

Phylogeny of the family Nemonychidae (Coleoptera) with descriptions of new taxa

Историческое развитие жуков семейства Nemonychidae (Coleoptera) с описанием новых таксонов

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Key words: Coleoptera, Curculioniformia, Obrieniidae, Nemonychidae, phylogeny, trophic links, new taxa, new placements, Mesozoic, Cainozoic.

Ключевые слова: Coleoptera, Curculioniformia, Obrieniidae, Nemonychidae, филогения, трофические связи, новые таксоны, новое положение, мезозой, кайнозой.

Abstract. The phylogeny of the Nemonychidae family has been reconstructed and the composition of this family and 12 subfamilies determined. Two monophyletic groups are assigned to this family. The position of the families Nemonychidae (Curculionoidea) and Obrieniidae (Obrienoidea) in Curculioniformia system is clarified. The distribution of fossil evidence and recent Nemonychidae records is discussed. Data on trophic relations are summarised. Four new taxa (*Martynovirhynchus* Legalov, **gen.n.**, *Martynovirhynchus arnoldii* Legalov, **sp.n.**, *Medmetrioxenoidesini* Legalov, **trib.n.** and *Megametrioxenoidesini* Legalov, **trib.n.**) are described. New systematic placements are made: the genera *Ampliceps* L. Arnoldi, 1977, **placem.n.** and *Scelocamptus* L. Arnoldi, 1977, **placem.n.** are transferred from tribe Oxycorynoidini to tribe Karataucarini, the genus *Belonotaris* L. Arnoldi, 1977 from tribe Oxycorynoidini to tribe Probelini, and *Distenorrhinus* (*Distenorrhinus*) *ponomarenkoi* (L. Arnoldi, 1977), **comb.n.**, **placem.n.** from genus *Oxycorynoides* of tribe Oxycorynoidini (Eobelinae) to nominate subgenus of genus *Distenorrhinus* (Distenorrhininae).

Резюме. В статье реконструирована филогения жуков семейства Nemonychidae. Определён объём семейства Nemonychidae и входящих в него 12 подсемейств. Семейство состоит из двух монофилетических групп. Уточнено положение семейств Nemonychidae (Curculionoidea) и Obrieniidae (Obrienoidea) в системе долгоносикообразных жуков (Curculioniformia). Рассмотрено распространение ископаемых и современных Nemonychidae. Обобщены данные о трофических связях. Описаны новые таксоны (*Martynovirhynchus* Legalov, **gen.n.**, *Martynovirhynchus arnoldii* Legalov, **sp.n.**, *Medmetrioxenoidesini* Legalov, **trib.n.** и *Megametrioxenoidesini* Legalov, **trib.n.**). Роды *Ampliceps* L. Arnoldi, 1977, **placem.n.** и *Scelocamptus* L. Arnoldi, 1977, **placem.n.** перенесены из трибы Oxycorynoidini в трибу Karataucarini, род *Belonotaris* L. Arnoldi, 1977 — из трибы Oxycorynoidini

в трибу Probelini, *Distenorrhinus* (*Distenorrhinus*) *ponomarenkoi* (L. Arnoldi, 1977), **comb.n.**, **placem.n.** — из рода *Oxycorynoides* L. Arnoldi, 1977 трибы Oxycorynoidini подсемейства Eobelinae в номинативный подрод рода *Distenorrhinus* L. Arnoldi, 1977 подсемейства Distenorrhininae.

Introduction

The curculionid-beetles are the biggest group by species number of the world fauna (more than 150000) but it is also one of a weakly studied group. On the one hand, many thousands of new taxa, mainly from tropical areas, are not described, and on the other hand, a system of this superfamily is insufficiently developed. The volume of the majority of the genera, tribes, subfamilies and number of the families are controversial. Curculioniformia are distributed practically everywhere. Similar adaptive characters complicate the natural system construction. Studying of the fossil material and the recent representatives of primitive groups can be one of the possible ways of revealing phylogenetic relationships. Promising methods of molecular researches for phylogenetic researches have not given appreciable results yet [Wink et al., 1997; Marvaldi et al., 2002, 2009; Hundsdörfer et al., 2009; McKenna et al., 2009; McKenna, Farrell, 2009]. A study of the family Nemonychidae Bedel, 1882, the most primitive of recent Curculionoidea [Crowson, 1955; Voss, 1965; Zherikhin, Egorov, 1991; Thompson, 1992; Kuschel, 1995; Gratshev, Zherikhin, 2003; Legalov, 2006, 2010a, b; Oberprieler et al., 2007] should take on a special significance. A distinct primitiveness practically in all morphological characters attracts special attention to them.

Material and methods

Studied specimens of the recent species of Nemonychidae are stored in the following museums: the Moscow State University Zoological Museum (Russia: Moscow), the Siberian Zoological Museum of the Institute of Animal Systematics and Ecology of the Siberian Branch of the Russian Academy of Sciences (Russia: Novosibirsk), the Zoological Institute of the Russian Academy of Sciences (Russia: St. Petersburg), Institut Royal des Sciences Naturelles de Belgique (Brussels), Lund University (Lund), the National Museum of Natural History (USA: Washington) and Staatliches Museum für Tierkunde (Dresden). Fossil forms of Obrieniidae and Nemonychidae are kept in the Palaeontological Institute (Russia: Moscow). The author used such literary sources as [Martynov, 1926; Kuschel, 1954, 1959, 1989, 1993, 1994, 2003; Arnoldi, 1977; Zherikhin, 1986, 1993; Kuschel, Poinar, 1993; Zherikhin, Gratshev, 1993, 2003, 2004; Gratshev, Zherikhin, 1995, 1996, 2000; Ren, 1995; Gratshev et al., 1997; Kuschel, May, 1997; Liu et al., 2006a, b; Soriano et al., 2006; Soriano, 2009; Riedel, 2010].

The phylogenesis reconstruction was carried out according to principles offered by Rasnitsyn [2002]. The construction of cladograms was carried out with the programs PAUP 2.4.1 and SYNAP 500.

Results

There are still a lot of questions about the origin of the suborder Polyphaga and the infraorders Chrysomeliformia and Curculioniformia, which are associated with insufficient safety of a known palaeontological material in the first place. In this work the author adhere to Ponomarenko's idea [1969, 1983, 2002] that Polyphaga were descended from Archostemata, similar to the family Ademosynidae Ponomarenko, 1968. Grimaldi and Engel [2005] also support this hypothesis. The Ademosynidae descendants, which gave birth to Chrysomeliformia, probably had a reduced notopleural suture (1) (Fig. 1) that was a synapomorphy for Polyphaga, and they also had false 4-segmented tarsi. Perhaps two branches originated from this group had an open pro- and metacoxa, a scutellar striole and the absence of an antennal clava (plesiomorphic conditions of characters).

The first branch is a superfamily Chrysomeloidea (2) (Fig. 1) with the antennae located near eyes and the absence of a hypopharyngeal bracon at a larva [Reid, 1995]. It should be noted, that a primitive group Protoscelinae Medvedev, 1968, described as a subfamily of the family Chrysomelidae Latreille, 1802 from the Middle–Late Jurassic of Karatau [Medvedev, 1968], is sometimes considered as an independent family [Tan et al., 2004] characterised by reduced elytral striae, emarginate eyes and possibly closed procoxa. *Tarso-megamerus mesozoicus* Zhang, 2005, recently found in the Middle Jurassic of China [Zhang, 2005], concerns to Elateriform beetles [Yan, 2009; Yan, Van,

2010]. Sufficiently primitive families Megalopodidae Latreille, 1802 and Orsodachnidae Thomson, 1859 similar to this group are usually characterised by enlarged metafemora with teeth, an elongated 5th ventrite and according to data reported by Reid [1995], by absence of a spiculum gastrale at females. There is an interesting suggestion by Kirejtshuk [1991] that Cucujiformia and Chrysomeliformia are possibly monophyletic specialised group from the infraorder Cuñujiformia. This consolidation explains later occurrence of Chrysomeloidea in the palaeontological record.

The second branch is a superfamily Curculionioidea (3) (Fig. 1) or a special infraorder Curculioniformia according to Kirejtshuk [1991], the most primitive representatives of which possibly have an elongated rostrum, and a designated clava of antennae. As far as Obrieniidae Zherikhin et Gratshev, 1993 are known from the border of the Middle and Late Triassic, it can be supposed that their ancestor group has arisen earlier in the Middle Triassic.

The following stage of evolution was a separation of the families Obrieniidae (4) (Fig. 1) and Nemonychidae. Obrieniidae (Fig. 2) from Obrienioidea is the most ancient family of curculionid-beetles existed from the Late Triassic almost to the end of the Jurassic [Zherikhin, Gratshev, 1993]. After the description, its systematic position was doubted [Zherikhin, 2002; Legalov, 2002; Gratshev, Zherikhin, 2003; Kuschel, 2003]. Kuschel [2003] has specified 9 characters which do not permit to consider it among curculionid-beetles. The Curculioniformia analysis showed that all these characters appeared in different groups of the superfamily. We should examine those characters in details.

1. «Middle coxae owing to direct contact with mesepimera and metepisterna». A similar condition of a character besides Obrieniidae is observed at the subfamily Cretonemonychinae Gratshev et Legalov, 2009 (Nemonychidae) and at primitive Ithyceridae Schoenherr, 1823.
2. «Absence of a scutellar striole». For example, the striae reduction is observed at Rhynchitidae Gistel, 1848 where only primitive representatives have it.
3. «The sutural interstria width is the same throughout, instead of the distinctly broader in the basal area». This condition of a character was noticed at Dryophthoridae Schoenherr, 1825, some Anthribidae Billberg, 1820, Rhynchitidae and Curculionidae Latreille, 1802.
4. «A sternopleural suture touching fore coxae anterolaterally, instead of fully laterally on the outer side of the coxae». A similar character shows up at some Brentinae Bilberg, 1820 (Brentidae Bilberg, 1820).
5. «Absence of distinct tibial combs». An apex of tibiae is not visible on the studied typical material of Obrieniidae. It should be noted, that Zherikhin and Egorov [1991] regarded the absence of tibial combs as a plesiomorphic condition of a character but the presence of them as an apomorphic one. Tibial combs are absent at many curculionid-beetles, for example, at Allocoryninae Sharp, 1890 (Belidae Schoenherr, 1826), Dryophthoridae, some Brentidae and Curculionidae.
6. «First three antennal segments equally robust

instead of two at most». A similar structure is observed at the genus *Eccoptarthrus* L. Arnoldi, 1977 (Nemonychidae: Eccoptarthrinae L. Arnoldi, 1977). 7. «A compact antennal club instead of a loosely articulated club». A similar clava is observed at many Curculionoidea including Anthribidae, Brentidae, Dryophthoridae, Curculionidae, and a tendency to its compacting is traced at Ithycerinae Schoenherr, 1823 (Ithyceridae), Oxycoryninae Schoenherr, 1840 (Belidae) and Attelabidae

Billberg, 1820. 8. «Elytral striae well marked throughout, instead of weak or effaced posteriorly». Sharp striae probably are a plesiomorphic character preserved from an ancestral group, but weakening of striae, especially to the apex, and the further reduction are an apomorphic character. Sharp striae are observed at many Brentidae, Dryophthoridae and Curculionidae (as reversions). 9. «Interstriae 2 and 3 joining 9 and 8, instead of joining 10 and 9». This character is noted in

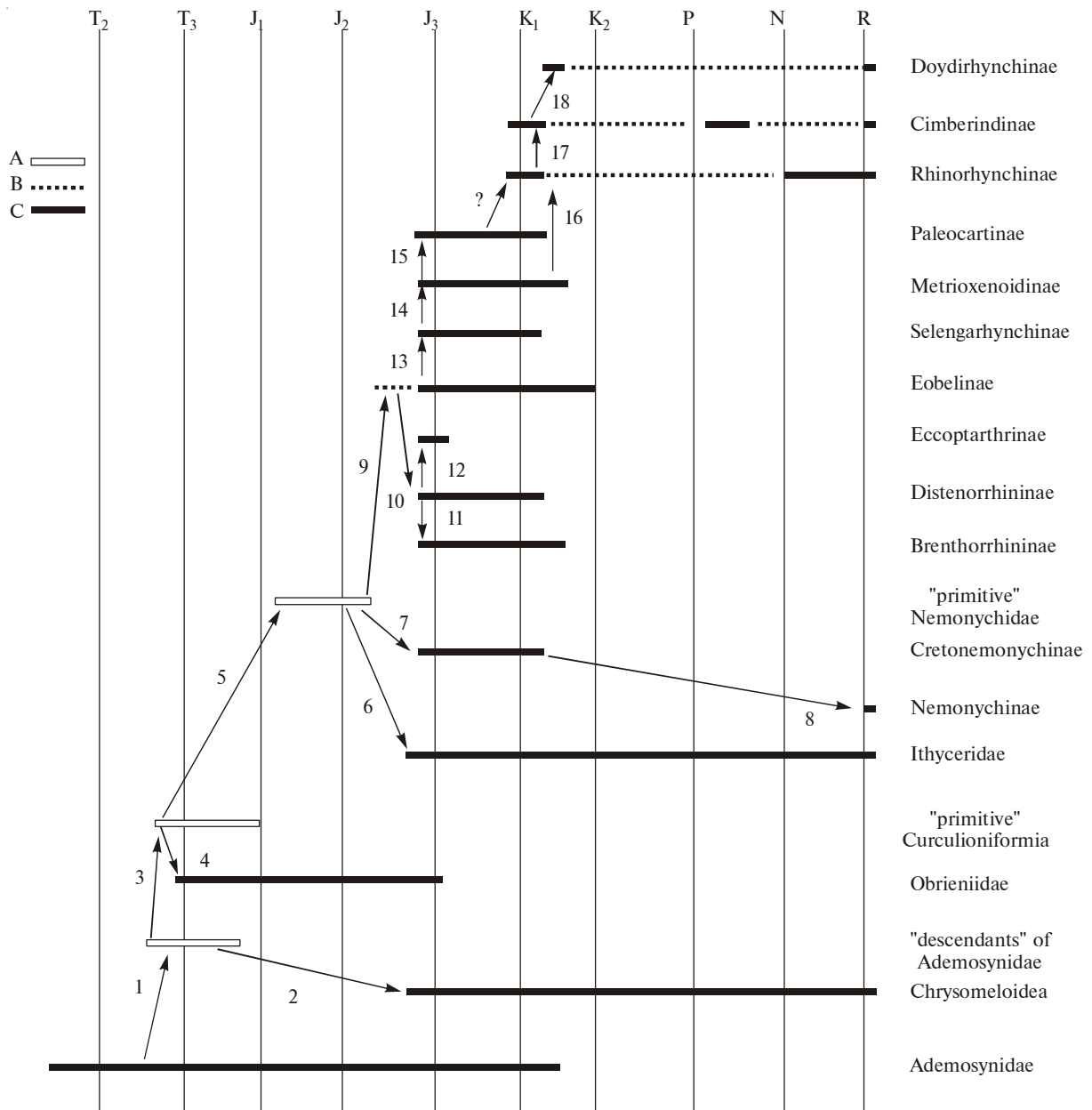


Fig. 1. Phylogeny of the family Nemonychidae. A — hypothetical ancestral group, B — group is absent in palaeontologic record, C — group is present in the palaeontological record or the recent fauna; Figures — synapomorphies (see in text); T₂ — Middle Triassic, T₃ — Late Triassic, J₁ — Early Jurassic, J₂ — Middle Jurassic, J₃ — Late Jurassic, K₁ — Early Cretaceous, K₂ — Late Cretaceous, P — Palaeogene, N — Neogene, R — Recent fauna.

Рис. 1. Историческое развитие семейства Nemonychidae. A — гипотетическая предковая группа, B — группа отсутствует в палеонтологической летописи, C — группа присутствует в палеонтологической летописи или современной фауне; цифры — синапоморфии (см. в тексте); T₂ — средний триас, T₃ — поздний триас, J₁ — ранняя юра, J₂ — средняя юра, J₃ — поздняя юра, K₁ — ранний мел, K₂ — поздний мел, P — палеоген, N — неоген, R — современная фауна.

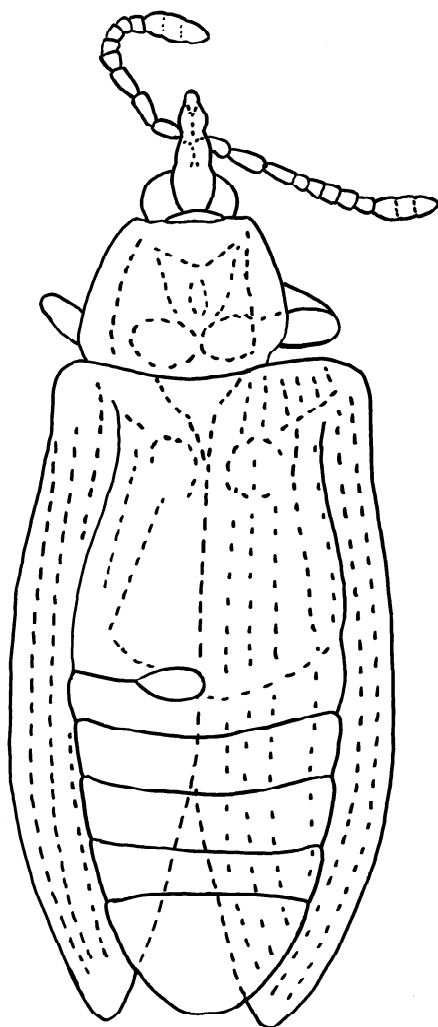


Fig. 2. *Obrienia kuscheli* Zherikhin et Gratshev, 1993 (holotype, ventral view).

Рис. 2. *Obrienia kuscheli* Zherikhin et Gratshev, 1993 (голотип, вид снизу).

the genus *Gymnaetron* Schoenherr, 1825 (Curculionidae: Curculioninae). Hereby characters, on the ground of which Kuschel [2003] suggested to exclude the family Obrienidae from curculionid-beetles, show up in different including primitive families of the Curculioniformia. As a rule, they have an adaptive character to life inside generative organs.

The most primitive Nemonychidae (5) (Fig. 1), which probably lived in the Middle or Early Jurassic, remain unknown. This family has been already well differentiated and varied on the border of the Middle–Late Jurassic. However, the author can assume with what characters one should differ. In the first place, they are certainly plesiomorphies (average sizes of a rostrum with the antennae located on the middle, a scutellar striae of the elytra, a weakly sclerotized body and an open mesocoxa). We can assume the presence of two apomorphies (a distinct clava of the antennae and a closed procoxa) in this group.

Probably, the first Ithyceridae (6) (Fig. 1) with an elongated rostrum and antennae located at its basis (Fig. 12), from which Belidae and other primitive families of Curculionoidea were originated [Legalov, 2009a], had been separated from this group.

We suppose that two subfamilies Cretonemonychinae (7) (Fig. 1) and Eobelinae L. Arnoldi, 1977 were branched from «primitive» Nemonychidae. Cretonemonychinae (Figs 3, 9, 13) had a long rostrum (Fig. 11), subapical antennae (Fig. 11), reduced striae of the elytra and an elongated 1st or 1st and 2nd ventrites (among the most advanced forms) (Fig. 4). We consider that a descendant of this group is a recent subfamily Nemonychinae Bedel, 1820 (8) differs by the sides of the pronotum without a lateral carina, strongly convex eyes, partially closed mesocoxae and a short rostrum.

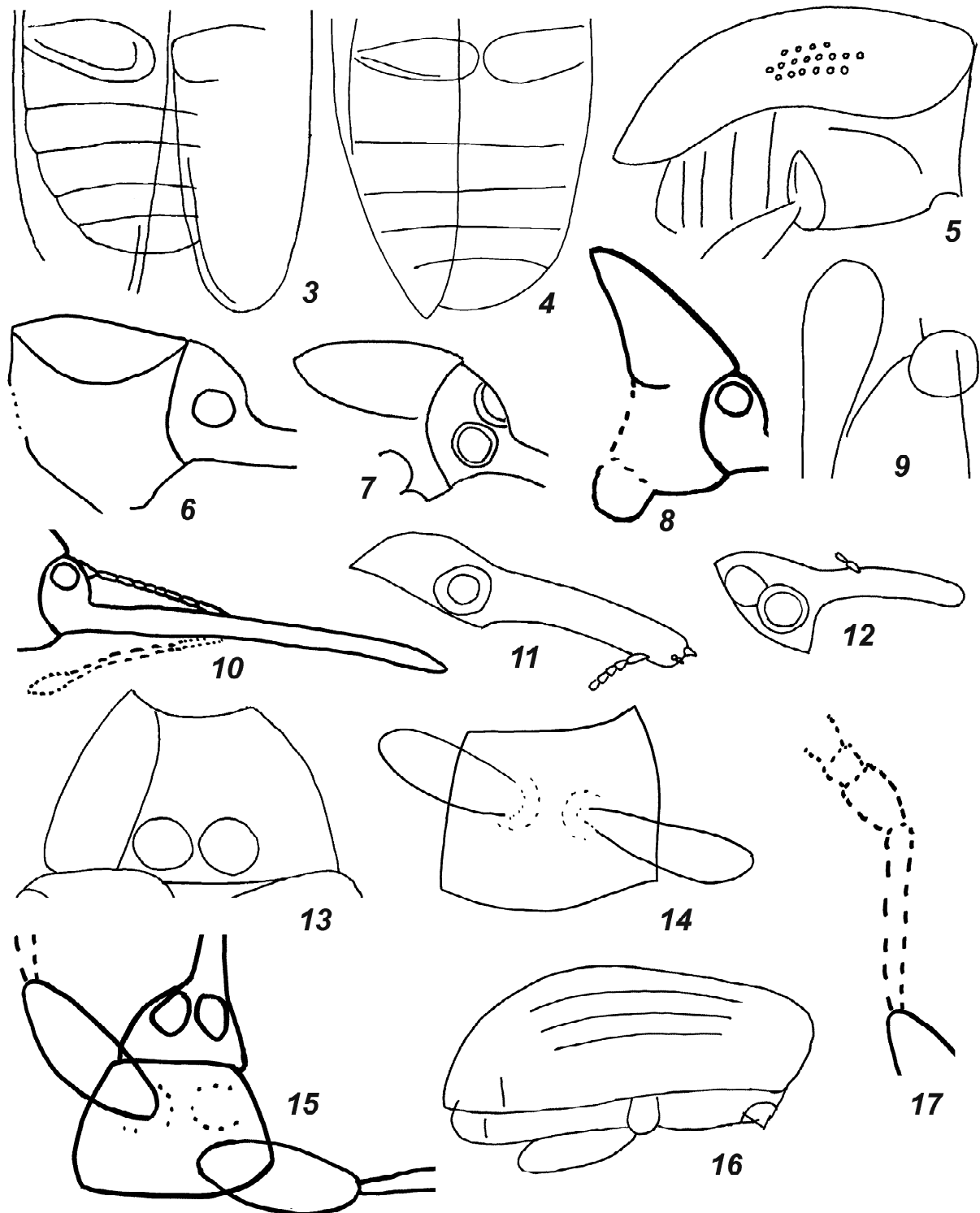
The subfamily Eobelinae (9) (Fig. 1) is characterised by closed mesocoxae. In spite of the fact that the majority of characters have a plesiomorphic condition (antennae located near the middle of the rostrum (Fig. 23), an elongated precoxal part of the prothorax

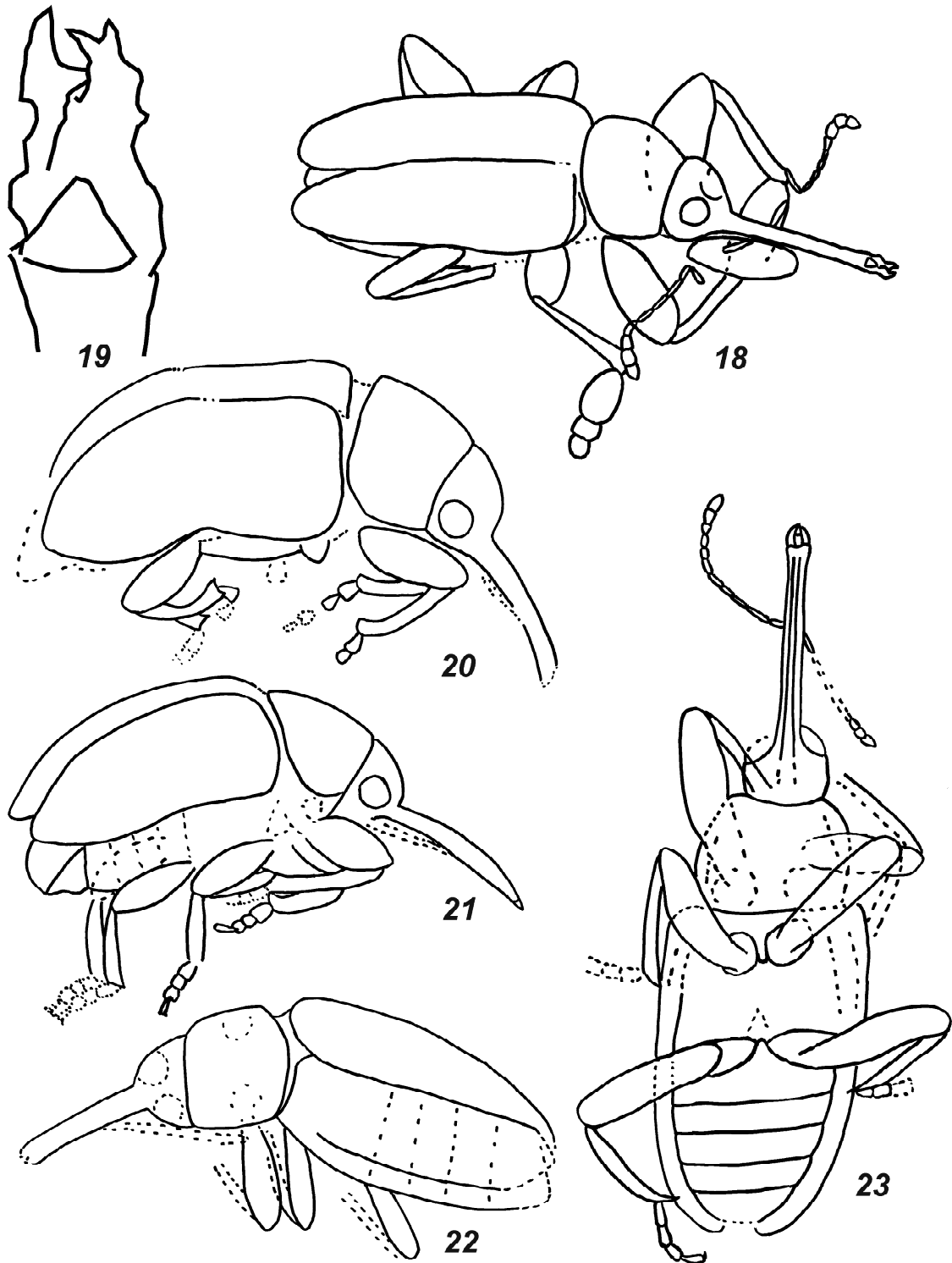
Figs 3–17. Curculionoidea gen. sp.: 3 — ventrites of *Pseudonemonyx stupendus* Gratshev et Legalov, 2009 (holotype, ventral view), 4 — ventrites of *Cretonemonyx profligatus* Gratshev et Legalov, 2009 (holotype, ventral view), 5 — elytra of *Selengarhynchus ovalis* Gratshev et Legalov, 2009 (holotype, lateral view), 6 — head, pronotum and prothorax of *Arnoldibelus* sp. from Karatau (holotype, lateral view), 7 — pronotum and prothorax of *Nanophydes ovatus* L. Arnoldi, 1977 (holotype, ventral view), 8 — pronotum and prothorax of *Arnoldibelus karatavicus* (L. Arnoldi, 1977) (holotype, lateral view), 9 — mesocoxal cavity of *Cretonemonyx profligatus* Gratshev et Legalov, 2009 (holotype, lateral view), 10 — rostrum of *Arnoldibelus karatavicus* (L. Arnoldi, 1977) (holotype, lateral view), 11 — rostrum of *Cretonemonyx profligatus* Gratshev et Legalov, 2009 (holotype, lateral view), 12 — rostrum of Ithyceridae gen. sp. from Karatau (lateral view), 13 — prothorax of *Cretonemonyx longirostris* Gratshev et Legalov, 2009 (holotype, ventral view), 14 — prothorax of *Distenorrhinus sinuatifus* Gratshev et Zherikhin, 1995 (holotype, dorsal view), 15 — head and prothorax of *Eccoptarthroides pomomarenkoi* Legalov, 2010 (holotype, lateral view), 16 — elytra of *Medmetrioxenoides prodromus* Gratshev et Legalov, 2009 (holotype, lateral view), 17 — proleg of *Eccoptarthroides pomomarenkoi* Legalov, 2010 (holotype, ventral view).

Рис. 3–17. Curculionoidea gen. sp.: 3 — вентриты *Pseudonemonyx stupendus* Gratshev et Legalov, 2009 (голотип, вид снизу), 4 — вентриты *Cretonemonyx profligatus* Gratshev et Legalov, 2009 (голотип, вид снизу), 5 — надкрылья *Selengarhynchus ovalis* Gratshev et Legalov, 2009 (голотип, вид сбоку), 6 — голова, переднеспинка и переднегрудь *Arnoldibelus* sp. из Каратау (голотип, вид сбоку), 7 — переднеспинка и грудь *Nanophydes ovatus* L. Arnoldi, 1977 (голотип, вид снизу), 8 — переднеспинка и переднегрудь *Arnoldibelus karatavicus* (L. Arnoldi, 1977) (голотип, вид сбоку), 9 — средние тазиковые впадины *Cretonemonyx profligatus* Gratshev et Legalov, 2009 (голотип, вид сбоку), 10 — головотрубка *Arnoldibelus karatavicus* (L. Arnoldi, 1977) (голотип, вид сбоку), 11 — головотрубка *Cretonemonyx profligatus* Gratshev et Legalov, 2009 (голотип, вид сбоку), 12 — головотрубка Ithyceridae gen. sp. из Каратау (вид сбоку), 13 — переднегрудь *Cretonemonyx longirostris* Gratshev et Legalov, 2009 (голотип, вид снизу), 14 — переднегрудь *Distenorrhinus sinuatifus* Gratshev et Zherikhin, 1995 (голотип, вид сверху), 15 — голова и переднегрудь *Eccoptarthroides pomomarenkoi* Legalov, 2010 (голотип, вид снизу), 16 — надкрылья *Medmetrioxenoides prodromus* Gratshev et Legalov, 2009 (голотип, вид сбоку), 17 — передняя нога *Eccoptarthroides pomomarenkoi* Legalov, 2010 (голотип, вид снизу).

(Figs 6, 8, 23), a convex body, homonomic ventrites (Fig. 23) etc.), in different genera of this extensive subfamily we can observe the appearance of different advanced characters, for example, an elongated (Fig. 10) (Eobelini L. Arnoldi, 1977 and Probelini Legalov, 2009) or short rostrum (*Khetanamonyx* Legalov, 2009), reduced elytral striae (all tribes), shortening of a precoxal part of the prothorax (Fig. 7)

(Nanophydini L. Arnoldi, 1977 and some Oxycorynoidini L. Arnoldi, 1977), widened tarsi (Fig. 17) (Eobelini and Karataucarini Legalov, 2009) and an increase of a body size (Eobelini and Probelini etc.). It should be mentioned that a place and a structure of this group were understood differently. Arnoldi [1977], who described them, considered that the representatives of this group (with 4 subfamilies: Eobelinae, Oxycory-





Figs 18–23. Nemonychidae gen. sp.: 18 — body of *Martynovirhynchus arnoldii* Legalov, sp.n. (holotype, ventral view), 19 — mandibles and labrum of *M. arnoldii* Legalov, sp.n. (holotype, dorsal view), 20 — body of *Scelocamptus tenuirostris* L. Arnoldi, 1977 (holotype, lateral view), 21 — body of *Ampliceus dentitibia* L. Arnoldi, 1977 (holotype, lateral view), 22 — body of *Distenorrhinus (Distenorrhinus) pomomarenkoi* (L. Arnoldi, 1977) (holotype, dorsal view), 23 — body of *Probelus tibialis* L. Arnoldi, 1977 (holotype, ventral view).

Рис. 18–23. Nemonychidae gen. sp.: 18 — внешний вид *Martynovirhynchus arnoldii* Legalov, sp.n. (голотип, вид сверху), 19 — мандибулы и верхняя губа *M. arnoldii* Legalov, sp.n. (голотип, вид сверху), 20 — внешний вид *Scelocamptus tenuirostris* L. Arnoldi, 1977 (голотип, вид сбоку), 21 — внешний вид *Ampliceus dentitibia* L. Arnoldi, 1977 (голотип, вид сбоку), 22 — внешний вид *Distenorrhinus (Distenorrhinus) pomomarenkoi* (L. Arnoldi, 1977) (голотип, вид сверху), 23 — внешний вид *Probelus tibialis* L. Arnoldi, 1977 (голотип, вид снизу).

noidinae L. Arnoldi, 1977, Nanophydinae L. Arnoldi, 1977 and Brenthorrhinae L. Arnoldi, 1977) were an extinct family close to the family Belidae. Kuschel [1983] placed Eobelidae as synonyms to the family Nemonychidae, and later Zherikhin [1986] substantiated this synonymy. Zimmerman [1994] disagreed with this synonymy and considered Eobelidae as a family close to Belidae. While studying the hind wing venation of the superfamily Curculionoidea Zherikhin and Gratshev [1995] paid attention to a mixed character of this group and assumed that a part of forms should belong to the family Belidae. In the following works [Soriano et al., 2006; Soriano, 2009] those authors considered three first subfamilies as a part of the family Belidae. «The body not flattened dorsoventral, a short precoxal part of the prothorax, and also that the labrum is not visible in any impressions» [Gratshev personal report]. It was a basic argument in favour of a placement of these beetles in Belidae. First two characters do not show the belonging to Belidae, so at the majority of Eobelinae (exceptions are specified above) can be observed an elongated precoxal part of the prothorax (Fig. 23), and not flattened body is typical for the majority of Nemonychidae (except for the subfamilies Distenorrhinae L. Arnoldi, 1977, Eccoptarthrinae and Brenthorrhinae). A widening of the rostrum on the apex is typical for all Nemonychidae (including recent). This character (Fig. 23) is well appreciable on a dorsal impression of *Probelus (Probeloides) tibialis* L. Arnoldi, 1977. Unfortunately, a distinct isolated labrum is not possible to be examined practically at any fossil species of Nemonychidae. In conclusion, a rank of Oxycorynoidinae and Nanophydinae was downgraded to tribes [Legalov, 2009b] as a part of the subfamily Eobelinae. A distinct labrum was visible on the holotype of *Archaeorrhynchoides arnoldii* Legalov, sp.n., it should be noted the presence of teeth at an external margin. A study of the typical species of the genera *Ampliceps* L. Arnoldi, 1977, placem.n. and *Scelocampus* L. Arnoldi, 1977, placem.n. showed that the segments of tarsi were widened and that they belonged to the tribe Karataucarini Legalov, 2009. The genus *Belonotaris* L. Arnoldi, 1977, placem.n. should be transferred from the tribe Oxycorynoidini to the tribe Probelini.

The two groups (Distenorrhinae and Selengarhynchinae) were separated from Eobelinae. The subfamily Distenorrhinae (10) (Fig. 1) differs by submedial procoxae (Fig. 14) and a flattened body. In this quite varied group the most advanced representatives have a widened body, a strengthening of its sclerotization, a rostrum lengthening, a displacement of a place of an attachment of antennae from the middle, closer to the apex or to the basis, a reduction of elytral striae and widened tarsi. Brenthorrhinae and Eccoptarthrinae have stood apart from Distenorrhinae in the process of further divergence. A study of the type of *Oxycorynoides ponomarenkoi* L. Arnoldi, 1977 has shown that coxae are located on the middle of the prothorax and it concerns to a nominate subgenus of the genus *Distenorrhinus* L. Arnoldi, 1977 (*Distenorrhinus (Disteno-*

rrhinus) ponomarenkoi (L. Arnoldi, 1977), comb.n., placem.n.).

Subapical antennae and a short rostrum characterise the subfamily Brenthorrhinae (11) (Fig. 1). The genus *Brenthorrhinoides* Gratshev et Zherikhin, 1996 has a tooth on an exterior margin of the mandibles.

Procoxae located on the prothorax of the first line (Fig. 15) distinguish the subfamily Eccoptarthrinae (12) (Fig. 1). Different genera of this subfamily have an elongated mandible, subapical antennae, a reduction of elytral striae and widened tarsi (Fig. 17).

The subfamily Selengarhynchinae Gratshev et Legalov, 2009 (13) (Fig. 1), probably formed in the Middle Jurassic, differs from Eobelinae by a strongly sclerotized body, large and rough points on the pronotum and striae of the elytra, and a strongly cutout exterior margin of the elytra (Fig. 5).

We consider Metrioxenoidinae Legalov, 2009 (14) (Fig. 1) as a subfamily originated from Selengarhynchinae. They have an elongated body and almost straight exterior margin of the elytra (Fig. 16). Most of the genera of this group are characterised by subapical antennae and fabiform eyes. The subfamily is well differentiated on three tribes; two of them are described as new in this work. The most primitive tribe Medmetrioxenoidesini Legalov, trib.n. with the genus *Medmetrioxenoides* Gratshev et Legalov, 2009 from the Jurassic of Karatau differs by the antennae attached on the middle of the rostrum, roundish eyes, weak elytral striae and a strongly elongated precoxal part of the prothorax. A distinctive tribe Megametrioxenoidesini Legalov, trib.n. is close to the tribe Medmetrioxenoidini with also strongly elongated precoxal part of the prothorax and weak striae of the elytra, but with transversal widened fabiform eyes, almost subapical antennae and claws with teeth. The tribe Metrioxenoidini with 3 genera is characterised by the rough punctate striae of the elytra, shorter precoxal part of the prothorax, longitudinal elongated fabiform eyes and claws without teeth (well visible at *Libanorhinus* Kuschel et Poinar, 1993) [Kuschel, Poinar, 1993]. It can be assumed that these tribes show consecutive development of this subfamily.

Systematic place of the subfamily Paleocartinae Legalov, 2003 (15) (Fig. 1) presents some difficulties: on the one hand, lateral impressions are absent, and on the other hand, known representatives are specialised enough and they differ by reduced striae of the elytra, mandibles with a tooth on an exterior margin and a strongly widened profemora at the tribe Nebrenthorrhini Legalov, 2007. Probably this group is a transitional group between Metrioxenoidinae and the recent subfamilies, but until new and more primitive fossil forms are not found, this statement will not be proved, as according to Cope's law, «the evolutionary novelties associated with new major taxa are more likely to originate from a generalized member of an ancestral taxon rather than a specialized member».

A rather isolated group is formed by the recent subfamilies Rhinorhynchinae Voss, 1922 (16) (Fig. 1),

Cimberindinae des Gozis, 1882 and Doydirhynchinae Pierce, 1916 characterised by convex eyes and a reduction of a lateral carina of the pronotum. In the palaeontological record first two appear simultaneously (the border of the Jurassic and the Cretaceous), but judging by morphological characters, it can be assumed, that Rhinorhynchinae is more primitive, and possibly it is the ancestor for Cimberindinae because of the following plesiomorphies: submedial attached antennae at some species (at the majority of forms antennae are subbasal), the elytra with striae, simple tarsi and claws with teeth. A mesonotum with stridulatory files and the right mandible with a tuft or a brush of setae next to mola [Kuschel, 1989] are at recent forms of this subfamily. The subfamily includes two close tribes Mecomacerini Kuschel, 1994 and Rhinorhynchini Voss, 1922 differ by the setae number on a labrum and the antennae located closer or further from apex of the rostrum. A specialised genus *Brarus* Kuschel, 1997 with a reduced rostrum and wide tibiae, forms the subtribe Brarina Legalov, 2009 of the tribe Mecomacerini.

The author supposes that the subfamily Cimberindinae (17) (Fig. 1) has separated from Rhinorhynchinae in the Late Jurassic in connection with a change to other pabular plants (from Araucariaceae to Pinaceae). This subfamily has such characters as: subapical antennae, a reduction of elytral striae, 2nd of the tarsi medially lobed projecting over the base of a 3rd segment and setiferous sex patches on ventrites at females.

The subfamily Doydirhynchinae (18) (Fig. 1) is very close to the previous subfamily but mainly differs by the antennae, located in the first quarter of the rostrum, placement of the mandibles, and a spermatheca channel shorter than a bursa [Kuschel, 1989].

Last three subfamilies are represented each of them by the one genus in the palaeontological record. The genera *Chinocimberis* Legalov, 2009 and *Renicimberis* Legalov, 2009 (The Late Jurassic – Early Cretaceous) are very close to the recent genera. The genus *Auletomacer* Zherikhin, 1993 is known owing to a badly remained specimen from the end of the Early Cretaceous (Albian) and it is conditionally placed in the subfamily Doydirhynchinae.

In spite of the boundedness of an application of cladistic methods in studying of fossil forms proved by Zherikhin [1998], it has been decided to try to analyse the phylogenetic relationships with the help of the SYNAP [Baikov, 1999] and PAUP [Swofford, 1986] methods. Two cladograms (Figs 24–25) have been received. There were used the following 26 characters (Table 1): 1. Body convex (0) — body flattened (1); 2. Mandible without a tooth at an exterior margin (0) — mandible with a tooth at an exterior margin at some representatives (1); 3. Mandible located lateral (0) — mandible located dorsal (1); 4. Rostrum absent (0) — rostrum developed (1); 5. Antennae located near the middle of the rostrum (0) — antennae located near the apex among the majority of representatives (1); 6. Antennae located not near eyes (0) — antennae located near eyes (1); 7. Eyes not convex or weakly convex (0) — eyes strongly convex (1); 8. 1st and 2nd segments of the funicle not widened (0) — 1st and 2nd segments of the funicle widened, wider than the subsequent segments (1); 9. Antennae without a distinct clava (0) — antennae with a distinct clava (1); 10. Pronotum with a lateral carina (0) — pronotum without a lateral carina (1); 11. Elytra with weakly marked to the apex striae (0) — sharp well marked to the apex striae (1); 12. Elytra with a scutellar striole (0) — scutellar striole absent (1); 13. Elytra with distinct striae (0) — striae

Table 1. Matrix table for subfamilies of family Nemonychidae
Таблица 1. Матрица данных подсемейств семейства Nemonychidae

Taxa	Characters*																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Megalopodidae	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1
Obreniidae	0	0	?	1	1	0	0	1	1	0	0	1	0	0	0	1	0	?	1	0	0	0	0	?	?	?
Cretonemonychinae	0	0	?	1	1	0	0	0	0	0	0	0	1	0	0	0	1	?	0	1	0	0	0	?	0	?
Nemonychinae	0	0	?	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Eobelinae	0	1	?	1	0	0	0	0	0	0	1	0	1	0	1	0	1	?	0	1	0	0	1	?	1	?
Selengarhynchinae	0	0	?	1	0	0	0	0	0	0	1	0	0	1	1	0	1	?	0	1	0	0	1	?	0	?
Paleocartinae	?	1	?	1	1	0	0	0	0	0	1	0	0	0	1	0	1	?	0	0	0	0	1	?	0	?
Metrioxenoidinae	0	0	?	1	1	0	0	0	0	0	1	0	0	1	1	0	1	?	0	1	0	0	1	?	0	1
Distenorrhinae	1	1	?	1	0	0	0	0	0	0	1	0	1	1	1	0	0	?	0	1	1	0	1	?	1	?
Brenthorrhinae	1	0	?	1	1	0	0	0	0	0	1	0	0	0	1	0	0	?	0	0	1	0	1	?	1	?
Eccoptarthrinae	1	0	?	1	1	0	0	1	0	0	1	0	1	0	1	0	0	?	0	0	1	1	1	?	1	?
Rhinorhynchinae	0	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Cimberindinae	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1
Doydirhynchinae	0	0	1	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1

* 0 — plesiomorphic state of the character; 1 — apomorphic state of the character; ? — unknown state of the character.

* 0 — плезиморфное состояние признака; 1 — апоморфное состояние признака; ? — состояние признака неизвестно.

reduced (1); 14. Elytra with a gentle sculpture, weak punctate (0) — sculpture of the elytra rough, large punctate (1); 15. Sutural interval of elytra of identical width from the basis to the apex (0) — sutural interval narrowed to the apex (1); 16. 2nd and 3rd intervals joining with 10th and 9th intervals (0) — 2nd and 3rd intervals joining with 9th and 8th intervals (1); 17. Prothorax elongated (0) — prothorax more or less short (1); 18. Mesonotum without stridulatory files (0) — mesonotum with stridulatory files (1); 19. Sternopleural suture laterally (0) — sternopleural suture anterolaterally (1); 20. Ventrites homonomic (0) — 1st ventrite or 1st and 2nd ventrite little elongated (1); 21. Procoxae located near the basis of the prothorax (0) — procoxae located near the middle or the apex of the prothorax (1); 22. Procoxae located near the middle of the prothorax (0) — procoxae located near the apex of the prothorax (1); 23. Mesocoxae opened or partially opened (0) — mesocoxae closed (1); 24. 2nd segment of tarsi medially truncate not projecting over the base of a 3rd segment (0) — 2nd segment of tarsi medially lobed projecting over the base of a 3rd segment (1); 25. Tarsi narrow enough (0) — tarsi wide flattened (1); 26. Claws with teeth (0) — claws without teeth (1). The families Megalopodidae and Obrieniidae were taken as outgroups.

On the received cladogram (Fig. 24) the family Megalopodidae is a sisterly group to other families that confirms the division of this groups into two infraorders Chrysomeliformia and *Nurculioniformia*. It should be noted that recent Megalopodidae is an advanced group characterised by 8 apomorphic characters.

First of all the Chrysomeliformia is marked by an advanced rostrum.

The following branch is the family Obrieniidae (Obrienioidea), which is a sisterly family to Curculionoidea superfamily with widened 1st and 2nd segments of the funicle, wider than the subsequent segments, antennae with a distinct clava, reduced scutellar striae, a 3rd interval of the elytra merges with an 8th interval and an anterolaterally elongated sternopleural suture.

The calculation algorithm of the method SYNAP did not reveal the synapomorphy of the Nemonychidae subfamilies but they were separated only as a sisterly group to Obrieniidae. This statement supports the opinion expressed by Zherikhin and Egorov [1991], who considered that Nemonychidae was separated in the first place on the basis of similesiomorphies.

The subfamilies are joined in two groups. The first group is formed by Cretonemonychinae and Nemonychinae with the reduced striae of the elytra and a little elongated 1st ventrite. The second group (Eobelinae, Paleocartinae, Metrioxenoidinae, Selengarhynchinae, Rhinorhynchinae, Cimberindinae, Doydirhynchinae, Eccoptarthrinae, Distenorrhinae and Brenthorrhinae) differs by the striae of the elytra weakly marked to the apex, narrowed to the apex sutural interval of the elytra and closed mesocoxae. It should be noted that first two characters separate this group from Obrieniidae. These characters are absent in the first group in

connection with the reduction of striae. Thereby the basic character is a structure of cavities of mesocoxae.

The subfamilies Eccoptarthrinae, Distenorrhinae and Brenthorrhinae considered by Gratshev and Zherikhin [1996] as one subfamily at the expense of a change of a position of procoxae and flattened body are sharply separated. The status of these groups has been revised by the author [Legalov, 2009c]. The explanation can be made to the name «Eccoptarthrinae» that was used earlier [Zherikhin, Gratshev, 1995] for the other subfamily. An investigation of Ithyceridae Schoenherr, 1823, Ulyanidae Zherikhin, 1993, Slonikinae Zherikhin, 1977 and Eccoptarthridae (=Caridae Thompson, 1992), helped the author to conclude that they assigned to one group and the oldest valid name for the family is Ithyceridae Schoenherr, 1823 [Legalov, 2009a]. The result of studying of the typical material has shown that the name *Eccoptarthrus* L. Arnoldi, 1977 (type species: *Eccoptarthrus crassipes* L. Arnoldi, 1977) refers to the genus *Pseudobrenthorrhinus* Gratshev et Zherikhin, 1996 (type species: *Pseudobrenthorrhinus crassicornis* Gratshev et Zherikhin, 1996), and species *Eccoptarthrus crassicornis* (Gratshev et Zherikhin, 1996), *E. crassipes* L. Arnoldi, 1977, *E. magnus* (Gratshev et Zherikhin, 1996) and *E. tenuicornis* (Gratshev et Zherikhin, 1996) from the Jurassic of Karatau are alike. Consequently, the name *Procurculionini* L. Arnoldi, 1977 has been combined in synonyms to *Eccoptarthrini* L. Arnoldi, 1977, and the subfamily of the family Ithyceridae, named earlier *Eccoptarthrinae*, has acquired the name *Carinae* [Legalov, 2009c].

Among other subfamilies, the primitive Eobelinae is sisterly to other subfamilies. The recent subfamilies have such synapomorphies as: strongly convex eyes and a pronotum without a lateral carina. The Rhinorhynchinae subfamily with the stridulatory files on mesonotum is sisterly to other subfamilies of this group. The subfamilies Cimberindinae and Doydirhynchinae are close to each other very much and have synapomorphies (the reduced elytral striae, 2nd of the tarsi medially lobed projecting over the base of a 3rd segment and claws without teeth). Fossil Paleocartinae, Metrioxenoidinae and Selengarhynchinae are joined because of simpleiomorphies. Metrioxenoidinae and Selengarhynchinae with a rough sculpture are a sisterly group to Paleocartinae.

Comparing the received cladogram (Fig. 24) with a historical development of Nemonychidae (Fig. 1), it should be noted that a separation of Chrysomeloidae, Obrieniidae and Nemonychidae is confirmed. The subfamilies of Cretonemonychinae and Nemonychinae are separated from the other subfamilies. Specific Mesozoic subfamilies such as: Eccoptarthrinae, Distenorrhinae and Brenthorrhinae are connected. Eobelinae show the primitiveness and the relationship with the other subfamilies. The recent forms have synapomorphies and are isolated from the fossil groups.

The cladogram (Fig. 25), received with a help of the PAUP method, is similar to the previous cladog-

ram. The family Nemonychidae is distinguished by the basis of the reversions (elytra with scutellar striole, 2nd and 3rd intervals of the elytra joining with 10th and 9th intervals and a lateral sternopleural suture). It is the basic difference of this cladogram. The consolidation of Nemonychinae with the subfamilies Rhinorhynchinae, Cimberindinae and Doydirhynchinae on the basis of the strongly convex eyes and a pronotum without a lateral carina retraces the results received by Kuschel [1989] at the analysis of the recent Nemonychidae genera. At the expense of the synapomorphy (more or less shorted prothorax) Cretonemonychinae is included in a cluster with the other fossil subfamilies. Eobelinae show a relationship with the subfamilies Eccoptarthrinae and Distenorrhinae, on the ground of the antennae inserted near the middle of the rostrum (reversion) and wide flattened tarsi. Synapomorphic on the reversion of a 13th character (elytra with distinct striae), the subfamilies Selengarhynchinae, Metrioxenoidinae, Paleocartinae and Brenthorrhinae are united into two groups. Selengarhynchinae and Metrioxenoidinae are differed by the rough sculpture of the elytra and a large punctuate pronotum and the elytra. The subfamilies of Paleocartinae and Brenthorrhinae are characterised by the mandible with a tooth at an exterior margin (at some representatives) and a little elongated 1st ventrite (reversion).

In spite of a certain incorrectness of this method, shown in a considerable quantity of the reversion and with no account taken of some important characters, for example, positions of the procoxa, this cladogram confirms some relationships (Eobelinae, Eccoptarthrinae and Distenorrhinae; Selengarhynchinae and Metrioxenoidinae; Rhinorhynchinae, Cimberindinae and Doydirhynchinae). These relationships were established by the previous methods.

Hereby the phylogenesis was reconstructed on the basis of the relations ancestor – descendant (Fig. 1), it seems to be optimal in comparison with cladograms (Figs 24–25) that were received from the computer methods. It should be noted that cladograms confirm many phylogenetic relationships, revealed at the manual reconstruction of the phylogenesis. In the process of the evolution Nemonychidae formed two monophyletic groups. The subfamilies of Nemonychidae and Cretonemonychinae formed the first group, and all the other families formed the second. Crowson [1985] suggested to divide them into two families. The author can assume that if we accept Kirejtshuk's idea [1991] about the independence of the infraorders Chrysomeliformia and Curculioniformia, it will be possible to take into account specificity and the earlier branch of Obrienidae. It should be sorted out of two superfamilies of curculionid-beetles (Obrienioidea with Obrienidae and Curculionioidea with Nemonychidae and other families).

The recent representatives of Nemonychidae (72 species from 21 genera) are widely distributed in the Northern, Central and South America, the greater part of the Palaearctic region, New Guinea, Australia,

New Caledonia and New Zealand [Legalov, 2009b]. Fossil forms (more than 100 species from more than 50 genera) are known from the border of the Middle–Late Jurassic of Kazakhstan (Karatau) and China, the Early Cretaceous of Brazil (Santana), Spain (Montsec, Las Hoyas), England (Purbeck), Lebanon (Saida), Mongolia (Erdeni-Uul, Sharyn-Gol, Bon-Tsagaan, Khutuliy-Khira, Gurvan-Ereny-Nuruu and Hutel-Hara), China (Yixian, Xiazhuang), the Asian part of Russia (Baissa, Khasurtyi, Khetana) and also the Eocene of Green River (USA) and Baltic amber (Russia). The fauna of Karatau is the richest (27 genera and 68 species). It also surpasses all known faunas (Table 2) though concedes all of them together (31 genera and 46 species). In other 17 localities, there were revealed from 1 to 5 genera (as a rule 1–2) with 1–7 species. If we look at a parity genus/species, it acquires 1.48 that is 1 genus with 1 species as a rule.

An interesting question is a change of species, genera number and the abundance of Nemonychidae in the taphocoenosis. The maximum diversity of species and genera were located on the border of the Middle–Late Jurassic and the Early Cretaceous (Fig. 26). Further, the family is very poor in species comparing with the other families of *Nurculioniformia* (Figs 26–27). A decrease in the number of species and genera probably began with the Late Jurassic. More detailed consideration of the Mesozoic fauna shows a decrease in number of the Nemonychidae genera and species to the end of the Early Cretaceous against the backgrounds of an increase in number of species of other curculionid-beetles (Fig. 27).

The Nemonychidae abundance in the taphocoenosis (Figs 28–29) was very high on the border of the Middle–Late Jurassic and was comparable with the abundance of Curculionidae (in the taphocoenosis) on the Eocene – Oligocene (Fig. 29). In the Cretaceous the Nemonychidae number is much less than the other Curculionioidea. In the Late Cretaceous (since the Cenomanian) Nemonychidae had been disappearing from the palaeontological record (Fig. 28) that was explained by the Cretaceous biocenotic crisis [Zherikhin, 1978].

The recent species develop in the male strobili of *Araucaria* and *Agathis* (Araucariaceae), *Dacrycarpus*, *Dacrydium*, *Halocarpus*, *Lepidothamnus*, *Mamoo*, *Phyllocladus*, *Podocarpus*, *Prumnopitys*, *Saxegothaea* (Podocarpaceae), *Pinus* (Pinaceae), the anthers of *Notofagus* (Fagaceae) and the ovaries of *Consolida* and *Delphinium* (Ranunculaceae) [Kuschel, 1954, 1959, 1983, 1989, 1994, 2003; Dieckmann, 1974; Ter-Minassian, 1984; Kuschel, May, 1997; Legalov, 2009b]. More complicated situation is with trophic links of the fossil species. Crowson [1975] supposed that the first beetles, which started its development on the generative organs of plants (particularly Cycadoidea from Bennettitales) in the Jurassic, were primitive curculionid-beetles. He supposed that «it is possible the rostrum of early Curculionioidea was adapted to penetrating between the scales on Cycadooid receptacles» [Crowson, 1975]. Crowson [1981] noted that Nemo-

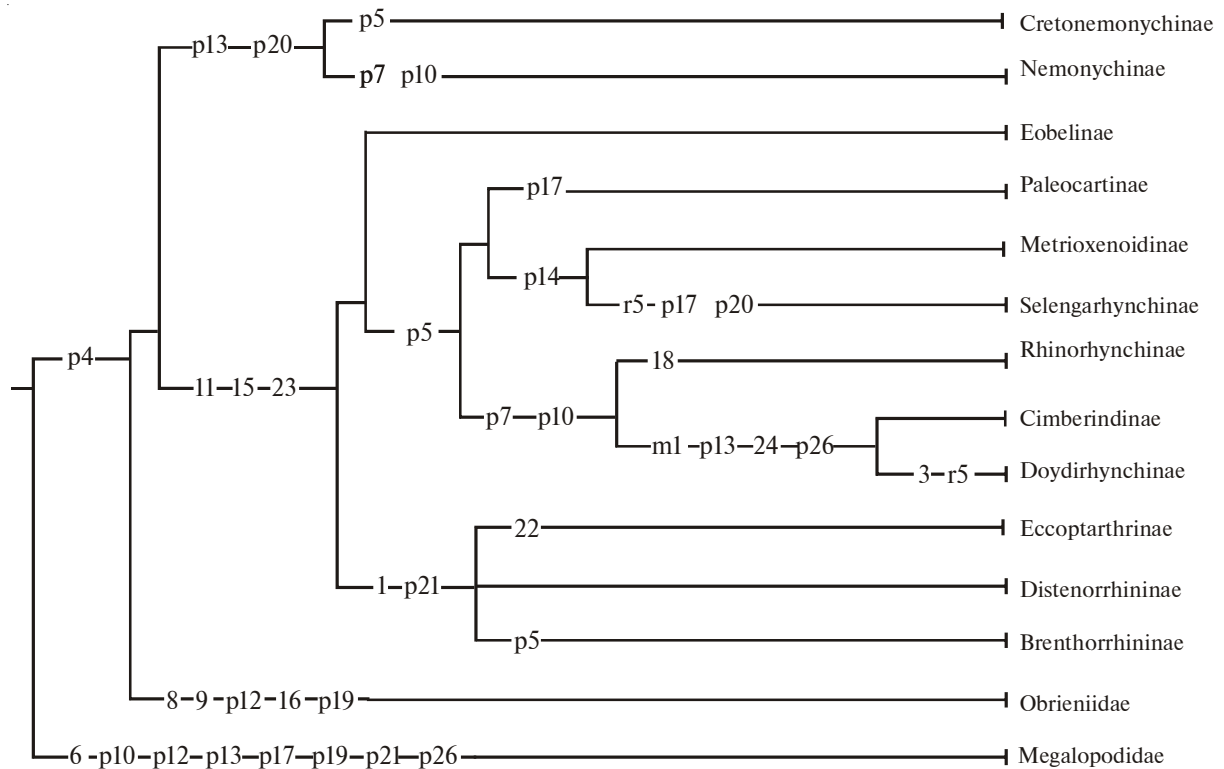


Fig. 24. Cladogram of the subfamilies of the family Nemonychidae is received by the method SYNAP. Figures — apomorphic conditions of characters; p — parallelisms; r — reversions; m — absence of character.

Рис. 24. Кладограмма подсемейств семейства Немонучидае, полученная методом SYNAP. Цифры — апоморфные состояния признаков; p — параллелизмы; r — реверсии; m — отсутствие признака.

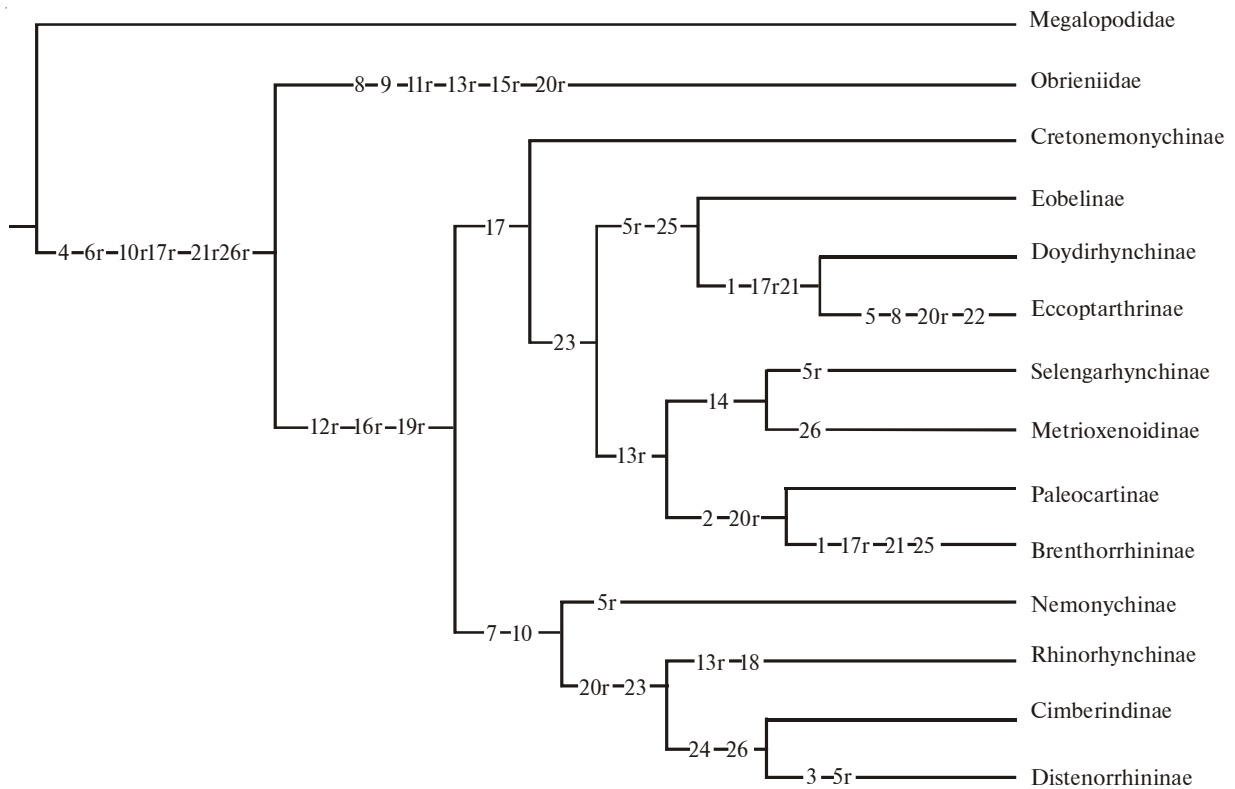


Fig. 25. Cladogram of the subfamilies of the family Nemonychidae received by the method PAUP. Indications as in Fig. 24.

Рис. 25. Кладограмма подсемейств семейства Немонучидае, полученная методом PAUP. Обозначения как на рис. 24.

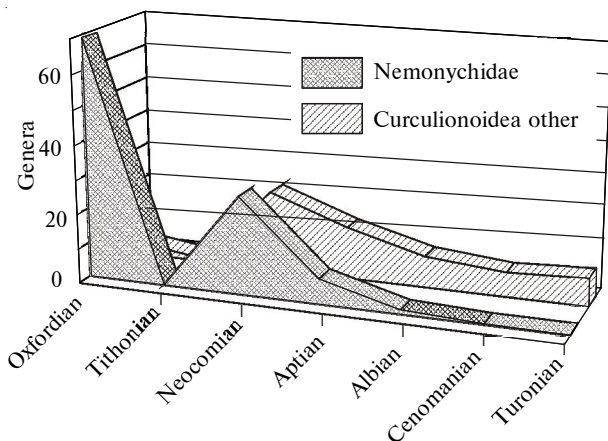


Fig. 26. Abundance of the genera Nemonychidae and other Curculioniformia in the Mesozoic.

Рис. 26. Изменение числа родов Nemonychidae и прочих Curculioniformia в мезозое.

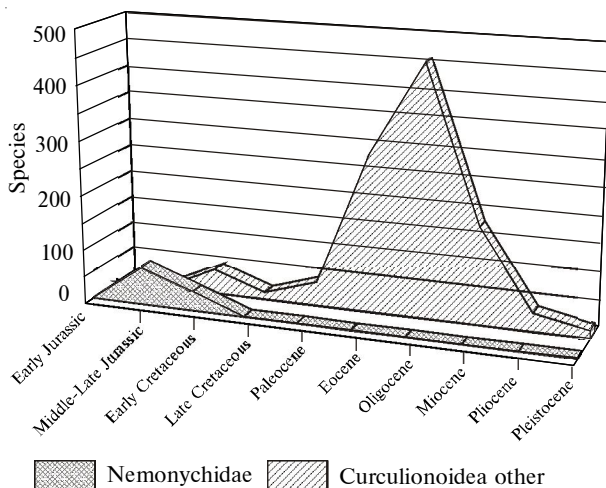


Fig. 27. Abundance of the genera Nemonychidae and other Curculioniformia in the Mesozoic and Cainozoic.

Рис. 27. Изменение числа родов Nemonychidae и прочих Curculioniformia в мезозое и кайнозое.

nymphidae were the oldest among modern pollen-eating beetles. Ponomarenko and Zherikhin [1980] assumed that Eobelidae were spermophages. Kuschel [1983] supposed that fossil Nemonychidae from Karatau were associated with Bennettitales. Poinar and Milki [2001] assumed the possibility of the development of *Libanorhinus succinus* Kuschel et Poinar, 1993 on *Agathis levantensis* Poinar et Milki, 2001. In my opinion, the most primitive Nemonychidae are representatives of the subfamily Cretonemonychinae and the tribe Oxycorynoidini (Eobelinae). We can assume their relations both with the Coniferous and the Bennettitales on the assumption of the fact that they probably have been associated with male fructifications. The following development of the female fructifications has led to the formation of Eobelini and Probelini, and a transition to the Coniferous has led to a formation of the branch of the recent subfamilies.

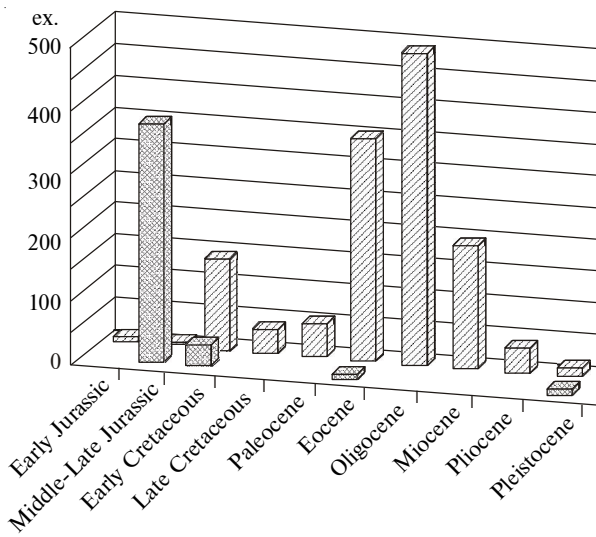


Fig. 28. Abundance of the specimens Nemonychidae and other Curculioniformia in the Mesozoic.

Рис. 28. Изменение числа экземпляров Nemonychidae и прочих Curculioniformia в мезозое.

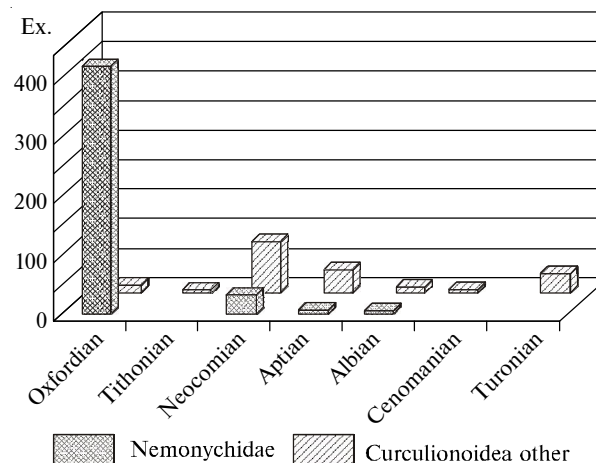


Fig. 29. Abundance of the specimens Nemonychidae and other Curculioniformia in the Mesozoic and Cainozoic.

Рис. 29. Изменение числа экземпляров Nemonychidae и прочих Curculioniformia в мезозое и кайнозое.

A systematic list of supraspecific taxa of the families Obrienidae and Nemonychidae

Superfamily **Obrienioidea**
Zherikhin et Gratshev, 1993

Family **Obrienidae** Zherikhin et Gratshev, 1993

Subfamily **Obrieninae** Zherikhin et Gratshev, 1993

Genus *Obrenia* Zherikhin et Gratshev, 1993: 3 species; Kyrgyzstan (Madygen), Middle–Upper Triassic.

Genus *Guillermia* Zherikhin et Gratshev, 1993: 1 species; Kyrgyzstan (Madygen), Middle–Upper Triassic.

Table 2. Fossil faunas of Nemonychidae
Таблица 2. Ископаемые фауны семейства Nemonychidae

Geological periods and epochs	Localities	Genera	Species
Middle-Late Jurassic	Karatau	27	68
Late Jurassic - Early Cretaceous	Yixian	3	4
	Khutuliy-Khira	1	1
Neocomian	Baissa	5	7
	Khasurtyi	3	5
	Hutel-Hara	2	2
	Gurvan-Ereny-Nuruu	1	2
Lower Berriasian	Purbeck	1	1
Berriasian - Barremian	Montsec	3	3
Hauterivian - Barremian	Las Hoyas	1	1
Middle Neocomian	Sharyn-Gol	2	2
	Erdeni-Uul	1	1
Middle Neocomian - Lower Aptian	Saida	1	1
?Lower Aptian	Bon-Tsagaan	1	3
Aptian - Albian	Santana	2	3
	Xiazhuang	1	1
Middle Albian	Khetana	2	2
Eocene	Green River	1	1
	Baltic amber	1	1

Subfamily Kararhynchinae
Zherikhin et Gratshev, 1993

Tribe Kenderlykanini Legalov, 2009

Genus *Madygenorhynchus* Zherikhin et Gratshev, 1993: 1 species; Kyrgyzstan (Madygen), Middle–Upper Triassic.

Genus *Kenderlyka* Zherikhin et Gratshev, 1993: 1 species; Kazakhstan (Kenderlyk), Upper Triassic.

Tribe Kararhynchini Zherikhin et Gratshev, 1993

Genus *Kararhynchus* Zherikhin et Gratshev, 1993: 2 species; Karatau, Middle–Late Jurassic.

Superfamily **Curculionoidea** Latreille, 1802

Family **Nemonychidae** Bedel, 1882

Subfamily Cretonemonychinae
Gratshev et Legalov, 2009

Genus *Pseudonemonyx* Gratshev et Legalov, 2009: 1 species; Russia (Baissa), Early Cretaceous.

Genus *Cretonemonyx* Gratshev et Legalov, 2009: 3 species; Karatau, Middle–Late Jurassic — Russia (Baissa), Early Cretaceous.

Subfamily Nemonychinae Bedel, 1820

Genus *Nemonyx* Redtenbacher, 1845: 4 species; Western and Central Palaeartic.

Subfamily Eobelinae L. Arnoldi, 1977

Tribe Oxycorynoidini L. Arnoldi, 1977

Genus *Belonotaroides* Legalov, 2009: 1 species; Karatau, Middle–Late Jurassic.

Genus *Cratomacer* Zherikhin et Gratshev, 2004: 2 species; Brazil (Santana), Early Cretaceous.

Genus *Khetanemonyx* Legalov, 2009: 1 species; Russia (Khetana), Early Cretaceous.

Genus *Microprobelus* Liu, Ren et Shih, 2006: 1 species; China (Yixian), Late Jurassic – Early Cretaceous.

Genus *Oxycorynoides* L. Arnoldi, 1977

Subgenus *Oxycorynoides* s. str.: 5 species; Karatau, Middle–Late Jurassic — Mongolia (Gurvan-Ereny-Nuruu), Early Cretaceous.

Subgenus *Pseudoxycorynoides* Legalov, 2009: 1 species; Karatau, Middle–Late Jurassic.

Tribe Karataucarini Legalov, 2009

Genus *Karataucar* Legalov, 2009: 1 species; Karatau, Middle–Late Jurassic.

Genus *Gratshevica* Legalov, 2009: 1 species; Karatau, Middle–Late Jurassic.

Genus *Ampliceps* L. Arnoldi, 1977: 2 species; Karatau, Middle–Late Jurassic.

Genus *Scelocamptus* L. Arnoldi, 1977: 2 species; Karatau, Middle–Late Jurassic.

Tribe Nanophydini L. Arnoldi, 1977

Genus *Nanophydes* L. Arnoldi, 1977: 1 species; Karatau, Middle–Late Jurassic.

Tribe Probelini Legalov, 2009

Genus *Belonotaris* L. Arnoldi, 1977: 1 species; Karatau, Middle–Late Jurassic.

Genus *Probelus* L. Arnoldi, 1977

Subgenus *Probelus* s. str.: 6 species; Karatau, Middle–Late Jurassic.

Subgenus *Probeloides* Legalov, 2009: 1 species; Karatau, Middle–Late Jurassic.

Genus *Arnoldibelus* Legalov, 2009: 10 species; Karatau, Middle–Late Jurassic.

Tribe Eobelini L. Arnoldi, 1977

Genus *Eobelus* L. Arnoldi, 1977: 1 species; Karatau, Middle–Late Jurassic.

Genus *Archaeorrhynchus* Martynov, 1926: 6 species; Karatau, Middle–Late Jurassic.

Genus *Archaeorrhynchoides* Legalov, 2009: 3 species; Karatau, Middle–Late Jurassic.

Genus *Martynovirhynchus* Legalov, gen.n.: 1 species; Karatau, Middle–Late Jurassic.

Subfamily Distenorrhiniinae L. Arnoldi, 1977

Genus *Buryatnemonyx* Legalov, 2010: 3 species; Russia (Khasurtyi), Early Cretaceous.

Genus *Distenorrhinus* L. Arnoldi, 1977

Subgenus *Distenorrhinus* s. str.: 9 species; Karatau, Middle–Late Jurassic — Russia (Khasurtyi), Early Cretaceous.

Subgenus *Parabrenthorhinus* Gratshev et Zherikhin, 1996: 2 species; Karatau, Middle–Late Jurassic — Spain (Las Hoyas), Early Cretaceous.

Subgenus *Astenorrhinus* Gratshev et Zherikhin, 1995: 2 species; Karatau, Middle–Late Jurassic.

Genus *Megabrenthorhinus* Gratshev et Zherikhin, 1996: 2 species; Karatau, Middle–Late Jurassic.

Genus *Microbrenthorhinus* Gratshev et Zherikhin, 2000: 2 species; Spain (Montsec), Russia (Khasurtyi), Early Cretaceous.

Subfamily Brenthorhininae L. Arnoldi, 1977

Tribe Brenthorhinoidini Legalov, 2003

Genus *Brenthorhinoides* Gratshev et Zherikhin, 1996: 2 species; Karatau, Middle–Late Jurassic.

Tribe Brenthorhinini L. Arnoldi, 1977

Genus *Abrenthorhinus* Legalov, 2009: 1 species; Karatau, Middle–Late Jurassic.

Genus *Brenthorhinus* L. Arnoldi, 1977: 1 species; Karatau, Middle–Late Jurassic.

Genus *Chinabrenthorhinus* Legalov, 2009: 1 species; China (Xiazhuang), Early Cretaceous.

Genus *Gobibrenthorhinus* Gratshev et Legalov, 2009: 1 species; Mongolia (Khutuliyn-Khira), Early Cretaceous.

Subfamily Eccoptarthrinae L. Arnoldi, 1977

Genus *Eccoptarthrus* L. Arnoldi, 1977: 4 species; Karatau, Middle–Late Jurassic.

Genus *Eccoptarthroides* Legalov, 2010: 4 species; Karatau, Middle–Late Jurassic.

Genus *Procurculio* L. Arnoldi, 1977: 3 species; Karatau, Middle–Late Jurassic.

Subfamily Metroxenoidea Legalov, 2009

Tribe Medmetroxenooidesini Legalov, trib.n.

Genus *Medmetroxenooides* Gratshev et Legalov, 2009: 1 species; Karatau, Middle–Late Jurassic.

Tribe Megametroxenooidesini Legalov, trib.n.

Genus *Megametroxenooides* Gratshev et Legalov, 2009: 1 species; Mongolia (Hutel-Hara), Early Cretaceous.

Tribe Metroxenooidini Legalov, 2009

Genus *Metroxenooides* Gratshev, Zherikhin, Jarzembowski, 1998: 1 species; UK (Purbeck), Early Cretaceous.

Genus *Cretoxenooides* Legalov, 2010: 1 species; Mongolia (Erdeni-Uul), Early Cretaceous.

Genus *Libanorhinus* Kuschel et Poinar, 1993: 1 species; Lebanon amber, Early Cretaceous.

Genus *Brasilnemonyx* Legalov, 2009: 1 species; Brazil (Santana), Early Cretaceous.

Subfamily Selengarhynchinae Gratshev et Legalov, 2009

Genus *Selengarhynchus* Gratshev et Legalov, 2009: 1 species; Mongolia (Sharyn-Gol), Early Cretaceous.

Genus *Selengarhynchoides* Legalov, 2010: 1 species; Mongolia (Sharyn-Gol), Early Cretaceous.

Subfamily Paleocartinae Legalov, 2003

Tribe Paleocartini Legalov, 2003

Genus *Paleocartus* Legalov, 2003: 1 species; Karatau, Middle–Late Jurassic.

Tribe Nebrenthorhinini Legalov, 2007

Genus *Nebrenthorhinus* Legalov, 2003: 1 species; Spain (Montsec), Early Cretaceous.

Subfamily Rhinorhynchinae Voss, 1922

Tribe Mecomacerini Kuschel, 1994

Subtribe Mecomacerina Kuschel, 1994

Genus *Renicimberis* Legalov, 2009: 1 species; China (Yixian), Late Jurassic – Early Cretaceous.

Genus *Mecomacer* Kuschel, 1954: 4 species; Argentina, Chile.

Genus *Notomacer* Kuschel, 1994: 8 species; Australia, New Caledonia.

Genus *Aragomacer* Kuschel, 1994: 5 species; Australia, Papua New Guinea.

Genus *Eutactobius* Kuschel, 1994: 1 species; Australia.

Genus *Bunyaesus* Kuschel, 1994: 2 species; Australia.

Genus *Rhynchitomacerinus* Kuschel, 1954: 1 species; Argentina, Chile.

Genus *Rhynchitoplesius* Voss, 1952: 1 species; Brazil.

Subtribe Brarina Legalov, 2009

Genus *Brarus* Kuschel, 1997: 1 species; Brazil.

Tribe Rhinorhynchini Voss, 1922

Genus *Atopomacer* Kuschel, 1989: 4 species; North and Central America.

Genus *Rhinorhynchus* Sharp, 1882: 4 species; New Zealand.

Genus *Nannomacer* Kuschel, 1954: 2 species; Argentina, Chile.

Genus *Basiliorhinus* Kuschel, 1994: 1 species; Australia.

Genus *Basilogeus* Kuschel, 1994: 2 species; Australia.

Genus *Pagomacer* Kuschel, 1994: 1 species; Australia.

Genus *Rhynchitomacer* Voss, 1937: 14 species; Argentina, Chile.

Subfamily Cimberindinae des Gozis, 1882

Tribe Cimberindini des Gozis, 1882

Genus *Chinocimberis* Legalov, 2009: 2 species; China (Yixian), Late Jurassic – Early Cretaceous.

Genus *Cimberis* des Gozis, 1881

Subgenus *Cimberis* s. str.: 4 species; Holarctic.

Subgenus *Amerocimberis* Legalov, 2009: 4 species; North America.

Genus *Pityomacer* Kuschel, 1989: 3 species; North America.

Genus *Acromacer* Kuschel, 1989: 1 species; North America.

Tribe Kuschelomacerini Riedel, 2010

Genus *Kuschelomacer* Riedel, 2010: 1 species; Baltic amber, Eocene.

Subfamily Doydirhynchinae Pierce, 1916

Genus *Doydirhynchus* Dejean, 1821: 2 species; Western Palearctic.

Genus *Lecontellus* Kuschel, 1989: 3 species; USA.

Genus *Auletomacer* Zherikhin, 1993: 1 species; Russia (Khetana), Early Cretaceous.

New taxa

Martynovirhynchus Legalov, **gen.n.**

Figs 18–19.

Material. Holotype — PIN, No. 284/508, South Kazakhstan, Chimkent Oblast, Algabass District, Kara-Tau Range, outcrops near villages of Kitaevka and Uspenovka, right bank of Kashkar-Ata River valley, Kara-Bas-Tau, Tchokhay, Mikhailovka, Galkino; Middle–Upper Jurassic, Oxfordian, Karabastau Formation; part and counterpart of beetle impression.

Description. Body elongated, flattened, weak sclerotized, yellowy-brown. Head and rostrum darker. Rostrum long, almost straight. Mandible long, with tooth at exterior margin. Labrum triangular, free. Eyes roundish, flat. Frons narrow, weakly convex. Temples short. Antennae located in the first thirds of the rostrum. Scapus elongated. Funicle segments elongated. Clava compact. Pronotum wide. Disk flattened. Elytra longer than their width. Points in striae small. Legs long. Procoxa basal. Pro- and mesofemora strongly widened. Tibiae almost straight. Tarsi elongated. 1st segment of pro- and metatarsi strongly widened and elongated. Length of body: 9.0 mm.

Diagnosis. This new genus differs from the close genera *Archaeorrhynchus* Martynov, 1926 and *Archaeorrhynchoides* Legalov, 2009 by the strongly widened pro- and metatarsi, weaker widened rostrum and femora, and weaker convex frons.

Диагноз. Новый род отличается от близких родов *Archaeorrhynchus* Мартынов, 1926 и *Archaeorrhynchoides* Legalov, 2009 сильно расширенными лапками не только передних, но и средних ног, слабее утолщёнными головами и бёдрами, а также слабее выпуклым лбом.

Etymology. New genus is named in honour of A.V. Martynov.

Martynovirhynchus arnoldii Legalov, **sp.n.**

Figs 18–19.

Material. Holotype — PIN, No. 284/508, South Kazakhstan, Chimkent Oblast, Algabass District, Kara-Tau Range, outcrops near villages of Kitaevka and Uspenovka, right bank of Kashkar-Ata River valley, Kara-Bas-Tau, Tchokhay, Mikhailovka, Galkino; Middle–Upper Jurassic, Oxfordian, Karabastau Formation; part and counterpart of beetle impression.

Description. Body narrow, flattened dorsoventrally, not strong sclerotized, and yellowy-brown. Head and rostrum brown. Rostrum long, almost straight, 1.73 times longer than pronotum and 9.0 times longer than width on the basis. Mandible long, with tooth at exterior margin. Labrum large, free. Head capsule little wider than length. Eyes roundish, flat. Frons narrow, weakly convex. Temples short, shorter than diameter of the eye. Antennae located in the first third of the rostrum, long and reaching the basis of the elytra. Scapus elongated, 7.6 times longer than width. 1st segment hardly shorter and narrower than scapus. 2nd–5th segments elongated, shorter. 6th and 7th segments elongated, trapezoid. Clava compact. 1st and 2nd segments trapezoid, wide. 3rd segment tear-shaped, pointed. Pronotum wide, 1.35 times wider than length. Disk flattened, small punctate. Elytra 1.77 times longer than width and 3.19 times longer than pronotum, flattened. Striae possibly weak. Points in them small. Intervals between points little wider than diameter of the points. Legs long. Procoxa basal. Profemora strongly widened, 2.4 times longer than width. Protibiae almost straight. 1st segment strongly widened and elongated, little narrower and shorter than profemora, 3.0 times longer than width. Mesofemora widened, narrower than profemora. Tib-

iae almost straight, widened to apex. Tarsi elongated, little shorter than tibiae, widened. 1st segment 1.46 times wider than length. 2nd segment 2.67 times shorter than 1st segment, narrower. 3rd segment narrower than 2nd segment. Metafemora narrow, narrower than mesofemora. Metatibiae narrow, hardly widened to apex. Length of body: 9.0 mm.

Etymology. New species is named in honour of L.V. Arnoldi.

Medmetrioxenoidesini Legalov, **trib.n.**

Type genus: *Medmetrioxenoides* Gratshev et Legalov, 2009

Description. Body narrow, not dorsoventral flattened, not strong chitinized. Rostrum short, very weakly and smoothly curved, of equal length to pronotum, 4.2 times longer than width at the basis, with small mandibles. Antennae located more basally the rostrum middle. Head slightly elongated. Frons weakly convex. Eyes almost round, average size. Temples equal to third of diameter of the eye. Antennae reaching pronotum apex. Scapus not widened, 2.0–2.5 times longer than width. Pronotum elongated, with distinct lateral carina and flattened disk. Elytra 2.6 times longer than pronotum, flat in the basic half and strongly convex in back, with weak punctate striae. Intervals wide. Precoxal part of the prothorax strongly elongated, more than twice longer the diameter of procoxa. Procoxae basal. Femora not widened. Tibiae straight, not thick. Length of body: 3.2 mm.

Diagnosis. This new tribe differs from the other tribes of this subfamily by the submedial located antennae, rounded eyes, weakly elytral striae, significantly long precoxal part of the pronotum.

Диагноз. Новая триба отличается от остальных триб подсемейства усиками, прикреплёнными на середине головотрубки, округлыми глазами, слабыми бороздками надкрылий и сильно удлинённой перкоксальной частью переднегруди.

Composition. Genus *Medmetrioxenoides* Gratshev et Legalov, 2009 from Middle–Late Jurassic of Karatau.

Remarks. For the figure, refer to Gratshev and Legalov's work [2009, fig. 8].

Megametrioxenoidesini Legalov, **trib.n.**

Type genus: *Megametrioxenoides* Gratshev et Legalov, 2009

Description. Body narrow, more or less strongly chitinized. Rostrum short, weakly and smoothly curved, 1.15 times shorter than pronotum and 4.1 times longer than width on the basis, with small mandibles. Antennae located on the border of the third quarter of the rostrum. Head elongated. Frons convex. Eyes beanlike, average size. Temples little shorter than the smallest diameter of the eye. Antennae reaching pronotum apex. Clava noncompact, much wider than funicle. Pronotum elongated, with distinct lateral carinae and flattened disk, small and densely granular. Elytra, probably, with weak punctate striae, 2.7 times longer than pronotum. Precoxal part of the prothorax strongly elongated, more than twice longer than the diameter of the procoxa. Procoxae basal. Profemora not widened. Metafemora strong widened. Tibiae straight and not thick. Metatarsi long, hardly shorter than metatibiae. 1st and 2nd segments triangular. 3rd segment weakly sinuate at apex and only little wider than the 2nd segment. Clausal segment on length equal to the first three segments altogether, thin and strongly curved. Claws with teeth. Length of body: 5.8 mm.

Diagnosis. This new tribe is very close to the tribe *Medmetrioxenoidini* but differs by very weak elytral striae,

transversal fabiform eyes and almost subapical located antennae.

Диагноз. Новая триба близка к трибе *Medmetrioxenoidini* и отличается очень слабыми бороздками надкрылий, поперечно вытянутыми бобовидными глазами и почти субапикальными усиками.

Composition. Genus *Megametrioxenoides* Gratshev et Legalov, 2009 from Neocomian of Mongolia.

Remarks. For the figure, refer to Gratshev and Legalov's work [2009, fig. 4].

Acknowledgements

The author is thankful to his colleagues for the help with the work.

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