

## Evolution of mode of life as the basis for division of the beetles into groups of high taxonomic rank

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### SUMMARY

Mode of life may be considered as an inherited group feature which is intimately connected with conservatism of ontogenetic development. Modification of it seems to be more important for formation of the taxonomic syndrome of a group of related species than structural characters (Linnaeus principle of group determinism of characters). Thus the evolution of mode of life should be used not only for testing of the phylogenetic models, but also as a base for reconstruction of the past of groups and the biota as a whole.

Mode of beetle's life as an integrated unit is characterized with significant plasticity in imaginal stage and conservative demands in immature instars. Peculiarities of ontogenetic development of the beetles are significantly reflected in possible trends of evolutionary modifications of different groups. According to this point of view the historical development of Coleoptera is interpreted and taxa of rank of suborder and infraorder are grounded.

KEY WORDS: Coleoptera, Evolution, Life history, Ordinal classification, Ontogeny, Phylogeny.

### INTRODUCTION

Many versions of the system of the order Coleoptera give the impression of a more or less formal (artificial) construction in spite of their authors frequently using evolutionary arguments for substantiation, including various concepts of naturalness of taxa. A considerable defect of many versions is that they are grounded on mainly structural peculiarities formalized in distinguishing characters. Many properties of organisms are lost after this procedure (HALL, 1988). Thus recent cladistic methodology allows a through analysis of characters but it has also some theoretical difficulties which have rise to accusation of it in high degree of metaphysics (GHISELIN, 1981). It is impossible to find correct evidence of sequence in the lineage ancestor-descendant.

Models of vector divergence of any hypothetical archetype with consequent acquisition of innovations (phylogenetic tree, cladogram etc.) bear a certain degree of typology and preformistic tradition of thinking (LUBISCHEV, 1925 and others). "Underlying synapomorphy" (SAETHER, 1988 and so on), which admits appearance of any apomorphic trend before its character is expressed, is rather feeble theoretical argument for explanation of parallel structural development in many groups. At the same time we have no means of separating the cladogenetic and anagenetic components of evolutionary process resulting in organisms under study. Difficulties in establishment of character polarity, transitive polymorphism, common occurrence of homeoplasy in evolutionary process lead us to considerable uncertainty of phylogenetic reconstructions (MEYEN, 1988). Especial difficulty is associated with possibility of regression of archaic features together with developmental progress of more recent ones. As a result the recent characters which became similar and independently raised in some organisms may be much more expressed than traces of their initial differences ("nomogenesis" in the sense of L. S. BERG, 1926).

#### SOME WAYS OF CORRECTIONS OF PHYLOGENETIC RECONSTRUCTIONS

Structural characters emerge during the individual development under any combination of conditions and at a certain stage of ontogenesis which is strictly consequent on previous one. Interferences in normal conditions (if they are not lethal) cause bigger or smaller changes in regular course of developmental process, in the extreme cases such as morphosis, classic "modification" and so on. Studies of ontogenesis of beetles show that this process in most representatives of the order has some common levels of structural differentiation with unequal distribution through free (larva, imago) and concealed (egg, pupa) stages (for example, TIKHOMIROVA, 1976). "Equifinality" in developmental strategy (as tendency to reach similar definitive stage in spite of differences in intermediate and initial conditions: SHISHKIN, 1988) makes immature stages more dependent and steady than imaginal one. In general, beetles were originally characterized by significant plasticity of imaginal stage and conservative demands in larval instars. This difference in reaction on environment is partly connected with capacity to migration of adults. However it is supplemented with initial predisposition of coleopterous larvae to inhabit inside substrate (primary attribute of the Holometabolan insects).

Mode of life may be considered as a set of inherited group features intimately connected with conservatism of ontogenetic development. This conservatism is explained by necessity of comparatively similar and more or less stable influence of environment on ontogeny in each generation of organisms. As a result more or less neutral deviation in genome or little adaptive modifications in structures at both population and species levels are scarcely significant for existence of organisms in comparison with disturbances of organisms with environmental conditions. Therefore essential modification

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\* "Taxonomic syndrome" is used as the term for designation of peculiar combination of characters attributing to any group and distinct from combinations of all other groups. This combination includes a lot of heterogeneous features with different origin and significance, though they in peculiar combination are

of mode of life seems to be more important for formation of taxonomic syndrome\* of a group of related species than structural characters which may lag behind this modification because of ontogenetic, morphogenetic or other reasons (from this is Linnaeus' principle of group determinism of characters follows). Thus the evolution of mode of life may be used for testing of phylogenetical models, but also a base for reconstruction of the past of groups and for determination of taxonomic limits.

View on evolution of beetles as mainly transformation of their ecological and larval peculiarities was formerly expressed in many authors. According to this viewpoint the imagines of beetles reached comparatively high perfection at an earlier stage of its historical development (perhaps, even during the Palaeozoic era), and later coleopterous groups were improving their preimaginal structures and larval reactions on environment (for example, PONOMARENKO, 1973). Indeed investigations of mode of life in many cases help to reconstruct possible ways of evolution of different groups (a great numbers of the R.A. CROWSON's works, CHEN, 1985 and many others).

Atavistic ecological features and traces of ancient behaviour may bear better evidence of evolutionary stages overcome by group than structural characters. The significance of relict feeding of the Bruchidae, females of whose avoid ovipositing before eating on pollen, for interpretation of their early evolution is formerly pointed (KIREJT-SHUK, 1984). Feeding on pollen of the both Coccinellid larvae and adults seems to be also atavistic. Predaceous and phytophagous Coccinellidae may frequently feed on pollen, especially in cases when the basic resources of food is in shortage or lost (SAVOJSKAYA, 1961; GRINFELD, 1978 and others). Analogously the feeding on flowers of imagines from primitive groups of the Cerambycidae (Lepturinae and Cerambycinae) may be understood as plesiotypic, as the advanced groups of this family are not anthophagous. Distribution of pollinophagy among different groups of the Polyphaga makes clear the ecological transition passed in the past by the modern Chrysomeloid groups from complete anthophagy (partly carpophagy) in both active stages of metamorphosis.

Pupation of almost all Nitidulid species in soil (in spite of diversity of ecological localizations of active immature and mature stages) may be regarded as plesiotypic or atavistic peculiarity which allows a supposition that their ancestral larvae inhabited in more or less wet or liquid substrate and these larvae left it for pupation and sought comparatively drier conditions in soil. It is very probable that these substrata included tree sap and soft fruits fermented with yeast and attendant microorganisms. Similar substances attract adults of many modern Nitidulid species from different subfamilies, but only some of them use these localities for larval breeding (mainly Carpophilinae including Epuraeini and Amphicrossini and also Cryptarchinae). It is notable that adults of some tropical Meligethinae visit soft fruits while all the known larvae of the subfamily are anthophagous (i.e. pollinophagous). Similar interpretation is possible for many Erotylidae which also pupate in soil. Soil pupation is preferred by many archaic groups of different infraorders of the Polyphaga, which allows an assumption of plesiotypic locality for this suborder as a whole.

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characteristic for the group. We may define this combination even in cases when possible ways of appearance of each character of it are unknown. Of course we may suppose any synapomorphy for any group of similar organisms before detailed study although it seems to be better to use "taxonomical syndrome" without indication on character origin.

## INITIAL MODE OF LIFE AND FIRST STAGES OF EVOLUTION

Unfortunately we have no recent species which may be regarded as any immediate descendant of the Palaeozoic coleopterous groups ("living fossil"). The CROWSON's substantiation (1975, 1981) of subcortical life of the Lower Permian Tschekardocoleidae seems fairly obvious, though his assumption concerning the structural features of larvae of these first beetles needs further confirmation. Evidence for the Lower Permian larva of beetles (PONOMARENKO, 1969; LAWRENCE & NEWTON, 1982) is insufficient to provide any syndrome of the larvae of the Protocoleoptera. PONOMARENKO (cit.) supposed that these larvae were rather diverse as he observed among the fossils attributed to this period some Holometabolan larvae with quite various levels of their structural differentiation (recent personal communication). At least it seems fairly likely that the mentioned larvae were xylomycetophagous (*sensu* MAMAYEV, 1977) and lived in subcortical spaces with their adults. In any case it is not safe to say that the Tschekardocoleidae and groups possibly allied to this family (Protocoleoptera, including Archecoleoptera *sensu* CROWSON, 1981) are correlated with the rest of beetles as ancestors and descendants (HENNIG, 1981). The Protocoleoptera are distinct from other suborders by 13-segmented antennae, comparatively long elytra and hind wings much surpassing their abdominal apices, and seemingly their venation (KUKALOVA, 1969; PONOMARENKO, 1969). A possible relation between the Protocoleoptera and the rest of Coleoptera is as problematical as that between Archaeopteryx and true Aves. Nevertheless it is important that the Protocoleoptera and Archostemata retain membraneous rudiments in their elytral cells (MACHATSCHKE, 1962). The Permocupedidae, Taldycupedidae and, perhaps, Labrodorocoleidae from upper layers of the Permian and the latter from the Cretaceous may be more or less definitely regarded as members of the Protocoleoptera, but the Rhombocoleoidea and Asiocoleoidea have more obscure taxonomic and phylogenetic connections. If the remains of fore part of body with 13-segmented antennae of *Rhombocoleites adumbratus* PONOMARENKO, 1969 are erroneously treated as a member of the Rhombocoleidae, all the families of the lastly indicated superfamilies include only fossil elytra. Therefore for more precise determination of systematic position of these groups further data is needed, especially in remains of fore part of body borne reliable correlation with conspecific elytral structures. The Rhombocoleoidea show evident aquatic or semi-aquatic structural adaptations, but the supposition of similar mode of life for the Asiocoleoidea may be more disputed.

## EARLY DIVERGENCE OF ORDER AND EVOLUTION OF SCHIZOPHOROID LINEAGE

Probable basic trend of evolution of the order at the end of Palaeozoic and beginning of Mesozoic eras consisted in attempts of many groups to leave subcortical localities or to get into dead wood as borers. The emergence from subcortical space by beetles proceeded through an intermediate stage of inhabitation in strongly wet or submerged trees, and then further spread of amphibious mode of life of both larvae and imagines in continental basins. This assumption conforms with palaeoecological data. The Palaeo- and Mesozoic terrestrial plants lived in conditions shared with weak antie-

rosive property, therefore dead organic matter was not detained, by soil and washed, and then amassed into valleys and depressions with hydrological circumstances comparatively ephemeral and, perhaps, quite distinct from those in the most types of the Cainozoic soil (PONOMARENKO, 1984). Thus there was considerable accumulation of organic matter with periodical or constant water in certain localities. This ancient ecological situation was conducive to the development of aquatic and semi-aquatic characteristics of beetles. Moreover, success in transition of the beetles to aquatic and amphibious life was facilitated by development of freshwater flora appearing from the Triassic (KALUGINA, 1980).

"Schizophoroid lineage", formulated by PONOMARENKO (1973), became the most successful group in the transition of the beetles from under-bark habitat into continental basins or localities near them which occurred at the Rubicon of the Palaeo- and Mesozoic eras. Features of this ancient transition are maintained in some modern representatives sprung from this lineage (families of the Sphaeriiformia (Mixophaga) and the Haliplidae (Adephaga)). In this case the initial (xylo) mycetophagy was replaced by mainly algophagy, detritophagy and so on with use as food of both algae and to a certain extent aquatic fungi (Saprolegniales etc.). The Schizophoriformia s.str. including only the Mesozoic Schizophoridae and Catiniidae with expressed aquatic adaptations (PONOMARENKO, 1973, 1983) represent the group close to basic one of the above lineage from which were originated the recent Myxophaga and Adephaga. First localities of them might be under loose bark or near the dead flood trees.

Similarity of the larvae of recent Myxophagan and Polyphagan groups may be explained by similar shift in sequence of structural differentiation distributed in their free and concealed stages of ontogenesis (in sense of TIKHOMIROVA, 1976), but not by close ancestral roots of both suborders (as treated by many authors: CROWSON, 1955, 1981; REICHARDT, 1973 and so on). Desembryonization of larva during postembryonic development had led to comparatively similar levels of differentiation ("silphoid stage") among the both Myxophaga and Polyphaga. But the stage of more differentiated larva ("caraboid" one) in these cases had concealed inside pupa. The alternative process leads to secondary embryonization and development of more differentiated larva with level of differentiation more similar to imaginal one (imaginization of larva as in some cases among the Staphyliniformia). This process occurs when mode of larval life is characteristic by active movement and more or less on substrate surface or in water.

PONOMARENKO (1977, 1983) believes that the unique structural combination of the Adephagan metathorax and abdominal base is evidence of aquatic origin of the suborder from ancestors related to the Mesozoic Schizophoriformia, to which the recent Haliplidae and Triassic Triaplidae are closer than other Adephaga. According to PONOMARENKO the fusion of metasternum, metacoxae and abdominal base resulted in a mechanism for strong rowing by hind legs in water. LAWRENCE & NEWTON (1982) noted that the enlarged plates of the Haliplid metacoxae serve to maintain an air bubble. This opinion corresponds with current studies on the Hydradephaga (KAVANAUGH, 1986 and others). The appearance in aquatic beetles of prothoracic and pygidial defensive glands may be explained by their multifunctional significance. Secretions of these glands in aquatic groups are used for moistening of body before the beetles plunge into water and protection from predaceous vertebrates as well as pathogenic microorganisms (DETTNER, 1985). Thus similar adaptations might be initially

raised in amphibious beetles or forms, larvae of which were aquatic but their adults left water for migrations. Plesiomorphic Adephagan larvae have a rather high level of differentiation beginning from their first instar ("caraboid stage"). POMOMARENKO (1983) considers this feature as a result of imaginization of larval development (like of that in some Neuropteran larvae), but not as a very ancient one.

Thus the formation of the Adephaga was conditioned by adaptations in the both larva and imago to more active movement in water with corresponding imaginization of the entire ontogenetic development and modification of trophic habit from mainly primary algophagy and mycetophagy. Only later the predation developed and widely spread among the more advanced aquatic and terrestrial Adephaga. Archaic characters of the Adephagan adults are explained by gerontomorphosis of their individual development on the whole (PONOMARENKO, 1983), which appears to be connected with comparatively long individual life of the generalized Adephaga in both active stages.

#### POSITION OF THE ARCHOSTEMATA s.str.

Simultaneously with the development of early Myxophaga, some groups were specialized to larval boring of trunks and branches of dead trees, which might have been available in certain conditions (for example, lack of bark). The earliest Cupedidae as well as traces of insect boring in trees are known from the Triassic (CROWSON, 1981). This modification of larval life with possible preservation of imaginal mode of life determined the peculiarities of this group, perhaps, little changed from the Triassic up to now in the Cupedidae. At the same time the head capsule of known larvae of the Archostemata s.str. shows some resemblance in configuration and shape of its appendages to that of *Micromalthus* LECONTE however the Cupedidae have larval antennae 4-segmented and maxillae with both lobes well raised.

The position of the xylomycetophagous relict *Micromalthus debilis* LECONTE, 1878 is to a certain extent questionable. This species is regarded as either a member of the Archostemata (most authors) or a form related to the Myxophaga s.str. (STEFAN, 1964; after KLAUSNITZER, 1975) and the Schizophoroid lineage as a whole (PONOMARENKO, 1969, 1973). Admitting argumentation of the latter authors we may put this species into a separate infraorder Micromalthiformia (or at least superfamily) and regard it as a sister-group of the modern aquatic and amphibious Sphaeriformia. However not only larval structures, but also imaginal ones of the *Micromalthus*, including genitalia, are quite similar to those of many Cupedidae. Therefore, some similarity between *Micromalthus* and Myxophaga should be explained as sequence of structural miniaturization, if they are not plesiomorphic. The *Micromalthus*, however, unlike many Archostemata shows some expressed paedomorphic evolutionary changes, which were more characteristic to the Myxophaga and Polyphaga. At the same time within the Archostemata and Adephaga we may rather find trace of gerontomorphic evolutionary process with changes by means of anabolies.

PONOMARENKO (1973) formulated the "Cupedoid lineage" in contrast with the Schizophoroid one. He regarded both lineages as derived branches of common stem uniting the known Tschekardocoleidae. The chief differences between them according to his viewpoint consists in the hind wing structure and superseding the elytral cells

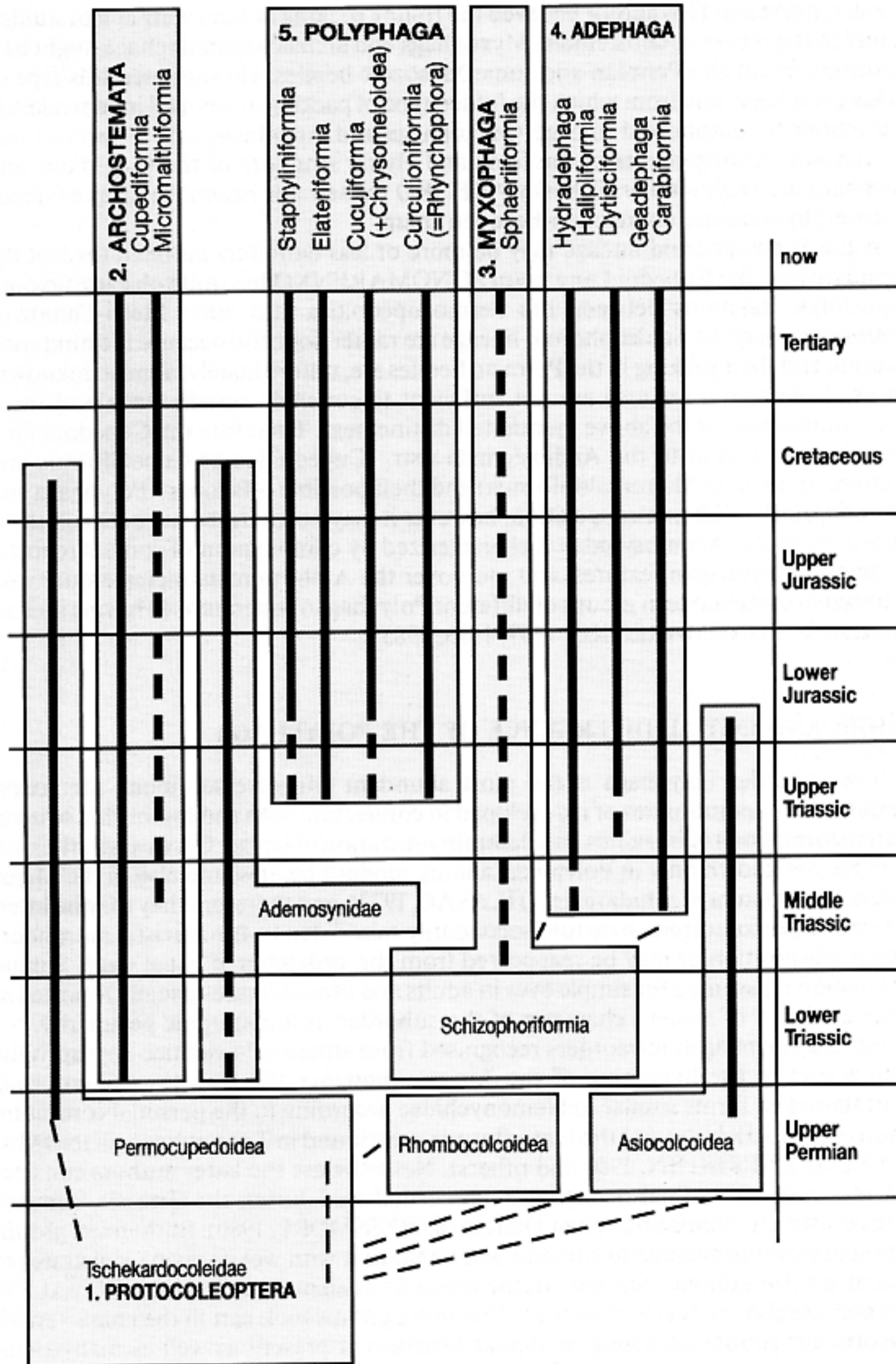


Fig. 1 - Scheme of phylogenetic relationships among coleopterous groups with high taxonomic rank.

by enlarging veins. This author believed the rolling packing of hind wing apices studied mainly in the recent Archostemata, Myxophaga and archaic Hydradephaga might be a characteristic for the Permian and some Mesozoic beetles. He supposed this type of packing was basic one from which the folded type of packing developed independently in the both Schizophoroid lineage (Myxophaga and Adepaga) and Cupedoid one (Polyphaga). Arrangements of the folds and elytral structure of the Cupedidae and Polyphaga are fairly similar. PONOMARENKO treated this resemblance as evidence of close phylogenetic connection between them.

If the Schizophoroid lineage may be more or less definitely outlined (except the *Micromalthus*), the Cupedoid one *sensu* PONOMARENKO has quite obscure taxonomical links. Relations between the Permocupedoidea and other Meso-Cainozoic beetles excluding the Schizophoroid lineage are rather doubtful because the hind wing venation and their packing in the Permian beetles are, unfortunately, almost unknown, but available elytral features are not sufficient to conclude certain kinship of these superfamilies having the above mentioned distinctness. Therefore the Cupedoid lineage is here restricted to the Archostemata s.str. (Cupedoidea or Cupediformia and Micromalthoidea or Micromalthiformia) and their possible offshoots - Polyphaga and Ademosynidae (with unclear position, however it may be intermediate between these suborders, as the Ademosynidae is characterized by combination of some Archostematan and Polyphagan features, and moreover the Archostemata metasternum may be traced in some modern groups of different Polyphagan superfamilies having archaic appearance: PONOMARENKO, 1969; 1973; 1983).

## ORIGIN AND INITIAL DIVERGENCE OF THE POLYPHAGA

The suborder Polyphaga is the most abundant and diverse among the recent beetles. Many apomorphies of it developed in connection with paedomorphic structural transformations of imagines and desembryonization of larvae. Cervical sclerites, for example, are known only in Polyphaga among modern beetles, and also in the Megaloptera, Neuroptera, Raphidioptera (HLAVAC, 1972), and therefore they may be interpreted as a plesiomorphic structure secondarily raised due to the atavistic morphogenetic predisposition or may be reappeared from the structures of pupal stage. Similar explanation is assumed for simple eyes in adults and other features usually regarded as either evidence of ancient character of the suborder or apomorphic peculiarity.

All the polyphagan infraorders recognised from structural evidence appear in the fossil record at the beginning of the Jurassic, however the true Curculioniformia (represented by forms similar to Nemonychidae according to the personal communication of ZHERIKHIN) and the Elateriformia were found in Triassic beds (PONOMARENKO & ZHERIKHIN, 1980 and others). Nevertheless the latter authors consider that the basic subordinal divergences proceeded just during the Triassic, simultaneously with the Bibionomorphan Diptera (RODENDORF, 1980). Both insect groups were seemingly connected in trophics and habitation with wet decaying substrates of dead plants (for example, fermented tree sap and soft plant fructification) (KOVALEV, 1984 and see above). It is very possible that these groups took part in the characteristic consortii (or guilds) appearing in similar localities at present as well as many times before. Joint inhabitation of the Polyphaga and Dipteran larvae caused conditions for multiple transitions of beetles from initial mycetophagy to predation.



Thus the main circumstance, which caused separation of the Polyphaga, was a change in mode of larval life for existence in conditions preserving during short periods of fermentation of the mentioned substances. In this connection the overall trend for the suborder of comparatively rapid larval life and paedomorphic modifications in imaginal structures were developing.

PONOMARENKO (1983) and LAWRENCE (1987) suppose that the Dascilloidea represent a group closest to ancestor of the Polyphaga, although many authors traditionally interpret the Staphiliniformia as the most archaic infraorder of the Polyphaga. The latter view looks more probable, especially because primitive characters of larvae and their mode of life occur in some recent Staphylinoid and Hydrophyloid groups (with "silphoid stage" of larval differentiation according to TIKHOMIROVA 1976, 1982). Amphibious and aquatic larvae and adults of the Hydrophiloidea appear to be more deviated from initial state (NIKITSKY, 1977; NEWTON & LAWRENCE, 1982). The progressive imaginization of larval instars is observed in the predaceous and actively moving Staphylinimorphan groups of Staphylinidae (as in terrestrial and aquatic Adephaga).

The infraorder Elateriformia including the Scarabaeiformia and Eucinetiformia, as defined by LAWRENCE & NEWTON (1982), may be well interpreted, though the arguments for its monophyly based on structural characters are not quite convincing (LAWRENCE, 1987). All the groups uniting into the Elateriformia *sensu lato* are characterized by comparatively long life of moderately differentiated larvae together with the trend to paedomorphic modifications of imagines well-expressed in some advanced groups (especially in the Cantharoidea). Such characteristics might originate in conditions of larval inhabitation in substrate poor in food matter and unfavourable for larval active movement. It seems quite likely that such conditions were in dead wood and organic litter after prolonged decay.

Widespread opinion on soil origin of these groups (for example, CROWSON, 1975) conflicts with the arguments of PONOMARENKO in connection with differences between conditions in the recent soil and those in the past (see above). If these arguments are adopted, life of the Elateriform ancestors may have been in places of drift of organic matter. These places were frequently flooded. These localities were more probable thanks to comparative richness of organic matter in contrast with insufficient conditions of most types of Mesozoic soil. Moreover hydromorphic soil conditions were being more or less persistent in the past. This explains the preservation of closing apparatus of larval spiracles and transition in aquatic environment of different groups of the infraorder. Long larval life in substrate poor in food was preadaptive for further expansion in the Cainozoic soil.

### SOME CAUSES OF EVOLUTIONARY SUCCESS OF HIGH POLYPHAGA

During the Mesozoic era the progressive expansion of the Gymnosperm plants was proceeding and this caused increasing and complicating in this connection of interrelations between the appearing arboricolous fungi and beetles, including living in more exposed situations than those at the original state of coleopterous evolution. These situations frequently gave favourable conditions for larval development only for a short time. The fast individual life-span, perhaps, was the basic factor of formation of

the Cucujiformia at initial stage of their evolution. Some recent Derodontidae, Nosodendridae and Nitidulidae seem to have a mode of life the closest to ancient one for the infraorder. CROWSON (1975) considered that larvae of the Derodontidae bear extremely archaic characters. PONOMARENKO (1969) pointed to the trace of an archostematan feature in the metathorax of this family, and later LAWRENCE & HLAVAC (1979) assumed that this family had present by the middle of the Triassic. The Nitidulidae are known only beginning from Cretaceous deposits (KIREJTSHUK & PONOMARENKO, 1990), however the distribution of primitive groups of this family suggests their much earlier evolution.

Inhabitation of the early Cucujiformia in very ephemeral terrestrial conditions may give a key to the exceptional diversity of ecological niches which are occupied by the recent representatives of this infraorder. Many authors (for example, LAWRENCE & NEWTON, 1982) conclude that the infraorder consists of groups (families) some of which seem to be paraphyletic and which may be more easily composed in grades than in phylogenetic branches. It may be demonstrated also that ecological grades correspond to some structural transformations, especially concerning the transition from initial (xylo)mycetophagy to complete phyllophagy crossing in some certain stages through larval and complete antho- and carpophagy (MANN & CROWSON, 1981; KIREJTSHUK, 1984, 1989).

The Chrysomeloidea may be regarded as one of highly organized and specialized groups of the infraorder which has secondarily acquired rather prolonged individual life (especially in some Cerambycidae). Nevertheless this superfamily retains some archaic traces making evident its relationship to the Cucujiformia. There are the Cucujoid type of hind wing venation, characteristics in aedeagal structure, reduced spiracles on 8th abdominal segments of imago, atavistic or secondarily complicated bi- and multisetose empodium in adults of the Megalopodidae and so on.

## POSITION OF THE CURCULIONIFORMIA

The infraorder Curculioniformia is usually regarded as a superfamily which is sister-group to the Chrysomeloidea. At the same time there is a unique combination of features of the Curculionoidea more or less distinct from the Chrysomeloidea (namely, imago: structure of head capsule with extremely modified mouthparts, including almost monocondylate mandibles with pharyngeal process, and proventriculus, not complicate tarsal sensilla (SCHMITT, 1988), presence of spiracles on 8th abdominal segment (MORIMOTO, 1962), tendency to the Staphylinid-like type of hind wing venation (CROWSON, 1955); larvae: "bruchoid stage" of differentiation with additional reduction of all appendages (TIKHOMIROVA, 1976, 1982), with traces of very archaic features in hypopharyngeal bracon and mandibular mola).

If we want to interpret the earlier appearance of the Nemonychidae (from the Triassic: PONOMARENKO & ZHERIKHIN, 1980 and others) than Chrysomeloidea (from the Jurassic) and reflect this difference in ordinal system, we should regard the Curculionoidea in composition of the Cucujiformia as a possible sister-group to other superfamilies given together or we should elevate rank of this group up to a separate infraorder. It is suggested that the Curculioniformia represent the descendants of a

very early divergence of the Polyphagan stock from the groups evolved into modern Cucujiformia. This separation was connected with an ancient transition and high structural specialization to complete "anthophagy" (mainly pollinophagy) with short larval development (corresponding to the period of "flowering" of the Triassic Gymnosperm plants). Thus it seems very likely that this group became phyllophagous much before than the Chrysomeloidea and other Cucujiformia. In further evolution, some groups among the Curculioniformia reversed back to mycetophagy.

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