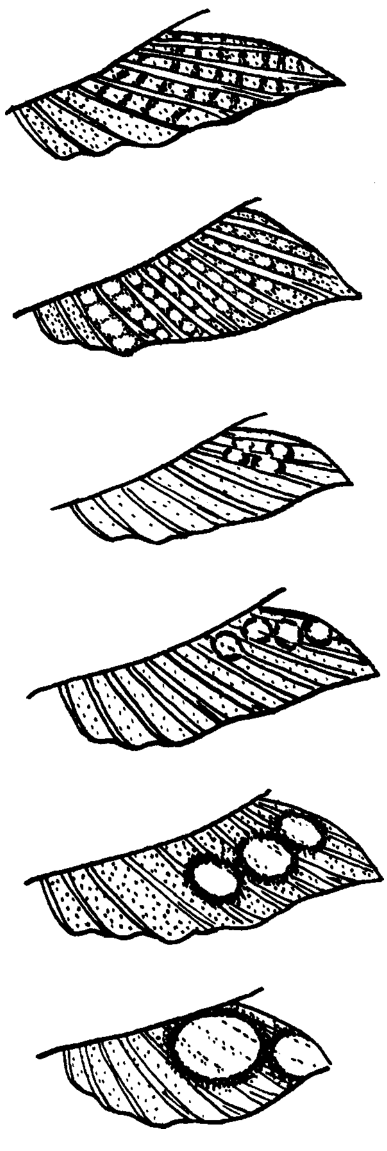
A large number of other authors in Germany in the years before and between the war researched adaptive coloration and mimicry – **Vosseler**, **Schröder**, from a Darwinian point of view **Study** (see the *Bibliography*), and others. **O. Prochnow**, who first worked in the small town Wendisch-Buchholz, later in Berlin, studied adaptive coloration in great detail. The **pseudaposematic coloration** theories (*Schreckfärbung*), which include eye-spots (at this time the influence of eye-spots on bird predators was being studied by **Steiniger**, 1938a, b) and snake imitations by caterpillars as well, were first thought of (1906, 1907, 1923) by him. His very extensive work on insect coloration (**Prochnow**, 1927) also includes a detailed summary of literature dealing with „Lamarckian" experiments with various moths from 1880 to 1928 and so is very interesting material for the study of the history of biology. **Exaggerated structures** in animals interested for example **Krieg**, 1936, **Frankenberg**, 1937, **Eggers**, 1935, **Haupt**, 1953, and also marginally **B. Rensch**, 1947. **Krieg** thought they (and this includes „exaggerated" movement or reproduction) were a way to work off surplus in diet, which is realized according to the species' constitution in a direction which is not in conflict with selection; if these influences work for a long enough period of time, the „exaggerated" structure is maintained at a certain level by selection, and if sudden changes in the environment occur, these structures can even become fatal. In contrast **Rensch** (1947) believed that luxurious or exaggerated structures are formed by allometric (faster than the rest of the body) growth of certain body parts during the enlarging of the body, which, in accordance with Cope's rule, he considers always positive in non-flying organisms - **Cope** himself did not speak of an advantage in this situation, he only noted a tendency to enlarge (it is true that species which have formed exaggerated structures are among the largest in their respective groups – lamellicorne (leaf-horned) beetles, deer, etc. - but exceptions do exist). The „exaggerated" character of horns and antlers of Bovidae and Cervidae is further amplified by their variability within the whole family (including extinct species), which makes use of every conceivable form, or even branching, in spite of the fact that the most effective weapon would be a short and sharp horn (see also **Bubeník**, 1966, **Modell**, 1969, **Riedl**, 1978, **Goss**, 1983, **Geist**, 1991). The time period between the wars produced much work on interspecific parallelisms in variability, where related (and sometimes less related) species have individual color variations which are more similar to corresponding variations in different species than to other variations within the species itself (**Gredler**, 1903, **Vavilov**, 1922, **Bryk**, 1923, 1928, **Philiptschenko**, 1927, **Kleinschmidt**, 1937). **Möbius**, 1905, was also concerned with the esthetic aspect of the appearance of organisms in this time period.

One often cited work on the mimicry of coral snakes was published in the German region after the war (**Mertens**, 1956). The author, **Robert Mertens**, was for quite some time the herpetologist of the Senckenberg Museum in Frankfurt. On the basis of his visit to a Brazilian vaccine production station in Butantan in 1954 he decided that species of the coral snake, *Micrurus*, which from **Wallace's** time were considered to be models for imitation by the less poisonous or non-poisonous members of the "true" snakes, family Colubridae, actually occur less often (about 1:5) than their imitators and are also poisonous to the extent that a bitten predator dies before even realizing the situation. For this reason Mertens concludes that the moderately poisonous Colubridae of the genera *Erythrolamprus,* and *Pseudoboa* serve as „models" (which are imitated), and the „imitators" are the most poisonous species of the coral snake, *Micrurus*, as well as the non-poisonous and mildly poisonous members of the genera *Atractus*, *Lampropeltis, Simophis*, *Pliocercus*, *Sibynophis*, *Cemphora*, etc. (to make sure that the whole affair has the „narrative and mythopoetic" components of Darwinian works, Mertens assumes that members of the genus *Micrurus* were less poisonous in the past and truly served as „models" for *today's* „models", only the evolution of their drastic toxicity in time moved them into the place of „mimics" of other various very poisonous imitators from the genera *Erythrolamprus* and *Pseudoboa*). This concept became generally well known especially thanks to the extensive references in Wickler's popular book (**Wickler**, 1968); occasionally the concept is mentioned under the general term „**Mertens' mimicry**" (*Mertensche Mimikry*). Even though the viewpoint is thought out very well, it belongs rather to the realm of fantasy than to mimicry interpretations. The numeric ratio between the coral snake, *Micrurus* and its imitators are quite different in areas outside of the region around Sao Paulo; in Panama (**Dunn**, 1954) for example the genus *Micrurus* occurs more often than its imitator species. In addition, Mertens numbers are derived from samples sent to the Butantan institute by collectors instead of being derived from actual field research. If we ignore possible ethological differences between the genus *Micrurus* and others (e.g. a higher rate of night-time activity than day-time activity - people are „predators" only in the day-time), it is not surprising that, since the reward of one ample of serum is given for any four snakes sent, the natives naturally catch non-poisonous or mildly poisonous snakes rather than deadly ones (Mertens believed that the natives were not capable of differentiating between various „coral" snakes, but this could have been a result of the typical arrogance of a museum specialist towards the „common native"). The following short recapitulation will show that the problem of „coral" snakes in not trivial and allows for many different interpretations.

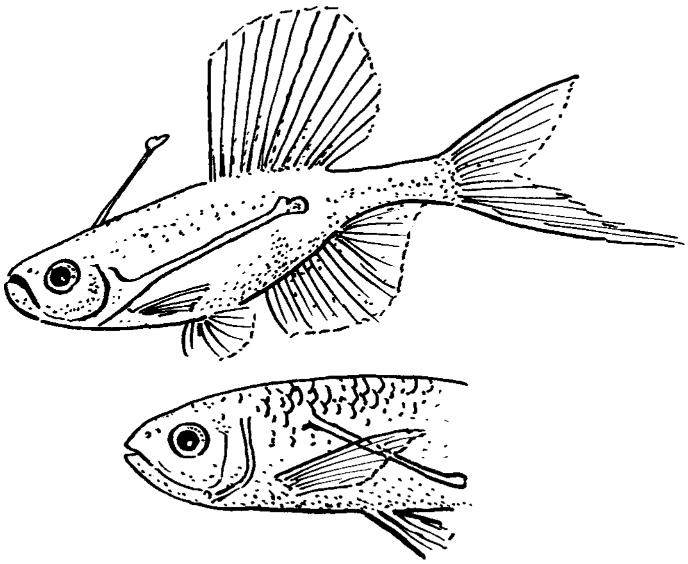
The first work which mentions that the folk-term „*cobra coral*" applies to a number of different species was written by the Brasilian traveller prince **von Wied** (1820). The problem also interested **Cope** (1860, 1893), who suggested explanation by postulating of the idea of a limited amount of freely combinable attributes of species, as was mentioned in the second chapter. After **Wallace's** (1867) interpretation of these phenomena as being an example of Batesian mimicry the whole problem was considered a closed chapter and was not opened for a long time. **Werner** (1907, 1908, 1917) considered these similarities to be a clean convergence more or less in the sense of **Eimer's** homeogenesis. **Gadow** (1911) thought the genesis of these phenomena was in **isotely**, the goalful targeting of development through similar, successive steps toward the same or similar results without any great selective influence, but through the influence of the „*genius loci*" (the problem of „*genius loci*" was even discussed by **Mertens**, 1956, under the influence of **Heikertinger** /1954/). **Gadow's** orthogenetic concept was criticized from a Darwinian standpoint by **Sternfeld** (1913), who noticed an interesting fact, mainly that the „coral" color pattern occurs only on snakes which are from 40 to 100 cm in length. **Dunn** (1954) added his observations from Panama to this; he found that 85% of these snakes feed on other snakes (ophiophagus) and because most of them are active at night he concludes that predators which rely on eyesight and mainly color do not play an important role. **Brattstrom** (1955) thought that the similarities between these snakes arose due to convergence, and that the effect is not aposematic, but basically cryptic (the white lines are important in this case, because they are visible even in twilight and confuse predators - the predator concentrates on the lines of the moving snake, and the lines seem to „shrink" and after a while the snake disappears). The „classical" explanation of the given phenomenon by mimicry is given by **Hecht & Marien** (1956) and lastly **Grobman** (1978), from the fact that the extensive area of the U.S.A. is inhabited by non-poisonous imitators (without a model of the coral snake, *Micrurus*), came to the conclusion that these night species are not under significant pressure from predators and develop these bright and interesting colors in „free spaces" because they can „afford to" (in the same way that many cryptically colored snakes are brightly colored on their undersides as well, even though the underside is almost never seen). **Gehlbach** (1972) in contrast believes that the whole phenomenon is related to so-called *self-mimicry*, because of the indistinguishable similarity between the head and tail portions of coral snakes (in **Garstka**, 1982). In addition it was proved that American birds, without prior experience, refuse objects which have a color pattern similar to the coral snakes, therefore this behavior is inborn to the birds and does not have to be learned through a life-threatening experience (**Smith**, 1975, 1977, 1978, 1980). This short overview, if nothing else, shows the truth of **Mayr's** (1982) theory that a biological concept which could clearly and unambiguously explain mimetic phenomena would also solve all other biological problems.

Compared to the period between the wars in Germany, the years after the war produced significantly fewer authors. The most important is **W. Wickler**, who worked at the ethological institute in Seewiesen in Bavaria, which was founded by **K. Lorenz**. In 1968 he published a book on mimetic phenomena, which, although wide in scope, is more of a compilation of other works, but is nonetheless a very instructive, richly illustrated work which is meant not only for experts but to the same extent for the more educated amateurs. The book became very popular and was translated into English, French, and Spanish (**Wickler**, 1968). Wickler, as a student and successor of K. Lorenz in the study of classical ethology was mainly interested in the study of the ethology of fish. His achievements include the before-mentioned discovery of the mimicry of the false cleanerfish of the genus *Aspidontus*, which imitate the cleanerfish of the genus *Labroides* and instead of cleaning the „customers" feed on them (**Wickler**, 1960, 1961, 1963, 1966a, b) and also the study of the development of egg dummies on the anal fins of the females from the African fish genus *Haplochromis* (Cichlidae) /in this genus the male carries the eggs in his mouth until they are born, the pattern which imitates the eggs - sometimes extremely exaggerated - on the anal fin of the female force the male to attempt to gather these „eggs" and so he also gathers real ones, which the female lets out from her reproductive opening, located nearby - the dummies evolved, like the eye-spots of butterflies, from what were originally cryptic traverse lines on the fin - **Wickler**, 1962a, b/. Classical ethology also points out another source of mimetic phenomena in nature - it is ritualization, where a complete action is replaced by representational action or displacement activity (the domestic cock offers a grain or other food to the hen before mating, while the pheasant cock of the genus *Lophura* only acts out this behavior without actually offering anything - the action here has a representational value, it is symbolic, and do not simply have a factual value, which then *eo ipso* gains some value, which is different from its original one; even human behavior is full of ritualizations, a good example can be found in children's behavior or in the Church's rituals, for example). On the level of the body the **dummy** (*Attrappe*) plays the role of the ritual, the forms more or less imitate certain objects, but their nature is different and their whole function is deceptive (an excellent analogy can be found in fake food products displayed by supermarkets in their display cases). The similarity between the dummy and the imitated object can be either very distant - the males of certain species of the fly family Empididae (dance flies) give during copulation as a „gift" only an empty case made of fiber, instead of the whole insect, which was originally tied up in the fibers. The South American fish from the sub-family Glaundulocanodinae (family Characidae) have in the male sex on their bodies formations with a very rough imitation of their prey on the end; this is used during epigamic ceremonies to gain the attention of the females (it is interesting to note that these formations often have a different morphological origin in different genera - the genus *Corynopoma* has this on the operculum, on the genus *Pterobrycon* they are formed by the lengthening of one scale on the body). In other cases the dummies can be very realistic, like the „illustration" of eggs on the fins of members of the genus *Haplochromis* or for example the very accurate dummies of red female genitalia swelling, which signalize that the female is ready to mate, on the male baboon hamadryas, *Papio hamadryas*, which is presented to the dominant male by submissive males to abate his anger, or for copulation as a sign of dominance of the stronger over the weaker (**Wickler**, 1967). Certain dummies in the animal kingdom exhibit one quite interesting attribute; instead of being overly realistic, some dummies are „beyond-normal", *„übernormale Attrappen"* (e.g. certain species fish from the genus *Haplochromis* have an imitation of only one extremely large „egg" on their anal fin). This difference is usually quantitative, but it can also be qualitative (**Tinbergen's** experiments with young seagulls showed that the bills of the adults, which normally have a red spot and serve as signals for the young to announce feeding points, can be of different color and still attract the attention of the young better than the natural red). This contradiction between the ideal (child, parent, partner, boss, or state for example) and the more or less not so perfect reality appear in humans as well. Exaggerated and unrealistically large egg dummies are very popular for birds, for men various industries make a living by making use of this conflict (e.g. pornography, parenting magazines, and in a wider sense all commercials and trivial literature in general). Why expectations are so far from reality is a difficult question to answer (many birds would like eggs which would weigh more than the bird itself - an egg like that would be not only impossible to lay, but impossible to keep warm as well). We can consider this special case of tension between polarities as an example of a typical attribute of the living world; even the suffering caused by this tension is in principle an indispensable part of life. An uncountable amount of dummies also exists in the world of human artifacts and their study would take a very long time. **M. Rothschild** (1967) mentions in this context not only a number of humorous artifacts and various devices intended for sexual self-presentation and self-beautification, but also sugar-coated pills as examples of the „mimetism" of a different artifact (a sweet) by another (the medicine), without giving the overall impression that the two are or look identical. We can actually say that artifacts or behavior that do not have any ritualized aspect or are not in some way dummies make up a minority and are an exception to the rule.

The development of spawns dummies (in the end even overdeveloped) from vertical bands on the anal fin of various African cichlids (according to Wickler).



The problem of aposematism and mimicry in the years after the war also interested **W. Schuler** from Göttingen University (e.g. **Schuler & Roper**, 1992), who was mainly concerned with the reaction of birds to fake imitations of aposematics and mimetics. Another post-war scientist, **E. Curio**, from the University of Bochum, was interested especially in the ethology of predation and optical adaptations of the prey (see also the *Bibliography*). On the whole though we can say that the interest in mimicry and related phenomena on the Continent after the war greatly diminished and in Germany, with the exception of



Dummies of food which lures females during epigamic ceremonies in two fish genera of the South American family Characidae, *Corynopoma* (the dummy is formed from operculum) and *Pterobrycon* (the dummy is formed from a change in one scale); (according to Wickler)

branches derived from the traditional Lorenz-Tinbergen ethology, practically does not differ from the Anglo-Saxon model.

In France, in the time period between the wars and especially the post-war years, mimicry research interested **L. Chopard**. His book, *Le mimétisme*, from 1949 contains, besides other data, another new system of categorization of mimetic phenomena, as is in any case the individualistic style prevalent in many French schools of thought, especially in the humanities. He primarily distinguishes between „travesties“ (*travestie*) /that is „dressing up“ as someone else/ and „camouflage“ (*camouflage*) /melting into the surrounding environment/ - in a phytomimetic situation for example these two categories merge. **R. Callois** (1960, 1963), whom we have already mentioned on a number of occasions, tackles the problem of mimetism from a humanitarian and intellectual point of view. He also deals with the psychological roots of mimetism in great detail: myths concerning changes, masks, carnivals, myths and folklore about invisibility (caps and capes which cause invisibility), fatal bites, bewitchment, charms, turning bodies to stone and other ways of making a body immovable (historicity occurs only after the end of the time of Infinite Return, after the laying aside of masks and the loss of belief in their omnipotence and constitutive ability). The analogy makes for a „transversal“ natural regularity, which can be best understood by the „transversal“ disciplines and hermetism. Especially unpleasant, according to Callois, is fitting mimetic phenomena into biological functioning and usefulness - if the phenomenon does not work, then it is an optical illusion, if on the other hand it does work, then mimesis exists. The book is literally „filled“ with thoughts from a different end of the intellectual spectrum than the biological sciences *sensu stricto* and in this way it represents one of the very few views on mimetic phenomena which is not wholly biological in perspective and so is an unusually valuable resource for anyone who is interested in mimetism from a different perspective than is offered by the purely scientific view.

Bernardi, **Pierre**, and **Guillaumin** were all interested in mimicry in African butterflies, Boulard was interested in the mimicry of cicadae (see also the *Bibliography*). Another scheme for the division of mimetic phenomena and a new nomenclature for the same were proposed in the works of **Pasteur** (1972, 1982) - the work itself is very shrewd and ingenious, but it is good to know that mimetic phenomena can be classified indefinitely according to many criteria without bringing any new information to light (the only new thing being is that every important new system, which catches on, allows, in the sense of **Foucault's** epistémé, a new discussion to commence and in the system lie implicitly and ahead of time all the possible results of the discourse).

Mimicry in plants and fungi

The problem of mimicry in plants is much harder to systematically analyze than the problem of mimicry in animals. Deception and imitation are on one hand a relatively common phenomenon in plants, but on the other hand literature on the subject is very disperse and is relatively hard to find. Mimetic phenomena in plants are also incomparable to animal mimicry and it is impossible to create a unified system of classification which covers every plant and animal mimetism without „bending“ the facts in at least some cases. Mimetic phenomena in plants were described as early as the first half of the 19th century, but the first well-arranged book on this theme was written by **Hildebrandt** (1902), who was very skeptical of the very existence of mimetic phenomena in plants. A composite, well-arranged work was written in the near past by **Wiens** (1978), or the unpublished diploma thesis written by **D. Müller** from the University of Freiburg (**D. Müller**, 1979). **Van der Pijl & Dodson**, 1966, and **Faegria & van der Pijl**, 1971, also allotted much space to flower mimicry. Because the individual categories of similarity in the plant kingdom are quite disparate, the historical development of the various points of view in various branches will be discussed separately (firstly we will deal with higher plants).

In contrast to animals, higher plants only rarely display **cryptic** phenomena. Succulent plants from South and East Africa and Madagascar often imitate abiotic substrates such as stones, pebbles, or the surface of the ground or sand. The first mention of the cryptic imitation of stones in the substrate by the "living stones", *Lithops* (Mesembryanthemaceae), which grow on the substrate, comes from **Burchell** (1822) (this author also mentions the South African „*curious little* Crassula ... [which is] *mistaken for the dung of birds*“, p. 310, this being the first mention of this curious case of crypsis). This phenomenon was later often described and commented (for example **Marloth**, 1904, 1905, 1929 among others - see the *Bibliography*). This mainly concerns the families Mesembryanthemaceae, Crassulaceae, Euphorbiaceae, Liliaceae, and Portulacaceae (a summary of these and many other mimetic plants can be found in **Wiens**, 1978). Certain North American cacti also imitate stones and boulders, mainly the genera *Pediocactus* , *Sclerocactus* and *Ariocarpus* (Cactaceae) - **Weins**, 1978, **Purpus**, 1914. It is interesting that earlier authors, especially **Marloth** (1929), but basically **Schwantes** (1957) as well, did not think that selection could have been the cause of these cryptic phenomena. People have at first great difficulties in discerning these cryptic plants, but after discovering the first it is easy yet surprising to discover how many actually exist in the biotop (the time of flowering is of course an exception, because the flowers are easy to discern). Stones and pebbles are also imitated by various larger seeds, for example of the castor bean, *Ricinus* (Euphorbiaceae) and **Sherzer** (1896) describes the excellent cryptic mimesis of the seeds of a unspecified shore plant from the Philippines, which in detail imitates pebbles with silicon veins and which come in a great many variations.

The region of Southern and Eastern Africa contains many genera of succulent plants (from the same families as those which have a „stone-type“ crypsis, and Asteraceae as well) which have developed an imitation of dried twigs on the above-ground part of their bodies. These mimetics always grow under a diverse group of bushes, where in semiarid conditions there is an abundance of fallen, dry twigs. Certain genera of cacti in South and North America (*Pediocactus, Sclerocactus, Opuntia,* etc.) have spikes which imitate dried grass (**Wiens**, 1978). Certain South African plants, e.g. the genus *Anacampseros* (Portulacaceae), even imitate the excrements of birds and smaller mammals (**Wiens**, 1978).

Crypsis in plants is not limited to arid regions, as it would seem from the above text. The massive leaves of the titan arum, *Amorphophallus* (Araceae), from South-Eastern Asia have petioles which grow from the rainforest soil which imitate lichens, which makes them appear similar to the bases of smaller trees. An interpretation on the basis of the apparent functionality is very difficult. The African climber from the genus *Fockea* (Asclepiadaceae) has leaves which imitate the leaves of the tree that it climbs, this includes for example the species *Euclea undulata* (**Wiens**, 1978).

The imitation of the host by a semi-parasite is a special category of plant mimicry, where the imitation includes the shape and size of the leaves, the form of the branches and their branchings, etc. The phenomena, which has a certain similarity with its counterpart from the animal kingdom, can be found in the family Loranthaceae, and is prevalent especially in Australia (**Barlow & Wiens**, 1977, **Wiens**, 1978). This phenomenon was observed quite early (**Drumond**, 1840) and was later described (**Hemsley**, 1896, **Moore**, 1899) but the selectionist explanations were quite forced and generally not persuasive (tree-climbing phytophagous marsupials, which are in any case night creatures and are predominantly olfactory-based, were proposed as the selective agent by **Barlow & Wiens**, 1977 - other selective pressures, for example butterflies of the genera *Delias* and *Ogyris* /Pieridae/, whose larvae feed on these plants, were discounted by the same authors). It is interesting to note that in Australia 78% of non-tropical species from the family Loranthaceae are mimetic in this sense, but on different continents they usually are not - **Wiens**, (1978) also describes other cases form South Africa and North America. This phenomenon is definitely caused genetically and not by the environment - during an incidental attack of a non-typical host the mimetic parasite does not of course change its appearance. Many other examples of interesting mimicry cases by vegetative parts of plants, which are intended for phytophags, also exist - Some North American plants from the mustard family Brassicaceae (Cruciferae) have red dummies of eggs of butterflies from the family Pieridae on their stems or on the bases of their leaves (the butterfly females are optically oriented and usually do not lay eggs on „occupied“ leaves or stems - **Shapiro**, 1981). Similarly many species from the passion flower, *Passiflora* (Passifloraceae), from neo-tropical regions (e.g. *Passiflora cyanea, P. oesterdi*) have models of eggs of butterflies from the genus *Heliconius* (**Williams & Gilbert**, 1981), other species from the same genus (e.g. *P. adenopoda*) have optical petiole or leaf imitations of caterpillars of the before-mentioned butterfly genus (**Gilbert**, 1971, **Rothschild**, 1974), which serve to dissuade females from laying eggs on the leaf. Plants from the genus *Passiflora* also characteristically display extremely varied and notable leaf forms (individual species are in this respect unusually different). Evidently they optically imitate the shape of the leafs of different plants from their own locality in order to escape the attention of females of the butterfly genus *Heliconius*, which obviously are not interested in such plants.

The family Moraceae presents a very curious case of leaf mimicry - certain genera and certain species (the mulberry, *Morus*,the common fig tree, *Ficus carica* and especially the East Asian genus *Broussonetia*,papper mulberry) imitate in their youth or on new branches at the base of their stem (this is always limited to about 1.5 meters /4.5 feet/ above ground) leafs which have been chewed up by catterpillars, in certain cases the leaf seems to be chewed down to the veins (**Nimelae & Tuomi**, 1987). Due to the height limit, this adaptation is obviously meant for phytophages from lesser ungulates, but the function itself is not quite clear. The *Columnea kalbreyeri* (Gesneriaceae) also presents a very interesting leaf mimicry - it uses red transparent spots on the leafs to simulate flowers, which are hidden and grow for only a short time (**Vogel**, 1975). The mimicry of leaves is a very delicate question. A great many species have leaves which are similar to the leafs of members of different, quite often very distant genera and the confused quantity of species' names ending with *-folia* clearly show the abundance of this phenomenon (e.g. *Cyclamen hederifolia* /Primulaceae/ x *Hedera* /Araliaceae/, *Platanus* /Hamamelidaceae/ x *Acer* /Aceraceae/, *Thalictrum aquilegiifolium* x *Aquilegia* / both Ranunculaceae/, *Rosa berberidifolia* /Rosaceae/ x *Berberis* /Berberidaceae/). In rare cases this phenomenon is interpreted as classic mimicry formed through the selective pressure of phytophages, but usually it is considered to be a form of „convergence“, an adaptation to the abiotic factors of the environment (the question of the phytophagal predatorial pressure on the morphology of plants interested even **Heikertinger**, 1914, 1915, in his early works). Even the first glance at the leaf types found in a specific locality shows that the abiotic factors do not correlate very well with the leaf shapes and allow for an almost unlimited variability of form (the habitat is directly related to the form of the leaf only in a few specific cases, such as the fact that wide leafs do not occur in desert plants, or the occurrence of „drip tips“ found on many rainforest tree leaves, etc.). The form of plant leaves (or the fruiting bodies of fungi, as will be seen later), like the form of deer antlers, is a phenomenon which does not rely on selective pressure much, but rather occurs in practically any conceivable amount of variations (it is therefore understandable that the large number of higher plant species - over 100,000 - causes many leaf forms to be repeated in various groups). Certain „untypical“ species of plants are similar to quite distant species not only in the form of their leaves, but in their general appearance as well (for example the South Chinese oak *Quercus bambussifolia* (Fagaceae) imitates not only the leafs but the overall appearance of bamboos (Poaceae), with which the oaks sparsely co-exist in mountain forests (the bamboo also imitates in its overall appearance a certain species from the genus *Begonia*). Another example of a similarity of overall appearance between non-related species in the same locality is the Mexican agave cactus, *Leuchtenbergia principis*, which imitates the slow-growing agaves *Agave lechuguilla*, which grows together with the cactus. Another example concerns certain American eryngo species, the genus *Eryngium* (*E. bromeliifolium*, Mexico, *E. agavaefolium*, Argentina) which imitate the overall appearance of bromelias or agaves (the genus *Eryngium* belongs to the family Daucaceae). This phenomenon is much more common than is generally belived and gradually fades into the category of the imitation of the so-called „life forms" (cykads and palms, grasses and sedge /*Carex*/, cacti and succulents /*Euphorbia*/, etc.), which is a phenomenon which does not by far have to concern plants from one locality and which also is not strongly (if at all) influenced by selective pressure (a similar situation occurs in flowers, as will be shown further). Sometimes the question of „true" mimicry according to **Bates'** scheme is discussed in literature - usually concerning European plant species with a similar appearance to e.g. nettles (*Urtica*), for example *Campanula trachelium, Lamium album* (the problem of the similarities between the vegetative parts of plants and their life forms was discussed in the first ever works on plant mimicry, e.g. **Bennet**, 1877, **Dyer**, 1871, **Lubbock**, 1886). Convincing experiments on this topic with herbivores have not yet been carried out, even though it is probable that they can optically discern various plant forms (certain optical modifications, such as the imitation of the central leaf rib perpendicular to the actual rib found in certain species of the genus *Begonia*, are more than inexplicable).

A special category of plant mimesis is the mimicry of weeds, which was first described by Russian authors at the beginning of the twentieth century (**Zinger**, 1909, **Sutulov**, 1914, **Baroulina**, 1920, **Vavilov**, 1922). The phenomenon concerns weeds which thrive in cultured field and due to the selective pressure of humans or machines during hoeing and later during the sorting eventually gain an overall appearance, or size and weight of seeds, which is similar to the primary crop. The problem is quite instructively and extensively described by **Wickler** (1968), which is why it will not be in detail described here. Especially well known are weeds which grow in cultures of flax (*Linum usitatissimum*, Linaceae), a plant which in the past required a very careful weeding by hand, which selected weeds of a direct, unbranched appearance (e.g. *Camelina linicola*, Brassicaceae; *Polygonum linicola*, Polygonaceae; *Spergula maxima*, Silenaceae), or even in *Cuscuta epilinum* (Cuscutaceae) whose seeds have the same size as their host plant (in this case the two connected seeds of the *C. epilinum* correspond to the one "host" seed). The above mentioned taxa, at times considered species, other times sub-species or forms, are obviously derived by human selection from forms which are closely related but not mimetic (the phenomenon is analogous to the selection of domestic animals to the „owner's own image", as was mentioned earlier, with the difference that this phenomenon occurs involuntarily and against the will of the farmers - basically it does not matter whether the selective agent is man or machine, both cases concern one form of mimetism where the mechanism of its formation is quite obvious and guaranteed). There is a large group of mimetic weeds, for example, spring vetch, *Vicia sativa* in the lentil (*Lens esculenta*, both Fabaceae) or *Lolium remotum* in barley (both Poaceae) (**Shaw & Base**, 1929, **Rowlands**, 1959). The problem of the mimicry of sprouting plants was also discussed in literature (**Kalačevskaja**, 1929).

Insectivorous plants are a group which present very distinctive leaf mimicry (**Wickler**, 1968, **Joel**, 1987), the most extreme being the venus flytrap, *Dionaea muscipula* (Droseraceae), whose inner catching-leaf imitates a flower. Even the tentacles from the sundew, *Drosera* are often interpreted as imitation of nectaries. Also the trap leafs of members of the families Nepenthaceae, Saraceniaceae, and Cephalotaceae have certain indications of flower simulation, especially their red-brown coloration and also the actual production of nectar, while at the same time the imitation of the flower is not perfect, but only faintly familiar in appearance (this is in a way analogous to Peckhamian mimicry in animals).

A special group of mimics, found only in tropical regions, is composed of species which imitate pulpy fruits of certain plants by seeds, especially by trees from the family Fabaceae, but includes others as well (see also **McKey**, 1975, **Wiens**, 1978) - the phenomenon itself was first discovered by **van der Pijl** (1969). This phenomenon concerns the fact, that seeds without pulpy components simulate, often quite perfectly, berries (usually red) which have this component or fruits which have pulpy arilus (red and black color combination) and are then swallowed and spread by deceived berry-eating birds, who gain nothing by this because the imitators pass through the digestive tract basically unchanged. **Wallace's** interpretation of the bright colors of pulpy fruits as being intended to optically lure birds and use them to spread was described earlier.

A large group of mimetic phenomena between plants has to do with flowers. The question of the mimicry of flower appearance has been discussed quite extensively in literature - the targets of that mimicry are pollinators, usually insects, occasionally hummingbirds as well. The first example of this type can be found in **Wallace**, 1889, from South Africa, where the

Impatiens capensis and *Ajuga ophrydis*, the only members of their genera in South African flora, imitate in the outward appearance of their flowers orchids and in this way „borrow" their pollinators. Many cases of plants which imitate the form and color of flowers of other non-related species and at the same time produce little or no nectar are known and can be found especially in **Wiens** (1978) and **Dafny & Bernhard** (1990). Cases where the flower mimicry is also related to semi-parasitism, similarly as with the leaf mimicry of the family Loranthaceae mentioned before, should also be examined. This case concerns the North American elephant head, *Pedicularis groenlandica* (Scrophulariaceae), and the shooting star, *Dodecatheon pulchellum* (Primulaceae – the host) (**Macior**, 1971) and the South African orchis *Orthopenthea fasciata* (Orchidaceae) and *Adenandra* (Rutaceae – the host). Flower mimicry of this type smoothly changes into convergence, as long as both species produce enough nectar and have the same pollinators, and at the same time the group can include many species from various families, from which only a few are different in their general appearance of their flowers from the usual garb of their genera or family - see also **Proctor & Yeo**, 1972, **van der Pijl & Dodson**, 1966. This phenomenon is occasionally analogously called the "Müllerian" floral mimicry.

The problem of the similarity of flowers of plants from different families is close to the problem of such similarities on the leaves (e.g. the similarity of the flower of the *Helianthemum* - *Potentilla* - *Ranunculus*) and in addition it is strongly influenced by the fact, that flowers of a similar type lure similar pollinators. The relation of flower colors to their pollinators is one of the cardinal examples of addressed proper phenomena in Portmann's sense in the living world was first noted by **Ch. Sprengel** (1793), a German parson and natural theologian, who interpreted the genius of these interdependencies from the standpoint of a religious Creationist, who marveled at the perfect sophisticatedness of all Creation (because Sprengel worked with European plants, he considered only insects and not hummingbirds, which pollinate flowers which are usually brightly red, or bats, which pollinate flowers which usually are not vividly colored, white, or are another light shade and the luring agent is their strong odor). It is interesting to note that even Linné considered the main pollinating agent to be the wind, insects were only secondary. The fact that **Darwin** overestimated the meaning of flower color and other adaptations which are related to it was discussed in the chapter about Darwin, **H. Müller** and their colleagues. **Sprengel** (1793) was one of the earliest to note that certain flowers are deceptive in the sense that in spite of the "promising" appearance they contain no nectar (e.g. the genus *Orchis* and many others). This phenomenon is sometimes formally considered "mimetic", which is basically not true, because it does not contain any active imitation. This aspect is fulfilled even in the case that the flower pretends to contain nectar and pollen or that the flower optically deceives the pollinators into thinking that there are more of these attractive sources of pollen and nectar than there really are. This phenomenon has been known the longest in the bog star, *Parnassia palustris* (Saxifragaceae), where the staminodia imitates with their projections of hyaline parenchyma drops of nectar (which is actually really present, but only at the very base of the flower - this case is mentioned by **Wallace**, 1889, and furthermore by **Daumann**, 1933, 1935, 1971). Similarly the imitation of pollen is quite common, either by partial optical „multiplication" of real pollen on the stamina by yellow hairs (e.g. the mullein, *Verbascum*), or the optical imitation of either sterile stems (the fertile ones are hidden in deeper parts of the flower) or by yellow spots on the petals, which sometimes bulge outward. This phenomenon was already described near the end of the 19th century using orchids from the genus *Calopogon* (**Robertson**, 1887). A separate type of mimicry is made up of plants whose stigma in the female flowers of those species with divided sexes imitate pollen - *Begonia, Carica, Anguria*, and others (this quite common phenomenon is occassionally called "automimicry"). An interesting imitation is the joined stamina found in many members of the family Cucurbitaceae which optically imitates the gynaeceum (the purpose of this imitation is not really understood). "Inner-flower" mimicry is covered by **Gack**, 1979, or **Müller**, 1979 for example.

A wholly specific category of floral mimicry concerns the flower imitation of a substrate which is attractive for many Diptera and usually serves as a material for the development of their larvae. Generally this includes carcasses, infected wounds, excrements, urine, and also fungi. Very often this adaptation is related (especially in the "snake root", *Aristolochia,* or the family Araceae) to the short-term imprisonment of the insect in the flower or inflorescence (*"Kesselfallenblumen"*), which is made possible by reversed hairs, smooth walls, or steep windows in the spatha (which makes use of the positive phototaxis of most Diptera). Only after the unsuccessful escape attempts have finished the pollination or have covered the insect in enough pollen does the flower "free" the trapped insect. These adaptations belong to the most ingenious in the whole of nature and from the 19th century have been described many times in literature (a summary can be found in **Faegri & van der Pijl**, 1971, **Kugler**, 1955, 1970, **Wickler**, 1968, or **Müller**, 1979). The imitation of carcasses or wounds relies heavily on an appropriate scent in combination with dark colors, especially red-brown, in certain cases also with hairs which imitate the fur of the carcass (certain members of the genera *Aristolochia* and *Stapelia*). The impression can be very convincing not only for Diptera, which often attempt to lay their larvae or eggs on these interesting objects (this type of substrate mimicry on the mimetic flowers typically does not allow the larvae to fully develop), but can deceive humans as well. This mainly applies to the families Araceae (e.g. *Amorphophallus* and many other genera), Asclepiadaceae (*Stapelia, Ceropegia*), Rafflesiaceae, Burmanniaceae, Aristolochiaceae (*Aristolochia*), and Orchidaceae from Australia (e.g. the genus *Pterostylis*). It is analogous in groups which imitate excrements, with the exception that the olfactory impression is more important than the optical - certain genera, e.g. *Arum*, simulate fresh excrements even through an increased temperature in the spatha, which is caused by the high metabolism of sacharids (the phenomenon is quite noticeable - the difference being often up to 10° C higher than the surroundings - and was mentioned even by **Lamarck** near the end of the 18th century). Certain other families, e.g. Anonnaceae, imitate rather the smell of rotting fruit and lure mainly beetles (see also **Gottsberger**, 1970, 1975, **van der Pijl**, 1960). The imitation of fungi by flowers is also very interesting - it serves to lure members of the family Mycetophilidae (fungus gnats), which serve as pollinators (a summary can be found in **Vogel**, 1978). Here the imitation includes a typical mushroom scent and structure, whether the gilliform (the labellum of the flower of the Australian orchid of the genus *Masdevallia*, the inside of the perigon of certain species of the genus *Asarum* /Aristolochiaceae/ or the spatha of the genus *Arisaema* /Araceae/) or porous mushrooms (a part of the perigon of the flower of the Mexican *Aristolochia arborea*, or the spadix in the flower of the Italian mouse plant, *Arisarum proboscideum*). Mushroom mimicry of the latter was clearly recognized quite early by **Arcangeli** (1891) and the first description of this phenomenon by **Savi** (1825) used the term "*fungoso - rimosus*".

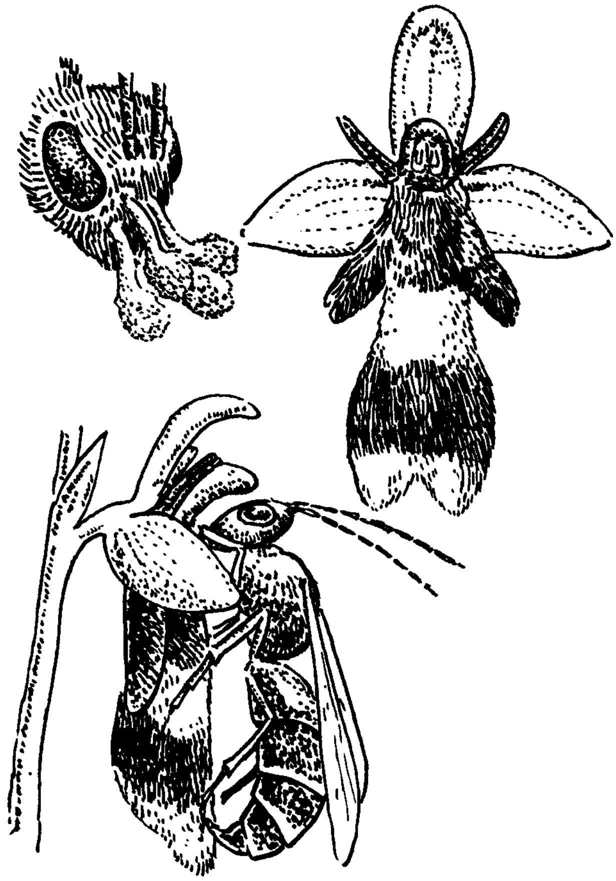
The appearance of containing an insect is a specific form of flower mimicry. **Hutchinson** (1946) describes an example from South Africa concerning the beetle daisy, genus *Gorteria* (Asteraceae), which (in comparison with the related genus *Arctotis*, which grows in the same locality) does not suffer from intrusive beetles as does the latter genus. The genus *Gorteria* has for this a dummy of a living beetle in the middle of its flowers - the flower is therefore already "taken" and real beetles have no interest in it. The flowers of certain European members of the genus *Pulsatilla* (Rannunculaceae) have in their centers something which seems like a bumblebee or some other large hairy insect (the function here is not very clear). The unique dark flower in the middle of the inflorescence of the cultivated carrot, *Daucus carota,* and certain other members of the family Daucaceae is sometimes interpreted as being an insect dummy (**Detto**, 1905b considered it an adaptation which protected the carrot from large herbivores, which would be afraid of stinging insects sitting on the flower, **Daumann**, 1973, considered it a method for luring pollinators, something which appealed to the aggregate instinct of flies - the furry nipple-shaped structures on the petals of the orchid *Paphiopedilum* is interpreted in a similar way - **van der Pijl & Dodson**, 1966). Another phenomenon which is often considered an optical lure for Diptera are the "glittering bodies", "*Flimmerkörper*", on the flowers from the genus *Ceropegia* (Asclepiadaceae) and certain orchids (*Cirrhopetalum, Megaclinium*), which is formed in the first case from individual hairs, in the second from the entire labellum (**Vogel**, 1954, 1975). Two orchids, the Mediterranean *Epipactis consimilis* (**Ivri & Dafni**, 1977) and the Sri-Lankan *Oberonia thwaitesii* (**Faegri & van der Pijl**, 1971) have aphid dummies on their labellum - the first is pollinated by hoverflies, family Syrphidae, which searches for a adequate place for laying eggs (the larvae are aphidophagous), the second is pollinated by ants.

A wholly unique group of floral mimicry is made up of "sexual" mimicry of orchids from the genus *Ophrys* and certain other genera, where the flowers imitate dummies of the females of certain Hymenoptera through olfactory, optical, and tactile sensations and are pollinated (by transporting pollinaria, as is usual for orchids) by the efforts at copulation by the males. The genus *Ophrys* has always attracted attention because of its unique "psychedelic" flowers, whose form reminds even amateurs of insects and which have a certain "animalness", especially the red-brown color tones of their flowers remind us of coagulated blood, the color patterns of the flowers are unusually complicated and optically enhance the third dimension of these flowers. The Syrian magical tradition in Antiquity used it (or rather its bulb) for their sexual - magical rituals (it is interesting to note that a certain "sexual inappropriateness" in flowers was noted even then, although the aberrant mechanism of pollination was of course not yet known). Even Renaissance authors, such as **J.-B. de la Porta** (1608) introduce this genus as a typical example of an imitation of bees or flies in flowers /in the same way as for example the flowers of peas or the *Lathyrus* represent an imitation of butterflies, according to him/. Even the species names given to various species by **Linné** and other botanists (*O. insectifera, apifera, muscifera,* etc.) very widely spread this similarity between the flowers and insects. The opinion that the striking imitation of insects by flowers is supposed to deter ordinary pollinators (bees, bumblebees, etc.) by making it seem that the flower is already taken, prevailed for quite a long time. This thought was formulated already in 1831 by **R. Brown** (quote **Wickler**, 1968) and was in more detail expressed and by observation strengthened by **Detto** (1905a). But why it would be necessary to deter pollinators from flowers which in any case have no nectar is not clear. Already in 1829 **H. Smith** in his work on flora found in Kent observed the "attacks" of solitary bees on the flowers of the genus *Ophrys*, but he did not observe the sexual motivation and pseudocopulatory character of the behavior (the observation was quoted by **Darwin**, 1862, as well). A modern interpretation was given by **Correvon & Pouyanne** (1916) and **Pouyanne** (1917), which was based on their Algerian observations and for this reason the phenomenon is sometimes called **Pouyannian mimicry**. In the twenties this theme interested another British entomologist **M. J. Godfery** and in 1927 **E. Coleman** described another analogous example from Australia, where a number of species of terrestrical orchids of the genus *Cryptostylis* are pollinated in a similar way by the ichneumon wasp *Lissopimpla semipunctata* (later it was shown that a whole group of Australian orchids, especially *Chiloglottis, Drakea, Spiculaea,* and *Caladenia*, present a dummy of wingless females from the digging wasps family Thynnidae / Hymenoptera/ and are pollinated in a similar pseudocopulatory way by the males, for more see the *Bibliography*). The theme of pseudocopulation was greatly discussed in the twentieth century, especially in the second half, and a large amount of literature was published concerning it, most of which dealt with this problem in connection with the genus *Ophrys*, either from the standpoint of the ethology of pollinators, or from the standpoint of the chemical aspects of pheromones (e.g. **B. Kullenberg**, **H. F. Paulus** and **C. Gack**, **F. Schremmer**, and many others - more details can be found in the *Bibliography*), substantially fewer works were written on Australian genera (e.g. **W. P. Stoutamire**, more details in the *Bibliography*). As is apparent, the perfect imitation of the female is not really that important (only a rough schematic is necessary), but the imitation of the surface texture and of course of the reproductive pheromones is essential. During pseudocopulation ejaculation does not occur and this evidently does not in any way injure the pollinators. The pollinaria are in certain cases transported on the head, in other cases on the abdomen, according to whether the "head" of the "female" is located at the base or at the end of the flower labellum (some species from the genus *Ophrys* are different than this). Some cases of pseudocopulation in insects from different orders than Hymenoptera have also been observed, for example the hoverflies (Syrphidae) and melolonthid "chafers" (Melolonthidae) on the orchid *Ophrys* (Engel, 1985) or flies from the family Tachinidae (*Paragymnomma*) on the orchid *Trichoceros antennifera* (**van der Pijl & Dodson**, 1966). One single observation of the pseudocopulation of a flower which is not a member of the family Orchidaceae exists, and that in the sabara, *Guiera senegalensis* (Combretaceae), from tropical Africa, the pollinators are solitary wasps from the family Sphecidae (**Kullenberg**, 1961).

The family Orchidaceae displays a number of other examples of aberrant pollinating techniques on a mimetic base - the neo-tropical orchids *Ada, Brassia*, and *Encyclia* imitate through the form of their labellum larvae, into which female parasitical wasps lay their eggs - during this "pseudoparasitism" the flowers are pollinated (**van der Pijl & Dodson**, 1966). The orchid genus *Oncidium* imitates the flying males of the neo-tropical solitary bees from the genus *Centris* and during territorially motivated attacks the flowers are pollinated (**Dodson & Frymire**, 1961, **Dodson**, 1962). The Mediterranean orchid genus *Serapias* allegedly imitates the „sleeping burrows" of the males of solitary wasps and uses their rest period for pollination. Extensive literature exists about bees from the South American subfamily Euglossinae, where males collect from the flowers of certain orchids and other flowers (Gesneriaceae, Araceae) various substances, which they later use as sexual pheromones (**Dodson**, 1962, **Dressler**, 1968, and many other later works) - This case, even though it is often considered mimetic, does not really belong in this category.

A wholly unusual category of form in higher plants are galls, which are caused by the activities of parasitical insects – the gall wasps, Cynipidae (Hymenoptera) or the gall midges, Cecidomyidae (Diptera). They form a unique attachment to the form of leafs and fruits, especially from the standpoint that their external appearance is evidently caused by the activities of parasites, but hardly has any functional or therefore selectional value. This form is often quite different from the forms which the plant would develop under normal circumstances (e.g. structures evoked by the gall wasp *Rhodites rosae* on wild roses) and at first glance does not

The terrestrial orchid *Ophrys insectifera* is pollinated by male solitary bees during attempts at copulation with the dummy of the female, which is in fact the flower; the head of the male then carries pollinaria (according to Wickler).



have to appear pathological. Certain unique works which indicate mimetism by galls also exist (**Rainbow**, 1895, **Fuller**, 1896, **Thomas**, 1897, **De Stefani-Perez**, 1905).

From the lower plants mosses from the family Splanchnaceae (*Splanchnum, Tetraplodon*) display very conspicuous mimicry - the discs, which are up to 1 cm wide, formed by the widening of the seta under the capsule, imitate through their yellow to red, or purple, color the flowers of higher plants (according to different theories the color serves only for an optical illumination of the entire body, which emanates a carcass-like odor). In any case these structures lure Diptera, which then spread the spores (in addition these mosses thrive on rotting substrates and carcasses). Works on this theme have sporadically appeared since the end of the 19th century (**Bryhn**, 1897, **Bequaert**, 1921, **Erlanson**, 1930, **Steere**, 1958, **Schremmer**, 1963, **Crum**, 1976).

Observation and understanding of form, coloration, and mimicry in fungi as a wholly specific phenomena is necessary for understanding form, coloration, and mimicry in live nature in general. The fruiting bodies of higher fungi present an amazing array of variability, which is not dependant on the function of the fruiting body (basically the formation of conspicuous fruiting bodies is not necessary for the spreading of the spores, in the same way as the external structure of the mushroom is not determined by its internal anatomy - they are something like „free-style creations“ made from water and mycochitine). These fruiting bodies also present an large array of various colors, from wholly cryptic (*Tricholoma equestre, Xerocomus badius*), which cannot be seen almost at all, to brightly colored „aposematic“ (*Amanita muscaria*). It is true that the cryptic colorations are usually found in species which can be eaten by warm-blooded vertebrates and the „aposematic“ species tend to be toxic or unpalatable, but this relation works only statistically and in addition optically oriented mushroom eating animals are quite rare (in temperate regions maybe squirrels). This whole color scale, including all other possible variations, in the same way as the whole scale of smells, which are produced by fungi and whose meaning is not clear, create the impression that the colors found in nature (and to an extent the various forms and smells) were sort of „tested“ or „allowed to freely develop“ here. This phenomenon interested (in the same way as the metallic coloration of certain insects) an amazingly small group of people, it is not mentioned even by **Portmann**. The interpretation of the form and coloration of mushrooms can be seen as one of the conspicuous applications of **Möbius'** (1896) postulate of the „principle of beauty". On occasion mycological literature describes the close similarity between certain non-related mushrooms (e.g. *Suilus luteus* x *Cortinarius* sp.) as an example of mimicry, the world of mycological folklore also includes an observation about the color and form analogy between the stem base of certain mushrooms and the base of the trunk of their symbiotic tree (*Leccinum aurantiacum* and the birch, *Boletus reticulantus* and the oak). Only a minimum of form and color creations in the mushroom world can be clearly interpreted as mimicry in the Darwinian and later meanings of the word - one example is the stinkhorn, *Phallus impudicus* (the mimicry does not concern form, but the stench emanating from its slime, which includes spores that are then spread in the digestive system of flies which feed on carcasses- e.g. **Schremmer**, 1963). A whole range of members of the same family (Phallaceae) more or less remind us (through their form) of actinomorphic flowers of higher plants and their spores are likewise spread by flies (e.g. *Aseroe rubra, Anthurus aseroeformis*, to a lesser extent *Dictyophora indusiata* or *Clathrus*). Especially the first two examples seem to imitate the „carcass" flowers of higher plants, sometimes it is considered a form of mimicry, other times convergence (**Wickler**, 1968, **Ingold**, 1971).

A whole range of rust fungi (Pucciniaceae) creates a carcass-like or on the other hand fruit or flower-like smell to spread their spores through flies or other insects. An especially nice example of this is a recently described case of the Agrentinian rust species *Puccinia monooica*, which changes the morphology of the rockcress, *Arabis* (Brassicaceae) in such a way that the top level of its leafs are completely covered in spores and perfectly resemble the yellow radially symmetrical flower and lures butterflies not only optically but also olfactorily as well - the butterflies then spread the spores (**Roy**, 1993). **Saville** (1976) describes a different adaptation in rusts of the genus *Ravenelia* which parasite on the leafs of mimosa, whose pycnidia reminds us of dropped pollen from the plant and are collected and spread by bees.

In connection with plant and generally biological form I cannot in the end not mention **van Iterson's** (1907) book about the application of mathematical principles on plant forms and protist shells of Foraminifera, which makes for a nice addition to the before mentioned book by **D'Arcy Thompson** (1917) about animal forms and the possibilities of their mathematical transformation. Iterson's study continues in the study of German romantic biology concerning the so called spiral theory of the location of leafs on plants (**K. B. Schimper** and **A. Braun** in **Sachs**, 1875) and is also a continuation of another work from this era concerning the form of the living world in general (**Bronn**, 1858).

Summary

The problem of mimicry in nature cannot be separated from the general problem of the form and external appearance of organisms, as can be seen in general in Portmann's work. The ingenious system of components of the external appearance of organisms obviously exceeds the narrow functional explanation given by biology and this type of interpretation is a greater barrier for true understanding than for example the „artistic-historical" principles of explanation, which can often turn out to be more adequate. The problem of mimicry also cannot be separated from the problem of similarities in the living world and it is necessary to realize that the various categories and terms, which are used to explain coloration and the external appearance of organisms, represent help in desperation in a situation where we are not able to grasp this basically unified phenomenon with a unified theory (basically in the same sense as the fact that electricity and magnetism were originally considered separate phenomena). The reference to „coincidence" in such phenomena is a resignation on any possibility of grasping the phenomena and at the same time it is an attempt to lighten the whole phenomena, to take away its value and meaning. An especially misleading method is using a dichotomy of coincidence and necessity in the world of the biology of external appearance, because such a dichotomy is an invented extreme of a certain continuity, in the middle of which we find something like creative freedom, which is neither „coincidental", nor „necessary", but has many varieties which require explanation, even though this does not have to be clear or simple (in arts this is quite natural and to be expected, but in organisms such a view has yet to be accepted, even though is possible that the world, especially the living one, is basically unified - a snail creates its shell in the same way as a writer creates a novel). Organisms most probably have something which we can compare with human will, intentionality, and creativity, if only on an unconscious level. It would in any case be strange if these human traits sometime in the Paleolithic period suddenly just „popped up" from nowhere - it is more probable that they just emerged from the unconscious and took up place in the conscious sphere and that they belong to organisms in general.

The problem of deceptive imitation, which we can call mimicry in the narrow sense, cannot be easily reduced to biological effects; if only for the reason that whoever notices the similarity must necessarily be human and must study phenomena of the living world. Merging the study of mimicry with a sociomorphical view of goals and usefulness is, as Callois notes, unusually un-good - if the phenomena does not work, it is an optical illusion, if it does, then mimicry exists. The phenomenon itself is one thing, sensing the phenomena by bird predators for example is another thing, even though it is very interesting. It is not truly possible to underrate the role of the selective pressure of predators on the formation of mimetic phenomena, the absolutization of selection is also misguiding and causes other aspects to be left out. It seems that the role of selection is often limited to „delicate fine-tuning" of mimetic similarities, while the basic direction of the development of the similarity is given by the autonomous inner dynamics of the given organism (a living organism has the „freedom" to create or not create a mimetic adaptation, only in this way can we explain the „preference'" of certain groups of organisms, for example longhorn beetles, family Cerambycidae, for certain mimetic phenomena in the sense of imitating other groups - if selective pressure was the sole cause of these phenomena, then the frequency of their distribution would be more or less equal in all groups). It is true though that within the framework of the current paradigm of modern science the explanations for mimetic phenomena can hardly be different than they currently are, but at the same time it is necessary to realize which unvoiced presumptions exist (e.g. the understanding that matter is a passive material which fills space and which has only inertia, and lacks its own activity). It is also necessary to realize whether the goal of the paradigm and of the science as a whole is to attain a more complex understanding of the world (including the living world) or whether the goal is maximal reductionism with ideological undertones (a certain amount of reduction is necessary for any system of knowledge of the world, but like everything else there is a optimal level, which is not equal to the maximum). These suppressed aspects of the world can especially be seen in systems such as Jungian psychology, which takes seriously even those things which modern sciences ignore. This is why „complementary" explanations of mimetic phenomena based on the principle of synchronicity (or syntopicity) or on the principle of

the *psýché* as terms which designate the totality of the autonomous dynamics and the self-building aspects of an organism (*anima est forma corporis*); also because interpsychic connections do not enter the framework of modern science, which is not built to use such terms, but which does not make them any less relevant (other aspects of knowledge and truth also lie outside of the competence of modern science). It is not this author's goal to undermine the many praiseworthy achievements in knowledge and interpretation of the world and manipulation with it made by modern sciences, but it is especially mimetic phenomena that best show the limits and borders of these sciences, which, if put forward in an absolute, give rise to scientism of a religious type, which is not dissimilar to the dogmatism and self-centeredness of other religions.

Glossary

aposematic, aposematism - a warning coloration, mostly contrasting and conspicuous, found on unpalatable or toxic animals
dummy - the imitation of some object using different means, e.g. the imitation of female genital swelling by males in the hamadryas, *Papio hamadryas*
centricity - inwardness, the sum of hidden aspects of an organism's (from the cell physiology to psychic properties), Portmann's „*Innerlichkeit*"
coloration - an optical impression of an organism based primarily on color
countershading - an optical method of camouflage, where the dorsal part of an organism has a darker color than the ventral part
cryptic, crypsis - a concealing coloration, camouflage, the reverse of semantic
epigamic - connected with courtship and mating behavior
exaggerated structures - overlarge, luxurious structures on the organism, e.g. deer antlers
eye-spot - the optical simulation of an eye by concentric rings or similar color patterns
false head - the simulation of a head on a different part of an organism
flash coloration - a short showing of a pseudaposematic coloration to the predator
hypertely - an adaptation which surpasses the „required" level, e.g. „hyperrealistic" cryptic adaptations
mimetic, mimetism - the imitation of other organisms or inanimate objects in a broad sense
mimic - an organism which imitates a model organism
model - an organism which is imitated by a mimic organism
myrmecoidy - the imitation of ants, to be ant-like
Oudemans' phenomenon - a linking color pattern which ignores the natural morphological structures of the organism
pattern - an optical impression of an organism based primarily on pigment ornaments
phytomimesis - the extreme cryptic imitation of plant parts by animals
proper phenomenon (p. manifestation) - the externalization of an organisms **centricity**, Portmann's „*eigentliche Erscheinung*"
pseudaposematic, pseudaposematism - a conspicuous coloration of palatable animals, mostly found on hidden body parts (hind-wings, etc.)
self-presentation, self-display - Portmann's „*Selbstdarstellung*" of the organism's external appearance
semantic - conspicuous, carrying some optical message, the reverse of cryptic
somatolysis - a disruptive cryptic coloration which optically divides an animal into parts

Bibliography

Agassiz L. (1858): Essay on classification. Philadelphia, Little, Brown &Co.

Aitken E. H. (1894): The larva and pupa of *Spalgis epius*, Westw. Journ. Bombay Nat. Hist. Soc. 8:485–485.

Allen G. (1879): The colour sense: its origin and development. An essay in comparative psychology. London, Trübner.

Allen G. (1882): The colour of flowers as illustrated in the British flora, with illustrations. London, J. Murray.

Allen J. A. (1874): On geographical variation in color among North American squirrels, with a list ... . Proc. Bost. Soc. Nat. Hist. 16:276–294.

Anonymus (1896): Resemblance of pupa of *Fenisca* to human head. Ent. News. 7:193.

Arcangeli G. (1891): Sull' *Arisarum proboscideum* Savi. Nov.Giorn. Bot. Ital. 23:545–549.

Argyll, Duke of (1869): The reign of law. London., Longman & Comp.

Autumn K., Batur H. (1989): Mimicry of scorpions by juvenile lizards, *Teratoscincus roborowskii* (Gekkonidae). Chin. Herpetol. Res. 2(2):60–64.

Baker E. C. S. (1923): Cuckoos' eggs and evolution. Proc. Zool. Soc. Lond. 1923: 277–294.

Bard J. B. L. (1977): A unity underlying the different zebra striping patterns. Journ. Zool. 183:527–539.

Bard J. B. L. (1981): A model for generating aspects of zebra and other mammalian coat patterns. Journ. Theor. Biol. 93:363–385.

Bard J. B. L., French V.(1984): Butterfly wing patterns: How good a determining mechanism is the simple diffusion of a single morphogen? Journ. Embryol. Exper. Mophol. 84:255–274.

Barlow B., Wiens D. (1977): Host-parasite resemblance in Australian mistletoes: The case for cryptic mimicry. Evolution 31:69–84.

Baroulina E. I. (1920): On vetches (*Vicia sativa*) weeds in lentils (mimicry in plants). (in russ.) Rep. 3-th. All- Russian Conf. Plant- Breeding, Saratov.

Bates H. W. (1858): Excursion to St. Paulo, Upper Amazonas. Zoologist 16:6160–6169.

Bates H. W. (1859): Notes on South American butterflies. Trans. Ent.Soc.Lond. 1859:1–11.

Bates H. W. (1862a): Contribution to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. Trans.Linn. Soc.Lond. 23:495–566.

Bates H. W. (1862b): Contribution to an insect fauna of the Amazon valley. Coleoptera:Longicornes. Ann. Mag. Nat. Hist. 9 (3.ser.):446–458.

Bates H. W. (1863): The naturalist on the River Amazons. (2nd ed.1892) London, J. Murray.

Bates H. W. (1867): On a collection of butterflies formed by Thomas Belt, Esq., in the interior of the Province Maranham, Brazil. Trans. Ent. Soc. Lond. 1867:535–546.

Bates H. W. (1868): Descriptions of three new species of *Ctenostoma* (tribe Cicindeles) Ent. Month. Mag. 4:276–279.

Bates H. W. (1870): Contribution to an insect fauna of the Amazon valley. Trans. Ent. Soc. Lond. 1870:391–444.

Bateson G. (1979): Mind and nature. London, Wildwood.

Beal F. E. L. (1908): The relations between birds and insects. Yearb. Dept. Agric. Wash. 1908:343–350

Beccari (1884): Fioriturі dell' *Amorphophallus titanum* (in Piepers, 1903).

Becker K. (1949): Untersuchungen über die Farbenmuster und das Wachstum der Molluskenschale. Biol. Zentralbl. 68: 263–288.

Beddard F. E. (1892): Animal coloration. London, S.Sonnenschein &Co.

Beehler B. M. (1987): Birds of paradise and mating system theory. Emu 78(2):78–89.

Bell Ch. (1833): The hand its mechanism and vital endowements, as evincing design. The Bridgewater treatises ... Treatise IV. London, W. Pickering.

Belt T. (1874): The naturalist in Nicaragua. New York, E. P. Dutton.

Bemmelen J. F. van (1889): Ueber die Entwicklung der Farben und Adern auf den Schmetterlingsflügeln. Tijdschr. Nederl. Dierk. Ver. (2) 2: 235–247.

Bemmelen, J. F. van. (1912): Über die Phylogenie der Flügelzeichnung bei Tagschmetterlingen. Zool. Jahr. (Suppl.) 15(3):453–478.

Bemmelen. J. F. van. (1916a): Die Flügelzeichnung der Hepialiden. Zool. Anz. 48:167–187.

Bemmelen. J. F. van. (1916b). On the phylogenetic significance of the wingmarkings in Hepialids. Kon. Akad. Wet. Proc. Lect. Sc. 8:1255–1265.

Bemmelen. J. F. van (1917): The markings of Arctiidae. Proc.Kon.Akad.Wet. Amsterdam 20:849–860.

Bemmelen J. F. van (1918): The value of generic and specific characters tested by the wing-markings of Sphingides. Proc. Kon. Akad. Wetensch. Amsterdam 21.

Bemmelen J. F. van (1919): De vleugelteekening der Chaerocampinen. Versl. Wis. Nat. Afd. K. Akad. Wet. Amsterdam 28:380–390.

Bemmelen. J. F. van (1921): Das Farbenmuster der mimetischen Schmetterlinge. Zool.Anz. 52.269–277.

Bennett A. W. (1870): Is protective mimicry due to natural selection? Am. Nat. 11:3–7.

Bennett A. W. (1872): On the theory of natural selection looked from a mathematical point of view. Nature 3:30–33.

Bennett A. W. (1877): Mimicry in plants. Popular Sci. Rev. 11:1–10.

Bequaert J. (1921): On the dispersal by flies of the spores of certain mosses of the family Splanchnaceae. Bryologist 14:1–4.

Berg L. S. (1926): Nomogenesis or evolution determined by law. London, Constable.

Bianki V. (1961): Lesnaja gazeta. Leningrad, Dĕtgiz.

Biedermann W. (1904): Die Schillerfarben bei Insekten und Vögeln. Tn: Festschrift zum 70. Geburtstag von Ernst Haeckel. Jena, G. Fischer.

Blest A. D. (1957): The function of eyespot patterns in the Lepidoptera. Behaviour 11:209–256.

Blest A. D. (1963): Longevity, palatability and natural selection in five species of New World saturniid moths. Nature 197:1183–1186.

Boisduval J. B. (1836): Histoire naturelle des Insectes. Species géneral des Lépidoptčres. I. Paris,Roret.

Bonnier G. (1879): Les nectaires, étude critique, anatomique et physiologique. Ann. Sci. Nat. 8 (6 –me sér.).

Bosio G. (1610): La trionfante e gloriosa croce. Roma.

Botke J. (1916a): Les motifs primitifs du dessin des ailes des Lépidoptres et leur origine phyletique. Tijdschr.Nederl.Dierk. Ver. 25(2).

Botke J.(1916b): Bijdrage tot de kennis van de phylogenie der vleugelteekening bij de Lepidoptera. Versl. Meded. K. Akad.Wet.Amsterdam 24.

Bougainville L.-A. de (1772): Voyage autour du monde ... en 1766–1769. Paris, Saillant & Nyon.

Boulard M. (1973): Le pronotum des Membracides: camouflage sélectionné ou orthogense hyperthélique? Bull. Mus. Nation. Hist. Nat. Paris (3e sér.) 109, Zool. 83:175–156.

Bowden S. R. (1988): How the butterfly lost its spots – a cladistic excursion Br. Journ. Entomol. Nat. Hist. 1(3):101–104.

Brakefield P. M., French V. (1995): Eyspot development on butterfly wings: the epidermal response to damage. Develop. Biol.168: 98–111.

Brattstrom B. H. (1955): The coral snake „mimic“ problem and protective coloration. Evolutin 9: 217–219.

Braun W. (1936): Über das Zellteilungsmuster im Puppenflügel der Mehlmotte *Ephestia kühniella* Z. in seiner Beziehung zur Ausbildung des Zeichnungsmusters. W. Roux Arch. Entwicklungsmech. 135:494–520.

Braun. W. (1939): Contributions of the study of development of wing-pattern in Lepidoptera. Biol. Bull. 76:226–240.

Brinckmann A. (1958): Die Morphologie der Schmuckfeder von *Aix galericulata*. Rev. Suisse Zool. 65:485–608.

Bronn H.G. (1858): Morphologische Studien über die Gestalfungsgesetze der Naturkörper überhaupt und der organischen insbesondere. Leipzig & Heidelberg.

Brower J. v. Z. (1958). Experimental studies of mimicry in some North American butterflies. I.–III.. Evolution 12:32–47(I.),123–136 (II.), 273.–285 (III.).

Brower L. P. (1968): Automimicry, a new extension of mimicry theory. Am. Zool. 8:745.

Brower L. P., Calvert H. W. (1985): Foraging dynamics of bird predators on overwintering monarch butterflies in Mexico. Evolution. 39(4): 852–868.

Brower L. P., Horner B. E., Marty M. M., Moffit C. M., Villa R. B. (1985): Mice (*Peromyscus maniculatus labecula*, *P.spicilegus*, and *Microtus mexicanus salvus*) as predators of overwintering monarch butterflies (*Danaus plexippus*) in Mexico. Biotropica 17:89–99.

Brown K. S. Jr. (1984): Adult-obtained pyrrolizidine alcaloids defend ithomiinae butterflies against a spider predator. Nature 309:707–709.

Brown K. S. Jr. (1987): Chemistry at the Solanaceae-Ithomiinae interface. Ann. Mo. Bot. Gard. 74(2): 359–397.

Brun R. (1969): Untersuchungen über die Dynamik im Federkeim, unter besonderer Berücksichtigung der Musterbildung beim Argusfasan (*Argusianus argus L.*) Acta Zool. Pathol. Antverp. 49: 64sq.

Brunner v.Wattenwyll C. (1873): Über die Hypertelie in der Natur. Verh. Zool.-Bot. Ges.Wien 23:133–138.

Brunner v. Wattenwyll C. (1883): Über hypertelische Nachahmungen bei Orthopteren Verh. Zool.-Bot. Ges. Wien 33:247–249.
Brunner v.Wattenwyll C. (1897): Betrachtungen über Farbenpracht der Insekten. Leipzig,Engelmann.
Brunner v.Wattenwyll C. (1899): Die Färbung der Insekten. Wien.
Brunner v.Wattenwyl C. (1900): Note on the coloration of insects. Ent.Rec.12:2–4.
Brunner v. Wattenwyl C. (1906): Orthoptares. Expedition Antractique Belge. Résults Belg. Zool. Inst. 1906:9–11.
Bryhn A. (1897): Beobachtungen über das Ausstreuen der Sporen bei den Splanchnaceen. Biol. Centralbl. 17:48–55.
Bryk F. (1923): Parnassidae. Lepidopterorum Catalogus 27. Berlin, Junk.
Bryk F. (1928): Über den Mimetismus der afrikanischen Papilio-Arten. Ein Versuch zu einer neuen Mimikrytheorie. Soc. Ent. 43:9–12, 13–16.
Bubenik A. B. (1966): Das Geweih. Berlin, P. Parey.
Buck J., Buck E. (1976): Synchronous fireflies, Sci. Am. 234:74–85.
Buckland W. (1836): Geology and mineralogy considered with refetrence to natural theology. London., Longman & Co.
Bürgin –Wyss U. (1961): Die Rückenanhänge von *Trinchesia coerulea* (Montagu). Eine morphologische Studie über Farbmuster der Nudibranchiern. Rev. Suisse Zool. 68: 461–582.
Burchell W. J. (1822): Travels in the interior of Southern Africa. I. London, Longman & Co.
Butler A. G. (1868): The larva of *Abraxas grossulariata* distastefull to frogs. Ent. Month. Mag. 5:131–132.
Butler A. G. (1869): Remarks upon certain caterpilar etc., which are unpalatable to their enemies. Trans. Ent.Soc.Lond. 1869:27–29.
Butler A. G. (1889): A few remarks respecting insects supposed to be distasteful to birds. Ann. Mag. Nat. Hist. (6th ser.) 4:171–173,463–473.
Butler A. G. (1890): Notes made during the present year on the acceptance or rejection of insects by birds. Ann. Mag.Nat. Hist. (6th ser.) 6:324–327.
Butler A. G. (1910): A few words respecting insects and their natural enemies. Trans. Ent. Soc. Lond. 1910:151–154.
Buytendijk F. J. J. (1928): Anschauliche Kennzeichen des Organischen. Philos. Anz. (Bonn) 2(4).
Buytendijk F. J. J. (1958): Mensch und Tier. Hamburg., P. Parey.
Callois R. (1960): Les trois fonctions du mimétisme. pp. 71–166 in: Méduse et cie. Paris, Galimard.
Callois R. (1963): Le mimétisme animal. Paris, Hachette.
Campbell K. (1973): Swallows mobbing bat. Bird Life 7:36.
Carpenter G. D. H. (1920): A naturalist on Lake Victoria. London, Unwin.
Carpenter G. D. H. (1925): A naturalist in East Africa. Oxford, Univ. Press.
Carpenter G. D. H., Ford E.B. (1933): Mimicry. London, Methuen.
Carpenter F. M. (1970): Fossil insects from New Mexico. Psyche 77:400–412.
Carpenter G. D. H. (1942–44): Edward Bagnall Poulton (1856–1943). Obituary Not. Fellows Roy. Soc.: 655–674.
Caspari.E. (1941): The morphology and development of the wing pattern of Lepidoptera. Quart. Rev. Biol. 16:249–273.
Catala R. (1940): Variations experimentales de *Chrysiridia madagascarensis* Less. (Lep.Uraniidae). Arch. Mus. Nat. Hist. Natur. 6:1–262.
Chai P., Srygley R. B. (1990): Predation and the flight, morphology, and temperature of neotropical rain – forest butterflies. Am. Nat. 135: 748–765.
Chambers R. (1844): Vestiges of the natural history of creation. London.
Charlesworth D., Charlesworth B. (1975): Theoretical genetics of Batesian mimicry. Journ. Theor. Biol. 55: 283–303 (I)., 305–324 (II.), 325–337 (III.).
Chopard L. (1949): Le mimétisme. Paris, Payot.
Clodd E.(1892): Memoir of the autor. In:Bates H.W.: The naturalist on the river Amazons (2.nd ed.). London, J.Murray.
Cloudsley –Thompson J.L. (1984): How the zebra got this stripes – new solution to a old problem. Biologist 31(4): 226–228.
Cockerell T. D. A. (1891): The evolution of metallic colours in insects. Ent. News 1:3–6.
Coleman E. (1927): Pollination of an Australian orchid *Cryptostylis leptochila* F.V. Muell. Victoria Nat. 44:333–340.
Cope E. D. (1860): Catalogue of the colubrid snakes in the Museum of the Natural Sciences in Philadelphia, with notes and descriptions of new species. Proc. Acad. Sci. Philadelphia 12:241–266.
Cope E. D. (1887): The origin of the fittest . New York.
Cope E. D. (1893): The color variation of the milk snake. Am. Nat. 27:1066–1071.

Correvon H., Pouyanne A. (1916): Un curieux cas de mimétisme chez les ophrydées. Journ. Soc. Nat. Hort. France 17:29–31.
Cott H. B. (1938): Camouflage in nature and war. Roy Engineers Journ. 1938(2):501–517.
Cott H. B. (1940): Adaptive coloration in animals. London, Methuen.
Cott H. B. (1946): Relative edibility in birds. Proc. Zool. Soc. London 384:1–155.
Cott H. B. (1964): Colouration, adaptive. Palatability of birds and eggs in: Thomson A.L: (ed.): A new dictionary of birds. London, Nelson.
Cott H. B., Nelson C.W. (1970): The palatability of birds, mainly based of a tasting panel in Zambia. Ostrich Suppl. 8:357–384.
Crum H. (1976): Mosses of the Great Lakes Forest, rev. ed.. Ann Arbor. Univ. Herbarium, Univ. of Michigan.
Csiki E. (1905–1915): Positive Daten über die Nahrung unserer Vögel. Aquila (Budapest) 11–12.
Cundale G., Katz D., Shrubb M., Peers M. (1988): Systematic list for 1988 (Chiroptera chased by *Delichon urbica*). Breconshire Birds 4:5–21.
Cunningham J.T. (1900): Sexual dimorphism in the animal kingdom, a theory of the evolution of secondary sexual characters. London, A. Black.
Curio E. (1978): The adaptive signification of avian mobbing. Teleonomic hypotheses and predictions. Zeitschr. Tierpsychol. 48:175–183.
Cuvier G. (1815): Discours sur les révolutions de la surface du globe. Paris, Déterville.
D'Arcy Thomson E. (1917): On growth and form. (2nd ed.1961) Cambridge, Univ. Press.
D'Urban (1865): No title. Ent. Month. Mag. 2:108.
Dafni A., Bernhardt P. (1990): Pollination of terrestrial orchids of Southern Australia and the Mediterranean region. Systematic, ecological and evolutionary implications., Evol. Biol. 24: 193–252.
Darwin E. (1794): Zoonomia or the laws of organic life. I.London, J. Johnson.
Darwin F. (ed.) (1887): The life and letters of Charles Darwin. I.–III. London, J. Murray.
Darwin F., Seward A. C. (1903): More letters of Charles Darwin. I.–II. London, J. Murray.
Darwin Ch. (1859): On the origin of species by means of natural selection. London, J. Murray.
Darwin Ch. (1862): On the various contrivances by which orchids are fertilized by insects, London. J.Murray.
Darwin Ch. (1871): The descend of man and selection in relation to sex. London, J. Murray.
Darwin Ch. (1872): The expression of emotions in man and animal. London, J. Murray.
Darwin Ch. (1880): The power movements in plants. London. J. Murray.
Daumann E. (1933): Über „Scheinnektarien“ von *Parnassia palustris* und anderen Blütenarten. Jahrb. Wiss. Bot. 77: 104–119.
Daumann E. (1935): Über die Bestäubungsökologie der *Parnassia*- Blüte II. Jahrb. Wiss. Bot. 81: 707–717.
Daumann E. (1971): Zum Problem der Täuschblumen. Preslia 43:304–317.
Daumann E. (1973): Über die vermeintliche Bedetung der Zentralblüten in der Dode von *Daucus carota* L. für die Bestäubungsökologie und als Schutz vor Weidetieren. Preslia 47:320–326.
Dawkins R. (1976): The selfish gene. Oxford, Oxford Univ. Press. (česky 1998, Praha, Ml. fronta)
De Meijere J. C. H. (1915): Zur Zeichnung der Insekten – im besonderen des Dipteren und Lepidopterenflügels.Tijdschr. Entomol.59:55–147.
De Meijere J. C. (1918): Zur Evolution der Zeichnung bei den holometabolen Insecten. Tijdschr. Entom. 61.
De Stefani – Perez G. (1905): Mimismo di una galla. Marcellia 3:66–70.
Dean B. (1902): A case of mimicry outmimicked? Science 16:832 sq.
Dean B. (1908): Accidental resemblance among animals. A chapter in un-natural history. Popul. Sci.Month. 72:304–312.
Derham W.(1713): Physico-Theology … London.
Derham W.(1714): Astro-Theology …, London.
Detto C. (1905a): Blütenbiologische Untersuchungen. Über die Bedeutung der Insektenähnlichkeit der Ophrysblüte. Flora 94.
Detto C. (1905b): Mimikry der Pflanzen. Natur u. Schule 4:192–213.
Dixey F. A. (1890): On the phylogenetic signification of the wing markings in certain genera of Nymphalidae. Trans. Ent. Soc. Lond.1890:89–129.
Dixey F. A. (1894): On the phylogeny of the Pieridae, as illustrated by their wing markings and geographical distribution. Trans. Ent. Soc. Lond. 1894:249–334.
Dixey F. A. (1896): On the relations of mimetic patterns to the original form. Trans. Ent. Soc. Lond. 1896:65–78.
Dixey F. A. (1897): Mimetic attraction. Trans. Ent.Soc.Lond.1897:317–332.

Dixey F. A. (1908): On diaposematism or the interchange of characters between distasteful forms. Rep. Brit. Assoc. Adv. Sci 1908:733sq.
Dixey F. A. (1913a): The geographical relations of mimicry. Rep. Brit. Assoc. Adv. Sci 1913:518sq.
Dixey F. A. (1913b): Geographical relations of mimicry. Nature 92:286–387.
Dixey F. A. (1913c): Mimicry in relation to geographical distribution. Proc. Ent. Soc. Lond. 1913: 60–69.
Dobkin D.S. (1979): Functional and evolutionary relationship of vocal copying phenomena in birds. Zeitschr. Tierpszchol. 50:348–363.
Dodson C. (1962): The importnace of pollination in the evolution of the orchids of tropical America. Am. Orchid. Soc. Bull. 31: 525–534, 641–649, 731–735.
Dodson C., Frymire G. (1961): Natural pollination of orchids. Missouri Bot. Gard. Bull. 49: 133–152.
Dohrmann. C. E. & Nijhout H. F (1988): Development of the wing marking in *Precis coenia* (Lepidoptera:Nymphalidae) Journ..Res.Lepid.27:151–159.
Dorfmeister G. (1864): Über die Einwirkung verscheidener während der Entwicklungsperioden angewendeter Wärmegrade auf die Färbung und Zeichnung der Schmetterlinge. Mitteil. Naturwissenschaftl.Verein Steiermark, 1864:99–108.
Dressler R. (1968): Pollination by Euglossine bees. Evolution 22: 202–210.
Drumond J. (1840): Swan River Journal. Hook. Journ. Bot. 2:343–372.
Dumbacher J. P., Beehler B. M., Spande T. F., Garraffo H. M:, Daly J. W. (1992): Homobatraachotoxin in the genus *Pitohui*: chemical defense in birds? Science 258:799–801.
Dunn E. R. (1954): The coral snake „mimic“ problem in Panama. Evolution 8:97–102.
Durrer H. (1965): Bau und Bildung der Augfeder des Pfaus (*Pavo cristatus L.*). Rev. Suisse Zool. 72:263–411.
Dyer J. (1871): On so-called „mimicry“ in plants. Nature 4:335.
Edmunds M. (1972): Defensive behaviour in Ghanian praying mantids. Zool. Journ. Linn. Soc. 51:1–32.
Edmunds M. (1974): Defence in animals. A survey in antipredator defences. Essex, Longman.
Edmunds M. (1976): The defensive behaviour of Ghanian praying mantids with a discussion of territoriality. Zool. Journ. Linn. Soc. 58:1–37.
Eggers F. (1935): Zur Sinndentung harmonischer und extremer Farben und Formen bei Tieren. Verh. Deutsch. Zool. Ges. 37:114–121.
Eibl-Eibesfeldt I. (1959): Der Fisch Aspidontus taeniatus als Nachahmer des Putzers *Labroides dimidiatus*. Zeitschr.Tierpsychol. 16:19–25.
Eibel-Eibesfeldt I. (1984): Die Biologie des menschlichen Verhaltens. Grundriss der Humanethologie. München & Zürich, Piper.
Eimer G. M. Th. (1874): Zoologische Studien auf Capri II.*Lacerta muralis coerulea*,ein Beitrag zur Darwin'schen Lehre. Leipzig, Engelmann.
Eimer G. M. Th. (1881): Über das Variren der Mauereidechse. Berlin, Nicolai.
Eimer G. M. Th. (1882): Ueber gesetzmässige Zeichnung der Reptilien, speziell der Eidechsen. Jahresber. Ver. Württemb. 38:114–115.
Eimer G. M. Th. (1883): Ueber die Zeichnung der Vögel und Säugethiere I. Jahresber. Ver. Württemb. 39: 56 sq., Zool. Anz.5:685–690.
Eimer G. M. Th. (1885): Ueber die Zeichnung der Thiere. II.Raubthiere. Zool. Anz. 7: 13,34,56.
Eimer G. M. Th. (1887): Uebere die Zeichnung der Thiere. III.–V. Humboldt 1887: 136–143.
Eimer G. M. Th. (1888a): Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften nach den Gesetzen organischen Wachsens. I. Jena, G. Fischer.
Eimer G. M. Th. (1888b): Ueber die Zeichnung der Thiere. VI. Humboldt 1888: 173–181.
Eimer G. M. Th. (1889): Die Artbildung und Verwandtschaft bei den Schmetterlingen. I. Eine systematische Darstellung der Abänderungen, Abarten und Arten der Segelfalterähnlichen Formen der Gattung *Papilio*. I. Jena, G. Fischer.
Eimer G. M.Th. (1895a): Ueber die Artbildung und Verwandtschaft bei den Schwalbenschwanzartigen Schmetterlingen. Verh. Deutsch. Zool. Ges. 5:125–130.
Eimer G. M. Th. (1895b): Über die Artbildung und Verwandtschaft bei den Schmetterlingen II. Eine systematische Darstellung der Abänderungen, Abarten und Arten der Schwalben-schwanzähnlichen Formen der Gattung Papilio. Jena, G. Fischer.
Eimer G. M. Th. (1897): Die Entstehung der Arten auf Grund von vererben erworbener Eigenschaften nach den Gesetzen organischen Wachsens. II. Orthogenesis der Schmetterlinge ... . Leipzig, Engelmann.
Eisner T. (1985). A fly mimicking jumping spiders. Psyche 92(1):103–104.
Eisner T., Kafatos F. C., Linsley E. G. (1962): Lycid predation by mimetic adult Cerambycidae (Coleoptera). Evolution 16:316–324.

Ekkens D. (1972): Peruvian treehopper behaviour (Homoptera: Membracidae). Ent. News 83 (10): 257–271.
Eltringham H. (1910): African mimetic butterflies. Oxford, Clarendon.
Eltringham H. (1916): On specific and mimetic relationship of the genus *Heliconius*. Trans. Ent. Soc. Lond. 1916:104–148.
Engel R. (1985): La pollinisation d'*Ophrys fuciflora* (Schmitt) Moensch par un diptre. Bull. Assoc. Philom. Alsace Lorraine 21: 263–283.
Erlanson C. (1930): The attraction of carrion flies to *Tetraplodon* by an odoriferous secretion of the hypothesis. Bryologist 33: 13–14.
Ettingshausen Cv., Krašan F. (1890): Untersuchnugen über Ontogenie und Phylogenie der Pflanzen auf paleontologischer Grundlage. Denkschr. Akad. Wiss. Wien 57.
Faegri K., Pijl L. van der (1971): Principles of pollination ecology. London, Pergamon Press.
Fairmaire I. (1846): Revue de la tribu Membracidés. Ann. Soc. Ent. France 4: 235–320, 479–528.
Fassl A. H. (1910): Ein eigenartiger Fall von Mimikry. Zeitschr. Wiss. Insekt.-Biol. 6:310sq.
Feldotto W. (1933): Sensible Perioden des Flügelmusters bei *Ephestia kühniella* Z. W. Roux. Arch. Entwicklungsmech. 128:208–341.
Fernandez J. M. (1949): La *Spheniscomyia filiola* Loew y su mimetismo. Graellsia (Madrid) 7:19–21.
Fickert K.(1889): Die Zeichnungsverhältnisse bei der Gattung *Ornithoptera*. Zool.Jahrb.Syst.4.
Filippov N. N. (1961): Zakonomernosti aberativnoj izmenčivosti risunka nadkrylij žestokokrylych. Zool. Žurn.40(3):372–385.
Fioroni P. (1961): Zur Pigment- und Musterentwicklung bei squamaten Reptilien. Rev. Suisse Zool. 68: 727–874.
Fisher R. A. (1927): On some objection to mimicry theory, statistical and genetic.Trans.Ent.Soc.Lond. 1927:269–278.
Fisher R. A. (1930): The genetical theory of natural selection. Oxford, Clarendon.
Fischer E. (1895): Transmutation der Schmetterlinge infolge Temperaturveränderungen. Zürich.
Fischer E. (1896): Neue experimentelle Untersuchungen und Betrachtungen über das Wesen und die Ursachen der Aberrationen in der Faltergruppe *Vanessa*. Berlin, Friedländer u. Sohn.
Fischer E. (1901): Experimentelle Untersuchungen über die Vererbung erworbeer Eigenschaften. Allgem. Zeitschr. Entomol.6: 49–51, 363–365, 377–380.
Fischer E. (1902): Weitere Untersuchungen über die Vererbung erworbener Eigenschaften. Allgem. Zeitschr. Entomol. 7: 129sq.
Fischer E. (1907): Zur Physiologie der Aberrationen und Varietäten-Bildung der Schmetterlinge. Arch. Rassen-Gesellschafts-Biol. 4:761–793.
Forbes H. O. (1885): A naturalist's wandering in the Eastern Archipelago. London, Murray.
Forbes W. T. (1941): Line elements in butterfly patterns (Lepidoptera, Nymphalidae). Ent.News 52.
Ford E. B. (1936): The genetics of *Papilio dardanus* Brown (Lep.). Trans. Ent. Soc. Lond. 1936: 435–466.
Ford E. B. (1964): Ecological genetics. London, Methuen.
Ford E. B. (1965): Genetic polymorphism. London, Faber & Faber.
Ford E. B. (1976): Genetics and adaptation. London, Methuen.
Fowler W. W. (1918): A combined instance of protective resemblance and mimicry in a locust larva. Ent. Month. Mag. 54(3–4):92
Frankenberg G. v. (1937): Unzweckmässigkeit im Organismenreich. Natur u. Volk 67:521–534.
Freeman R. B. (1852): Life of the Rev. William Kirby, M.A. London,Longman & Comp.
Freiling H. (1938): Das Zeichnungs- und Farbmuster der Vögel als Anpassungs – und Wesensausdruck. Mitt. Ver. Sächs. Ornith. 5:213–219.
French V. (1984): Pattern formation in animal development. in: (Graham, C. F. Warreing P.F., eds.).Developmental control in animals and plants. Oxford, Blackwell Scient. Publ.
French V, Brakefield P. M. (1995): Eyespot development on butterfly wings: the focal signal. Develop. Biol. 168: 112–123.
French V., Brakefield P. M. (1995): Eyespot development on butterfly wings: the focal signal. Develop. Biol. 168: 112–123.
Fries E. (1821–32): Systema mycologicarum. Gryphiswaldiae.
Frisch K. von (1958): Über Zeichnungsmuster auf Schmetterlingsflügeln. Sitzungsber. Bayer. Akad. Wiss. (Mathem.-naturw. Kl.),1958:157–166.
Froschammer J. (1877): Die Phantasie als das Grundprinzip des Weltprozesses. München, Oldenburg.
Fryer J. C. F. (1913). An investigation by pedigree breeding into the polymorphism of *Papilio polytes* Linn. Phil. Trans. Roy. Soc., Ser. B. 204:227–254.
Fuller C. (1896): Plant-galls formed by insects. Notes on some passive means of defense. Agric. Gaz. New South Wales 6(8): 695–699.
Funkhouser W. D. (1950): Membracidae. Genera insectorum 208 (P. Wytsmann ed.). Bruxelles.

Gack C. (1979): Zur Ausbildung, Evolution und Bedeutung von Staubgefässimitationen bei Blüten als Signal für die Bestäuber. Dissertationsarbeit, Freiburg i.B..

Gadow H. (1903): Evolution of the colour-pattern and orthogenetic variation in lizards . Proc. Roy. Soc. Lond. 72:109–125.

Gadow H. (1911): Isotely in coral snakes. Zool. Jahrb. Syst. 31: 1–24.

Garstka W. R. (1982): Systematics of the mexicana group of the colubrid genus *Lampropeltis*, with an hypothesis mimicry. Breviora Mus. Comp. Zool. Cambridge 466:3–35.

Gebhardt F. A. (1912): Die Hauptzüge der Pigmentverteilung im Schmetterlingsflügel im Lichte der Liesegangschen Niederschläge in Kollodien. Verh.Deutsch. Zool. Ges. 22.

Gehlbach F. R. (1972): Coral snake mimicry reconsidered. The strategy of self-mimicry. Forma Functio 5:311–320.

Geist V. (1991): Bones of contention revisited: did antlers enlarge with sexual selection as a consequence of neonatal security strategies? Appl. Anim. Behav. Sci 29: 453–469.

Gerstäcker A. (1836): *Scepastus* und *Phylloscirtus*, zwei käferähnliche Gryllodengattungen, nebst Bemerkungen über Formanalogien unter den Insekten. Stett. Ent.Zeit. 24:408–436.

Gerstäcker A. (1874): Two remarkable instances of protective mimicry. Nature 9:470.

Gertsch W. J. (1940): The Houdini of the spider world. Nat.Hist. 45(3):154–156.

Gertsch W. J. (1947): Spiders that lasso their prey. Mag.Am.Mus.Nat.Hist.56:152–158.

Ghiselin M. T. (1969): The triumf of Darwinian methods. Berkeley, Univ. California Press.

Ghiselin M. T. (1974): The economy of nature and the evolution of sex. Berkeley, Univ. California Press.

Giersberg H. (1929): Die Färbung der Schmetterlinge I, Zeitschr. Vergl. Physiol.9:523–552.

Gilbert L. E. (1971): Butterfly – plant coevolution – has *Passiflora adenopoda* won the selection race with heliconiine butterflies? Science 172: 585–586.

Gilbert L. E. (1983): Coevolution and mimicry. Pp. 263–281 in: Futuyma D. J., Slatkin M. (eds.): Coevolution. Sunderland (Mass.), Sinauer.

Goethe J. W. (1790): Versuch, die Metamorphose der Pflanzen zu erklären. Weimar, Böhlau.

Goldschmidt R. B. (1920): Untersuchungen zur Entwicklungsphysiologie des Flügelmusters der Schmetterlinge I. W. Roux Arch. Entwicklungsmech. 47:1–24.

Goldschmidt R. B. (1938): Physiological genetics. New York, Mc Graw – Hill.

Goss R. J. (1983): Der antlers. New York, Academic Press.

Gottsberger G. (1970): Beiträge zur Biologie von Annoneeceen– Blüten. Österr. Bott. Zeitschr. 118: 237–279.

Gottsberger G. (1975): Some aspects of beetle polination in the evolution of flowering plants. Plant. Syst. Evol. (Suppl.) 1: 211–226.

Gould S. J. (1974): The origin and function of „bizarre“ structures: Antler size and skull size in the „Irish elk“ *Megaloceros giganteus*. Evolution 28:221–231.

Gould S. J. (1980): Wallace's fatal flaw. Nat.Hist. 89(1):26–40.

Graham M. W. R. (1950): Postural habits and colour-pattern evolution in Lepidoptera. Trans. Soc. Brit. Ent. 10:217–232.

Gray A. (1863): Variation and mimetic analogy in Lepidoptera. Am. Journ. Sci. Arts (2-nd ser.) 36:285–290.

Gredler P. V. (1903): Zoologische Parallelen. Ber. Nat. Ver. Innsbruck 27:57–64.

Green E. F. (1904): *Xylocopa* and Asilid fly. Spolia Zeylanica 2:158.

Greene E. (1988): Flies that fool spiders.Ent.Can. (Ottawa) 17(2):10.

Greene E., Orsak L. J.,Whitman D. W. (1987): A tephritid fly mimics the territorial displays of its jumping spider predators. Science 236:310–312.

Grobman A. B. (1978): An alternative solution to the coral snake mimic problem (Reptilia, Serpentes, Elapidae). Journ. Herpetol. 12:1–11.

Grote A. R. (1888): The origin of ornamentation in the Lepidoptera. Canad. Ent. 20:114–117.

Haase E. (1893): Untersuchungen über die Mimicry auf Grundlage eines natürlichen Systems der Papilioniden. I., II. Bibl. Zool. Nr.4. Stuttgart, Nägele.

Haldane J. B. S. (1932): The causes of evolution. London, Longmans&Green.

Hall B. P., Moreau R. E., Galbraith I. C. J. (1966): Polymorphism and parallelism in the African buh-shrikes of the genus *Malaconotus*. Ibis 108:161–182.

Hamilton W. D., Zuk M. (1982): Heritable true fitness and bright birds: A role for parasites? Science 218: 384–387.

Hampson G. F. (1898). Protective and pseudomimicry. Nature 57:364.

Handlirsch A. (1927): Biologie (Ökologie-Ethologie). in: Schröder Ch.(ed.):Handbuch der Entomologie II.Jena, G.Fischer.

Harnack M. (1953): Die Hautzeichnungen der Schlangen. Zeitsch. Morphol. Ökol. Tiere 41:513–573.

Harris A. C. (1978): Mimicry by a longhorn beetle, *Neocalliprason elegans* (Coleoptera: Cerambycidae), of its parasitoid, *Xanthocryptus novozealandicus* (Hymenoptera:Ichneumonidae). New Zeal.Ent. 6)4):406–408.

Harrison J. W. H. (1919): A preliminary study of the effects of administering ethylalcohol to the lepidopterous insect *Selenia bilunaria*, with particular reference to the offspring. Journ.Genet.9:39–52.

Harrison J. W. H. (1920): Genetical studies in moths of Geometrid genus Oporabia (Oporinia) with a special consideration of melanism in Lepidoptera Journ..Genet.9:195–280.

Harrison J. W. H. (1926): Some thoughts on melanism and melanochroism in the Lepidoptera. The Vasculum 13(3):103–105.

Harrison J. W. H.(1928): A further induction of melanism in the Lepidopterous insect, *Selenia bilunaria* Esp., and its inheritance. Proc. Roy. Soc. B. 102:338–347.

Harrison J. W. H. (1935): The experimental induction of melanism, and other effects, in the geometrid moth *Selenia bilunaria* Esp. Proc. Roy. Soc. B. 117:78–92.

Harrison J. W. H. (1956): Melanism in the Lepidoptera. Entomol. Rec. Journ. Var. 68:172–181.

Harrison J. W. H., Garrett F. C. (1926): The induction of melanism in the lepidoptera and its subsequent inheritance. Proc. Roy. Soc. B. 99:241–263.

Haupt H. (1953): Insekten mit rätselhaften Verzierungen. Neue Brehm-Bücherei 104, Leipzig, Geest & Portig.

Hecht M. K., Marien D. (1956): The coral snakes mimic problem: a reinterpretation. Journ. Morphol. 98:335–365.

Heikertinger F. (1914): Über die beschränkte Wirksamkeit der natürlichen Schutzmittel der Pflanzen gegen Tierfrass. Biol. Zentralbl. 34:81–108.

Heikertinger F. (1915): Die Frage von den natürlichen Pflanzenschutzmitteln gegen Tierfrass und ihre Lösung. Biol. Zentralbl. 35:257–281.

Heikertinger F. (1919a): Die motöke Myrmekoidie. Tatsachenmaterial zur Lösung des Mimikryproblems. Biol. Zentralbl. 39:65–102.

Heikertinger F. (1919b): Exakte Begriffsfassung und Terminologie im Problem der Mimikry und verwandter Erscheinungen. Zeitschr. Wiss. Insekt. Biol. 15:57–65.

Heikertinger F. (1921–1927): Welchen Quellen entspringen die Biologischen Trachthypothesen? Zool.Anz. 53–69 /I. H. W. Bates. Zool. Ant. 53:286–297 (1921), II. A. R. Wallace. 54:30–38 (1922), III. A. R. Wallace (Warntrachthypothese).54:39–47 (1922), IV. R. Trimen.54:177–184 (1922), V. Fritz Müller. 54:195–190 (1922), VI., Die Schrecktrachthypothese. 55:1–9 (1922), VII.Ch. Darwin (Sexualselektion).55:141–154(1922), VIII A. R. Wallace (Erkennungsfärbungen, Lockfärbungen, typische Färbungen).62:313–326 (1925), IX. Die Schutzfärbungen. 63:69–80 (1925), X. E.Wasmann (Ameisenmimese). 69:225–248(1927)/.

Heikertinger F. (1923): Zur metöken Myrmecoidie. Zeitschr. Wiss. Insekt. Biol.18:163–178.

Heikertinger F. (1925): Über die Begriffe „Mimikry“ und „Mimese“ mit besonderer Berücksichtigung der Myrmekoidie. Biol. Zentralbl. 45:272–289.

Heikertinger F. (1926–1927): Die Ameisenmimese I.–IV. Biol. Zentralbl. 45: 705–727 (1926), 46:351–405,593–625 (1926),47:462–501(1927).

Heikertinger F. (1929): Die Frage der Schutzanpassungen im Tierreich, mit besonderer berücksichtigung der Färbungsanpassungen. Wissen und Wirken, Bd. 57, Karlsruhe, Braun.

Heikertinger F. (1933–1941): Kritik der Schmetterlingsmimikry I.–VII. Biol. Zentralbl. 53: 561–599 (I.,1933), 54:365–389 (II., 1934), 55:461–483 (II., 1935), 56:151–166 (IV.,1936), 56:463–494 (V.1.,1936), 57:2–21 (V.2.,1937), Verh. Zool: Bot.Ges.Wien 86–87:35–72 (VI.,1936–37), 90:91:5–25 (VII,1940–41).

Heikertinger F. (1940): Exakte Mimikryforschung und angewandte Entomologie. Zeitschr.Angew. Ent. 26:608–623.

Heikertinger F. (1942): Eine Erwiderung an die Gegner der exakten Mimikryforschung. Zeitschr. Angew.Ent. 29:347–365.

Heikertinger F. (1946): Sind die Schmetterlingsbilder in naturkundlichen Werken richtig? Zeitschr. Wien. Ent. Ges.31:3–32.

Heikertinger F. (1949): Das Problem de „Totalzeichnung“ auf den Schmetterlingsflügeln. Zeitschr. Wien. Ent. Ges.34:85–89.

Heikertinger F. (1954): Das Rätsel der Mimikry und seine Lösung. Eine kritische Darstellung des Werdens, des Wesens und der Widerlegung der Tiertrachthypothesen. Jena, G. Fischer.

Hemsley W. B. (1896): Some remarkable phanerogamous parasites. Journ. Linn. Soc.Lond. Bot. 31:306–311.

Henke K. (1924): Die Färbung und Zeichnung der Feuerwanze *Pyrrhocoris apterus* L. und ihre experimentelle Beeinflußbarkeit. Zeitschr.Vergl. Physiol. 4:297–499.

Henke K. (1928): Über die Variabilität des Flügelmusters bei *Larentia sordidata* F.und einigen anderen Schmetterlingen. Zeitschr. Morphol. Ökol. Tiere 12:240–282.

Henke K. (1933a): Zur vergleichenden Morphologie des zentralen Symmetriesystems auf dem Schmettelingsflügel. Biol. Zentralbl. 53: 165–199.

Henke K. (1933b): Zur Morphologie und Entwickllungsphysiologie der Tierzeichnungen. Deutsch. Naturwiss. 21:633–639, 654–659, 665–673, 683–690.

Henke K. (1933c): Untersuchungen an *Philosamia cynthia* Drury zur Entwicklungsphysiologie des Zeichnungsmusters auf dem Schmetterlingsflügel. W.Roux'Arch. Entwicklungsmech. 128:15–107.

Henke K. (1935): Entwicklung und Bau tierischer Zeichnungsmuster. Zool. Anz. Suppl. (Verh.Deutsch. Zool. Ges.Stuttgart 1935)8:176–144.

Henke K. (1936): Versuch einer vergleichenden Morphologie des Flügelmusters der Saturniiden auf entwicklungsphysiologischer Grundlage. Nova Acta Leopoldina 4:1–137.

Henke K. (1943): Vergleichende und experimentelle Untersuchungen an *Lymantria* zur Musterbildung auf dem Schmetterlintsflügel. Nachr. Ges. Wiss. Göttingen, Math.-Phys. Kl.1943:1–48.

Henke K. (1944): Über die Determination der Querbindenzeichnung und die Entstehung der Scheinsymmetrie bei der Saturnide *Antherea pernyi* Guer. Biol. Zentralbl. 64:98–148.

Henke K., Kruse G. (1941): Über Feldgliederungsmuster bei Geometriden und Noctuiden und den Musterbauplan der Schmetterlinge im allgemeinen. Nachr. Ges. Wiss. Göttingen, Math.-Phys. Kl.1941:137–198.

Hering M. (1926): Biologie der Schmetterlinge. Berlin,Springer.

Hespenheide H. A. (1973). A novel mimicry complex: beetles and flies (Col.,Dipt.). Journ. Ent. 48(1):49–56.

Hildebrandt F. (1902): Über Ähnlichkeiten im Pflanzenreich, eine morphologisch – biologische Betrachntung. Leipzig, Engelmann.

Hingston R. W. G. (1933): The meaning of animal colour and adorment . London, Arnoldt.

Hinton H. F. (1958): On the pupa od *Spalgis lemolea* Druce. Journ. Soc. Brit. Ent. 6:23–25.

Hinton H. F. (1974): Lycaenid pupae that mimic anthropoid heads. Journ. Ent. 49:65–69.

Hinton H. F. (1977a): Mimicry provides information about the perceptual capacities of predators. Folia Ent. Mex. 37: 19–29.

Hinton H. F. (1977b): Subsocial behaviour and biology of some membracid bugs (Hom.) Ecol. Ent. 2(1): 61–79.

Hitler A. (1942): Mein Kampf. München, Zentralverlag d.NSDAP.

Hogue E. L. (1984): Observations on the host plants and possible mimicry models of „lantern bugs“ (Fulgora spp.) (Homoptera: Fulgoridae). Revista Biol. Trop. 32(1): 145–150.

Holland W. J. (1892): The life history of *Spalgis s-signata* Holl. Psyche 6:201–203.

Holm E. (1965): Tier und Gott. Mythik, Mantik und Magie südafrikanischer Urjäger. Basel & Stuttgart, Schwabe & Co.

Huey R. B., Pianka E.R. (1977): Natural selection for juvenile lizards mimicking noxious beetles. Science 195: 201–203.

Hustler K. (1990): Why do cuckoos look like accipiters? Honeyguide 36(1):38–39.

Hutchinson J. (1946): A botanist in Southern Africa. London, P. R. Cauthorn.

Huxley J. S. (1938a): Threat and warning colouration in birds. with a general discussion of the biological functions of colour. Proc. 8th Int. Ornithol. Congr. Oxford 1934: 430–455. Oxford, Univ. Press.

Huxley J. S. (1938b): The present standing of the theory of sexual selection. Pp. 14–42. in: Beer G.R. de (ed.): Evolutin. Oxford, Univ. Press.

Huxley J. S. (1945): Evolution, the modern synthesis. London, G.Allen.

Hyatt A. (1880): Transformation of *Planorbis* at Steinheim with remarks on the effects of gravity upon the forms of shells and animals. Proc.Amer.Acad.Sci 29.

Ingold C. T. (1971): Fungal spores, their liberation and dispersal. Oxford, Clarendon.

Iterson G. van (1907): Mathematische und mikroskopisch – anatomische Studien über Blattstellungen nebst Betrachtungen über den Schalenbau der Milioninen. Jena, G.Fischer.

Ivri Y. Dafni A. (1977): The polination ecology of *Epipactis consimilis* (Orchidaceae) in Israel. New Phytol. 79: 173–178.

Jacobi A. (1913): Mimikry und verwandte Erscheinungen. Braunschweig, Vieweg.

Japha A. (1909): Die Trutzstellung des Abendpfauenauges (*Smerinthus ocellata*) Zool. Jahrb. Syst. 27:321–328.

Joel D. M. (1988): Mimicry and mutualism in carnivorous pitcher plants (Sarraceniaceae, Nepenthaceae, Cephalotaceae, Bromeliaceae). Biol. Journ. Linn. Soc. 35:185–197.

Jones F. M. (1932): Insect coloration and the relative acceptability of insects to birds. Trans. Ent. Soc. Lond. 80:345–385.

Jones F. M. (1934): Further experiments on coloration and relative acceptability of insects to birds. Trans. Ent. Soc. Lond. 82:443–453.

Jourdain F. C. R. (1925): A study of parasitism on the cuckoos. Proc. Zool. Soc. Lond. 1925:639–667.

Jung C.G. (1952): Synchronizität als ein Prinzip akausaler Zusammenhänge. in: Jung C.G., Pauli W.: Naturerklärung und Psyche. (Studien aus dem C.G.Jung Institut IV.). Zürich, Rascher.

Kácha P., Petr V. (1995): Camouflage and mimicry in fossils, I.:general part.Acta. Mus.Nat Prague, Ser. B, Hist.Nat. 51(1–4):53–82.

Kalačevskaja K. (1929): The mimicry of weeds. (in russ.). Bull. Acad. Sci. Ukraine Kieff, Cl. Sci. Phys. Math. 4:67–71.

Kammerer P. (1919): Das Gesetz der Serie. Stuttgart & Berlin., Societäts-Verl.

Kant I., (1790): Kritik der Urteilskraft. (ed. 1968), Frankfurt, Suhrkamp.

Kaup J. (1844): Classification der Säugethiere und Vö. darmstadt.gel

Kaye W. J. (1903): Some considerations concerning mimicry. Ent. Rec. 15:177–179.

Kaye W. J. (1906): Notes on the dominant Mullerian group of butterflies from the Potaro district of British Guiana. Trans. Ent. Soc. Lond. 1906:401–439.

Kellog V. L. (1907): Darwinism to-day. New York, M.Holt &Co.

Kettlewell H. B. D. (1973): The evolution of melanism: A study of a recurring necessity.Oxford, Oxford Univ. Press.

Kimler W. C. (1982): Mimicry: a history of an evolutionary examplar. Ph.D. thesis, Cornell Univ., Ithaca, New York.

Kimler W. C. (1983). Mimicry: view of naturalists and ecologists before the modern synthesis. Pp. 97–129 in: Grene M. (ed.): Dimensions of Darwinism. New York, Cambridge Univ. Press; Paris, Ed. Mais. Sci. Homme.

Kipp F. A.(1942): Das Kompensationsprinzip in der Brutbiologie der Vögel 18:52–59, reprint 1983, pp.131–138 in: Schad W.(ed.): Goetheanische Naturwissenschaft III.: Zoologie. Stuttgart, Freies Geistesleben.

Kirby W. (1823): A description of some insects, which appear to exemplify Mr. William S. Mac Leay's doctrine of affinity and analogy. Trans. Linn. Soc. Lond. 14:93–111.

Kirby W. (1833): On the power, wisdom and goodnes of God as manifested in the creation of animals and in their history, habits and instincts. London, W.Pickering.

Kirby W., Spence W. (1815, 1817): An introduction to entomology or elements of the natural history of insects. I., II. London, Longman & Co.

Kirby W. F. (1883): Resemblance between East Indian butterflies, and those of the Atlantic Islands. Evolution and Natural Theology 1883:117–118.

Kirkpatrick T. W. (1957): Insect life in the tropics. New York, Longmans & Green.

Kistner D. H. (1968): Revision of the African species of the termithophilous tribe Crotocini. I. A new genus and species from Ovamboland and its zoogeographical significance. Journ. New York Ent. Soc. 76:213–221.

Kleinschmidt O. (1937): Parallelentwicklungen und Wiederholungserscheinungen in der Tierwelt. Nova Acta Leopoldina 5:367–391.

Kloft W. (1959): Versuch einer Analyse der trophobiotischen Beziehungen von Ameisen zu Aphiden. Biol. Zentralbl. 78:863–870.

Kluzinger C. B. (1899): Theodor Eimer. Ein Lebensabriss mit Darstellung der Eimerschen Lehren nach ihrer Entwickelung.Jahresber. Ver. Württemb. 55:1–22.

Koenig O. (1970): Kultur und Verhaltensforschung. Einführung in die Kulturethologie. München, Dt. Taschenbuchverlag.

Koenig O. (1975): Urmotiv Auge. München, Piper.

Koestler A. (1978): Janus. A summing up. London, Hutchinson & comp.

Köhler W. (1932): Die Entwicklung der Flügel bei der Mehlmotte Ephestia kühniella Zeller mit besonderer Berücksichtigung des Zeichnungsmusters.Zeitschr. Morphol. Ökol. Tiere 24: 582–681.

Köhler E., Feldotto W.(1935): Experimentelle Untersuchungen über Systeme und Elemente in den sensiblen Perioden von *Vanessa urticae* L.nebst einigen Beobachtungen an *Vanessa io* L.,Arch. Jul.Klaus.Stiftg.10:313–543.

Komárek S. (1989a): Deutung der belebten Natur im Spiegel der Gesellschaftsstruktur. Mitt. Österr. Ges. Gesch. Naturw. 9(3–4): 7–11.

Komárek S. (1989b): Vorkommen, Morphologie und Evolution der Augenmuster in der Flügelzeichnung der Familie Sphingidae. Zool. Jahrb. Syst. 116(3):217–254.

Komárek S. (1991): Die Augenmuster auf den Hinterflügeln der Gattung *Smerinthus* (Lepidoptera: Sphingidae) und ihre Evolution. Ann. Naturhist.Mus.Wien, Ser.B, Bot.-Zool. 92–112.

Komárek S. (1992): Mimikry und verwandte Erscheinungen. Europ. Journ. Semiotic. Stud. 4(4): 159–162.

Komárek S. (1998): Mimicry, aposematism and related phenomena in animals and plants. Bibliography 1800–1990. Praha, Vesmír.

Komárek S., Verhoog H. (1994): Adolf Portmann. Kritisch Denkerlexicon (H.J. Achternhuis ed.) 17: 1–15.Houten & Zaventem, Bohn, Stafleu & Van Loghum.

Kottler M.(1980): Darwin, Wallace, and the origin of sexual dimorphism. Proc. Amer. Phil. Soc. 124:203–226.

Kreslavskij A. G. (1977): Nekotore zakonomernosti izmenčivosti i evoljucii rysunka nadkrylyj žukov listojadok (Col.,Chrysomelidae). Zool. Žurn. 56.(7): 1043–1056.

Krieg H. (1937): Luxusbildung bei Tieren. Zool. Jahrb. Syst. 69: 303–318.

Kropotkin P. (1902): Mutual aid. New York, McClure Phillips.

Kugler H. (1955): Zum Problem der Dipterenblumen. Österr. Bot. Zeitschr. 102: 529–541.

Kugler H. (1970): Blütenökologie. Stuttgart, Fischer.

Kugler R. (1967): Philosophische Aspekte der Biologie Adolf Portmanns. Zürich, EVZ – Ed. Academica..

Kühn A. (1926): Über die Änderung des Zeichnungsmusters von Schmetterlingen durch Temperaturreize und das Grundschema der Nymphalidenzeichnung. Nachr.Ges.Wiss. Göttingen, Math.-Phys.Kl.1926:120–141.

Kühn A. (1932): Zur Genetik und Entwicklungsphysiologie des Zeichnungsmusters der Schmetterlinge. Nachr. Ges. Wiss. Göttingen, Math.-Phys.Kl.1932:312–335.

Kühn A. (1932): Entwicklungsphysiologische Wirkungen einiger Gene von *Ephestia kühniella*. Deutsch. Naturwiss.20:974–977.

Kühn A. (1935): Genetische und entwickl ungsphysiologische Untersuchungen an *Ephestia kühniella* Z. Zeitschr. Indukt. Abstam. Vererbungsl. 73:419–455.

Kühn A. (1937): Entwicklungsphysiologisch-genetische Ergebnisse an *Ephestia kühniella* Z.Zeitschr.Indukt.Abstam. – Vererbungsl.73:419–455.

Kühn A. (1955): Vorlesungen über Entwicklungsphysiologie., Berlin-Göttingen-Heidelberg,. Springer.

Kühn A., Engenhardt M. von (1936): Über die Determination des Flügelmusters bei *Abraxas grossulariata* L.Nachr.Ges.Wiss. Göttingen, Math.-Phys. Kl.,1936:171–199.

Kühn A., Engenhardt M. von (1944): Mutationen und Hitzemodifikationen des Zeichnungsmusters von *Ptychopoda seriata* Schrk. Biol. Zentralbl.64: 24–73.

Kühn A., Henke K. (1929,1932,1936): Genetische und entwicklungs-physiologische Untersuchngen an der Mehlmotte *Ephestia kühniella* Z., Nachr. Ges. Wiss. Göttingen,Math.-Phys. KI. 1929:1–121 (I–VIII),1932: 127–219 (VIII–XII),1936:1–272(XIII–XIV).

Kühn A.& M. von Engenhardt (1933): Über die Determination des Symmetriesystems auf dem Vorderflügel von *Ephestia kühniella* Z. W. Roux' Arch. Entwicklungsmech. 130:660–703.

Kullenberg B. (1961): Studies in *Ophrys* pollination. Zool. Bidrag (Uppsala) 34: 1–340.

Kuroda N. (1966): On the origin of raptor-pattern and hawk-mimicry in cuckoos. Misc. Rep. Yamashina Inst. Ornith. Zool. 4: 384–387.

Lamarck J.-B. (1809) Philosophie zoologique, ou exposition des considérations.... Paris, L' auteur etc.

Lambert D. M., Millar C. D., Hughes T. J. (1986a): On the classic case of natural selection. Riv.Biol. 79(1): 11–49.

Lambert D. M.,Millar C. D., Hughes T. J. (1986b): Teaching the classic case of natural selection. Riv. Biol. 79(1):117–123.

Lamborn. W. A. (Poulton comm.) (1911): The cocoon of *Deilemera antinorii*, Oberth. Proc. Ent. Soc. Lond. 1911:54.

Lamborn W. A. (1913): Cocoons of moths from the Lagos district (*Deilemera antinorii*, Hypsidae). Proc. Ent. Soc. Lond. 1913:5–7.

Lamborn W. A. (Poulton comm.) (1930): The construction of false braconid cocoons by the W.African bombycid larva *Norasuma kolga*, Dracc. Proc. Ent. Soc. Lond. 5:13.

Lamnot A. (1969): Prolegomena to aggressive mimicry and protective resemblance in early fishes, chelicerates, trilobites and brachiopods. Scot. Journ. Sci 1(2): 75–103.

Latreille P. A. (1802): Instinct et industrie des Insectes dans les moyens de defendre leur existnce. pp. 190–279 in: Histoire naturelle, géneralle et particuliere des Crustaceés et des Insectes. Paris, Dufart.

Lemche H. (1935): The primitive colour-pattern on the wings of insects and its relation to the venation. Vid. Medd.Dansk. Nat.For.99:45–64.

Lemche H. (1937): Studien über die Flügelzeichnung bei Insekten. Zool. Jahrb. Anat. 63:183–288.

Leser F. Ch. (1738): Insecto–Theologia..... Jena.

Leser F. Ch. (1744): Testaceo–Theologia...... Jena.

Linden M. von (1896): Die Entwicklung der Skulptur und der Zeichnung bei den Gehäusenschnecken des Meeres. Zeitschr. Wiss. Zool. 56: 261–317.

Linden M. von (1898): Untersuchungen über die Entwicklung der Zeichnung des Schmetterlingsflügels in der Puppe. Zeitschr. Wiss.Zool. 65:1–49.

Linden M. von (1901): Die Flügelzeichnung der Insekten... Biol. Zentralbl. 21:112–256.

Linden M. von (1902a): Die Farben der Schmetterlinge und ihre Ursachen. Acta Leopoldina 1902:124–134.

Linden M. von (1902b): Experimentelle Untersuchungen über die Vererbung erworbener Eigenschaften. Biol. Centralbl. 22:62–64.

Linden M. von (1902c): Zusammenfassende Darstellung der experimentalen Ergebnisse... Zool. Centralbl. 1902: 581–599.
Linden M. von (1902d): Le dessin des ailes des Lépidopteres... Ann. Sci. Nat. Zool. 15:1–196.
Linden M. von (1906): Untersuchungen über die Veränderung der Schuppenfarben... durch äussere Einflüsse. Biol. Centralbl.1906: 580–600.
Linnaeus C.(1749): Oeconomia naturae. Amoenitates Academicae Upsalienses.
Linnaeus C. (1750): Politia naturae. Amoenitates Academicae Upsalienses.
Lloyd J. E. (1965): Aggressive mimicry in *Photuris*. Firefly femmes fatales. Science 149:653–654.
Longstaff G. B. (1906): Some rest-atitudes of butterflies. Trans.Ent.Soc. Lond. 1906:97–118.
Longstaff G.B. (1912): Butterfly-hunting in many lands(Notes of a field naturalist.) London.
Lubbock J. (1878): Note on the colours of British caterpillars. Trans. Ent. Soc. Lond. 1878:139–258.
Lubbock J. (1886): Flowers, fruits and leaves. London, J.Murray.
Lucanus F. R. (1921): Zur Frage der Mimicry der Kuckkuckseier. Journ. Ornith. 69:239–258.
M'Clelland J. (1839): Indian Cyprinidae. Asiatic Res. 19(2): 230 sq.
Mac Leay W. S. (1819–1821): Horae entomologicae : or essays on the annulose animals. I.–II. London, S. Bagster.
Mac Leay W. S. (1823): Remarks on the identity of certain general laws which have been observed to regulate the natural distribution of insects and fungi. Trans. Linn. Soc. Lond. 14:43–68.
Macior L. W. (1968): Pollination adaptation in *Pedicularis groenlandica*. Am. Journ. Bot. 55: 927–933.
Magnus D. (1958): Experimentelle Untersuchungen zur Bionomie und Ethologie des Kaisermantels *Argynnis paphia* L. Zeitschr.Tierpsychol. 15:397–426.
Magnusen K.(1933) Untersuchungen zur Entwicklungsphysiologie des Schmetterlingsfügels. W.Roux'Arch. Entwicklungsmech. 128:447–479.
Malthus Th. R. (1798): Essay on the principle of population, as it affects the future improvement of society. London. J.Johnson.
Marden J. H. (1992): Newtons second law of butterflies. Nat. Hist. 1/92.
Marchant J. (ed.) (1916): Alfred Russel Wallace: Letters and reminiscences. New York, Harper.
Marloth R. (1904): Mimicry in plants. Trans. South Afr. Phil. Soc. 15: 97 sq.
Marloth R. (1905): Further observations on mimicry among plants. Trans. South. Afr. Phil. Soc. 16.
Marloth R. (1929): Stone-shaped plants. South Afr. Biol. Soc. 6:1–18.
Marshall G.A.K. (1908): On diaposematism with reference to some limitations of the Mullerian hypothesis of mimicry. Trans. Ent. Soc. Lond. 1908: 93–142.
Marshall G. A. K. (1909): Birds as a factor in the production of mimetic resemblances among butterflies. Trans. Ent. Soc. Lond. 1909:329–383.
Marshall G. A. K., Poulton E.B. (1902): Five years' observations and experiments (1896–1901) on the bionomics of South African insects chiefly directed to the investigation of mimicry and warning colours. Trans. Ent. Soc. Lond. 1902:287–584.
Martinet J. F. (1777–79): Katechismus der Natuur. I.–IV. Amsterdam, J. Allart
Mather M. H., Roitberg B. D. (1987): A sheep in wolfs clothing: Tephritid flies mimic spider predators. Science 236:308–309.
Mayer A. G. (1896): The development of the wing scales and their pigment in butterflies and moths. Bull. Mus. Comp.Zool. Harvard 29:209–350.
Mayer A. G. (1897): On the colour and colour-patterns of the moths and butterflies. Bull. Mus. Comp. Zool. Harvard 30:169–256.
Mayer A. G. (1902): Effects of natural selection and race – tendency upon the color-patterns of Lepidoptera. Bull. Mus. Inst. Art. Sci. Brooklyn, New York, 1:29–86.
Mayr E. (1982): The growth of biologieal thought. London & Cambridge (Mass.), Belknap, Harvard Univ.Press.
Mc Atee W. L. (1912): The experimental method of testing the efficiency of warning and cryptic coloration in protecting animals from their enemies. Proc. Acad. Sci. Philadelph. 64:281–364.
Mc Atee W. L. (1932): Effectiveness in nature of the so-called protective adaptations in the animal kingdom, chiefly as illustrated by the food habits of nearctic birds. Smith. Misc. Coll. (Wash.) 85(7) 1–201.
Mc Atee W. L. (1933): Rejoinder to papers on protective adaptations recently published by the Entomological Society of London. Proc.Roy.Ent.Soc.Lond.8:113–126.
McIver J. D., Stonedahl G. (1993): Myrmecomorphy: Morphological and behavioral mimicry of ants. Ann. Rev. Ent. 38: 351–397.
Mc Key D. (1975): The ecology of coevolution of animals and plants. Austin, Texas Univ. Press.
Meinhardt H. (1982): Models of biological pattern formation. London & New York, Academic Press.
Meinhardt H. (1995a): Dynamics of stripe formation. Nature 376:722.
Meinhardt H. (1995b): The algorithmic beauty of sea shells. New York, Springer.

Merian M. S. (1679): Der Raupen wunderbare Verwandlung und sonderbare Blumennahrung. Nürnberg, J. A. Graff.

Merian M. S.(1705): Metamorphoses insectorum Surinamensium. Amsterdam, M. Merian.

Merrifield. F.(1890): Systematic temperature experiments on some Lepidoptera in all their stages. Trans. Entomol. Soc. London, 1890.131–159.

Merrifield F.(1891): Conspicuous effects on the markings and colouring of Lepidoptera caused by exposure of the pupae to different temperature conditions. Trans.Entomol. Soc.London 1892:155–168.

Merrifield F. (1892): The effects of artificial temperature on the colouring of several species of Lepidoptera, with an account of some experiments on the effects of light. Trans.Entomol. Soc. London 1892:33–44.

Mertens R. (1956): Das Problem der Mimikry bei Korallenschlangen. Zool. Jahrb. Syst. 84:541–575.

Meyer A. B. (1870): Some remarks on the poison glands of the genus *Calliophis*. Proc. Zool. Soc.Lond. 1870:368–369.

Mivart S. G. (1871): On the genesis of species. New York, Appleton.

Möbius K. (1896): Über nutzlose Eigenschaften der Pflanzen und das Prinzip der Schönheit. Ber. Deutsch Bot. Ges. Berlin 1896:5–12.

Möbius K. (1905): Die Formen und Farben der Insekten ästhetisch betrachtet. Sitzungsber. Akad. Berlin 1905:159–166.

Modell W. (1969): Horns and antlers.Sci. Am. 220“ 114–122.

Möller A. (1915–21): Fritz Müller: Werke, Briefe und Leben. I.–III. Jena, G.Fischer.

Monte O. (1932). As cigarrinhas sugadoras. Bol.Agric. Zootec.Vet. Minas Geraes 9:1–27.

Monteith L. G. (1972): Status of predators of the adult apple maggot, *Rhagoletis pomonella*, in Ontario. Can. Ent. 104:257–262.

Moon H. P. (1976): Henry Walter Bates: Explorer, scientist and Darwinian. Leicester, Leicester Museums Press.

Moore M. (1899): The botanical results of a journey into the interior of Western Australia. Journ. Linn. Soc. Lond. Bot. 34.

Morgan T. H. (1903): Evolution and adaptation. New York, Mac Millan & Co.

Morris D. (1974): Manwatching: a field guide to human behavior. New York, London, Lausanne.

Morrison N. H. (1981): Fly mimicry by a jumping spider (Saitis, Salticidae) Aust. Ent. Mag. 8(2–3).:22.

Mortensen T. (Poulton comm. (1922): The shrew – like appearance of a Lasiocampid moth (*Suana concolor*) from Java. Proc. Ent. Soc.Lond. 1922:83.

Mueller H. C. (1972): Zone-tailed hawk and turkey vulture: mimicry or aerodynamics? Condor 74(2):221–222.

Müller D. (1979): Mimikry bei Pflanzen – Aspekte der Bestäubung, Verbreitung und des Frasschutzes. Staatsexamensarbeit, Freiburg i.B..

Müller F. (1878): *Epicalia Acontius*. Kosmos 4: 285–292.

Müller F. (1879): Ituna und Thyridia. Ein merkwürdiges Beispiel von Mimikry bei Schmetterlingen. Kosmos 3:100–108.

Müller H. (1879): Die Wechselbeziehungen zwischen den Blumen und den ihre Kreuzung vermittelnden Insekten. Breslau.

Müller H. (1879): Schützende Ähnlichkeit einheimischer Insekten. Kosmos 3:29–39,114–124.

Murray A. (1860): On the disquises of nature : being an inguiry into the laws that regulate external form and colour in plants and animals. Edinburgh New Phil.Journ., n.s. 11: 66–90.

Murray J. D. (1981a): A pre-pattern formation mechanism for animal coat markings. Journ.Theor. Biol. 88:161–199.

Murray J. D. (1981b): On pattern formation mechanisms for lepidopteran wing patterns and mammalian coat markings. Phil.Trans.Roy.Soc.Lond. B 295:473–496.

Murray J. D. (1982): Parameter space for turing instability in reaction-diffusion mechanisms: A comparison of models. Journ.Theor. Biol. 98:143–163.

Murray J. D. (1989): Mathematical biology. New York, Springer.

Murray J. D., Myerscough M. R. (1991): Pigmentation pattern formation in snakes. Journ.Theor. Biol. 149:339–360.

Mysterud J., Dunker H. (1978): Mammal ear mimmicry: a hypothesis on the behavioural function of owl „horns“. Behaviour 27:316.

Netolitzky F. (1936): Blonde Insektenrassen in Nord– und Ostseeraum. Forschung u.Fortschrit (Berlin) 12:103–104.

Neville A. C. (1977): Metallic gold and silver colours in some insect cuticles. Journ. Ins. Physiol. 23:1267–1274.

Newbigin M. I. (1898): Colour in nature: a study in biology. London, J. Murray.

Nicolai J. (1974): Mimicry in parasitic birds. Sci. Am. 231(4):93–98.

Niemelae P., Tuomi J. (1987): Does the leaf morphology of some plants mimic caterpillar damage? Oikos 50(2): 256–267.
Nicholson A. J. (1927): A new theory of mimicry in insects. Austral. Zool.5 :10–104.
Nijhout H. F. (1978): Wing pattern formation in Lepidoptera: a model.Journ.Exp.Zool. 206(2):119–136.
Nijhout H. F. (1980): Pattern formation on Lepidoptera wings:determination of an eyespot. Devel.Biol.80:275–288.
Nijhout H. F.(1981): The color patterns of butterflies and moths. Sci.Amer.245:145–151.
Nijhout H. F. (1984): Colour pattern modificaton by coldshock in Lepidoptera. Journ. Embryol. Exp. Morphol. 81:287–305.
Nijhout H. F. (1985a): Cautery-induced color patterns in *Precis coenia* (Lepidoptera:Nymphalidae). J. Embryol. Exp. Morphol.86:191–203.
Nijhout H. F. (1985b): The developmental physiology of color patterns in Lepidoptera. Adv. Ins. Physiol. 18:181–248.
Nijhout H. F. (1985c): Independent development of homologous pattern elements in the wing patterns of butterflies. Devel.Biol.108:146–151.
Nijhout H. F. (1986): Pattern and pattern diversity on Lepidopteran wings. Bioscience 36:527–533.
Nijhout H. F. (1990): A comprehensive model for colour pattern formation in butterflies. Proc.Roy. Soc. Lond. B 239:81–113.
Nijhout H. F. (1991): The development and evolution of butterfly wing patterns. Washington, D.C., Smithonian Inst.Press.
Nijhout H. F., Grunert L. W. (1988): Colour pattern regulation after surgery on the wing disks of *Precis coenia* (Lepidoptera: Nymphalidae). Development 102:377–385.
Nijhout H. F., Wray G. A. (1986): Homologies in the colour patterns of the genus *Charaxes* (Lepidoptera: Nymphalidae). Biol. Journ.Linn.Soc.28:387–410.
Nijhout H. F., Wray G. A. (1988): Homologies in the colour patterns of the genus *Heliconius* (Lepidoptera: Nymphalidae). Biol. Journ. Linn. Soc. 33:3456–365.
Nijhout H. F., Wray G. A. & E. Gilbert (1990): An analysis of the phenotypic effects of certain colour pattern genes in Heliconius (Lepidoptera:Nymphalidae). Biol.Journ.Linn.Soc.40:357–372.
Nikolskij A. A. (1984): Mammalian sound signals in the evolutionary process. (russ.) Moskva, Nauka.
Oberling J. J. (1978–87): Color patterns on molluscan shells: an interpretation. Jahrb.Naturhist.Mus.Bern 7:201–221 (Part 1);8:193–208 (Part 2); 8:209–216 (Part 3); 9:101–123 (Part 4).
Oliveira P. S., Sazima I. (1984): The adaptive bases of ant – mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). Biol. Journ. Linn. Soc. 22(2):145–155.
Oliviera P. S., Sazima I. (1985): Ant-hunting behaviour in spiders with emphasis on *Strophius* nigricans (Thomisidae). Bull. Brit. Arachnol. Soc. 6:309–312.
Osborn H. F. (1917): The origin and evolution of life. Philadelphia.
Otto R. (1907): Das Heilige. Über das Irrationale in der Idee des Göttlichen und sein Verhältnis zum Rationalen. München, Piper.
Oudemans J. Th. (1903): Étude sur la position du repos chez les Lépidopteres. Verh. Kon. Akad. Wetensch. Amster., II. sect., 10:11sq.
Owen D. F. (1980): Camouflage and mimicry. Chicago, Univ. Chicago Press.
Owen R. (1843): Lectures of the comparative anatomy and physiology of invertebrate animals. London, Longman & Comp.
Owen R. (1848): On the archetype and homologies of vertebrate skeleton. London, Longman & Comp.
Packard A. S. (1901): Lamarck, the founder of evolution. London, J.Murray
Paley W.(1802): Natural theology or Evidence the existence and attributes of the deity, London, R. Fauldner.
Papageorgis C. (1975). Mimicry in Neotropical butterflies. Why are so many wing-coloration complexes in one place? Am. Sci.63:522–532.
Pasteur G. (1972): Le mimétisme. Que sais-je? Paris, P.U.F. éd.
Pasteur G. (1982): A classificatory review of mimicry systems. Ann. Rev. Ecol. Syst. 13:169–199.
Pasteur L. (1857): Ann. Chim. Phys.3-e sér., 49:5–31 (in Callois,1960).
Peckham E. G. (1889): Protective resemblances in spiders. Occas. Papers Nat. Hist. Soc. Wisconsin (Milwaukee) 1:61–113.
Peterich L. (1972): Biological chromatology. The laws of colour and design in nature. Acta Biotheor. 21:24–46.
Peterich L. (1973). Chromatologie, eine Untersuchung der Chromatik der Fauna und Flora auf deren rein chromatische Gesetzlichkeiten hin. Tijdschr. Ent. 116(8):143–159.
Peters H. M. (1960): Soziomorphe Modelle in der Biologie. Ratio 1960: 22–37.
Philiptschenko J. (1927): Variabilitat und Variation. Berlin, Bornträger.
Piepers M. C. (1897a): Über das Horn der Sphingiden-Raupen. Tijdschr. Ent. 40:1–26.

Piepers M. C. (1897b): Über die Farbe und den Polymorphismus der Sphingiden-Raupen. Tijdschr. Ent. 40:27–105.
Piepers M. C. (1898): Die Farbenevolultion (Phylogenie der Farben) bei den Pieriden. Tijdschr. Nederl. Dierkund. Ver. (2. ser.) 5:70–289.
Piepers M. C. (1899): The evolution of colour in Lepidoptera. Not. Leyden Mus. 22:1–24.
Piepers M. C. (1903): Mimicry,Selection, Darwinismus. Leiden, Brill.
Piepers M. C. (1904): Über die sogenannten „Schwänze“ der Lepidoptera. Deutsche Ent. Zeitschr. Iris 16:247–285.
Piepers M.C. (1907): Noch einmal Mimicry,Selection, Darwinismus. Leiden, Brill.
Pigafetta A. de (1519–22) Relazione sul primo viaggio intorno al globo. (repr. 1894). Roma. Min. Publ. Inst.
Pijl L. van der (1960): Ecological aspects of flower evolution I. Evolution 14: 403–416.
Pijl L. van der (1969): Evolutionary actions of tropical animals on the reproduction of plants. Biol. Journ. Linn. Soc. 1:85–92.
Pijl L. van der, Dodson C. (1966): Orchid flowers: Their polination and evolution. Coral Gables (Flor.), Univ. of Miami Press.
Pocock R. I. (1911): Some probable and possible instances of warning characteristics amongst insectivorous and carnivorous mammals. Ann. Mag. Nat. Hist. 8:750–757.
Porta J.-B. de la (1608): Phytognomonica Lib. VIII. Francofurti, N. Hoffmann.
Portmann A.(1948): Die Tiergestalt. Basel, Reinhardt.
Portmann A. (1953): Das Tier als soziales Wesen. Zürich, Rhein-Verl.
Portmann A. (1955): Biologie und Geist. Zürich, Rhein Verlag
Portmann A. (1956): Tarnung im Tierreich. Heidelberg, Springer.
Portmann A. (1960): Neue Wege der Biologie. München, Piper. (engl. ed.: Animal forms and patterns, New York, 1967)
Portmann A. (1966): Um das Menschenbild. Biologische Beiträge zu einer Anthropologie. Stuttgart, Reclam.
Portmann A. (1970): Entläßt die Natur den Menschen? Gesammelte Aufsätze zur Biologie und Anthropologie. München, Piper.
Portmann A. (1974): An den Grenzen des Wissens. Wien, Düsseldorf, Econ.
Portschinsky J. (1891–1897): Coloration marquante et tachés ocelés, leur origine et leur développement. I.–IV. (Lepidopterorum Rossiae biologia II.–V.) (in russ.), Horae Soc. Ent. Ross. 25:3–120 (1891.I.), 26: 258–411 (1892,II.), 27:139–223 (1893,III.), 30:358–428 (1897,IV.)..
Poulton E. B. (1887): The experimental proof of the protective value of colour and markings in insects in refetrence to their vertebrate enemies. Proc. Zool. Soc. Lond. 1887:191–274.
Poulton E. B. (1890). The colours of animals, their meaning and use. Especially considered in the case of insects. London, Kegan, Paul, Trench, Trübner & Co.
Poulton E. B. (1891): On an interesting example of protective mimicry discovered by Mr. W. L. Sclater in British Guiana. Proc. Zool.Soc. Lond. 1891: 462–464.
Poulton E. B. (1896): Charles Darwin and the theory of natural selection. London, Longmans, Green & Co.
Poulton E. B. (1898): Causes of mimetic resemblance and common warning colours. J. Linn. Soc. Lond. 26: 558–612 (reprint 1908,pp. 220–270 in: Essays on evolution 1889–1907).
Poulton E. B. (1903a): Suggestions as to the meaning of the shapes and colours of Membracidae in the struggle for existence. Pp.273–285 in: Buckton G. B.: A monograph of the Membracidae. London, Lowell Reeve.
Poulton E. B. (1903b): No title. Proc. Ent. Soc. Lond. 1903:63–66.
Poulton E. B. (1904a): The mimicry of Aculeata by the Asilidae and *Volucella*, and its probable significance. Trans. Ent. Soc.Lond.1904:661–665
Poulton E. B. (1904b): Resemblance between *Hyperechia* and *Xylocopa*. Proc. Ent.Soc.Lond.1904:76.
Poulton E. B. (1908): Essays on evolution 1889–1907. (The Place of mimicry in a scheme of defensive colouration, pp.293–382) Appendix. A classification and index of the examples of mimicry quoted in the text, pp. 383–394). Oxford, Clarendon.
Poulton E. B. (1909): Charles Darwin and the Origin of species. (Mimicry in butterflies of North America, pp. 144–212. Letters of Charles Darwin to Roland Trimen, 1863–1871,pp.214–246)
Poulton E. B. (1910): Art the comrade of science. Nature 84:532–536.
Poulton E. B. (1913): Protective resemblance and mimicry in the Membracidae. Proc. Ent. Soc. Lond. 1913: 33– 38.
Poulton E. B. (1916): Mimics ready – made. Nature 97:237–238.
Poulton E. B. (1918): Bud-and-flower-like Flatidae (Homoptera) from ex-German East Africa.Proc. Ent. Soc. Lond.1918:78.

Poulton E. B. (1924a): The relation between the larvae of the Asilid genus *Hyperechia* (Laphriinae) and those of Xylocopid bees. Trans. Ent. Soc. Lond. 1924:121–123.

Poulton E. B. (1924b): The larvae of Asilid flies of the genus *Hyperechia* (Laphriinae) prezing upon the larvae of Xylocopid bees. Proc. Ent. Soc. Lond.1924:21–22.

Poulton E. B. (1924c): The terrifying appearance of *Laternaria* (Fulgoridae)Founded on the most prominent features of the aligator. Proc. Ent. Soc. Lond. 1924:43–49.

Poulton E. B. (1925a): Some of the chief Asilid mimics with their Xylocopid models, from East Africa. Proc. Ent. Soc. Lond. 1925:13.

Poulton E. B. (1925b): The evolution of the colours and patterns of cuckoos'eggs and its relation to that of insect resemblances, such as mimicry. Proc. Ent. Soc. Lond. 1925:96–104.

Poulton E. B. (1931): Two specially significant examples of insect mimicry. Trans. Ent. Soc. Lond. 79:395–398.

Poulton E. B. (1932): The alligator-like head and thorax of the tropical American *Laternaria laternaria*, L. (Fulgoridae,Homoptera). Proc. Ent. Soc. Lond. 7:68–70.

Poulton E. B. (ed.) (1897–1913): The Hope reports. I.–XIII. Oxford, Oxford Univ. Press.

Poulton E. B., Sanderson A. R., Dixey F. A. (1920): Butterflies (*Delias*:Pieridae) migrating in evening from one valley to another in Selangor, F. M. S., and back in morning, accompanied by moth mimics (*Psaphis*:Chalcosinae:Zygaenidae). Proc. Ent. Soc. Lond. 1920:63–68.

Poulton E. B., Sanderson A. R., Harvey T. R. (1921): Pierine butterflies and mimetic moths migrating from one valley to another in Selangor, F. M. S. Proc. Ent. Soc. Lond. 1921:5–6.

Poulton E. B., Seitz A. (1913): A locustid and a reduviid mimic of a fossorial aculeate in the S. Paulo district of Brazil. Proc. Ent. Soc. Lond. 1913:100–103.

Pouyanne A. (1917): La fécondation des *Ophrys* par les insectes. Bull. Soc. Hist. Nat. Afr. Nord 8:6–7.

Povolný D., Gregor F. (1946): Burnet moths (*Zygaena* Fab.) in Moravia and Silesia . Entomologické příručky Entomologických Listů (Brno) 12:1–100.

Povolný D., Pijáček J. (1949): On the polymorphism by *Zygaena ephialtes* L. Přírodověd. Sbor. Ostr. kraje 10(4): 1–11.

Povolný D., Weyda F. (1981): On the glandular character of larval integument in the genus *Zygaena* (Lepidoptera, Zygaenidae). Acta Ent. Bohemoslov. 78(5): 273–279.

Proctor M., Yeo P. (1972): The pollination of flowers. New York, Taplinger.

Prochnow O. (1906): Über die Färbung der Lepidoptera. Ein Beitrag zur Deszendenz-Theorie. Einige Momente für und gegen Mimikry, Selektion und Deszendenz. Berlin, Börnträger. (též Intern. Ent. Zeit. Guben 1906:20sq.)

Prochnow O. (1907): Die Mimikry-Theorie. Intzern. Ent. Zeit. Guben 1907:2sg.

Prochnow O. (1927): Die Färbung der Insekten (nach Beobachtungen und Versuchsergebnissen). pp.430–572 in: Schröder Ch. (ed.):Handbuch der Entomologie II. Jena, G.Fischer.

Provine W. B. (1971): The origins of theoretical population genetics. Chicago, Univ. Chicago Press.

Przibram H., Brecher L. (1919–1924): Ursachen tierischer Farbkleidung I.–X.. Roux' Arch. Entwicklungsmech.45–50.

Punnett R. C. (1905): Mendelism.Cambridge, MacMillan &Bowes.

Punnett R. C. (1915): Mimicry in butterflies. Cambridge, Univ. Press.

Punnett R. C. (1933): Inheritance of egg-colour in the „parasitic“ cuckoos. Nature 132:892–893.

Purpus J. (1914): Mimikry bei Kakteen. Mueller's Deutsche Garten – Zeit. 29:73–78.

Rádl E. (1908): Geschichte der biologischen Theorien in der Neuzeit I,II . Leipzig, Engelmann.

Rainbow W. J. (1895). Hymenopterous galls simulating the appearance of larvae. Proc. Linn. Soc. New South Wales 1895:382.

Ralls K., Fiorelli P., Gish S. (1985): Vocalization and vocal mimicry in captive harbor seals, *Phoca vitulina*. Canad. Journ.Zool. 63(5):1050–1056.

Raup D. M. (1966): Geometric analysis of shell coiling: General problems. Journ. Paleontol. 40:178–1190.

Ray J. (1691): The wisdom of God manifested in the works of creation. London.

Reaumur R. A. F. (1734–42): Mémoires pour servir a l'histoire des Insectes. I.–IV. Paris, Impr.Royale.

Reimarus S. M. (1760): Allgemeine Betrachtungen über die Triebe der Theire. Hamburg,

Rensch B. (1924): Zur Entstehung der Mimikry der Kuckuckeier. Journ. Ornithol. 72:461–472.

Rensch B. (1947): Neuere Probleme der Abstammungslehre. Stuttgart, Enke.

Reuss T. (1918): Mimetik, Strukturfarben, Melanismus und die Eimer- Piepers'sche Farbenfolge. Ent. Rundschau 35.

Ridout B. V. (1987): The enigma of the lantern. Wildlife (Lond.) 19(5):209–211.

Riedl R. (1975): Die Ordnung des Lebendigen. Systembedingungen der Evolution. Hamburg, P. Parey.

Richards D. G. (1986): Dolphin vocal mimicry and vocal object labelling. Pp. 273–288 in: Schusterman R.J., Thomas J. A., Wood F. G. (eds.): Dolphin cognition and behavior. Hillsdale (N.J.)& London, L.Erlbaum.

Ritland D. B. (1991): Revising a classic butterfly mimicry scenario: Demonstration of Muellerian mimicry between Florida viceroy (*Limenitis archippus floridensis*) and queens (*Danaus gilippus berenice*). Evolution 45 (4): 918–934.
Ritland D. B., Brower L. P. (1991): The viceroy butterfly is not a Batesian mimic. Nature 350:497–498.
Robbins R. K. (1980): The lycaenid „false head“ hypothesis: Historical review and Luantitative analysis. Journ. Lepid. Soc. 34:194–208.
Robbins R. K. (1981): The „false head“ hypothesis: predation and wing pattern variation of lycaenid butterflies. Am. Nat. 118(5):770–785.
Röber J. (1905): Die sogenannten „Schwänze“ der Lepidoptera. Stettin. Ent. Zeit. 66:247–259.
Robertson C. (1887): Fertilization of *Calopogon parviflorus*. Bot. Gaz. Chicago 12: 288–291.
Roesel v.Rosenhof J. A. (1746–61): Insecten-Belustigungen I.–IV. Nürnberg, J. J.Fleischmann.
Rössler A. (1861): Gedanken über die Bedeutung der Malerei auf den Schmetterlingsflügeln. Wien. Ent. Monatschr.5:163–166.
Rössler A. (1880): Ueber Nachahmung bei lebenden Wesen (Organismen), insbesondere den Lepidopteren, mit einer Betrachtung über die Abstammungslehre. Jahrb. Nassau Ver. 31–32: 232–244.
Rothschild M. (1967): Mimicry, the deceptive way of life. Nat. Hist. 76:44–51.
Rothschild M.(1974): Modified stipules of *Passiflora* which resemble horned caterpillars. Proc. Roy. Ent. Soc. Lond. C 39:16.
Rothschild M. (1984): Aide mémoire mimicry. Ecol. Ent. 9(3):311–319.
Rothschild M. (1985): British aposematic Lepidoptera. pp. 9–62 in: Head J. & Emmets A. M. (eds.): The moths and butterflies of Great Britain and Ireland. II. Essex, Harley.
Rowlands D. (1959): A case of mimicry in plants – *Vicia sativa* L. in lentil crops. Genetica 30: 435–446.
Roy B. A. (1993): Floral mimicry by a plant pathogen. Nature 362:56–58.
Ruplinger P. (1975): Do pheasants mimic humans? Game Bird Breed. Gaz. 24:11.
Ruyer R. (1962): L'origine des formes vivantes. Paris, Roret.
Ruyer R. (1964): L´animal, L´homme, la fonction symbolique. Paris, Gallimard.
Sager E. (1955): Morphologische Analyse der Musterbildung beim Pfauenrad. Rev. Suisse Zool. 62:25–127.
Sachs J. (1875): Geschichte der Botanik. München, Oldenburg.
Saleh M. A. (1984): Does the ostrich bury its head in the sand? Courser 1:32–63.
Sargent T. D. (1968): Cryptic moths: Effects on background selections of painting the circumocular scales. Science 159:100–101.
Sargent T. D. (1969a): Background selection of the pale and melanic forms of the cryptic moth, *Phigalia titea* (Cramer). Nature 222:585–586.
Sargent T. D. (1969b): Behavioural adaptations of cryptic moths. I.–V. J. Lepid. Soc. 23:1–9 (I.), Journ.New York Ent. Soc. 77:75–79 (II.), Anim. Behav. 17:670–672 (III.), 112–114 (IV.), 123–128(V.).
Sargent T. D. (1969c): A suggestion regarding hindwing diversity among moths of the genus *Catocala* (Noctuidae). Journ.Lepid.Soc. 23:261–264.
Sargent T. D. (1970–82): Studies on the *Catocala* (Noctuidae) in southern New England I.–VI. Journ. Lepid. Soc. 24 (1970): 105–117(I)., 25(1971): 82–90 (II.), 26 (1972): 94–104 (III.), 27 (1973):175–192(IV.), 31 (1977): 1–16 (V.), 36 (1982): 42–53 (VI.).
Sargent T. D. (1976): Legion of night: The underwing moths. Amherst, Univ. Mass. Press.
Sargent T. D. (1978): On the maintenance of stability in hindwing diversity among moths of the genus *Catocala* (Lepidoptera:Noctuidae). Evolution 32:424–434.
Sargent T. D. (1980): Antipredator adaptations in underwing moths. pp. 259–284 in: Kamil A., Sargent T. D. (eds.): Foraging behaviour: ethological, ecological and psychological perspectives. New York, Garland.
Sargent T. D. (1990): Startle as a anti-predator mechanism, with special reference to the underwing moths (*Catocala*). pp. 229–249 in: Evans D. L., Schmidt J. O. (eds.): Insect defenses: adaptive mechanisms and strategies of predator and prey. Albany, State Univ. of New York Press.
Sargent T. D., Owen D. F. (1975): Apparent stability in hindwing diversity in samples of moths of varying species composition. Oikos 26:205–210.
Savi G. (1825): Botanicon etruscum, vol.4. Pisa.
Saville D. (1976): Evolution of the rust fungi (Uredinales) as reflected by their ecological problems. Pp. 137–207 in: Dobzhansky T., Hecht M., Steere W. (eds.): Evolutionary biology. New York, Plenum Press.
Scott W. B. (1894): On variations and mutations. Amer. Journ. Sci. 48:355–374.
Schad W. (1971): Säugetiere und Mensch.Stuttgart, Freies Geistesleben.
Schad W. (1981): Vom Leben im Lichtraum. Erziehungskunst 45(2):76–82. reprint 1983, pp. 42–49 in:Schad W. (ed.): Goetheanishe Naturwissenschaft III:: Zoologie. Stuttgart, Freies Geistesleben.
Schad W. (ed.) (1982): Goetheanische Naturwissenschaft II.: Botanik. Stuttgart, Freies Geistesleben.
Schad W. (ed.1983): Goetheanische Naturwissenschaft III.: Zoologie. Stuttgart, Freies Geistesleben.

Scherzinger W. (1986): Kontrastzeichnungen im Kopfgefieder der Eulen (Strigidae) als visuelle Kommunikationsmittel. Ann. Naturhist.Mus.Wien 88/89B:37–56.

Schilde J. (1879): Gegen pseudodoxische Transmutationslehre. Berlin, Friedländer.

Schilde J. (1884): Antidarwinistische Skizzen. Berlin, Friedländer.

Schilde J. (1890): Schach dem Darwinismus. Studien eines Lepidopterologen. Berlin, Friedländer.

Schremmer F. (1963): Wechselbeziehungen zwische Pilzen und Insekten. Beobachtungen an der Stinkmorchel, *Phallus impudicus* L. ex Pers.. Österr Bot . Zeitschr. 110:380–400.

Schuler W., Roper T. J. (1992): Responses to warning coloration in avian predators. Adv. Stud. Behav.21:111–146.

Schultz T. D., Bernard G. D. (1989): Pointillistic mixing of interference colours in cryptic tigre beetles. Nature 337:72–73.

Schultz T. D. (1986a): Role of structural colours in predator avoidance by tigre beetles of the genus Cicindela (Coleoptera: Cicindelidae). Bull. Ent. Soc. Am. 32(3):142–146.

Schultz T. D. (1986b): Structural colors of tigre beetles and their role in heat transfer through the integument. Physiol. Zool. 60:737–745.

Schuster von Forstner W. (1925): Blaublindheit der Vögel und blaue Schmetterlinge und Käfer. Intern. Ent. Zeitschr. Guben 19:241–242.

Schutz E. (1957): Das Occipitalgesicht bei Sperlingskauzen (*Glaucidium*). Vogelwarte 19:138–140.

Schwantes G. (1957): Flowering stones and mid-day flowers. London, E. Benn.

Schwanwitsch B.N.(1923): Observations on the wing-pattern in Rhopalocera. The modificatin of the wing-pattern in the family Nymphalidae. Proc.1-st Congr.Russ.Zool. Anat. Histol. Petrograd, 1923: 104–106, 106–107.

Schwanwitsch B. N. (1924): On the groundplan of wing-pattern in nymphalids and certain other families, of Rhopalocerous Lepidopetra. Proc.Zool.Soc. London 31.

Schwanwitsch B. N. (1925): On a remarkable dislocation of the components of the wing pattern in the Satyrid genus *Pierella*. Entomologist 58:266–269.

Schwanwitsch B. N. (1926a): On the modes of evolution of the wing – pattern of Nymphalids and certain other families of the Rhopalocerous Lepidoptera. Proc. Zool.Soc.London 33:493–507.

Schwanwitsch B. N. (1926b): The evolution of the wing-patern in Rhopalocera, Proc. Ent. Soc. London 1926:4–5.

Schwanwitsch B. N. (1927): The evolution of the wing-pattern in palearctic Satyridae (russ.) Proc.2-nd Congr. of Russ. Zool. Anat. Histo: 97–98. Moscow.

Schwanwitsch B. N. (1928a): Studies upon the wing-pattern of *Pierella* and related genera of South American Satyridan butterflies .Zeitschr.Morphol. Ökol.Tiere 10:499–520.

Schwanwitsch B. N. (1928b): Pierellisation of stripes in the wing-pattern of the genus Rhaphicera Btl. (Lepidoptera, Satyridae). Zeitschr.Morphol. Ökol.Tiere 11:1–12.

Schwanwitsch B. N. (1929a): Two schemes of the wing-pattern of butterflies. Zeitschr. Morphol. Ökol.Tiere 14:36–58.

Schwanwitsch B. N. (1929b): Evolution of the wing-pattern in palearctic Satyridae I.Genera Satyrus and Oeneis. Zeitschr.Morphol. Ökol.Tiere 13:559–654.

Schwanwitsch B. N. (1929c): Studies upon the wing-pattern of *Prepona* and *Agrias*, two genera of South-American Nymphalid butterflies. Acta Zool. 11:289–424.

Schwanwitsch B. N. (1930): Studies upon the wing-pattern of *Catagramma* and related genera of South American Nymphalid butterflies.Trans.Zool.Soc.London 21:218–291.

Schwanwitsch B. N. (1931): Evolution of the wing-pattern in palearctic Satyridae II. Genus *Melanargia*. Zeitschr.Morphol. Ökol. Tiere 21:316–408.

Schwanwitsch B. N. (1935a): Superposition of pattern components in a species of Amathusiid butterflies. Entomologist 68:15–12.

Schwanwitsch B. N. (1935b): Evolution of the wing-pattern in palaearctic Satyridae III. Pararge and five other genera. Acta Zool. 16:143–281.

Schwanwitsch B. N. (1935c): On some general principles observed in the evolution of the wing-pattern of Palaeartic Satyridae. Proc.VI-th.Int.Congr.Ent.

Schwanwitsch B. N. (1938): On the stereoeffect of cryptic colour-patterns in Lepidoptera. Dokl.Akad.Nauk SSSR 21 (4):179–182.

Schwanwitsch B. N. (1943): Wing-pattern in papilionid Lepidoptera. Entomologist 76: 201–203.

Schwanwitsch B. N. (1945a): Wing-pattern in Lycaenid Lepidoptera. Proc.Roy.Ent.Soc.London 20(A):97–100.

Schwanwitsch B. N. (1945b): Wing-pattern in Lycaenid Lepidoptera. Proc.Roy. Entomol.Soc.London 20(A):97–100.

Schwanwitsch B. N. (1948): Evolution of the wing – pattern in Palaearctic Satyridae IV. Polymorphic radiation and parallelism. Acta Zool. 29:1–61.

Schwanwitsch B. N. (1949): Evolution of the wing pattern in the lycaenid Lepidoptera Proc. Zool. Soc. London. ser. B, 119:189–263.

Schwanwitsch B. N. (1956a): Color-pattern in Lepidoptera. Entomol. Obozr. 35:530–301.

Schwanwitsch B. N. (1956b): Wing pattern of pierid butterflies (Lepidoptera, Pieridae). Entomol. Obozr. 35: 285–301.

Schwanwitsch B. N, Sokolov G. N. (1934): On the wing-pattern of the genus *Lethe* (Lepidoptera, Satyridae). Acta Zool. 15:134–196.

Schwartz V. (1962): Neue Versuche zur Determination des zentralen Symetriesystem bei *Plodia inerpunctella*. Biol. Zentralbl. 81:19–44. Seevers C. H. (1965): The systematics, evolution and zoogeography of Staphylinid beetles associated with army ants (Coleoptera, Staphylinidae). Fieldiana (Zool.) 47:137–351.

Seitz A. (1887): Betrachtungen über die Schutzvorrichtungen der Tiere. Zool.Jahrb. Syst. 3:59–96.

Selman B. J. (1985): The use and significance of color in the separation of paropsine chrysomelid species. Entomography 3: 477–479.

Sermonti G., Catastini P. (1984): On industrial melanism, Kettlewell's missing evidence. Riv. Biol. 77 (1): 35–52.

Sevastopulo D. G. (1977): Lycaenid pupae that mimic anthropoid heads. Ent. Rec. Journ. Var. 89(9): 253–254.

Shapiro A. M. (1980): Canalization of the phenotype of *Nymphalis antiopa* (Lepidoptera: Nymphalidae) from subarctic and montane climates. Journ. Res. Lepid. 19:82:87.

Shapiro A. M. (1981): The pierid red-egg syndrome. Am. Nat. 117:276–294.

Shaw F., Bose R. (1928): Studies in Indian pulses. I. Lentil (*Ervum lens*, Linn.). Mem. dept. Agric. India Bot. Ser. 16:159–189.

Shelford R. (1902): Observations on some mimetic insects and spiders from Borneo and Singapore. Proc. Zool. Soc. Lond. 1902:230–284.

Sherzer W. (1896): Pebble mimicry in Philippine Island beans. Bot. Gaz. Chicago 21: 235–237.

Shuckard W. E. (1836): A few observations upon the habits of the indigenous Aculeate Hymenoptera. Trans. Ent.Soc.Lond 1:52–60.

Shull A. F. (1937): The needs of the mimicry theory. Science 85: 496–498.

Sibatani A. (1987): Oudemans' principle and its extension in pattern formation on the wings of Lepidoptera (Insecta). Journ. Lib. Arts. Dep. Kansai Med. Univ., Osaka 11:1–10.

Sillén –Tullberg B. (1988): Evolution of gregariousnes in aposematic butterfly larvae. A phylogenetic analysis. Evolution 42: 293–305.

Sillén –Tullberg B. (1992): Does gregariousness reduce attacs on aposematic prey? A reply to Cooper. Anim.Behav.43(1):165–167.

Smith A. (1776): Inquiry into the nature and causes of wealth of nations. Edinburgh.

Smith D. A. M. (1984): Mate selection in butterflies: Competition, coyness, choice and chquvinism. Pp. 225–244 in:Vane-Wright R.I., Ackery P.K. (eds.): The biology of butterflies. Orlano, Academic Press.

Smith G. E. (1829): Catalogue of plants of south Kent. London.

Smith S. M. (1975): Innate recognition of coral snake pattern by a possible avian predator. Science 187:759–760.

Smith S. M. (1977): Coral-snake pattern recognition and stimulus generalization by naive great kiskadees (Aves:Tyrannidae): Nature 265: 535–536.

Smith S. M. (1978): Predatory behavior of young great kiskadees *Pitangus sulphuratus*. Anim. Behav.26:988–995.

Smith S. M. (1980): Responses of naive temperate birds to warning coloration. Am. Midl. Nat. 103:346–352.

Sokolow G. N. (1936): Die Evolution der Zeichnung der Arctiiden. Zool. Jahrb. Anat.61:140–194.

Sokolow G. N. (1947): Evoljucija risunka u kokonoprjadov (Lep.Lasiocampidae). Izv.Akad.Naauk SSSR, Ser.Biol.1: 212–246.

Sprengel Ch. K. (1793): Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. Berlin.

Standfuss M. (1894): Die Beziehungen zwischen Färbung und Lebensgewohnheiten bei den paläarktischen Großschmetterlingen. Vierteljahrschr. Naturf.Ges. Zürich 39:85–119.

Standfuss M. (1896): Handbuch der palearktischen Gross-Schmetterlinge für Forscher und Sammler. Jena, G. Fischer.

Standfuss M. (1906): Beispiele von Schutz – und Trutzfärbung. Mitt. Schweiz. Ent. Ges. 11:153–158.

Steel R. (1900): Imitation, or the mimetic force in nature and human nature. London, Simpkin & Marschall.

Steere W. (1958): Evolution and speciation in mosses. Am. Nat. 92:5–2.

Stecher R. M. (1969): The Darwin-Bates letters, correspondence between two nineteenth – century travellers and naturalists. Ann. Sci 25: 1–47 (Part I), 95–125 (Part II.)

Steiniger F. (1938a): Die ökologische Bedutung der Augenflecke bei Insekten. Verhandl. VII. Intern. Kongr. Ent. Berlin 2:1340–1346.

Steiniger F. (1938b): Warnen und Tarnen im Tierreich. Ein Bildbuch zur Schutzan-passungsfrage. Berlin, Bermühler.

Steinmann G. (1908): Die geologischen Grundlagen der Abstammungslehre. Leipzig, Engelmann.

Sternfeld R. (1913): Die Erscheinungen der Mimikry bei den Schlangen. Sitzungsber. Ges. Naturf. Freunde Berlin 1913:98–117.

Stradling D. (1976): The nature of the mimetic patterns of the brassolid genera *Caligo* and *Eryphanis*. Ecol. Ent. 9(2):135–138.

Strickland H. E. (1840): Observations upon the affinities and analogies of organized beings. Ann. Mag. Nat. Hist., 4:219–226.

Strickland H. E. (1841): On the true method of discovering the natural system in zoology and botany. Ann. Mat. Nat. Hist. 6: 184–194.

Strickland H. E. (1846): On the structural relations of organized beings. Phil. Mag. 28: 354–364.

Strong M., Cuffe E. (1985): Drongos pursue Microchiroptera. Sunbird 15:42–43.

Study E. (1919): Die Mimikry als Prüfstein phylogenetischer Theorien. Naturwissenschaft 7:21–23

Study E. (1926): Über einige mimetische Fliegen. Zool. Jahrb. Allg. Zool. 42:421–427.

Study E. (1930): Neuere Angriffe auf die Selektionstheorie. Arch. Rassen-u. Gesellsch. Biol. 22:353–393.

Süffert F. (1924): Bestimmungsfaktoren des Zeichnungsmusters beim Saison-Dimorphismus von *Araschnia levana-prorsa*.Biol.Zentralbl. 44:173–188.

Süffert F. (1925): Geheime Gesetzmäßigkeiten in der Zeichnung der Schmetterlinge. Rev.Suis.Zool. 32:107–111.

Süffert F. (1927): Zur vergleichenden Analyse der Schmetterlingszeichnung. Biol. Zentralbl. 47: 385 – 413.

Süffert F. (1929): Morphologische Erscheinungsgruppen in der Flügelzeichnung der Schmetterlinge, insbesondere die Querbindenzeichnung. W. Roux´ Arch.Entwicklungsmech. 120:299–383.

Süffert F. (1932): Phänomene visueller Anpassung I–III . Zeitschr.Morphol.Ökol.Tiere 26:147–316.

Süffert F. (1935): Neue Arbeit an den Fragen visueller Anpassung. Verh. Zool. Ges. 1935:248–295.

Süffert F. (1937): Die Geschichte der Bildungszellen im Puppenflügelepithel bei einem Tagschmetterling. Biol.Zentralbl. 97:615–628.

Suchantke A. (1964): Was spricht sich in den Prachtkleidern der Vögel aus? Die Drei 34(4): 278–298,reprint 1983, pp. 139–161 in: Schad W.(ed.): Goetheanische Naturwissenschaft III.: Zoologie. Stuttgart, Freies Geistesleben.

Suchantke A. (1965): Metamorphosen im Insektenreich. (2.ed. 1999) Stuttgart, Freies Geistesleben.

Suchantke A. (1974): Biotoptracht und Mimikry bei afrikanischen Tagfaltern. Elemente d.Naturwiss. 21:1–21. (reprint 1983, pp.91–118, in: Schad W. (ed.) Goetheanische Naturwissenschaft III., Zoologie. Stuttgart, Freies Geistesleben).

Suchantke A. (1976a): Biotoptracht bei südamerikanischen Schmetterlingen. Elemente d. Naturwiss. Nr. 25:1–8, reprint 1983,pp. 119–125 in: Schad W. (ed): Goetheanische Naturwissenschaft III: Zoologie. Stuttgart, Freies Geistesleben.

Suchantke A. (1976b): Die Buckelzirpen (Membracidae) und die Formensprache der Insekten. Elemente d.Naturwiss. Nr. 24:1–14, reprint 1983, pp. 74–90 in: Schad W. (ed.): Goetheanische Naturwissenschaft III. Zoologie. Stuttgart, Freies Geistesleben. Suchantke A. (2000): Über den Zusammenhang von Biotoptracht und Mimikry bei Schmetterlingen – Beobachtungen in Südasien und anderen Kontinenten. Tycho Brahe – Jahrbuch für Goetheanismus 2000 : 18-87. Stuttgart, Freies Geistesleben.

Sutulov V. (1914): On a species of *Polygonum* obstructing flax crops (*Polygonum linicola mini*). Bull. Seed Control Stat. Soc. Agric. 1(2):1–12.

Swainson W., Shuckard W. E. (1840): On the history and natural arrangement of insects. London, Longman & comp.

Swynnerton C. F. M. (1919): Experiments and observations bearing on the explanation of form and colouring, 1908–1913, Africa. Journ. Linn. Soc. Zool. 32:203–385.

Švanvič B. N. (1931): Evoljucija rysunka kryljev u baboček po novym issledovanijam(russ). Priroda 4:1.

Švanvič B. N. (1945): Ob osnovnom plane risunka kryla Lepidoptera(russ.). Zool. Žurn. 24: 515–546.

Švanvič B. N. (1948): O risunke kryla baboček tolstogolovok (Hesperidae)(russ.). Dokl.Akad.Nauk SSSR 59: 789–792.

Švanvič B. N. (1952): O rysunke kryla palearktičeskich Hesperidae i nekotorych Argynnis (Lepidoptera)(russ.). Entomol. Obozr. 32:137–147.

Švanvič B. N. (1952): Stereomorfizm v kriptičeskoj okraske Lepidoptera Heterocera i nekotorych pozvonočnych(russ.). Trudy Leningrad. Obšč. Est. 71:27–39.

Švanvič B. N. (1953): O rysunkge češuekrylych, preimuščestvenno Heterocera(russ.). Zool. Žurn. 32:874–885.

Thayer A. H. (1896): The law which underlies protective coloration. Auk 13(2):124–129.
Thayer A. H. (1909): Concealing coloration in the animal kingdom. An expression of the laws of disguise through color and patterns. New York, Moffat, Yard&Co.
Thieme O. (1884): Fragmentarisches über Analogien im Habitus zwischen Coleopterenspecies verschiedener Gattungen und Familien. Berlin. Ent. Zeit. 28:191–202.
Thomas F. (1897): Über Mimikry bei Eichenblatt-Gallen. Sitzungsber. Ges. Naturf. Freund. Berlin 1897:45–47.
Thomas of Cantimpré (asi 1250): Miraculorum et exemplorum memorabilium sui temporis libri duo (Bonum universale de apibus). ed. 1605, Duaci, B.Colvenerius.
Thorpe W. H. (1973): Duet-singing birds. Sci. Am. 229:70–79.
Thulborn T. (1994): Mimicry in ankylosaurid dinosaurs. Rsc. South Austr. Mus. 27(2): 151–158.
Tietz D., Zrzavý J. (1996) : Dorsoventral pattern formation : Morphogenesis of longitudinal coloration in Graphosoma lineatum (Heteroptera : Pentatomidae). Eur.Journ.Entomol. 93 : 15-22.
Tinbergen N.(1958): Curious naturalists. London,Wildwood.
Todd J. E. (1888): Directive coloration of animals. Am.Nat. 1888(3).
Tonner M., Novotný V., Lepš J., Komárek S. (1993): False head wing pattern of the Burmese Junglequeen butterfly and the deception of avian predators. Biotropica 25(4):474–484.
Topitsch E. (1958): Ursprung und Ende der Metaphysik. Wien, Springer.
Tower W. L. (1906): An investigation of evolution in chrysomelid beetles of the genus *Leptinotarsa*. Washington, Carnegie Inst.Publ.48, Papers Stat. Exp.Evol.Cold Spring Harbor, New York 4:1–320.
Trimen R. (1861): Rhopalocera Africae australis. I.Cape Town.
Trimen R. (1868): On some undescribed species of South-African butterflies, including a new genus of Lycaenidae. Trans. Ent. Soc. Lond. 1868:69–96.
Trimen R. (1869): On some remarkable mimetic analogies among African butterflies Trans. Linn. Socc. Lond.26:497–522.
Trimen R. (1874): Observations on the case of *Papilio merope*, Auct. with an account of the various known form of that butterfly. Trans. Ent. Soc. Lond. 1874:137–153.
Trimen R. (1885): Protective resemblance and mimicry in animnals (President's adress). Proc.South. Afr.Soc. 3:70–82.
Trimen R. (1897): Mimicry in insects (President's adress). Proc. Ent. Soc.Lond. 1897:74–97.
Trimen R., Bowkers J. (1887–89): South African buttrflies I. (1877), II, (1888), III. (1889) London.
Trotter A. (1903): Miscellanea cecidologiche. Macellia 2:29–35.
Tsacas L., Desmier C. R. de, Coutin R. (1970): Observations sur le parasitisme larvaire d'*Hypertrichia bomboides* (Dipt., Asilidae) Ann. Soc.Ent. France (n.s.) 6:493–512.
Tshirvinskij P. N. (1925): A propos de la compensation des couleurs sur les ailes des Lépidopteres. Rev. Russe Ent. 19: 79–82.
Turner J. R. G. (1983): „The hypothesis that explains mimetic resemblance explains evolution": the gradualist – saltationist schizm. Pp. 129–189 in: Grene M. (ed.): Dimensions of darwinism. New York, Cambridge, Univ. Press. Paris, Ed. Mais. Sci. Homme.
Turner J. R.G. (1984): Darwin's coffin and doctor Pangloss – do adaptationist models explain mimicry? Pp. 313 – 361 in: Shorrocks B. (ed.) : Evolutionary ecology. New York, Academic Press.
Tylor A. (1886): Colouration in animals and plants. London, Longman.
Urquhart F. A. (1957): A discussion of Batesian mimicry as applied to the monarch and viceroy butterlies. A contribution of the division of Zoology and Paleontology, Royal Ontario Mus., Univ. Toronto Press.
Vane-Wright R. I., Ackery P. R. (ed.) (1984): Biology of butterflies. Orlando, Academic Press.
Vavilov N. I. (1922): The law of homologous series in variation. Journ. Gen. 12: 47–89.
Vogel S. (1954): Blütenbiologische Typen als Elemente der Sippengliederung. Jena, G.Fischer.
Vogel S. (1975): Blütenökologie. Fortschr. Bot. 37: 379–392.
Vogel S. (1978): Pilzmückenblumen als Pilzmimeten I., II. Flora (Jena) 167:329–398.
Waddington E. R., Cowe R. J. (1969): Computer simulation of a molluscan pattern. Journ. Theor. Biol. 25:219–225.
Wagner M.(1880): Über die Entstehung der Arten durch Absonderung. II. Die Mimikry. Kosmos 7:89–96.
Waldbauer G. P.(1981): Phenological relationship of Batesian mimics, their models, and insectivorous birds in an Illinois sand area. Nat. Geogr. Soc. Res. Rep.13:651–654.
Wallace A. R. (1855): On the law which has regulated the introduction of new species. Ann. Mag.Nat.Hist., ser.2,16:184–196.
Wallace A. R. (1858): On the tendency of varieties to depart infinitely from the original type. Journ.Proc. Linn. Soc. (Zool.) 3:53–62.
Wallace A. R. (1865): On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of the Malayan Region. Trans. Linn. Soc. Lond. 25:1–71.

Wallace A. R. (1867): Mimicry and other protective resemblances among animals. Westminster For. Quart. Rew.,New Ser. 32:1–43.
Wallace A. R. (1869): The Malay Archipelago.London, MacMillan.
Wallace A. R. (1870): Contributions to the theory of natural selection. London, MacMillan.
Wallace A. R. (1878a): The colours of animals and plants. Am.Nat.11:641–662.
Wallace A. R. (1878b): Tropical nature, and other essays. London, MacMillan.
Wallace A. R. (1889): Darwinism, an exposition of the theory of natural selection. London, MacMillan.
Wallace A. R. (1891): Natural selection and tropical nature. London, MacMillan.
Wallace A. R. (1905): My life, a record of events and opinions I,II. London & New York, Dodd & Mead.
Wallace A. R. (1911): The world of life:a manifestation of Creative Power, Directive Mind and Ultimate Purpose. New York, Moffat, Yard&Co.
Walsh B. D. (H. W.Bates comm.) (1864): No title. Proc. Ent. Soc. Lond. 1864:104–105.
Walsh B. D., Riley C. V. (1869): Imitative butterflies. Am. Ent. 1:189–193.
Walsingham M. A. (1890): The presidents adress. Proc. Ent. Soc. Lond. 1890:48–60.
Walter J. (1904): Die Fauna der Solnhofener Plattenkalke (Oberjura). Pp. 133–214 in: Festschr. 70. Geburtstag E. Haeckel. Jena, Fischer.
Wasmann E. (1890): Vergleichende Studine über Ameisen- und Termitengäste. Tijdschr. Ent. 33: 27–97.
Wasmann E. (1899a): Die psychischen Fähigkeiten der Ameisen. Appendix. Zool. Hefte 26: 1–131.
Wasmann E. (1899b): Instinkt und Intelligenz im Tierreich. Freiburg i. Br.
Wasmann E. (1925): Die Ameisenmimikry, ein exakter Beitrag zum Mimikryproblem und zur Theorie der Anpassung. Abh. Theor. Biol. 19. Berlin, Bornträger.
Waterhouse G. R. (1839): Descriptions of some new species of exotic insects. Trans. Ent. Soc. Lond. 1839:188–196.
Weir J. J. (1869): On insects and insectivorous birds, and especially on the relation between the colour and the edibility of Lepidoptera and their larvae. Trans. Ent.Soc.Lond. 1869:21–26.
Weir J. J. (1870): Further observations on the relation between the colours and edibility of Lepidoptera and their larvae. Trans. Ent. Soc. Lond. 1870:337–339.
Weismann A. (1875): Studien zur Deszendenz – Theorie I. Über den Saison-Dimorphismus der Schmetterlinge. Leipzig, Engelmann.
Weismann A. (1876): Studien zur Deszendenz – Theorie II. 1.) Ontogenese und Morphologie der Sphingiden – Zeichnung. 2.) Über den phyletischen Parallelismus bei metamorphischen Arten. Leipzig, Engelmann.
Weismann A. (1902). Vorträge über Deszendenztheorie. I. Jena, G.Fischer.
Werner F. (1890): Untersuchungen über die Zeichnung der Schlangen.Wien.
Werner F. (1891): Weitere Beobachtungen über die Zeichnung der Reptilien und deren Deutung vom phylogenetischen Standpunkt. Biol. Centralbl. 11: 358–372.
Werner F. (1892–93): Untersuchungen über die Zeichnung der Wirbelthiere II.–III. Zool. Jahrb. Syst. 6: 155–229(II.),7:365–410(III.).
Werner F. (1893): Bemerkungen über die Schildkrötenzeichnung. Biol. Centralbl. 13: 201–206.
Werner F.:(1895): Nachträgliche Bemerkungen über die Schlangenzeichnung. Biol. Centralbl. 15:345–347.
Werner F. (1907): Das Ende der Mimikryhypothese? Biol. Centralbl. 27:174–185.
Werner F. (1908): Nochmals Mimikry und Schutzfärbung. Biol. Centralbl. 28:567–576, 588–601.
Werner F. (1917): Mimikry bei Schlangen. Blätter Aquar. Terrarienk. 28: 186–188.
Westwood J. O. (1840a): Observations upon the relationship existing amongst natural objects, resulting from more or less perfect resemblance, usually termed affinity and analogy. Mag.Nat. Hist., New Ser. 4:141–144.
Westwood J. O. (1840b): Illustrations of the relationship existing among natural objects usual termed affinity and analogy, selected from the class of insects. Trans. Linn. Soc. Lond. 18:409–421.
Westwood J. O., Wallace A. R., Bates H. W. et all. (1866): (Discussion about mimicry). Proc. Ent. Soc. Lond. 1866:36–41,44–48.
Whitman D. W., Orsak L., Greene E. (1988): Spider mimicry in fruit flies (Diptera: Tephritidae): Further experiments on the deterrence of jumping spiders (Araneae: Salticidae) by *Zonosemata vittigera* (Coquillett). Ann. Ent. Soc. Am. 81(3): 532–536.
Wickler W. (1960): Aquarienbeobachtungen an *Aspidontus*, einem ektoparasitischen Fisch. Zeitschr. Tierpsychol. 17:277–292.
Wickler W. (1961): Über das Verhalten der Blenniiden *Runula* und *Aspidontus* (Pisces, Blenniidae). Zeitschr. Tierpsychol. 18:421–440.
Wickler W. (1962a): Zur Stammesgeschichte funktionell kohärenter Organ- und Verhaltensmerkmale:Ei-Attrapen und Mulbrüten bei afrikanischen Cichliden. Zeitschr.Tierpsychol. 19:129–164.

Wickler W. (1962b): „Egg-dummies“ as natural releaser in mouth-breeding Cichlids.Nature 194:1092–1093.
Wickler W. (1963): Zum Problem der Signalbildung, am Beispiel der Verhaltensmimikry zwischen *Aspidontus* und *Labroides*. Zeitschr. Tierpsychol. 20:657–679.
Wickler W. (1966a): Mimicry and the evolution of animal communication. Nature 208:519–521.
Wickler W. (1966b): Mimicry in tropial fishes. Phil. Trans. Roy. Soc. (B) 251:473–474.
Wickler W. (1967): Socio-sexual signals and their intraspecific immitation among primates. Pp. 69–147 in:Morris D. (ed.): Primate ethology. London.
Wickler W. (1968): Mimikry. Nachahmung und Täuschung in der Natur. München, Kindler.(engl.ed.1968, London, World Univ. Library)
Wied M. v. (1820): Über die Cobra Coral oder Cobra Coraes der Brasilianer. Verh. Leop. Carol. Akad. Naturf. 2:105–110.
Wiens D. (1978): Mimicry in plants. Pp. 365–405 in: Hecht M. K., Steer W. C., Wallace B. (eds.): Evolutionary biology, Vol. II.
Wiernasz D. C. (1989): Female choice and sexual selection of male wing melanin pattern in *Pieris occidentalis* (Lepidoptera). Evolution 43: 1672–1682.
Williams K. S., Gilbert L. E. (1981): Insect as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. Science 212:467–469.
Willis E. O. (1963): Is the zone-tailed hawk a mimic of the turkey vulture? Condor 65:313–317.
Winhard W. (1996): Konvergente Farbenmusterentwicklung bei Tagfaltern. Spixiana (München), Suppl. 21:1–192.
Wohlfahrt T. A. (1989): Über die geographische Variabilität der Schwanzfortsätze an den Hinterflügeln des Segelfalters Graphium agamemnon (L.), Spixiana (München) 12(2):213–226.
Wolff Ch. von (1725): Vernünftige Gedancken von dem Gebrauche der Theile in Menschen ... . Jena.
Wood T. W. (1867): Remarks on the coloration of chrysalids. Proc. Ent. Soc. Lond. 1867:99–101.
Wood-Mason J. (1878): No title. Proc. Ent. Soc. Lond. 1878:12–13.
Wrigley A. (1948): The color patterns and sculptures of molluscan shells. Proc. Malacol. Soc. Lond.27 : 216–217
Young A. M. (1971): Wing coloration and reflectance in *Morpho* butterflies as related to reproductive behaviour and escape from avian predators (Lep., Nymphalidae). Oecologia 7:209–222.
Zahavi A. (1975): Mate selection – a selection for handicap. J.Theor. Biol. 53:205–214.
Zajciw D. (1971): Contribucao ao estudo do desenho dos élitros de *Colobothea* Serv.,1825 (Col. Cerambycidae, Lamiinae). Rev. Bras. Biol. 31(2): 133–140.
Zaret T. (1977). Inhibition of cannibalism in *Cichla ocellaris* and hypothesis of predator mimicry among South American fishes. Evolution 31:421–437.
Zenneck J. (1894): Die Anlage der Zeichnung und deren physiologische Ursachen bei Ringelnatterembryonen. Zeitschr. Wiss. Zool. 58: 364 –393.
Zimmermann D. A. (1976): Comments of feeding habits and vulture mimicry in the zone-tailed hawk (*Buteo albonotatus*). Condor 78(3):420–421.
Zinger N. V. (1909): On *Spergula* and *Camelina* obstructing flax crops. (in russ.). Trav. Mus. Bot. Acad. Sci. St.-Pétersbourg 6:1–303.
Zrzavý J. (1990) : Evolution of the aposematic colour pattern in some Coreoidea s.lat. (Heteroptera): a point of view. Acta Entomol. Bohemoslov. 87 : 470-474.
Zrzavý J. (1994) : Red bugs and the origin of mimetic complexes (Heteroptera: Pyrrhocoridae: Neotropical Dysdercus spp.). Oikos 69 : 346-352.
Zrzavý J. (1995): Morphological organization of abdominal colour patterns in pyrrhocorid bugs (Hemiptera-Heteroptera: Pentatomomorpha). Journ.Syst. Zool.Evol.Res. 33: 3-8.
Zrzavý J. (1997): Phylogenetics and ecology : all characters should be included in the cladistic analysis. Oikos 80 : 186-192.
Zrzavý J. (1999): Comparative and developmental morphology of the forewing color pattern in Pyrrhocoridae (Hemiptera). Acta Soc.Zool.Bohem. 63 : 279-289.
Zrzavý J., Nedvěd O. (1997): Phylogeny of the New World Dysdercus (Insecta: Hemiptera: Pyrrhocoridae) and evolution of their colour patterns. Cladistics 13 : 109-123.
Zrzavý J., Nedvěd O. (1999): Evolution of mimicry in the New World Dysdercus (Hemiptera: Pyrrhocoridae). Journ.Evol.Biol. 12 : 956-969.
Zrzavý J., Nedvěd O., Socha R. (1993): Metameric color pattern in the bugs (Heteroptera : Lygaeidae, Largidae, Pyrrhocoridae, Rhopalidae) : A morphological marker of insect body compartmentization. Zool.Sci. 10 : 133-140.

List of Illustrations

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About the author

Prof. Dr. Stanislav Komárek, born in 1958 in Jindřichův Hradec, Czech Republic, studied biology at the Faculty of Natural Sciences of Charles University in Prague. From 1983-90 he was an emigrant in Austria (The Ministry of Agriculture, the Zoological institute of the University of Vienna), then from 1990 he lectures on the mimicry phenomena in nature, history of biology, and on biological esthetics at the Department of Philosophy and History of Science at the Faculty of Science of Charles University in Prague.

This book complexly covers mimetic phenomena in nature and deals with the interpretation of the external appearance of organisms. The author made use of his extensive database of works on mimetic phenomena, which contains over 5000 entries and which is mainly the result of his work in Vienna, Leiden, and Amsterdam. In book form it was published by the Prague publishing house Vesmír in 1998 under the title ***Mimicry, Aposematism and Related Phenomena in Animals and Plants, Bibliography 1800-1990***.