

CAMOUFLAGE AND MIMICRY IN FOSSILS, I.: GENERAL PART

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Abstract. A brief review of camouflage and mimicry in fossils is given. It is suggested that the great majority of palaeontological articles have referred to camouflage and mimicry only in relation to discoveries of colours and colour patterns. The present authors stress the importance of morphology for the study of these phenomena in the fossil record and interesting possibilities of camouflage and mimicry (esp. in trilobites) are considered here. Finally, both the structuralists' as well as darwinists' explanations of camouflage and mimicry are thoroughly discussed, discarded and a true holistic approach is proposed and defined here.

■ palaeontology, mimicry, camouflage, structuralism, darwinism, holistic approach

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motto

"At the very least, as John Collier put it in a personal communication, "the separation of science from myth obscures the mythical character of science, and gives [it] more weight than it deserves."

(STANLEY N. SALTHER 1993)

Introduction

Camouflage and mimicry have long proved interesting and fascinating. Every observer probably knows something of "masking" in the living world because for every animal one easily discovers there are several scarcely distinguishable or almost "invisible". Such "protective strategies" are very common among animals. They are even overwhelming in the living world. Without doubt, the same situation must be observable in the fossil record.

However, any observation or idea is interesting, but it is not really a contribution to scientific knowledge until it is published for others to read. But looking at the literature we come to a mysterious conclusion: it seems that palaeontologists did not publish many articles on such common phenomena under consideration here. Why?

And what about zoologists? How far back in history we must go for the first written observation of the phenomena discussed in our present paper? Of course, the situation in zoology is different.

The writings of Greek philosophers contain material which is clearly scientific showing that the Greeks made great strides in beginning to understand the structure and function of the living world. In search for *camouflage* and *mimicry* (these terms themselves are of recent coinage) we come to the turning point in the history of Greek science, to a point of extensive empirical enquiries and the last great systems of the world as a whole. And we find that

camouflage through active colour changes (described thoroughly in the classical book, Parker 1948) in the octopus and chameleon was already described by Aristotle (384–322 B.C.), founder of the Lyceum, who mentioned it in his treatise "*Historia Animalium*". His observations became an important part of scientific literature on the subject. References to camouflage through colour changes in animals were made by Pliny, i.e. Gaius Plinius Secundus (A. D. 23/24–79), in his "*Naturalis Historia*", too. As a recognized distinct field in zoology, the interest in the phenomena of camouflage and mimicry dates from the 19th century, especially thanks to the early darwinists (see below). But what about the references to camouflage and mimicry in fossils?

Although ancient invertebrate shells, skeletons and carapaces displaying original colour patterns are among the rarest fossils, we can find a relatively considerable number of articles on this subject (see especially the summary and bibliography in Kobluk and Mapes 1989). Because of some special forms of some preserved colour patterns, possible presence of the phenomena of camouflage, warning coloration and mimicry in fossil marine organisms has been described by several previous authors. For example, Cowen, Gertman and Wiggins (1973), Kobluk and Hall (1976), Kobluk and Mapes (1989), and Boucot (1981, 1990) have reported colour, colour patterns, including the so-called countershading patterns (for the purpose of counteracting the differential illumination) and the so-called disruptive marginal patterns (which break up a sharply defined outline) of various fossil shells, skeletons and carapaces which may have served probably for offensive or defensive camouflage, partly for species or sex recognition. Gottfried (1989) has observed cryptic and the so-called disruptive coloration (colour markings which break up the shape of the body) in a single specimen of *Elonichthys* sp. (Upper Palaeozoic actinopterygian fish from Kansas), etc.

In general, the great majority of articles have referred to camouflage and mimicry in fossils only as in relation to discoveries of colours and colour patterns. On the other hand, many of the works on fossil colours and colour patterns did not refer to camouflage and mimicry at all. The oldest known fossil with preserved colour pattern (fan-like array of stripes on the pygidium) is the Middle Cambrian trilobite species *Anomocare vittata* (Raymond 1922). For illustration, several other patterned trilobites have been described by previous authors (except Raymond 1922, see e.g., Williams 1930, Wells 1942, Teicher 1944, Garretson 1953, Harrington 1959, Hessler 1965, Esker 1968 or Babcock 1982). For an interesting bibliography on colour patterns in Palaeozoic marine invertebrates see Kobluk and Mapes (1989). The latter includes also an article on the colour patterns of some Barrandian (Lower Palaeozoic) fossils (Kříž and Lukeš 1974). However, the bibliography does not include the studies on colour patterns of some fossil invertebrates from the Barrandian area which are to be published in a larger work by Vojtěch Turek on colour patterns in cephalopods as well as in two reports by Radvan Horný on colour patterns discovered in platyceratids and cyrtoneurids (both authors are members of the Department of Palaeontology, National Museum).

Well-known are findings of colour and colour patterns on wings of fossil insects (for summary see Boucot 1990, and Shear and Kukalová-Peck 1990) and their possible function as warning or mimetic coloration has been discussed. Also colour patterns on the insect's abdomen are known in the fossil record (see e.g., Becker 1965), colour patterns on the carapax of a turtle (Sullivan et al. 1988), chromatophores in fossil anurans, colour patterns on feathers of fossil birds, etc. (for bibliography see Boucot 1990). Some of these works also discuss the possible function of colour patterns in camouflage, warning coloration or mimicry.

Therefore, it is obvious again that to date, most of the work on fossil camouflage and mimicry has been concentrated on finding colours or colour patterns in the fossil record. Paradoxically, other characteristics of camouflage and mimicry (including those which are the best observable in the fossil record, i.e. *morphological* ones) do not play an important role in the research of fossils.

Do camouflage and mimicry represent only a simple function of colour and colour patterns?

In non-zoological literature, less weight has been put on other characteristics of the discussed phenomena and almost no palaeontologists were able to see them in their full com-

plexity, i.e. as a result of the interplay between colours, colour patterns, shape of the body, behaviour and the surrounding environment, both "physicochemical" and biological. This is the reason why palaeontologists did not publish many articles on the phenomena under consideration.

Of course, among zoologists it is well-known that not only the colour pattern but a combination of it with *shape* provides the animals with most elaborate and highly effective disguises. The zoologists (e.g. Cott 1940, Wickler 1968, Robinson 1969, Herán 1976 or Owen 1980) have also pointed to the importance of animal *behaviour* associated with the camouflage phenomenon because the latter works only under special conditions, i.e. in relation to the appropriate *environmental background* and the appropriate "positioning" of the camouflaged animal in that background. Of course, it seems questionable whether camouflage and mimicry in such a manifold sense have ever been recognized in the fossil record. But while it is generally accepted that there are many examples of similarities in the fossil record resulting from *close relationship* (i.e. because of common ancestry), there has been less enthusiasm for the notion that two similar species at the same place and time are related as a "model" and its "mimic" or that they were camouflaged in the same manner. For example, Jan Bergström (1973, p. 43) correctly stated that "*convergence-like similarities have been commonly taken to indicate a close relationship but the development of the same morphological characteristics along different phylogenetic lineages may be due to a similar mode of life*". Unfortunately, the "mode of life" is frequently related only to "abiological" environment. Palaeontologists typically discuss *parallelism* (i.e., development of similar characters in different lineages of common ancestry) and *convergence* (i.e., homeomorphism or similarity resulting from the same mode of life in unrelated phylogenetic lineages) but almost no palaeontologist is able to suppose that there are other possibilities. *The purpose of the present article is to point out that in the fossil record many similarities between species may have resulted from a similar type of camouflage or mimicry.*

In order to search for camouflage and mimicry in the fossil record, palaeontologists must study the external morphology of fossil shells, skeletons and carapaces and so take into account that some features of the external morphology can be of no systematic value (e.g. the granulation on the exoskeletons of trilobites discussed below). Such "taxonomically unuseful characteristics" are of great importance for reconstructions of life habits and - of the camouflage as well. Among trilobites, for instance, it seems very likely that well-camouflaged polymorphic species do occur in the fossil record (not only in recent arthropods), and that several external morphological similarities (e.g. between asaphids, scutelluids and lichids) do not result simply from an unspecified, in many cases *poorly abstract* and hypothetical "similar mode of life", but also from the same type of camouflage or mimicry.

Even though many aspects of camouflage and mimicry in fossils have never been thoroughly investigated, enough is known of living animals to provide comparison with fossils. Many questions still have no answers. Therefore, it seems important for the present authors to discuss these phenomena as thoroughly as possible (including at least a brief summary of zoological literature), so that other palaeontologists can use the informations given below to advance our knowledge in this very interesting but still almost intact field of palaeobiology. The presented first part of our study is for those interested in general aspects of camouflage and mimicry, including discussion on consequences for the evolutionary theory. The second part, which is in preparation, will be devoted to granulation (as camouflage) on trilobite carapaces (material from Lower Palaeozoic of the Barrandian area).

Recent camouflage and mimicry

Camouflage or *crypsis* is one of nature's most common "escape mechanisms". Typically, the various colours and colour patterns allow organisms to blend with their background (the so-called *cryptic coloration*). This "invisibility" is observable everywhere. In many cases the strategy of camouflage is directed only to a limited number of predators. For example, the stripes of a zebra (although seemingly conspicuous for us in the zoo) represent a type of effective camouflage in natural conditions. Surprisingly, after experienced hunters and travellers (see Herán 1976), the black and white stripes merge well with the surrounding vegetation so that the zebra cannot be seen even at a very short distance. Moreover, unlike humans, their main predators - lions - are colour-blind.

After Needham (1974), a colour-specialist, the main, but not the only, functions of integumental chromes are in the contrasting roles (camouflage) and *semasis* (advertisement). Camouflage (crypsis) is most crucial for animals preyed upon but is common also in predators, both those "*which lie in wait for the prey and those which approach by stealth*." Its types are diverse, extending to countershading, shadow-elimination, matching background colours, shape-disruption, including the phenomenon of "chromotropism", or better, *chromotaxis* (the latter represents an interesting behaviour of camouflaged animals in which they deliberately seek a matching background).

After Needham (1974), *advertisement* involves bright, conspicuous colours, in large patches, with sharp boundaries and contrasts, and may be interpreted by the "target" animal as either warning (*aposematic*) or welcoming (*episematic*). Warning coloration may be very effective. After Carpenter (1921), using the monkey *Cercopithecus* as a test-predator, about 84% of insect species bearing warning colours were distasteful, while, in camouflaged ones, only 18%(!). The contrasting colour bands of wasps are the best known warning pattern. Bright colours of male birds are the best-known examples of sexually attracting (*episematic*, *epigamic*) displays. Needham (1974) has pointed out that the latter "*must often compromise with camouflage requirements and in many cases the colours and bold patterns are hidden except during the actual process of courtship*." The *episematic* subdivision (i.e. *episematic patterns attracting for purposes other than reproduction*), is the least familiar. Perhaps the best known are the lures of some deep sea fishes (e.g., aggressive mimicry in anglerfishes) and certain trematodes (Needham 1974, p. 257). Possibly also the bright colours of sea anemones may have this significance. An example of *pseudaposematic* (Batesian) mimicry may be that of palatable insects (cockroaches) of unpalatable leaf beetles and lady-bird beetles. (The latter examples from Needham's work are given only to illustrate the terminology which is in various authors different; the term mimicry will be discussed below and only the simplest terminology will be applied here).

In the marine environment, many forms of camouflage and mimicry exist and some have been described in the literature (see e.g., Fricke 1975). However, despite the great interest in colour patterns in the sea, their function is still poorly understood. Possibly better known (especially in reef fishes) are brilliant colour patterns which do not serve as a means of camouflage but as *communication*. The "visual cues" (colour patterns of the reef fishes) are invaluable because other type of communication would be almost impossible in the clear-water high-energy environment on the reef (e.g. chemical cues are rapidly dispersed in such an environment). For example, according to observations of numerous eye-colour patterns in many reef fishes of the tropical western Atlantic less than 25% of the species have camouflaged eyes (i.e. patterns disrupting the outline of the eye for the purpose of concealment). On the other hand (see Tresher 1978), the most frequently encountered form of eye ornamentation is outlining (i.e., a way to make an eye conspicuous). Moreover, because reef fishes are best able to see blue and yellow, their pupil is often dark blue, while their iris generally bright yellow.

Many animals perfectly imitate plants or inanimate objects (but also plants may use such a technique), often with the aid of special behaviour, e.g. a horned frog, a fish or a bush-cricket looking all like leaves, a tropical mantid looking like a flower, etc. (see e.g. the summary in Owen 1980). Other interesting practice of "invisibility" is the camouflage of a nightjar with plumage like bark and withering leaves, or the camouflage of many bark-like bark-resting insects that spend much of their lives exposed on tree trunks. Well-known are camouflaged lepidopterous insects. Especially famous is the case of the so-called "*industrial melanism*" in peppered moth *Biston betularia* (which represents also a kind of "*adaptive polymorphism*" - see below, as well as of the above mentioned *chromotaxis*) described in the classical article of Kettlewell (1959). Camouflaged nonlepidopterous bark-resting insects are less well known (e.g. Silberglied and Aiello 1980).

The term *mimicry*, on the other hand, is generally used in connection with animals that (especially visually) imitate other animals or their parts (see Rothschild 1967) and, moreover, the "model" animal must be already protected by warning coloration (it was the co-author of the theory of natural selection, Alfred Russell Wallace, who first propounded the theory of warning coloration). Although Rothschild stressed in her article that this is a somewhat confusing restriction of the term, for specialists in this field it is still the situation of the present day (Owen 1980).

The term itself has been introduced into biology by Kirby and Spence (1817) but not in its present state of understanding. The true discoverer of the phenomenon of mimicry was the British naturalist Henry Walter Bates (*1825 †1892). Bates, while voyaging along the Amazon Valley, found a perfect visual resemblance of some butterflies to their highly protected heliconid "models". Bates's famous pioneering report – "*Contribution to an Insect Fauna of the Amazon Valley*" – was read before the Linnean Society in June 21, 1861. Therefore, the so-called disguises of "sheeps in wolf's clothing" are named *Batesian mimicry*. The second main subdivision (*Müllerian mimicry*, in which both the mim and model are unpalatable) is named after the German zoologist Fritz Müller (*1822 †1897).

George St. Mivart, a very popular opponent of Darwin, has summarized Bates's discovery and Wallace's theory:

"Let us take the cases of mimicry amongst Lepidoptera and other insects. Of this subject Mr. Wallace has given a most interesting and complete account, showing in how many and strange instances this superficial resemblance by one creature to some other quite distinct creature acts as a safeguard to the first. One or two instances must here suffice. In South America there is a family of butterflies, termed Heliconidae, which is very conspicuously coloured and slow in flight, and yet the individuals abound in prodigious numbers, and take no precautions to conceal themselves, even when at rest during the night. Mr. Bates (the author of the very popular book "The Naturalist on the River Amazons," and the discoverer of "Mimicry") found that these conspicuous butterflies had a very strong and disagreeable odour; so much so that any one handling them and squeezing them, as a collector must do, has his fingers stained and so infected by the smell as to require time and much trouble to remove it.

It is suggested that this unpleasant quality is the cause of the abundance of the Heliconidae; Mr. Bates and other observers reporting that they have never seen them attacked by the birds, reptiles, or insects which prey upon other Lepidoptera. Now it is a curious fact that very different South American butterflies put on, as it were, the exact dress of these offensive beauties and mimic them even in their mode of flight." (Mivart 1871, p. 33–34).

The present state of understanding is not very different. We can define the *visual mimicry* (the most common and possibly the only type of mimicry detectable in the fossil record) exactly as follows:

1) there must be an animal, so-called "mimic" which resembles another species or "model" (also animal) and (from this resemblance) gains some sort of advantage for itself,

2) there must be a model (typically more abundant than the mimic, esp. in the Batesian mimicry) in the same place and time (the latter restriction seems to be very important for zoologists as well as for palaeontologists) which leads a "warning way of life" and which is imitated by the mimic, and

3) there must be an "operator" (audience), generally a predator which mistakes the mimic for the model (see e.g., Owen 1980).

Batesian and Müllerian mimicry studied extensively among arthropods and some other invertebrates (see e.g., Poulton 1890, Brower and Brower 1962, Wickler 1968, Vane-Wright 1976 or Owen 1980) are relatively rare (but only relatively!) in vertebrates (see e.g., Cott 1940, Heráñ 1976, Greene and McDiarmid 1981, Diamond 1994).

A special case of mimicry (unfortunately, some authors have excluded it from the division of true mimicry), well-known in butterflies of the family Lycaenidae, so-called diverting "*false head*", seems to be also very effective form of disguise because a considerable number of predators are known to perform their initial strike at the prey's head (see e.g., Swynnerton 1926, Carpenter 1941, Curio 1965).

There are also other kinds of camouflage and mimicry and some of them will be discussed below. For understanding the further discussions it is crucial to remember again and again that *camouflage and mimicry do not represent only a function of colour and colour patterns!*

Morphological aspects of camouflage and mimicry in fossils

Because colours and colour patterns in fossils are rather a preservational curiosity (at least for collectors), there is no doubt that in the articles written by Lamont (esp. 1967, 1969) we can find the most important attempts to count camouflage and mimicry in fossils. It is because

the popular Scottish palaeontologist Archie Lamont has given the first real confirmation of the correctness of the way of explaining the function of camouflage and mimicry in fossils from the viewpoint of *morphological* characteristics of ancient animal skeletons. In other words, he has proved that *camouflage and mimicry are not curiosities in the fossil record*. His provocative conclusions include many aspects of the phenomena in many groups of Lower Palaeozoic marine animals, e.g. aggressive mimicry in the eurypterid *Stylonurus*, mimicry of "gaping mouth" threat in the tails of recent and fossil fish-shaped vertebrates, several types of imitations of algae in fossils, a considerable number of camouflaged trilobites (e.g., granulation imitating grit), several types of camouf in brachiopods, graptolite colonies imitating a brittlestar, etc.

The possibility of mimicry among trilobites has also been reported by the American palaeontologist and macroevolutionist, Niles Eldredge. He has mentioned calmoniids of the genera *Schizostylus* and *Probolops* and pointed to the striking similarity of their heads, their common occurrence in the same beds and to the rarity of the latter genus. Eldredge (1980, p. 50) has concluded that *Probolops* is a (probably Batesian) mimic of *Schizostylus*.

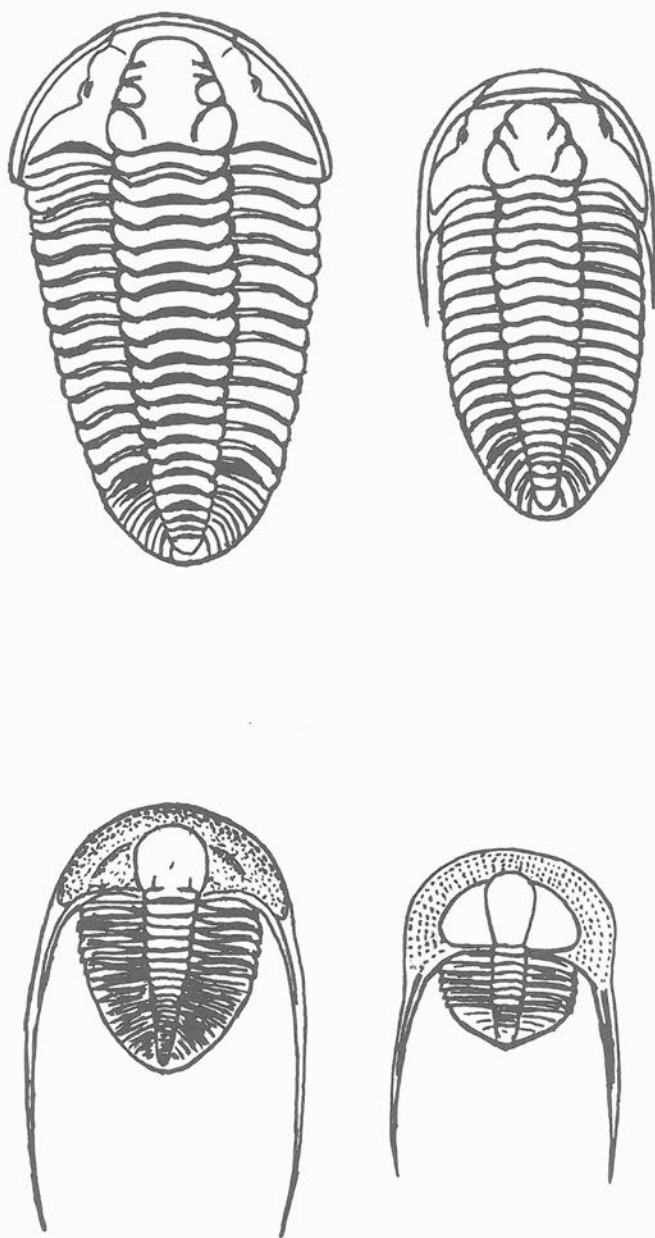
From the same point of view, the most recent description of a mimicry in the fossil record (and the first one among dinosaurs!) is that of the Australian vertebrate palaeontologist, Tony Thulborn. He found that there is a very limited flexibility in Late Cretaceous ankylosaurid tails, the clubs of which are usually regarded as a weapon to deter predators. His conclusion is that this is a kind of mimicry of a "false head" that may have diverted predator (which had tendency to bite the neck or head) from the true head. The ankylosaurid tail with its club may have imitated a generalized form of neck and head of some other ornithischian dinosaurs. According to Thulborn's model, the carnosaur was "*lured within reach of the tail club*" and "*the tail club would strike at the aggressor's head, rather than its feet, thereby achieving the greatest deterrent effect*" (Thulborn 1994). Such an effective advertisement may have possibly been multiplied by the "invisibility" of the true head. The author points to a similar situation in other ankylosaurids, nodosaurids and stegosaurids which have "*a shallow skull that merges insensibly into a short neck.*"

Camouflage and mimicry in Barrandian (Lower Palaeozoic) trilobites?

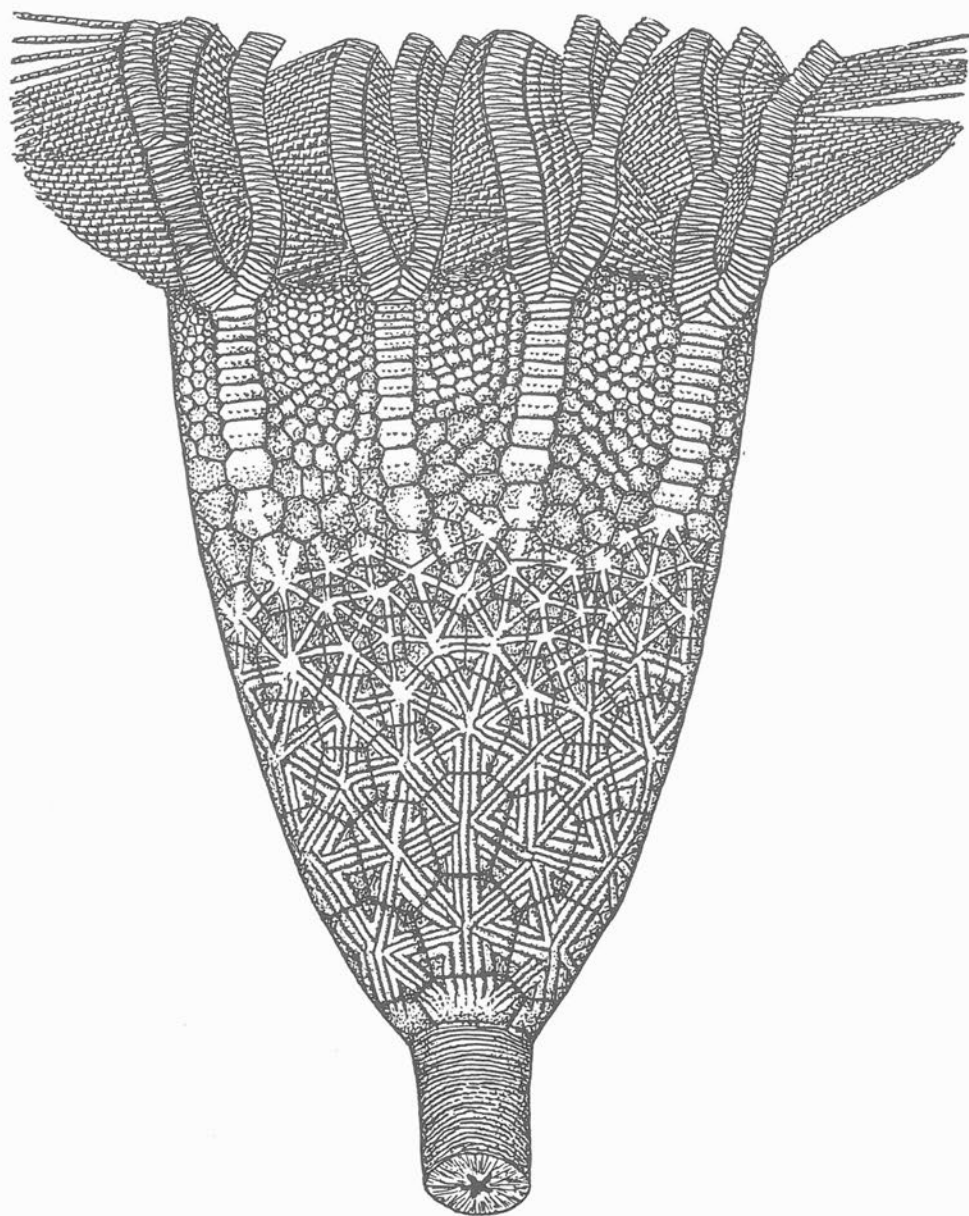
It is possible that some or very many examples of species diversity in the fossil record and even the so-called "ecophenotypic" variations in a single fossil species have resulted from camouflage. We argue that camouflage-related variability (and similarity, too) is common in recent seas as well as on the land. However, palaeontologists have traditionally searched only for the distinction of "environmental" from "genetic" variations (see Johnson 1981) but the ancient animals did not live in a sort of abiological laboratory environment.

As a preliminary result of our study of Lower Palaeozoic trilobites (supposed to be a typical prey of large predators in Palaeozoic seas) is that the size and density of granulation preserved on the external part of trilobite carapaces may have been (in many cases!) a function of sediment particle size. In other words, specimens of trilobites coming from fine-grained sediments bear dense, soft granulation on their carapaces (in extremely fine-grained sediments the carapax may be smooth), while those from coarse-grained ones are provided with large granules scattered on the outer surface of the exoskeletons. Such an interesting correlation has been previously recognized by Chlupáč (1977) in some phacopid trilobites from the Barrandian Lower Devonian, especially in *Boeckops boeckii* (Hawle et Corda), *Reedops bronni* (Barande), and *R. cephalotes* (Hawle et Corda) (personal communication). Similar relationship between the substrate particle size and the type of granulation on the trilobite carapax we have found in the common dalmanitid *Dalmanitina socialis* (Barande) from the Bohemian Middle Ordovician. There are good reasons (supported by shared knowledge and the kind personal indications by Ivo Chlupáč (Charles University) for the belief that the above mentioned examples represent a relatively frequent phenomenon which points to the presence of a specific and very common type of *camouflage* in trilobites, regardless of the conclusions of previous authors about the taxonomic or non-taxonomic value of the trilobite granulation.

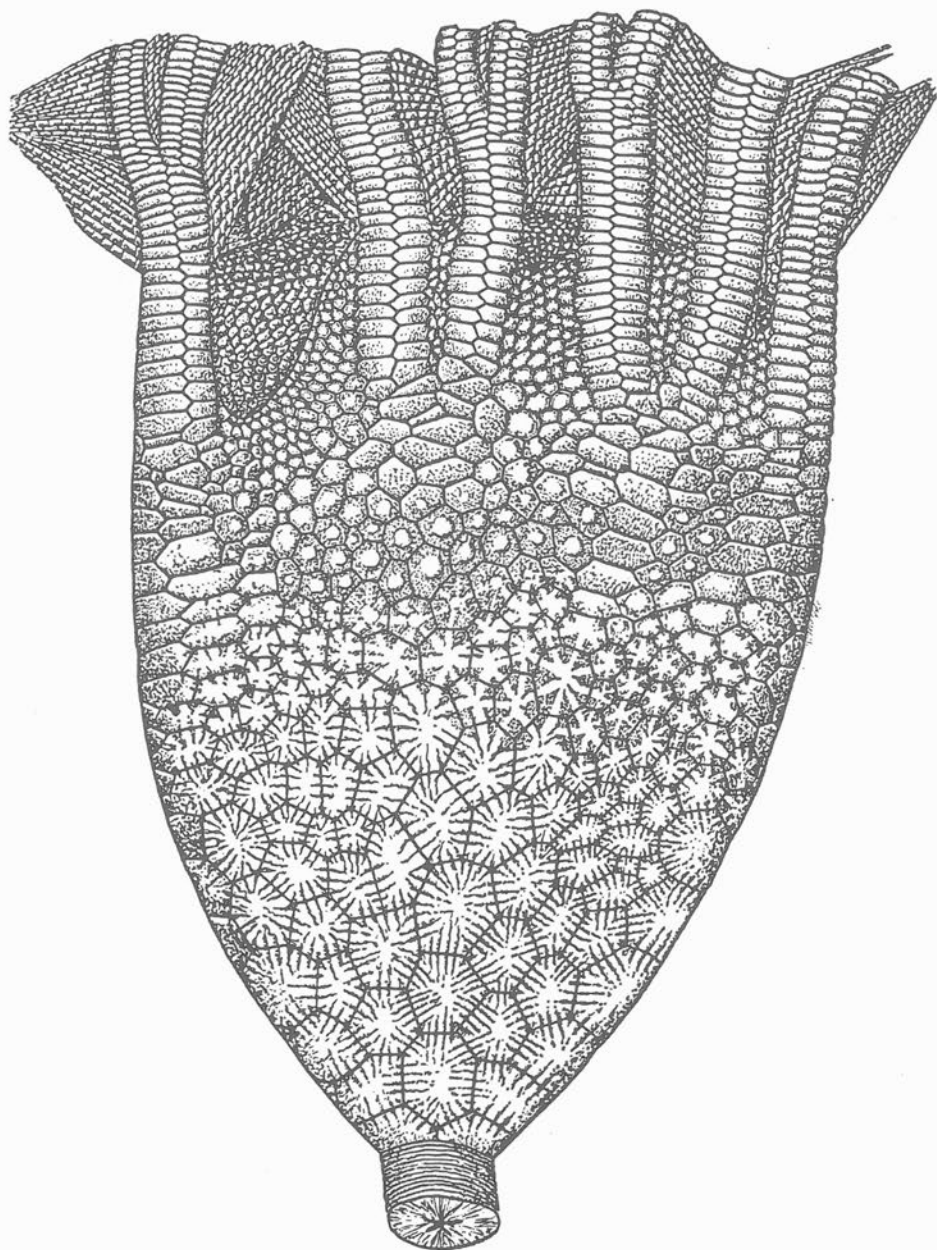
Kácha and Šarič (1991, 1994) stressed on some examples that the form and even presence of trilobite granulation is dependent on the stage of ontogeny. It is important because several previous works on Barrandian trilobites have overemphasized the role of granulation for



Text-fig. 1: Two examples of accidental homeomorphy or (Batesian) mimicry? Coexisting Ordovician trilobite genera from the Barrandian area: 1. *Prionocheilus* ROUAULT (upper left) and *Flexicalymene* SHIRLEY (upper right), 2. *Deanaspis* HUGHES, INGHAM et ADDISON (lower left) and *Dionide* GUERICH (lower right).

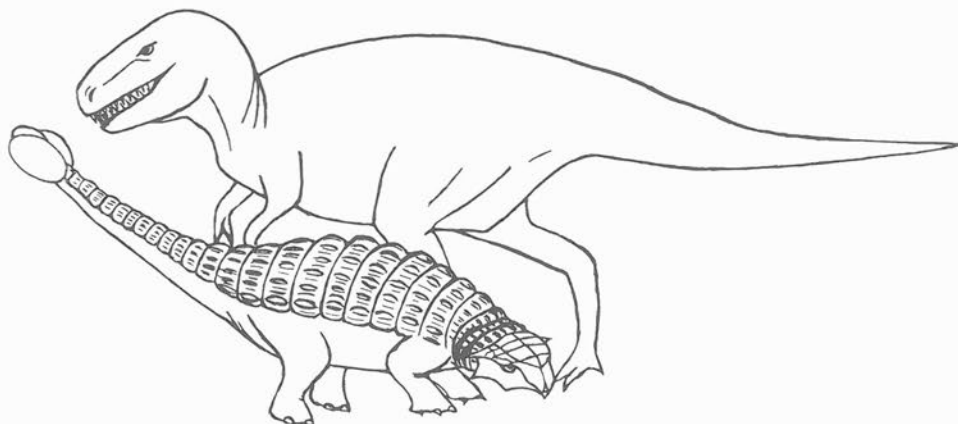


a



b

Text-fig. 2a, b: Müllerian mimics?: Float-bearing camerate crinoids *Scyphocrinites* ZENKER (a), and *Carolicrinus* WAAGEN et JAHN (b), coexisting in uppermost Silurian seas of the Barrandian area. Although both genera are very abundant in the so-called "*Scyphocrinites* Horizon", their common ancestry poses an unresolved question (see Prokop and Petr 1986, 1987, 1994).



Text-fig. 3: Mimicry of "false head"? Because of a very limited flexibility in Late Cretaceous ankylosaurid tails (the clubs of which are usually regarded as a weapon to deter carnosaurs), the club may have diverted predator (which had tendency to bite the neck or head) from the true head. The ankylosaurid tail with its club may have imitated a generalized form of neck and head of some other ornithischian dinosaurs. Such an effective advertisement may have been possibly multiplied by the "invisibility" of the true head which has merged insensibly into a short neck (modified after Thulborn 1994).

taxonomical purposes and many polymorphic species received two, three or even more specific names thanks to slightly different granulation. Moreover, although the changes in granulation throughout the trilobite ontogenies are well known in literature (e.g. Chatterton, Siveter, Edgecombe and Hunt 1990), they have been never related to camouflage. In some recent articles they are even attributed to characteristics invaluable for phylogenetic analyses (see e. g., Edgecombe, Speyer and Chatterton 1988). But the simple fact that the younger (ontogenetically) the individual the coarser and more sparse the granules on its exoskeleton indicates a *relatively stable diameter of the granules* and points to a possible connection between the granulation and the grain size of the substrate (rather than to any phylogenetical conclusion).

It is important to stress that some external features of the trilobite exoskeleton have previously related to the grain size of the inhabited substrate. A constructional morphologist Helmut Schmalfuss discovered that the "cuticular terraces" on the carapaces of some trilobites (as well as those of some recent decapods) may have functioned to provide frictional resistance in interaction with the grains of the substrate (Schmalfuss 1978a-c, 1981). The most interesting discovery is that the number of these terraces per *surface unit* remains constant during ontogeny (the grain-size of the inhabited substrate remains constant during the animals ontogeny, too). We argue that such a close relation to the grain-size of the substrate is also visible in the granulation: the number of granules per *surface unit* remains relatively constant during the development of many trilobites. Of course, this latter observation cannot be linked with burrowing life habits of these trilobites but rather to the purpose of camouflage.

The possibility of mimicry of a "false head" in illaenid trilobites is self-evident but the modern interpretation of illaenid morphology (cephalon extremely similar to pygidium) is a different one. Westrop (1983) has interpreted the life habits of the Ordovician illaenine trilobite *Bumastoides* on the basis of its smooth skeletal surface, strongly convex cephalon and the nature of the thoracic articulation as an "*infaunal trilobite that was poorly suited to epifaunal crawling*" and proposed for it a "*sedentary, infaunal suspension feeding existence*". The latter author has noted that this mode of life would be applicable to many other "illaenimorphs" and that "*convergence has led to the appearance of effaced, strongly convex morphotype in a number of unrelated families, including the Illaenidae, Asaphidae, Aulacopleuridae, Plethopeltidae and Scutelluidae*". However, we argue that the mimicry of a "false head" may also represent a plausible explanation - for illaenids as well as for almost all

other trilobites (the similarity of the cephalon and pygidium is almost universal among trilobites). Unfortunately, as we have incomplete information (some will probably remain incomplete forever) we cannot know exactly whether this type of mimicry has been accompanied by special colour patterns, "eye spots" or a special behaviour. Finally, in a somewhat similar way, species bearing large telsons, may have used them as diverting structures.

There is the possibility of a common presence of many types of camouflage and mimicry in trilobites and several types have been previously discussed by Lamont (1967, 1969). Unfortunately, his conclusions have been typically ignored and never followed in the works of specialists. It is possibly because palaeontologists like to work after the "fashion". Archie Lamont wrote:

"The study of mimicry at Birmingham University was unpopular, and Miss Stephenson (1946) had just left. Mimesis upset neat Darwinian lineages and introduced ideas of mutual aid instead of crude natural selection." (Lamont 1969, p. 88).

Punctuated equilibria and onshore-offshore pattern

The inevitable question for the present authors is whether the "mechanism" of the *diversification* of the trilobite fauna is well-explained in the literature. In the two following chapters we will see that the answer is very important for our further considerations on a specific type of camouflage.

Recent macroevolutionary theory, sometimes called "hierarchy theory", has originated from the famous concept of *punctuated equilibria* (the pioneering article is that of Eldredge and Gould 1972) which has been formulated to account for the incompatibility of the so-called "phyletic gradualism" with the evidence in the fossil record. The "punctuation" is consistent with rapid allopatric speciation, while the "equilibrium" with long periods of stasis. The hierarchy theory, at least in the American literature, has replaced in most cases the former neo-Darwinian "modern synthesis" and may be summarized as follows:

"'Hierarchy theory' accepts the neo-Darwinian paradigm of within-population variation, selection, and drift, but seeks to extend the list of evolutionary entities beyond genes, organisms, and populations. Specifically, species, monophyletic (higher) taxa, and ecosystems have come to be viewed as having real existence, and are variously termed 'systems', 'entities', or even 'individuals'. The goal of hierarchy analysis is to elucidate the nature of each kind of large-scale entity, and thus to determine their possible role(s) in the evolutionary process." (Eldredge 1990).

Some orthodox neo-darwinists (i.e. representatives of the so-called "modern synthesis") claim that this is a misleading and completely non-Darwinian approach to the evolutionary theory, while other neo-darwinists (also "synthetists") claim that there is nothing new under the sun and that a similar model was previously proposed in classical works by George Gaylord Simpson (e.g., Simpson 1944, 1949, 1953). There are many reasons for this curious situation but possibly the most distinct is that in the Eldredge's (seemingly holistic) definition – no smooth extrapolation of microevolutionary processes (i.e. processes within a population) can lead to macroevolutionary phenomena (i.e. among species) and, especially, that there are very different views of "natural selection" and its bearing on evolution.

The "punctuated equilibria" originated as an idea of Niles Eldredge (see e.g. Eldredge 1971) who studied Lower Palaeozoic trilobites and observed that *species persisted for long periods of time without change*. Therefore (especially in Eldredge 1974, 1980) the role of natural selection in creating new species has been deeply questioned. Eldredge and Gould (1972, see also Gould and Eldredge 1977) pointed to the fact that species are *real entities not only in space but in time as well* and proposed an allopatric model of speciation which gained (after a decade) nearly total acceptance among palaeontologists. From this point of view speciation is a fundamentally accidental fragmentation of a once coherent population and natural selection accounts only for a small (if any) part of this rapid change:

"There is as yet no proven, necessary relationship between natural selection and speciation. Though selection invariably plays an important role during speciation event, it has never been shown to be the effective 'cause' of speciation in the sense that the selective regime originates and is sustained for the 'purpose' of developing a new species." (Eldredge 1974).

"... natural selection per se does not work to create new species. The pattern of change

in so many examples in the fossil record is far more a reflection of the origin and differential survival (selective extinction) of species than the inexorable accumulation of minute changes within species through the agency of natural selection." (Eldredge 1980, p. 51).

From this point of view in the "punctuated equilibrium" model the change is not inevitable as it is in the orthodox selectionist model ("modern synthesis") where the "feeling that evolutionary change is almost inevitable is based upon the relentless logic of adaptation through natural selection: somehow, one feels, it is inevitable that environments must change, and organisms must modify their adaptations to keep pace, or face the grim consequence of extinction." (Eldredge 1984).

Because the more heterogeneous the environment, the greater the possibilities are of the establishment of isolates and of speciation. In the sea, it is far easier to find habitat heterogeneity along "onshore" than "offshore" areas. Therefore, for the evolution in environmentally monotonous Palaeozoic epeiric seas the most important issue of the speciation model of Eldredge and Gould (1972) is that proposed by Eldredge (1974). The latter pointed to the possibility that monotonous offshore areas of the epeiric seas "allowed little real opportunity for establishing genetic discontinuity among populations of a species." (Eldredge 1974, p. 544).

Therefore, Niles Eldredge has argued that offshore areas (areas with high diversity) have their source of new species in onshore areas (areas with low diversity). In other words, the latter author really agreed that *more species are found in offshore areas* (because of the greater degree of "niche subdivision" arising from environmental stability) but argued that *the exploitation of these areas resulted probably from speciation in onshore areas*.

Eldredge's theory, mounted, however, on the myth of competition between "primitive" and "advanced" animal groups, is now well-known as the "onshore – offshore pattern" or "onshore – offshore faunal change" and may be ascribed to J. J. Sepkoski, Jr. (see e.g., Sepkoski 1981, 1991, 1995, Sepkoski and Miller 1985, Sepkoski and Sheehan 1983).

The latter author proposed the "Archaic-Cambrian", "Palaeozoic" and "Modern" "Great evolutionary faunas" from which *each originated onshore and displaced the earlier one to offshore areas* during the course of time. However, some specialists disagree with Sepkoski's propositions. For example, Webby (1992) points to the fact that Sepkoski believes that Ordovician radiations are produced by a great expansion of the "Palaeozoic evolutionary fauna" (e.g. Trilobita and Eocrinoidea are assigned to the so-called "Cambrian fauna", while all other echinoderms, except Echinoidea and Holothuroidea to the "Palaeozoic fauna") but that the levels that produce the majority of new higher taxa and community types are in the mid-outer shelf and slope habitats, not onshore.

It is obvious that there is a problem with the so-called "incomplete fossil record". This is a problem as old as the Darwinian theory of evolution itself. In this case it is evident that, for example, during the Ordovician the "Palaeozoic" fauna diversified onshore while the evidence in the fossil record points to higher diversity offshore. But for neo-darwinists, both orthodox and heterodox, this is possibly (traditionally) only a minor pitfall. Even the macroevolutionists (heterodox neo-darwinists) argue, for example, that:

"These discordancies (in onshore-offshore pattern between well-preserved orders and well-preserved genera and poorly preserved orders in post-Palaeozoic marine benthic invertebrates) suggest that the pattern of preferential onshore origination (of post-Palaeozoic benthic invertebrates) is not an artifact of preservation or collection and that the origin of higher taxa cannot be regarded as a simple extrapolation of rates and patterns at lower levels." (Jablonski and Bottjer 1991).

A much more serious problem, however, poses the question of genetic variability within a species. In a recent textbook on biology there is well-expressed a common argument of neutralists against the evolution through natural selection: "These critics (i.e. neutralists) point out that if natural selection is so important, then species surviving in changeable environments should show more genetic variability, and those in stable environments should show less. One might predict, for example, that species in the chaotic intertidal zone would show more genetic variability than species living on the stable floor of the deep sea. Both groups, however, show equal genetic variability when tested." (Postlethwait and Hopson 1989)

So, the evidence conflicts with the predictions of orthodox selectionists for which the genetic variability must be greater in the intertidal (and for which the origin of higher taxa is a "simple extrapolation of rates and patterns at lower levels") as well as with those of

modern "holistic" macroevolutionists (accepting paradoxically "*the neo-Darwinian paradigm of within – population variation, selection, and drift*", but seeking "*to extend the list of evolutionary entities beyond genes, organisms, and populations*" because "*the origin of higher taxa cannot be regarded as a simple extrapolation of rates and patterns at lower levels*"). However, it seems to be evident that, at least in some cases, the places of maximum species diversity in particular groups tended to shift progressively offshore over time (Sepkoski 1991). Why?

So far, we have dealt only with a certain type of data interpretations but the "patterns" may be explained in other, much more plausible ways. Westrop, Tremblay and Landing (1995) studied the well-known declining importance of trilobites from Cambrian to Ordovician and the possible "onshore-offshore pattern" in trilobite evolution. They accepted that during the Cambrian and Ordovician there is a general gradient of increasing trilobite species diversity from nearshore (onshore) to offshore environments. However, they simply argued that the places with maximum species diversity (i. e., offshore environments) were really those in which trilobites (in situ!) attained their maximum species diversity. According to new data from northern North America, Westrop, Tremblay and Landing (1995) found that trilobite species in nearshore (onshore) settings maintained a constant(!), low level diversity between the Late Cambrian and Middle Ordovician (there is no evidence of the predicted trilobite species-diversity decline in nearshore environments).

Therefore, the latter authors pointed out that there is no observable replacement of "Cambrian fauna" (trilobite-rich palaeocommunities) by "Palaeozoic fauna" (brachiopod – dominated) and "Modern fauna" (mollusc – dominated), that the relative importance of trilobites declined rather through a "process of dilution" as species of newly radiating groups (e.g., gastropods, articulate brachiopods) joined them in their environments, and that the "*apparent offshore retreat of trilobite – dominated palaeocommunities (i.e. of the „Cambrian fauna”)*" is also at least partly a *reflection of this dilution process*". Moreover, these authors stressed that the data from the District of Mackenzie indicate little change in trilobite species diversity even in Middle Ordovician offshore environments.

They concluded that: "... *trilobite – dominated paleocommunities maintained their integrity longer in the offshore, and this produced an overall pattern of diachronous replacement. Similarly, progressive offshore replacements of other community types in younger strata may also be dilution phenomena related to species diversity gradients... There does not appear to have been any active ecological displacement of one group by another.*" (Westrop, Tremblay and Landing 1995).

Polymorphism as camouflage in trilobites

Keeping in mind the model of trilobite diversification outlined above and especially the exclusion of the hypothetical displacement of "primitive" groups by "advanced" ones, we come to polymorphic trilobite species.

After the classic of "modern synthesis", Theodosius Dobzhansky, the "adaptive polymorphism" is a widespread phenomenon in the living world. He pointed out that "*adaptively polymorphic populations should, in general, be more efficient in the exploitation of ecological opportunities of an environment than genetically uniform ones...*" and that "*A species will be polymorphic if it contains a variety of genotypes each of which is superior in adaptive value to the others in some habitats which occur regularly in the territory occupied by this species*" (Dobzhansky 1951).

The latter author argued that the so-called industrial melanism is a type of this phenomenon and that "*becoming inconspicuous in normal surroundings, or acquiring a resemblance to some object which is dangerous or distasteful to natural enemies, are among the possible ways in which an organism may become adapted to its environment*".

There seems to be an interesting application of the latter words in trilobites. It has been observed (e.g., Whittington 1966, Foote 1990) that the trilobite suprageneric taxa are morphologically more distinct from each other in the Ordovician than in the Cambrian. Hughes (1991) has argued that there was a progressive change in species discreteness in trilobites from the early Cambrian to late Ordovician and that also many other studies provide quantitative evidence which suggests that the degree of "canalization" in trilobite species increased

through the Palaeozoic. The latter author points out that results show that species belonging to "primitive" clades show greater allometry than species belonging to "advanced" clades, that the species from "primitive clades" often show striking changes throughout adult growth, and that higher levels of ontogenetically invariant intrapopulation variation also occur within trilobite species from "primitive clades".

We must ask again, however: Is it reasonable to see such a phenomenon as a result of "primitive" and "advanced" characteristics? Certainly not. Even Charles Darwin himself was well aware of the difficulties of the concept of "higher" and "lower" and Ghiselin (1969, p. 70) has pointed to the fact that Darwin made a memorandum in his copy of Robert Chamber's book "Vestiges of the Natural History of Creation" writing "*Never use the word higher and lower*"! Darwinists, including those from the time of "modern synthesis", all disagree with the words "primitive" and "advanced", "higher" and "lower" etc. since the classical work of Williams (1966). We can find the same opinion in works of all recent macroevolutionists – for possibly the best analysis of the problem see Benton (1987). The syntheticist Michael Chiselin even wrote:

"The idea of absolute scale for highness or lowliness is an example of essentialist metaphysics which is very common in our everyday thought, and which has profound social implications." (Ghiselin 1969, p. 71).

Foote (1990) analyzed mathematically morphological diversification of Cambrian and Ordovician trilobites and supported the opinion that "*morphospace became more discontinuously occupied from the Cambrian to the Ordovician*". He pointed out that the "*world became a progressively more constrained place for organisms*" and that this increase in morphological clustering might be interpreted as a reflection of a "*transition to an adaptive landscape marked by steeper peaks and deeper valleys*".

On the other hand, the latter author also observed a clear increase in clustering intensity from the Cambrian to the Ordovician (i.e., the morphological clusters are tighter in the Ordovician than in the Cambrian). He concluded that these tighter clusters "*might represent groups of species with more finely partitioned niches*". Moreover, Foote (1990) expected such results and suggested that the expansion of "morphospace" logically accompanied the diversification.

Yes, it seems to be self-evident that the tighter clustering "*may be an expected consequence of any diversification*", however, the validity of this conclusion rests implicitly on the curious assumption that there is an infinite number of "niches" in the "abiological" environment to which the organisms "are adapted". Moreover, the diversification is "implied" by adaptation which is "implied" by the action of natural selection.

However, the largest disparity of marine arthropods is observable in the fossil record from Lower and Middle Cambrian (Gould 1989), i.e. from the time in which the "niches" (from the orthodox view) were paradoxically extremely undifferentiated. Therefore, we agree with Rosen (1978, p. 372) that "*Although natural selection theory fails to explain the origin of evolutionary novelties, its greatest shortcoming in terms of evolutionary theory is that it fails to explain evolutionary diversity.*" However, we do not suggest that the interesting discoveries of Foote (1990) and Hughes (1991) are erroneous. Quite the contrary. We greatly appreciate their discoveries (not explanations) because they are very important for our purpose to search for camouflage and mimicry in the fossil record of trilobites.

The evidence that older or "primitive" trilobite species show a reduced degree of developmental "canalization" compared to younger or "advanced" ones meshes well with the hypothetical model of Kobluk and Mapes (1989) in which the colour patterns did not function originally as camouflage and warning displays. The latter authors studied Palaeozoic invertebrates (about 180 Palaeozoic genera are known with colour patterns preserved!) and pointed to distinctly increasing diversity of colour patterns in the fossil record. They proposed three developmental phases in the evolution of invertebrate colour patterns:

1. the origin of colour patterns during the Cambrian as simple incorporation of metabolic by-products into the invertebrate skeletons,
 2. use of these pigments for other purposes, e.g. light screening, and
 3. use of these pigments and colour patterns for camouflage, mimicry, and warning display.
- Kobluk and Mapes (1989) argued that the colour patterns in the earliest Palaeozoic may have developed prior to the evolution of predators with "*vision sufficiently sophisticated to see them*" (i.e., colour patterns).

Both the latter important discoveries (i.e., Foote 1990, and Hughes 1991 on the one hand, and Kobluk and Mapes 1989 on the other) are significant for our conclusion that both are very closely interrelated due to predators views of prey in the Palaeozoic seas. It is self-evident. The unusually high degrees of intraspecific and interspecific variations among trilobites within the earliest Palaeozoic "primitive" groups ("weakly canalized growth regulation" has been invoked to explain this variability by Hughes 1991) may have represent the only way to reduce the likelihood of being captured (and eaten) by a predator with a poorly developed vision.

This explanation is theoretical and is based on the above mentioned evidence in the fossil record and on what is believed to be the way in which some predators search for their prey. Predators learn by *experience* and consistently seek more of a species with which they have already had success. Because of previous experience, the predator forms an image of what it is looking for and goes on searching for the same species.

Recent species with distinct morphologies are typically camouflaged by colour patterns that match the background either by blending or by resemblance to a specific structure. In some cases, however, the species use the methodology of "being different" (see e.g., Owen 1980). For example, in the recent brittlestar *Ophiopholis aculeata*, there is an extraordinary variation in colour, colour patterns and morphological characteristics. The predator must examine hundreds of specimens before finding that two are alike. In the case of predators with poorly sophisticated vision in the earliest Palaeozoic seas, an important possibility to reduce their responsibility to learn may have been (for the prey) paradoxically to look all alike (no distinct species-specific morphologies developed) and being all different (almost each individual is different from others in a given species). And this forms a logical explanation of the trend discovered in trilobites, and for which the changing composition of ecological-ethological types of predators seems to be clearly responsible.

Who was the predator of trilobites?

This question has been thoroughly discussed in Babcock (1993a). We can only add some remarks.

The earliest predators were possibly large arthropods, unable to see colours. Babcock and Robison (1989) examined the scars on Palaeozoic trilobites and reported that those scars that result from unsuccessful (sublethal) predation (rather than from undefined causes) are significantly more frequently found on the posterior and right side of the trilobites. In Lower and Middle Cambrian trilobites these scars are frequently attributed to *Anomalocaris*. Babcock (1993b) stressed that this "*strong lateral asymmetry of predation scars is most likely due to handedness in either the predators or the trilobites or perhaps in both*". Therefore, Babcock and Robison (1989) concluded that handedness (or "lateralized behaviour") had developed in the Cambrian seas - about 500 million years earlier than previously supposed (see also Babcock 1993 a,b).

Regarding the evidence of large arthropods preying on trilobites in the Barrandian area, there are some possibilities found in the Ordovician rocks (cephalopods are important from the Silurian onward), e.g. in the Letná Formation. According to Ivo Chlupáč (personal communication, Institute of Geology and Palaeontology, Charles University), "*Nothozoe barrandei* CHLUPÁČ (see Chlupáč 1970) of the Letná Formation at Drabov represents the only phyllocarid attaining sufficient length (up to 40 cm) of a large predator. But there is a considerably larger predator than "*Nothozoe*" at the above mentioned locality. In the personal collections of Ivo Chlupáč there are several fragments of giant, smooth carapaces of a possible eurypterid. Prof. I. Chlupáč (personal communication) supposes that the length of this undescribed and poorly known creature was probably about 1 m.

Regarding Lower Palaeozoic cephalopods (in Barrandian they are important in Silurian and Devonian), almost no inference may be drawn from the evidence about their vision. Russel-Hunter (1968, p. 160) has pointed to the fact that there are behavioural indications of colour vision in recent cephalopods and that their eyes are certainly the dominant sense-organs in their behavioural patterns. However, the situation with *Nautilus* (possible nearest neighbour of Palaeozoic forms) is much more complicated. Wells (1962, p. 146-147) wrote that *Nautilus* "... has large eyes of simple structure, with no lens and no iris. There

is a very small circular pupil. The eyes can move backwards and forwards about a vertical axis, but the animals do not appear to recognize objects by sight. They are, however, clearly very sensitive to changes in light intensity, and in aquaria remain quiescent and withdrawn during the day, emerging to swim about only when the light intensity fades towards sundown. While they are attracted to lights and will follow an electric torch about an aquarium, they tend to seek shade from more general illumination..." and that "In the sea, as in aquaria, *Nautilus* seems to locate its food by smell rather than by sight..." and that "they depend on chemotactile sense rather than on sight to locate their food." The latter author and Lane (1957) also pointed to old observations of Arthur Willey (reference in Lane 1957, Wells 1962) who reported that "basket trap baited with cooked crustaceans concealed under coconut fibre caught more *Nautilus* than similar traps baited with freshly dead, clearly visible fish. The traps were set in clear water at a depth of about one hundred metres." On the other hand, we must stress that several different extinct groups of cephalopods are known from the Lower Palaeozoic rocks and we know nothing about their real capacity of vision. Ward (1982) has observed that *Nautilus macromphalus* commonly gains nutrition by eating the molted exoskeletons (exuviae) of spiny lobsters (only the hard cephalothorax is left untouched).

From the uppermost Silurian onward (in the Barrandian area as well as in the world) there is a real possibility of predators with sophisticated colour vision (i.e., true fishes). Such an occurrence meshes well with both the observations of Kobluk and Mapes (1989) as well as with those of Foote (1990) and Hughes (1991).

Homeomorphy, parallelism and convergence.

It is generally supposed that one measure of natural sciences is the understanding of natural phenomena and of man's place in nature. In the search for this understanding naturalists have called upon gods, evolution, archetypes, spirits, transcendentalism, lamarckism, functionalism, structuralism, darwinism, holism, reductionism, vitalism, etc. But the search does not constitute a steady progress of scientific advance or a continuous growth of scientific knowledge: it is rather a matter of changing paradigms (Kuhn 1962, 1970). Because camouflage and mimicry represent phenomena the explanations of which are extremely "paradigm-sensitive" (i.e., their existence may be either denied, as by some structuralists, or explained through "holistic downward causation", as by creationists and darwinists, see below), we must at least touch these related topics in the following chapters.

Niles Eldredge, involved in the study of Bolivian trilobites, has found specimens of the calmonioid trilobite *Bouleia* which was said to be closely related to *Phacops*. After a careful examination of well-preserved individuals, Eldredge (1980) concluded that the resemblance was entirely superficial and that *Bouleia* is an unrelated "homeomorph" of the latter genus, "adapted to similar environmental demands". He also observed that calmonioid *Cryphaeoides* is very similar to dalmanitids. What does this "homeomorphy" mean?

It means "being of the same shape". Typically, morphologically similar organisms, or *homeomorphs*, of different systematic position are supposed to evolve either during the so-called parallel or convergent evolution. Any morphological similarity between closely related species is commonly termed *parallelism* and any morphological similarity between unrelated species is termed *convergence*. According to neo-darwinists, in parallelism the morphological similarity (or the so-called "phenotypic" similarity) results "from joint possession of independently acquired phenotypic characteristics produced by a shared genotype inherited from a common ancestor", while in convergence the similarity results "from joint possession of independently acquired phenotypic characteristics that are not produced by a genotype inherited from a common ancestor" (Mayr 1969, p. 202). Of course, the demarcation between parallelism and convergence is necessarily arbitrary (Webb 1994).

Therefore, the convergence (Batesian and Müllerian mimicry represent also a case of "Convergence") is looked upon as a morphological similarity which is not based upon the shared genotype and darwinists generally suppose that it results from similar "selective pressure" in similar environments. But "similar selective pressure" seems to be a somewhat metaphysical explanation. Natural selection must operate on random variations but a repeated development of the same *bauplans* in different lineages may indicate that certain morpho-

logical solutions are established as “archetypes” (in the sense of Richard Owen rather than that of Charles Darwin).

The origin of similar species during the parallel and convergent evolution was discussed also by some structuralists: “According to neo-Darwinists the phenomenon (parallelism) is due to a combination of two effects, homology and analogy. Some of the resemblance between, say, a timber wolf and a Tasmanian wolf, is attributable to the fact that they are descended from a common ancestor. The cause of the remaining similarity, and especially of those traits which are found in the two wolves but not in other mammals of either kind, is that they occupy similar ecological niches. This explanation, however, depends on the assumption that the two species have been subjected to very much the same selection pressures in the same sequence, and there is no evidence for this, nor for a struggle for existence between them and other variants, with the wolf-type winning in both cases...” (Saunders and Ho 1984, p. 134).

Really, why only a “similar genotype” and “similar selective pressure”? To duplicate the process of the evolution of wolf independently in a marsupial mammal simply by random mutation followed by natural selection seems to be as metaphysical as a miracle. Why is there no other solution to the bauplan in the Tasmanian wolf? Is the Darwinian explanation of “optimal adaptation to common problems” (i.e., that both the placental and marsupial wolf are built for running and catching) sufficient? Are there some unknown non-Darwinian forces involved, familiar with the final goal?

And what about similar colours? Are “homeocoloration” and “homeomorphism” related to different causes? According to the “modern synthesis” every structure results from random variation and non-random natural selection. Herein, it seems to be very important to point out that A. R. Wallace (as a Darwin supporter but an opponent of Darwin’s theory of sexual selection) wrote:

“Yet of all characters this (i.e., colour) is the most difficult to bring under the laws of utility or of physical connection. Mr. Darwin – as you are well aware – has shown how wide is the influence of sex on the intensity of coloration; and he has been led to the conclusion that active or voluntary sexual selection is one of the chief causes, if not the chief cause, of all the variety and beauty of colour we see among the higher animals. This is one of the points on which there is much divergence even among the supporters of Mr. Darwin, and one as to which I myself differ from him. I have argued, and still believe, that the need of protection is a far more efficient cause of variation of colour than is generally suspected; but there are evidently other causes at work, and one of these seems to be an influence depending strictly on locality, whose nature we cannot yet understand, but whose effects are everywhere to be seen when carefully searched for.” and gave us several interesting examples (see Wallace 1878, p. 254–267).

Of course, the Wallace’s interesting “*unknown local action*” represents a designation of “unknown causes of known phenomena” and as such it was forgotten by evolutionists of the era of “modern synthesis” because the “*appeal to the unknown*” was supposed to be metaphysical, not scientific (see e.g. Simpson 1953, p. 133–134). However, the inexplicable “*Local Causes of Colour-development*” were attributed by Wallace (1878, p. 216–217) to “*probably... chemical peculiarities in the soil or vegetation*”.

Unfortunately, at present, with few exceptions, the view of natural phenomena is shaped and controlled by opinion-makers and scientific leaders who are heterodox neo-darwinists. Their worldview still yields a special picture of the world in which some phenomena, as e.g. the “influence depending strictly on locality”, simply do not exist. But in true science, fact must yield perception, not the other way around.

Darwinism and structuralism

Many works are devoted to theoretical explanations of the principles of camouflage and mimicry but the question remains, however, whether the most common Darwinian solution is correct.

Bates’s observations were especially invited by Charles Darwin (several years after his famous first issue of the “*Origin of Species*” in 1859) and since Bates’s preliminary study “*Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae*” (1862)

the interpretation of mimicry has been a sparring ground for supporters and opponents of Darwin's Theory of Natural Selection (see e.g. Panchen 1992, p. 270).

The opponents, for example, argued that selection cannot account for the evolution of mimicry because the latter would be of no "selective advantage" until well-developed and that the proposed "*small steps of increasing selective advantage*" was not really involved in the evolution of mimicry (e.g., Goldschmidt 1945). They also pointed to the fact that what to a human eye may seem to be a real similarity, e.g. between two different organisms, need not be such to the eyes of a predator. Thomas Hunt Morgan stressed that the "*so-called mimicry*" is "*purely imaginary, in the sense that the resemblance has not been acquired on account of its relation to the animal imitated. There is no need to question that in some cases animals may be protected by their resemblance to other animals, but it does not follow, despite the vigorous assertions of some modern Darwinians, that this imitation has been the result of selection.*" (Morgan 1903, p. 358-9).

Almost completely identical views have been proposed in numerous works of the Austrian zoologist Franz Heikertinger (for illustration see the selected bibliography of his most important articles, Heikertinger 1914-37). Certainly, the dangers of assuming that a given similarity is mimetic are great but, on the other hand, there can no longer be a doubt that many animals are really well-camouflaged in their habitats. Curiously, we are to face a situation that a century old study by some remarkable darwinists has shown only, that the very reality of the phenomena of mimicry and camouflage is still an open question. Recent structuralists (e.g., Edlinger, Gutmann and Weingarten 1991, and Gutmann, personal communication) give us the traditional answer that the very phenomena of camouflage and mimicry are almost purely imaginary and that for the predator they probably do not exist. They argue that because predators hunt primarily by smell and hearing, the coloration of the prey would provide no protection. Some structuralists also believe that the so-called parallel and convergent evolution are both inherently inadaptable.

We believe, however, that such a structuralist's view is oversimplified. The diet of predators which hunt by sight has been investigated in many experiments and the significance of camouflage, mimicry and warning coloration was determined in several serious studies. Moreover, Herán (1976) has correctly stressed that even though smell and hearing are important in the orientation of many predators, *visual clues are absolutely necessary for the execution of the final attack.*

Darwinian biologists have discovered that there is really no doubt that camouflage and mimicry act effectively together with the animal's other means of defence.

Despite a noteworthy lack of supporting data, on the other hand, for darwinists, at least for those which believe in the so-called "modern synthesis", there is their traditional "Theory of Natural Selection" explaining all parallelisms and convergences, as well as deceptive and protective adaptations in both predators and prey.

Darwinian biologists have "discovered" that parallelism, convergence, camouflage and mimicry are together the strongest sort of evidence for the efficacy of natural selection and its adaptive orientation in evolution. More exactly: "*The Darwinian theory of evolution states that some genotypes in a population of a given organism have a higher reproductive efficiency than others. As a result of this greater reproduction, the favored type will increase in frequency; possibly it will replace the less favored type.*" (Lewontin 1965).

They believe that natural selection acts as a "Great Unifying Principle" (including Owen 1980) and see camouflage and mimicry as a kind of a "*grand co-evolutionary arms race*" in which predators evolve more efficient ways to catch prey and the prey evolves better and better ways to escape (of course, in this philosophy only the best camouflaged prey survives). How strong are such orthodox views?

We argue that it is still an open question whether there is a "demon" of Natural Selection responsible for the development of camouflage and mimicry. Thanks to the American palaeontologist Stephen Jay Gould the neo-Darwinian "modern synthesis" has fallen down on both of its fundamental claims: that macroevolution is only an extrapolation of microevolution (i.e. of the gradual allelic substitutions) and that the only force in evolution is natural selection leading to adaptation (see Gould 1980). There can be no doubt of Gould's right to be called "first man" of the present-day evolutionary theory, at least in the United States. He has written many books and typically all the essays in his books were printed first in the journal *Natural History* (published by the American Museum of Natural History). What about his view of mimicry?

In an interesting essay entitled "A Darwinian Paradox" (Gould 1979, reprinted in his famous book *"The Panda's Thumb: More Reflections in Natural History"*, New York, W. W. Norton 1980) he has discussed an example of mimicry in the Philippine anglerfish *Antennarius maculatus* (Antennariidae, Lophiiformes) described by American ichthyologists Theodore Pietsch and David Grobecker (see also Grobecker 1981, Pietsch and Grobecker 1978, Pietsch and Grobecker 1990). Anglerfishes are certainly masters of aggressive mimicry among vertebrates and the mentioned species is characterized by an impressive luring apparatus, a fishlike bait (*esca*) placed on the end of a modified anterior spine (*illicium*) of its dorsal fin. The anglerfish, approximately 10 cm in length, rests inert on the bottom, looking like coral-, sponge- and algae-encrusted rock, moving the illicium (about 2.7 cm long) with the fishlike esca (about 1.4 cm long). The white and chocolate-brown-coloured esca is strongly compressed bearing lateral extensions simulating caudal, pectoral, pelvic, dorsal and anal fins. Moreover, this false "fish" is provided with four or five strongly pigmented vertical bands just behind false eyes (in area corresponding to the false shoulder and pectoral region) and two lighter bands (in area of the false caudal fin). So, the bait forms "nearly an exact replica of a small fish that could easily belong to any of a number of percoid families common to the Philippine region" (Pietsch and Grobecker 1978, p. 370). It is important to stress that the movements of the bait improve the mimicry and that the small reef fishes spotting the bait are captured by the voracious anglerfish in milliseconds (anglerfishes are fastest predators among vertebrates).

Gould's solution to the problem of evolution of such an extremely impressive mimicry is interesting. Gould points to the well-known formula "random variation followed by natural selection" as well as to the D'Arcy Thompson's vision of organisms directly shaped "by physical forces acting upon them". Stephen Jay Gould wrote:

"Organisms jump suddenly from one optimum to another when the regime of physical forces alters. We now know that physical forces are too weak, in most cases, to build form directly – and we look to natural selection instead. But we are derailed if selection can only act in a patient and piecemeal way – step by sequential step to build any complex adaptation."

I believe that a solution lies in the essence of Thompson's insight, shorn of the unsubstantiated claim that physical forces shape organisms directly. Complex forms are often built by a much simpler (often a very simple) system of generating factors. Parts are connected in intricate ways through growth, and alteration of one part may resound through the entire organism and change it in a variety of unsuspected ways." (Gould 1979, p. 42)

Gould's above mentioned "solution" of the case of aggressive mimicry, however, tells nothing. It seems to be that it is rather a solution to the problem of Darwinian theory itself – a "macroevolutionary" improvement of the synthetic theory. Orthodox neo-darwinists say that macroevolutionary theory is a non Darwinian destruction of "modern synthesis", the heterodox ones that it is "comeback" of true Darwin's "darwinism" (with Darwin's pluralism and his "mysterious laws of growth"), while structuralists are commonly pleased with Gould's critique of the adaptationist programme. But where is any explanation of our case? It is clearly hidden from us because structuralism and constructional morphology imposed on neo-darwinism does not seem to be the best way to explain the phenomena of camouflage and mimicry. It does not seem to be a way at all.

Curiously, it seems that only the "modern synthesis" (and "scientific" creationism, of course) has "explanatory powers" to give at least a sort of "solution" in the cases of camouflage and mimicry. Unfortunately, the explanatory power is based on metaphysical assumptions (see also below). All the history of the so-called "modern synthesis" shows that we can construct a theory or rather a dogmatic ideology that is proof against almost any real evidence. Thus, in darwinism, the idea of simple mechanical selection (of course, important but *destructive* and *secondary*) takes the place of serious searching for the very origin of camouflage and mimicry. This is both understandable and unsatisfying: understandable because of the selectionist's dogmatic belief in randomness of mutations, and unsatisfying because few (if any!) of the selectionist's adaptive scenarios are correct (there is no criterion of "fitness" other than survival, see esp. Macbeth 1978) over the full spectrum of evolutionary problems, particularly in the fossil record. The orthodox neo-darwinists still argue, for example, that a "key adaptation arose within a particular group of organisms which enabled that group to compete and replace a previously dominant group". Such a new group is regarded as competitively superior or advanced ("higher") to the one (primitive or "lower") that it replaced.

But no evidence for such an assumption is observable in the fossil record (see especially the study of Benton 1987). It becomes more and more difficult to understand how the new "random" mutation arises and how it is that the evolution is so creative.

The great Irish dramatist and winner of the Nobel Prize for Literature (1925), George Bernard Shaw wrote about the theory of natural selection:

"...what did Darwin really discover? Here, I am afraid, I shall require once more the assistance of the giraffe, or, as he was called in the days of the celebrated Buffon, the camelopard (by children, cammyleopard). I do not remember how this animal imposed himself illustratively on the Evolution controversy; but there was no getting away from him then; and I am old-fashioned enough to be unable to get away from him now. How did he come by his long neck? Lamarck would have said, by wanting to get at the tender leaves high up on the tree, and trying until he succeeded in wishing the necessary length of neck into existence. Another answer was also possible: namely, that some prehistoric stock-breeder, wishing to produce a natural curiosity, selected the longest-necked animals he could find, and bred from them until at last an animal with an abnormally long neck was evolved by intentional selection, just as the race-horse or the fantail pigeon has been evolved. Both these explanations, you will observe, involve consciousness, will, design, purpose, either on the part of the animal itself or on the part of a superior intelligence controlling its destiny. Darwin pointed out – and this and no more was Darwin's famous discovery – that a third explanation, involving neither will nor purpose nor design either in the animal or anyone else, was on the cards. If your neck is too short to reach your food, you die. That may be the simple explanation of the fact that all the surviving animals that feed on foliage have necks or trunks long enough to reach it. So bang goes your belief that the necks must have been designed to reach the food. But Lamarck did not believe that the necks were so designed in the beginning: he believed that the long necks were evolved by wanting and trying. Not necessarily, said Darwin. Consider the effect on the giraffes of the natural multiplication of their numbers, as insisted on by Malthus. Suppose the average height of the foliage-eating animals is four feet, and that they increase in numbers until a time comes when all the trees are eaten away to within four feet of the ground. Then the animals who happen to be an inch or two short of the average will die of starvation. All the animals who happen to be an inch or so above the average will be better fed and stronger than the others. They will secure the strongest and tallest mates; and their progeny will survive whilst the average ones and the sub-average ones will die out. This process, by which the species gains, say, an inch in reach, will repeat itself until the giraffe's neck is so long that he can always find food enough within his reach, at which point, of course, the selective process stops and the length of the giraffe's neck stops with it. Otherwise, he would grow until he could browse off the trees in the moon. And this, mark you, without the intervention of any stock-breeder, human or divine, and without will, purpose, design, or even consciousness beyond the blind will to satisfy hunger. It is true that this blind will, being in effect a will to live, gives away the whole case; but still, as compared to the open-eyed intelligent wanting and trying of Lamarck, the Darwinian process may be described as a chapter of accidents. As such, it seems simple, because you do not at first realize all that involves. But when its whole significance dawns on you, your heart sinks into a heap of sand within you. There is a hideous fatalism about it, a ghastly and damnable reduction of beauty and intelligence, of strength and purpose, of honor and aspiration, to such casually picturesque changes as an avalanche may make in landscape, or a railway accident in a human figure. To call this Natural Selection is a blasphemy, possible to many for whom Nature is nothing but a casual aggregation of inert and dead matter, but eternally impossible to the spirits and souls of the righteous. If it be no blasphemy, but a truth of science, then the stars of heaven, the showers and dew, the winter and summer, the fire and heat, the mountains and hills, may no longer be called to exalt the Lord with us by praise: their work is to modify all things by blindly starving and murdering everything that is not lucky enough to survive in the universal struggle for hogwash." (Shaw 1921, p. xliiv-xlvi).

We maintain that the Darwinian explanations take too narrow a view of the phenomena of camouflage and mimicry as a whole and that they tend to become one-sided, strongly overemphasizing the role of selection. There is an almost infinite array of interesting features in the fossil record (and of the living things, too) that could (and should) be more systematically exploited. The Darwinian reductionist's agenda cannot be complete until we know at least

something about the *origin* of "bauplan similarities" (not only about their preservation which is self-evident from *the* preservation). An understanding of the origin of bauplans is inseparable from the most important evolutionary questions. It is impossible to conduct a meaningful search for the so-called "mechanisms of evolution" without knowing more about the circumstances under which the phenomena of mimicry, camouflage, parallelism, convergence or Wallace's "locality influence" originated. It is not surprising that the latter is generally ignored or is supposed to be purely accidental because it does not fit the neo-Darwinian schemes.

Therefore, we point to the obvious paradox. Darwinians systematically overlook the very mechanisms that may have led to the emergence of any bauplan similarity. How, on the other hand, do they decide that a bauplan has a "fitness"? Of course, by the fact that it survives. But again, it is self-evident that a bauplan that survives or is repeated in the course of its history must be useful.

The well-known English sci-fi writer, Arthur C. Clarke, under the influence of the theory of natural selection, wrote (first words of his greatest space adventure "2001: A Space Odyssey") about the evolution of mankind: "*The drought had lasted now for ten million years, and the reign of the terrible lizards had long since ended. Here on the Equator, in the continent which would one day be known as Africa, the battle for existence had reached a new climax of ferocity, and the victor was not yet in sight. In this barren and desiccated land only the small or the swift or the fierce could flourish, or even hope to survive...*" (Clarke 1968) but, on the other hand, the very responsibility for the origin of man he clearly ascribed to "T.M.A.-1" constructed by intelligent extraterrestrials. Why?

It is probably because the author was unable to imagine the origin of man's intelligence as a result of infinite random variations stabilized by natural selection (orthodox neo-Darwinian view). On the contrary, members of the relatively newly established school of macroevolutionists (from this point of view we may say "Darwinian structuralists") are at least convinced that many developmental constraints impose important limitations on the evolution by natural selection (see especially the classical "*Critique of the adaptationist programme*" by Gould and Lewontin 1979, reprinted in 1984) and that it does not seem to be reasonable to assume that variations are infinite. This provided an important insight into the old "modern synthesis". Of course, also in the ideas of the very heterogeneous movement of constructional morphologists (see especially their large symposium volume edited by Schmidt-Kittler and Vogel 1991) there it is clearly stressed that in nature the structural possibilities are limited. White, Michaux and Lambert (1990) have pointed to Darwin's acknowledgement that there are some impossible forms.

The latter authors have also remembered two arguments of Hans Driesch (Driesch 1929) that: "... *natural selection, to some degree, is self-evident; at least as far as it simply states that what is incompatible with permanent existence cannot exist permanently*", and "*In speaking of an 'explanation' of the origin of the living specific forms by natural selection, one ... confuses the sufficient reason for the non-existence of what there is not, with the sufficient reason for the existence of what there is.*" White, Michaux and Lambert (1990) continue that "... *natural selection is not even a sufficient reason for 'the non-existence of what is not,' because some forms may not exist because they are not possible*" (the latter authors have also argued that the range of impossible forms is potentially infinite!).

A modern structuralist's view of the origin of a bauplan may be expressed in words of the famous British biologist and an expert in the so-called morphogenetic fields, Brian Goodwin: "... *there is evidence from the study of complex nonlinear systems describing morphogenetic processes that these have an intrinsic robustness that gives resultant structures the status of generic forms, arising within large attractors in morphospace...*" (Goodwin 1994). It must be stressed that for all modern structuralists, "*genes are not sufficient causes of biological form any more than last years elliptical passage of the earth around the sun is a sufficient cause of this year's elliptical trajectory.*" (Goodwin 1984).

Structuralists Nijhout (1978) and Saunders and Ho (1984) have argued that for one butterfly to mimic another requires nothing more than a few minor alterations and that the patterns on butterflies wings are far less complex than they look. The latter authors have expected similar arguments to apply in other cases of mimicry as well. They also pointed out that the advantage due to the Batesian mimicry is density dependent. It has a value only when the mimic is comparatively rare. The more Batesian mimics there are the more predators will learn to associate the mimics with a palatable prey.

Yes, the latter structuralist's arguments are important but, on the other hand, they represent a reduction again, overlooking the ecosystem. Analogically, why the structuralists do not ask, for example "*Why there is a predator-prey system which oscillates around an equilibrium?*". Possibly because they agree with neo-darwinists that the latter is set by external limits to the prey population? But there is an intrinsic rule of predator-prey stability in which predators increase or decrease their own numbers and rates of food consumption in proportion to prey density. We may ask as well: "*Which was the first: the prey overpopulation or the ability of foxes to produce more offspring in the years of prey increase?*" It is obvious that we must replace the structuralist's reductionism by a form of non-Darwinian holism.

Holism

It must be stressed that the majority of naturalists do not know the real meaning of the word "holism" (as well as its counterpart "reductionism"). Possibly the best analysis of the usage of the term was given by Wilson (1988) who has identified three different senses of holism:

1. *Mechanistic holism*, i.e. a "subdivision" of holism with a simple and very common tendency to explain a phenomenon with many (not only one) "factors". From this point of view (i.e. view of *complexity*) the great majority of naturalists are holists.

2. *Descriptive holism*, i.e. holism as a *practical tool* for making predictions. This kind says nothing about *causal* relationships among the parts. It is interesting that in very many cases such a holism seems to be the only route to true understanding. Herein, there is also embedded the essence of the third type of holism: "...*population problems may best be approached by starting with the ecosystem and working down rather than by starting the individual or species.*" From this point of view (i.e. view of practicality) the majority of naturalists are reductionists because they point to the fact that *practicality* is not an *explanation* itself.

3. "*Metaphysical*" holism, i.e. *true holism* which denies that higher-level processes of a hierarchy are simply caused by (or fully explicable in terms of) lower-level processes. The most important issue of this is that the higher levels of a hierarchy (or *integrated wholes*) impose order on lower levels (i.e. on their parts). This is also called "*downward causation*" and is commonly used also in a Darwinian sense (i.e. in relation to natural selection which is "imposed" on the organism from the "outside"), see e.g. Campbell (1974).

Keeping in mind Karl Popper's "*Darwinism as a metaphysical research program*" (1974, and "*Unended Quest*" 1974, 1976), we have a second reason to take selectionism as "metaphysical" (the first one is that the theory of natural selection is capable, on a *purely theoretical basis*, to "explain" *every thinkable* structure, every thinkable morphology or physiology of every individual organism, every state of ecosystem, etc.).

Of course, the best way for the present authors is to use the second "subdivision" of holism because it is practical. However, at least in this general part, it is inevitable to touch on the really "metaphysical" issues.

All darwinists must agree that the camouflage - related and mimetic structures of a given animal represent a self-evident case of "downward causations" (downward from the ecosystems to the animals). Therefore, all darwinists are *holists* (looking not only for the "upward causation") while many structuralists are reductionists (many of them stress only the so-called "internal factors" of the animal's structure without connection with the ecosystem). We argue, however, that the Darwinian holism is incorrect *especially* from the *metaphysical* point of view, i.e. incorrect in its vision of "*nature red in tooth and claw*" - overwhelming competition and strong selective pressures as the only "non-random factors of evolution". Such a kind of world is impossible because of its inability to produce organic diversity (Rosen 1978) and even survive.

It would be useful to define where we are taking holism here because non-holistic functionalist's and structuralist's speculations bring us to the old question: "*Which was the first: the chicken or the egg?*" and we are back to where we started.

The question is whether anything is overlooked in the ecosystem theories. It seems that there is really amazingly little known about the very function of a whole ecosystem because the commonly used argument against any concept of superorganism is that there are not

only "symbioses" in ecosystems but also many cases of predation. But this is clearly a misunderstanding because the latter constitutes one of the most important forms of ecosystem regulation. We may remember here at least the so-called Energy Quality Theory of the famous ecologist Howard T. Odum who said that: "all units in systems are symbiotic (mutually contributing to the other's survival, many species (and other kinds of units) have evolved very close mutual relationships wherein pairs operate almost as a single unit, each requiring the other." (see H. T. Odum 1983, p. 394-395).

A very important view of inseparable interrelatedness of living organisms and their abiotic environment we find in the classical and possibly the most enjoyed textbook on ecology by Eugene P. Odum: "*The ecosystem is the basic functional unit in ecology, since it includes both organisms (biotic communities) and abiotic environment, each influencing the properties of the other and both necessary for maintenance of life as we have it on the earth.*" (E. P. Odum 1971, p. 8).

Lewis Thomas, a well-known American writer, winner of the National Book Award in 1974 for his collection of essays "*The Lives of a Cell*", wrote about the life in the sea:

"Perhaps something is wrong in the way we look at them (i.e., living things). From our distance we see them as separate, independent creatures interminably wrangling, as a writhing arrangement of solitary adversaries bent on killing each other. Success in such a system would have to mean more than mere survival; to make sense, the fittest would surely have to end up standing triumphantly alone. This, in the conventional view, would be the way of the world, the ultimate observance of nature's law. It was to delineate such a state of affairs that the hideous nineteenth-century phrase, 'Nature red in tooth and claw', was hammered out.

What is wrong with this view is that it never seems to turn out that way. There is in the sea a symmetry, a balance, and something like the seance of permanence encountered in a well-tended garden." (Thomas 1971).

In the ecosystems there is a kind of an intrinsic homeostasis (i.e. self-maintenance and self-regulation) present. The order is a self-evident one and the existence of the living world throughout its long history is both a tremendous puzzle to us as well as a self-justification of it. As pointed out by Austin Hobbart Clark: "*The more we learn of the world in which we live the more clearly do we see that an orderly and definite plan underlies and dominates all the phenomena of nature. The living world of animals and plants is no exception. It is not chaotic. To picture it as chaotic is simply to confess our ignorance...*" (Clark 1930, p. 208).

We are impressed by W. I. Vernadsky (e.g. 1929, 1945) followed by E. P. Odum (1971) who raised the interesting possibility that individual organisms "*not only adapt to the physical environment, but by their concerted action in ecosystems they also adapt the geochemical environment to their biological needs.*" The latter view is also retained in the well-known (and at present days very discussed) Gaia theory (i.e., theory of the Earth as a superorganism) of James Lovelock (see especially his books, Lovelock 1979, 1988, 1994) as well as in the viewpoints of English-born Zen-philosopher Alan Watts who enjoyed popularity in San Francisco at least during the 1950s. In both the latter cases the *Earth is taken as a whole*. Both show that, although it is common to speak of the Earth as of a planet inhabited by life, it may be confusing. Beginning rather crudely, we may view the living things as having generally very short lives and being completely dependent on the surrounding "abiological" environment. In fact, this is not the way it is but the way we see it due to our reduction because life itself is as old as the Earth's record of its crust, water, and sedimentary rocks (see any recent textbook on historical geology). Therefore, we may say that the Earth "implies" Life as well as Life "implies" Earth. Really, there is not only the question "How does the planet control its life?" but also "How does the life control its planet?"

"Ecologists often speak of the 'evolution of environments' over and above the evolution of organisms. For man did not appear on earth until the earth itself, together with all its biological forms, had evolved to a certain degree of balance and complexity. At this point of evolution the earth 'implied' man, just as the existence of man implies that sort of a planet at that stage of evolution... But, as Douglas E. Harding has pointed out, we tend to think of this planet as a life-infested rock, which is as absurd as thinking of the human body as a cell-infested skeleton. Surely all forms of life, including man, must be understood as 'symptoms' of the earth, the solar system, and the galaxy - in which case we cannot escape the conclusion that the galaxy is intelligent..." (Watts 1966, reprint 1970).

Therefore, we believe that whatever is underlying all these regulating phenomena, whether mimicry, warning coloration, camouflage, mutualism, parasitism or predator-prey relationships, it is going to turn out to be universal. But the latter does not mean that it is anything analogical to the purely *metaphysical* "basic evolutionary mechanism" but rather to an intrinsic and really holistic *developmental* control of the gigantic planetary superorganism itself. The living world is much richer than all sorts of neo-Darwinian theories portray it to be and *development* seems to be a better word than "evolution".

Written by James Lovelock: "*I admit that we have often been provocative. We had to be or our work would have been ignored. I now realize that our provocation was a mistake. Nothing we could say or offer as evidence would convince the closed minds of our opponents. In the case of discoveries such as the global distribution of the chlorofluorocarbons and the finding that dimethyl sulfide is the natural sulfur carrier, I have found that the initial scorn and rejection was soon followed by the development of the topic as a major scientific interest. To the real scientists I say, be patient and don't knock Gaia too hard; before long she may be paying your grants.*" (Lovelock 1991).

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EXPLANATIONS TO THE PLATES.

Pl. 1–2: Two polymorphic camouflaged trilobite species from the Lower Devonian of the Barrandian area. The size and density of the granulation on the external face of their carapaces closely match the grain-size of the substrate inhabited. All photographs by H. Vršalová (generous gift of Prof. I. Chlupáč).

Plate 1

Boeckops boeckii (HAWLE et CORDA)

Fig. 1: medium-grained sculpture on the cephalon of an enrolled individual from Damil (Chlupáč 1977, Tab. XV, fig. 11). $\times 2.2$.

Fig. 2: almost smooth cephalon (Chlupáč 1977, Tab. XV, fig. 3) $\times 2.6$.

Fig. 3: coarse granulation on the cephalon of an enrolled specimen from Damil (Chlupáč 1977, Tab. XV, fig. 12) $\times 2.2$.

Plate 2

Reedops bronni (BARRANDE)

Fig. 1: coarse granulation on the cephalon from Praha – Konvářka (Chlupáč 1977, Tab. XXII, fig. 16) $\times 3.6$.

Fig. 2: left lateral view of *dtto* (Chlupáč 1977, Tab. XXII, fig. 17) $\times 3.6$.

Fig. 3: sparsely granulated to almost smooth cephalon from Branžovy near Loděnice (Chlupáč 1977, Tab. XXII, fig. 18) $\times 2.6$.

