Subcortical space as an environment for palaeoendemic and young groups of beetles, using mostly examples from sap-beetles (Nitidulidae, Coleoptera)

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Fermenting tree sap, particularly when concentrated in subcortical space is extremely attractive to many beetles of different families, and perhaps, a significantly greater diversity of species, genera and families occurs in this situation than in any other comparable environment. Tree sap, fermented by different fungi, myxomycetes and bacteria, attracts beetles with different trophic preferences (mostly mycetophagines, but also xylo- and zoophagines). In accordance with particular preference in places and modes of life, specialized inhabitants of tree trunks and branches can be divided into xylo-, myceto-, cortico- phloeobiontes (cambiobiontes). Subcortical space is inhabited by some insects during their entire life cycle, while others utilize it only for lesser and greater periods of their individual development. Subcortical situations are also frequently used by other beetles as a place to hide from enemies, or to survive unfavourable periods. Finally, subcortical coleopterous complex is the greatest component in xylobiotic fauna of the order as a whole.

Subcortical habitats played a rather important role in the evolutionary history of the order. The first beetles are thought to have been associated with them, i.e. the development of coleoptery seemed to be conditioned by adaptation to such habitats and, probably, the Lower Permian coleopterous fossils represent forms, which should be interpreted as subcortical inhabitants (Ponomarenko, 1969; Crowson, 1975 etc.). Appearance of these forms was linked with the development of the xeromorphous Gymnosperm flora at the end of the Carboniferous. Adults of some of the oldest recent relicts of ancient faunas are also mainly collected near or under bark (Archostemata). These include *Omma* Newman, 1839 and *Tetraphalerus* Waterhouse, 1901 (Ommatidae) as well as *Sikhotealinia* Lafer, 1992 (Jurodidae) (Kirejtshuk, 1999). Recent members of these taxa or their close relatives have scarcely changed from those found in the Mesozoic deposits.

Having originated in subcortical space, palaeozoic beetles at the end of the period showed numerous transitions to semi-aquatic and aquatic habitats (Ponomarenko, 1969; 2002). The initial type of coleopterous development can be characterized by desembryonization of larva and gerontomorphosis of imago, i.e. long larval life allowed them to reach complete structural differentiation and, if any change occured, it was a further structural transformation additional to the initial one. They are still thought to have been probable members of the paleoendemic suborder Protocoleoptera.

The recent suborders appeared in the palaeontological record during the Lower and Middle Triassic, and are therefore some of the oldest suborders in the recent invertebrate fauna, although Schizophoriformia (probable ancestors of Myxophaga and Adephaga) may have appeared in the end of the Permian.

A smaller proportion of Triassic beetles appear to have inhabited subcortical and arboreal localities, and the major structural and ecological diversification of the order, with some transformations of type of ontogenesis, took place at that time. Ancient Adephaga and Myxophaga appear to have mastered aquatic and semi-aquatic modes of life, with evident aquatic adaptations, while the first Archostemata became a xylophagous group adapted to live deep inside tree trunks during larval life and with adults leaving such substrate.

It is important to note that both Adephaga and Myxophaga have almost never returned to initial xylomycetophagy, while most Archostemata retain to now their more or less ancient diet and mode of life. The principal diversification of the ancient beetles, particularly the early Polyphaga, were also associated with some changes in the ecological circumstances of their life and corresponding transformations in individual development (Figs. 1 and 2).
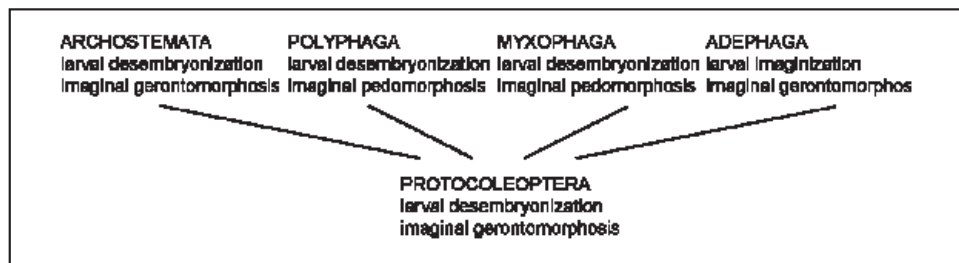

Fig. 1. *Scheme of different trends of ontogenesis in the suborders of Coleoptera (after Kirejtshuk, 2000).*
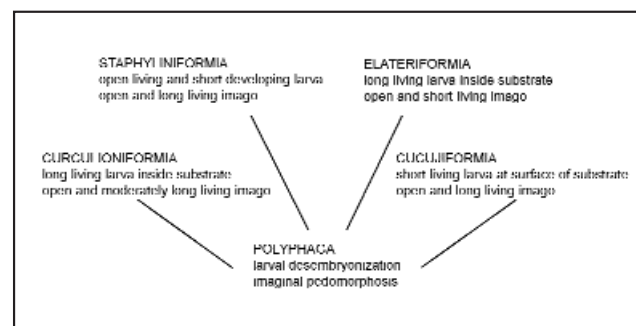

Fig. 2. *Strategies in generalized mode of life of infraorders of Polyphaga (after Kirejtshuk, 2000).*

Two infraorders of Polyphaga (Curculioniformia and Staphyliniformia) have been recorded the the Triassic, a few uncertain Elateriformia are also known from that period, and only Cucujiformia did not appear in the fossil records until the Upper Jurassic (FIG. 3). However, the Triassic groups formerly regarded as Curculionoidea were linked by some researchers to a lineage of Archostemata, convergently similar to weevils (Gratshev & Zherikhin, 2001), because their mesocoxal cavities are formed with the participation

of metepisterna (a characteristic feature for Protocoleoptera and Archostemata and rather exceptional for Polyphaga). The infraorder Staphyliniformia was mastering a more and more active mode of life inside loose (porous) substrate with concentrations of organic matter. Origin the infraorder Staphiliniformia with very active larva and imago, which in some groups demonstrate a secondary tendency to embryonization and imaginization of larval instars and more or less progressive pedomorphosis of imago, can be understood, if we suppose an inhabitancy of their ancestors in the dead trees after long periods of decay and later mastering the localities near decaying trees at border of freshwater basins. The infraorder Curculioniformia appeared as a separate group and started to live in generative organs of ancient plants. The infraorder Elateriformia seemed to be radiating inside nutrient-poor organic materials with a preference for rotting trees. Long larval life in substrate poor of food was a base for further mastering of the Cainozoic soil by many elateriform groups. However, the infraorder Cucujiformia seemed to retain its initial subcortical connections more strictly. In contrast to other suborders, all the infraorders of Polyphaga demonstrate many secondary transitions to mycetophagy sensu lato in subcortical and other arboreal habits, perhaps, at different times. For our consideration it is important to note that Cucujiformia seemed to retain the initial tendency towards a comparatively short larval life, particularly expressed in Cucujoidea. This is important for taxa living in ephemeral (sporadic) substrates, such as fermenting sap in cambium and phloem.

Despite the availability of forms with different trophic regimes, the main potential food resource in such places is represented, if not by
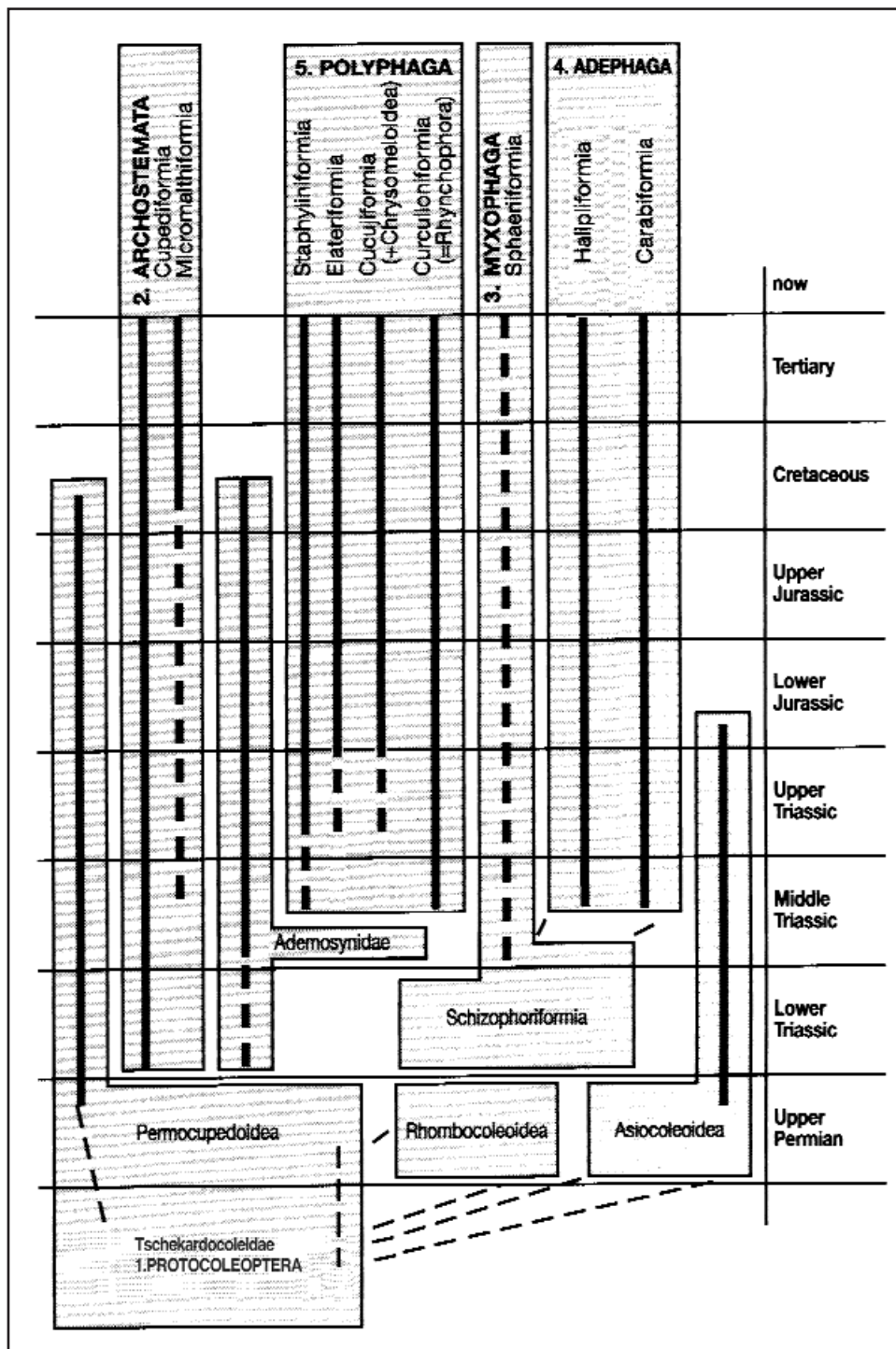

Fig. 3. *Taxonomic composition and distribution of basic coleopterous groups in the paleontologic chronicle (after KIREJTSHUK, 1991).*

actual-fungi and plasmodia, by products of fermentation by fungi, myxomycetes and bacteria. The substrate produced by the activity of these organisms is very accessible as a food, and has a higher concentration of nutritious components. To increase efficiency of food consumption some sort of mutualistic relationship between beetles, on the one hand, and symbiotic fungi, protozoans and bacteria, on the other, has appeared probably rather long ago. Extremely diverse and complicated interconnections between coleopterous, fungal and microbiotic components in consortia near and under bark draw the attention of many biologists and there are many publications on this topic. The yeast and yeast-like endosymbionts from Ascomycota have been found only within mycetophagous beetles [Staphylinoidea, Eucinetoidea, Scarabaeoidea, Dryopoidea, Dermestoidea, Bostrichoidea, Cleroidea, Cucujoidea, Tenebrionoidea, Chrysomeloidea (Cerambycidae), Curculionoidea (at least Anthribidae, Cryptorhynchinae, Scolytidae)], but there is no such record from phytophagous or predaceous forms.

During more than 250 millions years of its historical development the order had gone through many changes in relation to trees in ancient and recent forests. The history of these relationships had some dramatic episodes, but in general they reflect the long co-evolution of beetles, trees and fungi. Appearance of some immune reactions of plants, such as resin production, is usually thought to have appeared in connection with protection of trees against attacks of both insects and fungi. It is easy to suppose a progressive penetration of subcortical inhabitants more deeply inside tree trunks, or a step-by-step transition of them to more decomposed plant matter. Besides emergence of some beetles out of subcortical places, other coleopterous groups had an alternative tendency and became secondarily phloeo- and xylobiotic. Many xylobiotic beetles of the superfamilies Bostrichoidea, Lymexyloidea, Cucujoidea and Tenebrionoidea probably originated from the primary xylobionts, while others became xylocolous from forms, which were feeding on living plant organs (for instance, Chrysomeloidea and Curculionoidea) or which inhabited plant organics after long periods of decay [for instance, Staphyliniformia (including Scarabaeiformia) and Elateriformia]. Because the formation of interconnections between each group of beetles and subcortical fungi or myxomycetes occurred at different times, and particular biotic circumstances, these interconnections show a great diversity and many attempts to classify this diversity have been made (see MAMAYEV, 1977; LAWRENCE & MILNER, 1996 etc.). Appearance of mycetophagy among predatory beetles was not quite characteristic, although supposed cases are known, for example, in the family Rhysodidae.

The superfamily Cucujoidea with about 30 families represents one of the youngest lineages among coleopterous superfamilies (KIREJTSHUK, 2000). However, formerly, even R.A. Crowson (CROWSON, 1955, 1981 etc.) insisted that Cucujoidea should be closer to a common ancestor than Curculionoidea and Chrysomeloidea (CROWSON, 1955). And for a long time this superfamily has been expected in the deposits lower than those bearing Curculionoidea and Chrysomeloidea. However, all fossils formerly attributed to true Cucujoidea from the Jurassic should be placed in Cleroidea (KIREJTSHUK & PONOMARENKO, 1990; KIREJTSHUK, 1994), while both Chrysomeloidea and Curculionoidea appear in the Jurassic, and even significantly earlier (if the family Obrienidae represents Curculionoidea). [Many superfamilies of Cucujiformia appear later in the fossils record, and many families of Cucujoidea - in the Cretaceous and later, but

Table 1 *Appearance of superfamilies of suborder Polyphaga in fossil records (after KIREJTSHUK, 2000; T – Triasic, J – Jurassic, K – Cretaceous, Pg – Palaeogene)*

Infraordo STAPHYLINIFORMIA	
Staphylinoidea Latreille, 1802	J1
Hydrophiloidea Latreille, 1802	J1
Histeroidea Gyllenhal, 1808	Pg2
Infraordo ELATERIFORMIA (including Scarabaeiformia)	
Dascilloidea Guerin-Meneville, 1843	K2
Scarabaeoidea Latreille, 1802	J3
Scirtoidea Fleming, 1802	J3
Byrrhoidea Latreille, 1806	J1
Buprestoidea Leach, 1815	J2
Cebrionoidea Latreille, 1802 (= Elateroidea)	T2
Cantharoidea Latreille, 1802	Pg1
Infraordo CUCUJIFORMIA	
Derodontoidea LeConte, 1861	R
Bostrichoidea Latreille, 1802	K1
Lymexyloidea Fleming, 1921	N1
Cleroidea Latreille, 1802	J1
Cucujoidea Latreille, 1802	K1
Tenebrionoidea Latreille, 1802	J3
Chrysomeloidea Latreille, 1802	J3
Infraordo CURCULIONIFORMIA	
Curculionoidea Latreille, 1802	T2

Table 2 *Fossil records of families of Cucujoidea (after KIREJTSHUK, 2000 with corrections; T – Triasic, J – Jurassic, K – Cretaceous, Pg – Palaeogene, N – neogene, R – recent)*

Bothrideridae Erichson, 1845	Pg2–R
Byturidae Jacquelin du Val, 1858	K1–R
Cerylonidae Billberg, 1820	Pg2–R
Coccinellidae Latreille, 1807	K2–R
Corylophidae LeConte, 1852	Pg2–R
Cryptophagidae Kirby, 1837	K2–R
Cucujidae Latreille, 1802	Pg2–R
Endomychidae Leach, 1815	Pg2–R
Erotylidae Latreille, 1802	Pg2–R
Helotidae Reitter, 1876/Chapius, 1876	N1-R
Kateretidae Erichson, 1843	Pg3–R
Laemophloeinae Ganglbauer, 1899	Pg2–R
Languriidae Crotch, 1873	K1–R
Latridiidae Erichson, 1842	K2–R
Monotomidae Laporte, 1840	Pg2–R
Nitidulidae Latreille, 1802	K1–R
Passandridae Erichson, 1845/Blanchard, 1845	Pg2–R
Phalacridae Leach, 1815	Pg2–R
Propalticidae Crowson, 1952	N2–R
Silvanidae Kirby, 1837	Pg2–R
Sphindidae Jacquelin du Val, 1858	Pg2–R
Incertae Sedis:	
Parandrexidae Kirejtshuk, 1993	J2–J3

palaeoendemic Parandrexidae with unclear position – in the Jurassic – see TABLES 1 and 2].

As for the origin of Cucujoidea, it is necessary to say that, except miniaturization and simplification in structure of many archaic groups, as well as larval desembrionisation and imaginal pedomorphosis, the sole non structural difference between the superfamilies Cleroidea and Cucujoidea seems to be the duration and intensity of individual development, which can be estimated not only by absolute season time, but also by the level of their structural differentiation in larvae. The appearance of the first Cucujoidea partly coincides in time with the Cretaceous crises, and the formation of

the Cainophytic groups of plants. Intensification of development of this group with a respective maintenance of archaic bionomic features becomes explicable in the context of the general intensification of all processes in the biosphere, which was reflected in the fate of many groups of plants and animals.

During the Mesozoic era, the progressive expansion of the gymnosperm plants was causing a formation and increasing the interactions between beetles and fungi, including fungi living in more open localities. These localities frequently provided conditions suitable for larval development only for a short period. A comparatively fast larval life, perhaps, was a basic factor for formation of Cucujiformia as a whole. The superfamily Cucujoidea is also characterized by a rather short larval development and comparatively long-living imagines, both stages were and are quite shortly active in contrast to many coleopterous groups, because imagines were/are usually waiting a considerable time for optimal periods when the food was/is more accessible.

In addition to the continuity of initial ecological peculiarities, the comparative recency and apparently unsteady modes in diversification cause a not always apparent hiatus between cucujoid families, i.e. numerous homoplastic transformations in organs, characteristics of which are usually important for diagnostics of families in other cucujiform superfamilies with the earlier origin. In accordance with the general tendency in the evolution of the superfamily it is thought that characteristic cucujid peculiarities could have formed among some members of Cleroidea (and probably related groups) in the past. As localities and substrate for inhabitance of the earliest Cucujoidea were rather similar (live trees and fresh wood infested by fungi), and their mode of life changed only slightly, if at all, over a long period of time, divergences and specializations in many families not infrequently gave rise to parallel development or homoplasy. Consequently, partitioning of the superfamily into comparable groups or lineages of related families is still rather problematic.

The rather abundant sap-beetles (Nitidulidae), together with the small palaeotropical family Helotidae seem to represent an ancient branch of the archaic cucujoids, which can be considered in the context of evolutionary radiation of the superfamily as a whole. Some groups of this lineage are thought to have retained their archaic habitus and to have maintained a rather archaic mode of life. These are all Helotidae, Calonecrinae and Maynipeplinae of the Calonecrin lineage of sap beetles, most of Cryptarchinae, as well as

Table 4 *Subcortical and ambrosia sap-beetles (Nitidulidae):*

Calonecrinae	– probably all species
Maynipeplinae	– probably all species
Epuraeinae	– Epuraea Erichson,1843: at least many Epuraea sensu stricto, Epuraeanella Crotch, 1874
Carpophilinae	– Carpophilus Stephens, 1829: Carpophilus sensu stricto, Ecnomorphus Motschulsky, 1858 and 3 new subgenera (KIREJTSHUK, in press)
Amphicrossinae	– most species
Nitidulinae	– Soronia and Ipidia complexes (Soronia Erichson, 1843, including Platipidia Broun, 1893; probably most Lobiopa Erichson, 1843; probably Sebastianella Kirejtshuk, 1995; Temnoracta Kirejtshuk, 1988; Prometopia Erichson, 1843; Parametopia Reitter,1884; Platychora Erichson, 1843; Taracta Murray, 1867)
	– Megauchenia complex (Axyra Erichson, 1843; Megauchenia Macleay, 1825)
	– Phenolia complex (Phenolia Erichson, 1843, sensu stricto, Ussuriphia Kirejtshuk, 1992)
	– Aethina complex (some Aethina Erichson, 1843, sensu stricto)
Cillaeinae	– some Brachypeplus Erichson, 1842, sensu lato and members of many other genera
Cryptarchinae	– perhaps, most Cryptarchini

the *Soronia-* and *Ipidia*-complexes of genera of Nitidulinae (TABLES 3 & 4). These archaic Cryptarchinae and Nitidulinae are most similar to Helotidae, and like the latter these groups keep more or less regular connections with sap flows and subcortical space containing fermenting liquids, with yeasts, other fungi, protozoans and bacteria. Many of them are known to live in such places in both active stages of their life cycle (larva and adult). Such an archaic mode of life is also characteristic of Cillaeinae of the Nitidulin lineage, and Amphicrossinae of the Carpophilin lineage, although the appearance of members of these subfamilies looks more or less derived from that of primitive groups. To a certain extent it also pertains to some Epuraeinae, Carpophilinae and some other Nitidulinae not linked by very close relations. Many mycetophagous sap-beetles of different subfamilies more characteristic of fungal fruit-bodies regularly visit such places as well (LESCHEN, 1999 etc.).

Three main lineages of Nitidulidae have unclear relationships and probably not all of them are monophyletic (in the holophyletic sense). The previous phylogenetic analyses gave partly contradictory results. The Calonecrin lineage seems to represent only remnants of an ancient group including two subfamilies, which manifest a lot of similarities in many organs (different from those in members of all other subfamilies, but aedeagus of *Calonecrus* J. Thomson, 1857 from the Indo-Malayan region is greatly reminiscent of that of advanced members of the Carpophilin lineage, while the aedeagus of *Maynipeplus* Kirejtshuk, 1998 from the Afrotropical region strongly resembles that in advanced groups of the Nitidulin-lineage - KIREJTSHUK, 1998). The Nitidulin and Carpophilin lineagues both spread over the world, and share many similar features, which can be regarded as a sequence of a common ancestry, i.e. they can be interpreted as synapomorphic characters. The archaic members of

Table 3 *Composition of the family Nitidulidae (orig.)*

1. Calonecrin lineage:	Calonecrinae, Maynipeplinae
2. Carpophilin lineage:	Epuraeinae, Carpophilinae, Amphicrossinae
3. Nitidulin lineage:	Nitidulinae, Cryptarchinae, Cillaeinae, Meligethinae, Cybocephalinae

the Nitidulin lineage (i.e. the above-mentioned *Soronia-* and *Ipidia-*complexes of genera and Cryptarchinae) show stronger resemblances not only to Helotidae, but also to Peltidae (probably the most archaic family among Cucujiformia) and apparently old groups, such as Protocucujidae, Derodontidae, Nosodendridae, Jacobsoniidae, some Anobiidae (Dorcatominae), Othniidae and so on. Nevertheless, the first fossil record of this lineage was dated as the Upper Cretaceous (KIREJTSHUK & PONOMARENKO, 1990). On the contrary, the archaic members of the Carpophilin lineage show a more generalized appearance and resemble more advanced taxa, although this lineage first appears in the fossil record in the Lower Cretaceous. Both the latter lineages have some differences in distribution, which can be interpreted in a phylogenetic sense. The Nitidulin lineage is much better represented and with greater diversity in the Western Hemisphere, while the Carpophilin lineage shows there a comparatively poor representation and lack of any endemic genus [only some endemic subgenera of *Epuraea* Erichson, 1843 (Epuraeinae) and *Carpophilus* Stephens, 1829 (Carpophilinae)] and only a few forms of the latter are distributed in South America (mostly from groups including species with wide pantropical range). If the former conclusions on the greater antiquity of Nitidulinae and Cryptarchinae are true, it is possible to constitute the fact that the younger subcortical Epuraeinae, Carpophilinae and Amphicrossinae are present in most cases in a greater number of species and frequently in a higher density, but mostly in the Eastern Hemisphere.

The relationships of sap beetles and fungi are more or less simple in comparison with other groups demonstrating rather more complex relations with fungal symbionts. Nevertheless, many cases of mutualistic interdependence are known among some Nitidulidae. Transmission of fungal spores and conidia on the body surface is recorded in many subcortical and fruticolous inhabitants (for example, mycelial particles and ascospores of *Endoconiophora* or *Ceratocystis fagacearum* are transported by different species of the genera *Epuraea*, *Carpophilus* and *Glischrochilus* Reitter, 1873: JUZWIK & FRENCH, 1983 etc. – see FIG. 4; JUZWIK & MEYER, 1997 and so on). Some nitidulids have larger depressions on different sclerites of the body surface (usually on underside), which are sometimes interpreted as probable mycangia (FIGS. 5-6). Sometimes fungal infections are transmitted by mostly carpophagous species (such as
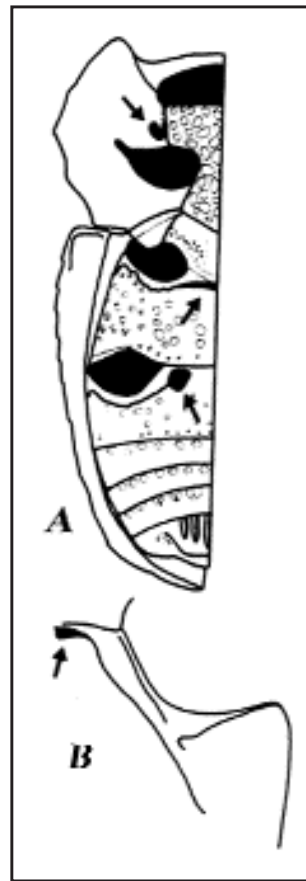

Fig. 5.
Underside of Taraphia gemina Audisio et Jelinek, 1993 (A) and Submesocoxal line of Megauchenoides corniger Audisio et Jelinek, 1993 (arrow points at mycangia) (after AUDISIO & JELINEK, 1993)
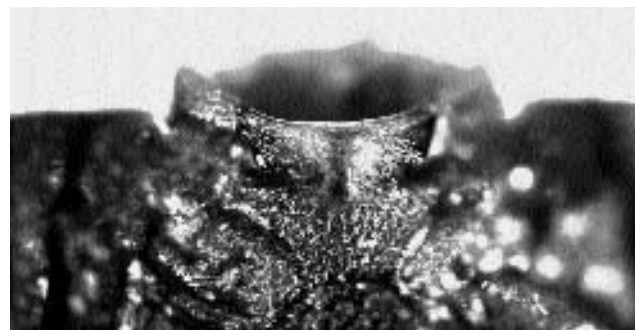
Fig. 6.
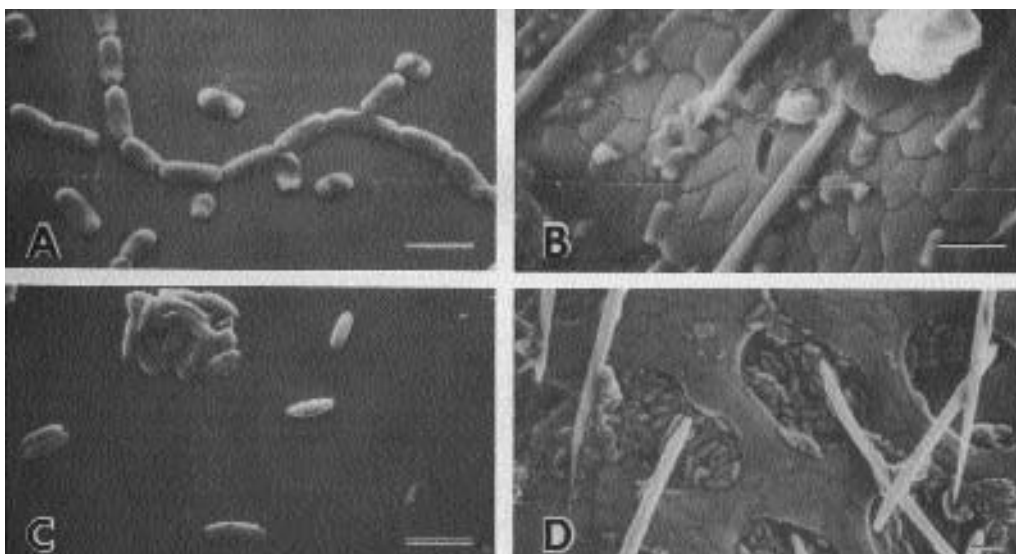*Mesosternum of Carpophilus sp. from Vietnam (orig.)*

Fig. 4.
Scanning electron micrographs of Ceratocystis: A – conidia from culture of fungi; B – conidia on nitidulid surface; C – ascospores from perithecia in nature; D – ascospores on nitidulid surface (after JUZWIK & FRENCH, 1983).

members of the genus *Urophorus* Murray, 1864 transmitting *Ceratocystis paradoxa*). Ascospores of *Ophiostoma pluriannulata, Graphium rugium* and *Ceratocystis fagacearum* have been found in excrement of some species of the genera *Carpophilus, Cryptarcha Shuckard*, 1839 and *Glischrochilus*, and therefore it seems reasonable to suppose that sap-beetles can serve as agents of spermatization, i.e. they not only transmit, but also facilitate fungal propagation (JUZWIK & FRENCH, 1983; CURRIE et all, 1996 etc.). Besides, there are facts of infection by hibernating beetles after surface cleaning (MÖLLER & DE VAY, 1968) supporting the viewpoint of usual dispersal of fungal species through the alimentary canal of sap beetles.

For this consideration, it is necessary to mention that mycangia are commonest in Cucujoidea, Tenebrionoidea (Cucujiformia) and also in Scolytinae (Curculioniformia), but seem to be rare in Elateriformia and hardly known in Staphyliniformia including Scarabaeiformia (CROWSON, 1981). In this connection an important ecological role of many sap beetles and some other Cucujoidea can be noted. A dominant element among assemblage of beetles visited oozing sap on damaged trees is constituted by different groups of Nitidulidae, some of them have been recorded as vector of tree-killing fungi. It means that the primary separation of weakened and damaged trees for further elimination is frequently made by these small insects, rather than the more famous species known as harmful pests from the families Buprestidae, Cerambycidae, Curculionidae (Scolytinae) etc. It is interesting also that the oak wilt (*Ceratocystis fagacearum*) particularly dangerous in North America is mainly transmitted by nitidulids of different genera and subfamilies (HIMELICK & CURL, 1958; CEASE & JUZWIK, 2001 etc.), but symbiotic connections of this fungal species could not appear in the common ancestor of these transmitters.

Many unrelated Epuraeinae and Cryptarchinae are regularly associated with ambrosia tunnels of Scolytinae and members of the *Megauchenia* complex of genera have been collected in such tunnels of Brentidae. Some, like *Glischrochilus, Pityophagus* and *Epuraea* species of the *laeviuscula*-group, are usually regarded as predators of Scolytinae. Their predatory ability is usually overestimated, however, these forms, as many other mycetophagous beetles, from time to time eat soft invertebrates as a protein supplement in their diet. Isolated larvae of these sap beetles, reared in substrate without any other larvae, usually complete their development and successfully produce normal adults. Like other mycetophagous commensals, most sap beetles attendant to Scolytinae invade and inhabit, alongside the host, ambrosia tunnels that, have already been prepared, while some sap beetles have been found to participate in the transmission of the fungi produced ambrosia form.

Besides obligatory subcortical sap beetles, many mycetophagines of this family, which are more characteristic of fruit-bodies of fungi, decaying cones of Gymnosperms, flowers and fruits Angiosperms as well as different types of fresh and decaying galls, will visit the places with oozing sap, and adults of some of these mycetophagous species rather regularly occur in such localities. The adults of species, whose larvae live under bark or in tunnels of Scolytinae, in comparison with other mycetophagous forms, are usually dorsally flattened and with rather raised pubescence, although species attendant to Scolytinae are frequently elongate and subcylindrical, as with a tendency to reduction of hairs on their integument.

Larvae of sap beetles living under bark and in tunnels of Scolytinae show a normal level of differentiation, characteristic of mycetophagous sap beetles in general, whose thoracic and abdominal segments, in contrast to phytophagous and predaceous members of the family, have tubes bearing biforous spiracles and air chambers inside the peritreme. Such tubes are particularly developed among some species, which inhabit a damper substrate or oozing sap. This feature can be treated as any kind of specialization, but this is also characteristic of genera of the tribe Strongylini, *Physoronia* and some other groups, whose larvae develop in fruiting bodies of Basidiomycota. However, the level of larval differentiation of all groups of sap beetles is lesser than in other Cucujoidea and can be compared only with some groups of the Monotomid lineage of this superfamily (KIREJTSHUK, 2000). This feature should be linked with a rather fast larval development, thought to be a preadaptation to larval life in other ephemeral localities, such as flowers.

It can be summarized that loose bark and the interstices under it were the probable initial locality for the ancestor of the order. Such habitats seemed to have been kept by beetles during the whole evolutionary history of the order, and the main phylogenetic transformations of the order took place in connection with the maintenance of this niche or changes to it. Nevertheless, some evolutionary progress can be traced in the groups specialized to live in subcortical places. Younger subcortical Cucujoidea appear to have some advantages in contrast to more ancient groups (Permian Protocoleoptera and early Mesozoic groups), the most important of these can be defined in terms of a shorter individual development [some species of *Carpophilus* can pass only two larval moults (HINTON, 1945 etc.)]. One sequence of this shortening, or at least the feature linked with it is a tendency to imaginal pedomorphosis, which reduces former structural specialization. Owing to these peculiarities, Cucujoidea could use many ecological gaps and narrow ecological niches, not accessible for groups, that are less mobile in development, or/and have less ecological plasticity. Therefore, this group could master and be accustomed to extremely different types of substrate, including the flowers of Angiosperms. Thus the superfamily Cucujoidea are better adapted to the intensification of biotic processes, quite characteristic as a general tendency of evolution of the Global biota as whole. Some analogy can be traced among fungivorous Staphylinidae, particularly from subfamily Oxyporinae, which are capable of rapid development in fungal substrates.

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