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Classification and taxonomy of the nitidulid-group of families (Coleoptera: Cucujoidea): comments on morphology, bionomics, phylogeny and methodology, with a key to species of the subgenus *Myothorax* Murray, 1864 of the genus *Carpophilus* Stephens, 1830 (Nitidulidae: Carpophilinae)

© A.G. Kirejtshuk

Zoological Institute of the Russian Academy of Sciences, Universitetskaya Embankment, 1, St Petersburg 199034 Russia. E-mail: agk@zin.ru, kirejtshuk@gmail.com

Abstract. The paper provides an overview of the author's methodological opinion, which became the basis for developing the system and phylogeny of the nitidulid-group of families. The proposals for changing the system and phylogeny of these families are discussed, including the justification for using the taxon Nitiduloidea. The most reliable evidence of ancient divergences of these families can be the structure of the genitalia of both sexes, and therefore, in a number of cases, fossils without exposed genitalia can be arranged to a certain supraspecies group only tentatively. According to the structure of the genitalia of both sexes, two subgroups of families are distinguished: kateretid-subgroup (Apophisandridae, Boganiidae, Kateretidae, Parandrexidae, and Smicripidae) and nitidulid-subgroup (Helotidae, Monotomidae, and Nitidulidae), which reveal significant antiquity and many parallelisms in structure and bionomy and seem to have diverged earlier than the Middle Jurassic. The family Nitidulidae is also clearly divided into two phyletic lineages based on the structure of the male genitalia: nitiduline-lineage (Cillaeinae, Cryptarchinae, Cybocephalinae, Maynipeplinae, and Nitidulinae) and carpophiline-lineage (Amphicrossinae, Calonecrinae, Carpophilinae, and Epuraeinae). Recent proposals for changing the system and phylogeny are discussed. These do not take into account the fundamental features discussed in this paper. They were obtained after preliminary comparisons of some sequencing that require careful additional checks and clarifications. There are also discussed the independent appearance of trophic interactions with the plant generative organs in representatives of many groups of the considered families; misinterpretations of these interactions have often led to hasty and insufficiently substantiated conclusions, including serious errors in constructing classifications and phylogenetic proposals. The latter methodological defects require verification, which can be achieved by the principle (method) of multiple parallelisms. This principle harmoniously complements the concept of integrated taxonomy and phylogenomics, providing the latter with an objective basis and a method of verification. The possible role of participation of representatives of the considered families in pollination of gymnosperms and angiosperms in the past, starting from the Middle Jurassic and up to the present day, are discussed. Using the method of multiple parallelisms, it has been shown that if the nitidulid-group of families has a common origin, then the kateretid-subgroup should be considered as mainly Mesozoic with some genera represented in the modern biota, then the nitidulid-subgroup should be considered, despite the antiquity of its origin, as prosperous in the Cenozoic, having given rise to a large number of modern forms with imaginal or complete anthophagy. At the same time, modern nitidulids, which usually live on dioecious palms, exhibit greatest convergent similarity of many structures with those of Mesozoic apophisandrids.

An overview of the *dimidiatus*-group of species of the subgenus *Myothorax* Murray, 1864 of the genus *Carpophilus* Stephens, 1830 is presented. This group includes widespread food pests that cause significant economic damages. Identification of these species has so far been an almost insoluble problem for pest control specialists. A key to these pests facilitating their identification is developed. New taxa are proposed: subfamily Vetunitidulinae **subfam. n.** (Apophisandridae, type genus *Vetunitidula* Zhao, Engel, Huang et Cai, 2025), tribe Plesiogethini **trib. n.** (Cybocephalinae, type genus *Plesiogethes* Zaitsev, Vasilenko et Perkovsky, 2025) and the genus *Mesohelotopsis* **gen. n.** (Helotidae, type species *Metahelotella monochromata* Liu, Šlipiński, Ren et Pang, 2019), as a result a new combination is established: *Mesohelotopsis monochromata* (Liu, Šlipiński, Ren et Pang, 2019), **comb. n.** The following new species are described: *Carpophilus* (*Myothorax*) *assignatus* **sp. n.** (Malaysia: Kalimantan, Sabah; Indonesia: Sulawesi), *C. (M.) fumatoides* **sp. n.** (India: Karnataka; Laos), *C. (M.) generosus* **sp. n.** (Indonesia: Java, Bali), and *C. (M.) languescens* **sp. n.** (Cambodia). In addition, new synonymy is introduced for the following species: Epuraeinae: *Epuraea* (*Epuraea*) *excisicollis* Reitter, 1872 = *E. (E.) dolosa* Kirejtshuk, 1995, **syn. n.**; Carpophilinae: *Carpophilus* (*Ecnomorphus*) *plagiatiipennis* (Motschulsky, 1858) = *C. (Ecnomorphus) jahari* Dasgupta et Pal, 2019, **syn. n.**, *Carpophilus* (*Myothorax*) *contegens* (Walker, 1858) = *C. (M.) maculatus* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *nigritus* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *testaceus* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *dilutus* Murray, 1864, **syn. n.**, non *Colastus dilutus* Motschulsky, 1858, *Carpophilus* (*Myothorax*) *fusciceps* Grouvelle, 1913 = *C. (M.) scotti* Grouvelle, 1913, **syn. n.**, *Carpophilus* (*Myothorax*) *lewisi* Reitter, 1884 = *C. (M.) signatus* Grouvelle, 1908, **syn. n.** = *C. (M.) signatus* var. *ornatus* Grouvelle, 1908, **syn. n.** = *C. (M.) subcalvus* Kirejtshuk, 1984, **syn. n.**, *Carpophilus* (*Myothorax*) *schioedtei* Murray, 1864 = *C. (M.) pallescens* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *limbalis* Murray, 1864, **syn. n.**, *Carpophilus* (*Myothorax*) *pilipennis* Macleay, 1873 = *C. (M.) davidsoni* Dobson, 1952, **syn. n.**; Nitidulinae: *Aethina* (*Aethina*) *aeneipennis* Reitter, 1873 = *A. (A.) zhizhuaca* Chen et Huang, 2024, **syn. n.**, *Atarphia quadripunctata* Reitter, 1884 = *A. cincta* Jelínek et Hájek, 2012, **syn. n.**, *Physoronia wajdelota* (Wankowicz, 1869) = *P. japonica* Reitter, 1873, **syn. n.**, *Pocadius nobilis* Reitter, 1873 = *P. fasciatus* Cline, 2008, **syn. n.** = *P. okinawaensis* Cline, 2008, **syn. n.** = *P. tenebrosus* Chen et Huang, 2020, **syn. n.** = *P. zhangjiajieensis* Chen et Huang, 2020, **syn. n.**; Cryptarchinae: *Glischrochilus* (*Glischrochilus*) *quadripunctatus* (Linnaeus, 1758) = *G. (G.) tremulae* Clayhills, Audisio et Cline, 2016, **syn. n.**; Cybocephalinae: *Cybocephalus bicinctus* Kirejtshuk, 1988 = *C. chlorocapitis* Hisamatsu, 2013, **syn. n.** Besides, lectotypes are designated for *Aethina suturalis* Reitter, 1884, *Carpophilus lewisi* Reitter, 1884, *C. ochropterus* Boheman, 1851, *C. pilosellus* Motschulsky, 1858, *C. (Ecnomorphus) nigricans* Grouvelle, 1897, *C. (Eidocolastus) bosschae* Grouvelle, 1892, *C. (Myothorax) vittiger* var. *limbalis* Murray, 1864,

C. (M.) luridus Murray, 1864, *C. (M.) maculatus* Murray, 1864, *C. (M.) vittiger* var. *nigritus* Murray, 1864, *C. (M.) nepos* Murray, 1864, *C. (M.) notatus* Murray, 1864, *C. (M.) pallescens* Murray, 1864, *C. (M.) vittiger* var. *robustus* Murray, 1864, *C. (M.) schioedtei* Murray, 1864, *C. (M.) vittiger* var. *testaceus* Murray, 1864, *C. (M.) vittiger* Murray, 1864, *Colastus dilutus* Motschulsky, 1858, non *Carpophilus (Myothorax) vittiger* var. *dilutus* Murray, 1864, *Colastus plagiaticipennis* Motschulsky, 1858, *Nitidula contegens* Walker, 1858, *Nitidula hemiptera* Fabricius, 1792, non *Dermestes hemipterus* Linnaeus, 1758. The name *Carpophilus (Myothorax) robustus* Murray, 1864, **stat. n.** should be used as valid for a separate species, which was originally proposed to designate a variety of *C. (M.) vittiger*, however, according to the studied lectotypes, the latter should be recognized as a junior synonym of *C. (M.) contegens*.

Key words: method of multiple parallelisms, structure of aedeagus, synonymy, individual development, pollinophagy, pollination.

**Классификация и таксономия группы семейств, близких к Nitidulidae (Coleoptera: Cucujoidea):
замечания по морфологии, биологии, филогении и методологии
с определительной таблицей для видов подрода *Myothorax* Murray, 1864
рода *Carpophilus* Stephens, 1830 (Nitidulidae: Carpophilinae)**

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Зоологический институт Российской академии наук, Университетская набережная, 1, Санкт-Петербург 199034 Россия

Резюме. Сделан обзор методологических взглядов автора, ставших основой для разработки системы и филогении группы семейств, близких к Nitidulidae. Обсуждаются предложения по изменению системы и филогении этих семейств, в том числе и оправданность использования таксона Nitiduloidea. Наиболее надежным свидетельством древних дивергенций этих семейств может быть строение гениталий обоих полов, и поэтому в ряде случаев ископаемые жуки, у которых не сохранились гениталии, могут соотноситься с определенной надвидовой группой только предположительно. По строению гениталий обоих полов выделены две подгруппы семейств: близкая к Kateretidae (Apophisandridae, Boganidae, Kateretidae, Parandrexidae и Smicripidae) и близкая к Nitidulidae (Helotidae, Monotomidae и Nitidulidae), – обнаруживающие значительную древность и многие исторические параллелизмы в строении и биологии и, по-видимому, имеющие общие корни ранее середины юры. Семейство Nitidulidae также отчетливо разделяется по строению гениталий самцов на две филогенетические линии: нитидулиновую (Cillaeinae, Cryptarchinae, Cybocephalinae, Maupyrinae и Nitidulinae) и карпофилиновую (Amphicrossinae, Calonecrinae, Carpophilinae и Epruraeinae). Обсуждены предложения последних лет по изменению системы и филогении, в которых не учитываются рассмотренные в этой статье фундаментальные особенности, а также которые получены из дендрограмм предварительных сравнений некоторых секвенированных, нуждающихся в тщательных дополнительных проверках и уточнениях. Обсуждается независимое появление трофической приуроченности к генеративным органам растений у представителей многих групп рассмотренных семейств, неправильная интерпретация трофики которых нередко приводит к неверным выводам, в том числе к серьезным ошибкам в построении классификаций и филогенетических реконструкций. Последние методологические дефекты требуют проверки, которую можно осуществить методом множественных параллелизмов. Этот принцип гармонично дополняет концепцию интегративных таксономии и филогеномики, обеспечивая последнюю объективной основой и методом проверки. Обсуждены возможности участия представителей рассмотренных семейств в опылении голосеменных и покрытосеменных в прошлом, начиная со средней юры, и в настоящее время. Благодаря методу множественных параллелизмов показано, что если группа семейств, близких к семейству Nitidulidae, имеет общее происхождение, то подгруппу семейств, близких к семейству Kateretidae, следует рассматривать как преимущественно мезозойскую с некоторыми родами, представленными в современном биоте, а подгруппа семейств, близких к Nitidulidae, должна рассматриваться, несмотря на древность ее происхождения, как процветающая в кайнозое, давшая большое число современных как имагинальных, так и полных антофагов. При этом современные нитидулиды, обычно обитающие на двудомных пальмах, обнаруживают наибольшее конвергентное сходство многих структур с таковыми у мезозойских апофизандрид.

Представлен обзор группы видов *dimidiatus* подрода *Myothorax* Murray, 1864 рода *Carpophilus* Stephens, 1830, в составе которой известны вредители продовольственных запасов, получившие широкое распространение и наносящие значительный экономический ущерб. Определение этих видов до сих пор представляло почти неразрешимую проблему для специалистов по борьбе с этими вредителями. Разработана определительная таблица, призванная облегчить их определение. Предложены новые таксоны: подсемейство Vetunitidulinae **subfam. n.** (Apophisandridae, типовой род *Vetunitidula* Zhao, Engel, Huang et Cai, 2025), триба Plesiogethini **trib. n.** (Cybocephalinae, типовой род *Plesiogethes* Zaitsev, Vasilenko et Perkovsky, 2025) и род *Mesohelotopsis* **gen. n.** (Helotidae, типовой вид *Metahelotella monochromata* Liu, Ślipiński, Ren et Pang, 2019), в результате, установлено новое сочетание: *Mesohelotopsis monochromata* (Liu, Ślipiński, Ren et Pang, 2019), **comb. n.** Описаны следующие новые виды: *Carpophilus (Myothorax) assignatus* **sp. n.** (Малайзия: Калимантан, Сабах; Индонезия: Сулавеси), *C. (M.) fumatoides* **sp. n.** (Индия: Карнатака, Лаос), *C. (M.) generosus* **sp. n.** (Индонезия: Ява, Бали) и *C. (M.) languescens* **sp. n.** (Камбоджа). Кроме того, установлена новая синонимия для следующих видов: Epruraeinae: *Epruraea (Epruraea) excisicollis* Reitter, 1872 = *E. (E.) dolosa* Kirejtshuk, 1995, **syn. n.**; Carpophilinae: *Carpophilus (Ecnomorphus) plagiaticipennis* (Motschulsky, 1858) = *C. (Ecnomorphus) jahari* Dasgupta et Pal, 2019, **syn. n.**; *Carpophilus (Myothorax) contegens* (Walker, 1858) = *C. (M.) maculatus* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *nigritus* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *testaceus* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *dilutus* Murray, 1864, **syn. n.**, non *Colastus dilutus* Motschulsky, 1858, *Carpophilus (Myothorax) fusciceps* Grouvelle, 1913 = *C. (M.) scotti* Grouvelle, 1913, **syn. n.**; *Carpophilus (Myothorax) lewisi* Reitter, 1884 = *C. (M.) signatus* Grouvelle, 1908, **syn. n.** = *C. (M.) signatus* var. *ornatus* Grouvelle, 1908, **syn. n.** = *C. (M.) subcalvus* Kirejtshuk, 1984, **syn. n.**, *Carpophilus (Myothorax) schioedtei* Murray, 1864 = *C. (M.) pallescens* Murray, 1864, **syn. n.** = *C. (M.) vittiger* var. *limbalis* Murray, 1864, **syn. n.**, *Carpophilus*

(*M.*) *pilipennis* Macleay, 1873 = *C. (M.) davidsoni* Dobson, 1952, **syn. n.**; Nitidulinae: *Aethina (Aethina) aeneipennis* Reitter, 1873 = *A. (A.) zhizhuaca* Chen et Huang, 2024, **syn. n.**, *Atarphia quadripunctata* Reitter, 1884 = *A. cincta* Jelínek et Hájek, 2012, **syn. n.**, *Physoronia wajdelota* (Wankowicz, 1869) = *P. japonica* Reitter, 1873, **syn. n.**, *Pocadius nobilis* Reitter, 1873 = *P. fasciatus* Cline, 2008, **syn. n.** = *P. okinawaensis* Cline, 2008, **syn. n.** = *P. tenebrosus* Chen et Huang, 2020, **syn. n.** = *P. zhangjiajieensis* Chen et Huang, 2020, **syn. n.**; Cryptarchinae: *Glischrochilus (Glischrochilus) quadripunctatus* (Linnaeus, 1758) = *G. (G.) tremulae* Clayhills, Audisio et Cline, 2016, **syn. n.**; Cybocephalinae: *Cybocephalus bicinctus* Kirejtshuk, 1988 = *C. chlorocapitis* Hisamatsu, 2013, **syn. n.** Кроме того, обозначены лектотипы для *Aethina suturalis* Reitter, 1884, *Carpophilus lewisi* Reitter, 1884, *C. ochropterus* Boheman, 1851, *C. pilosellus* Motschulsky, 1858, *C. (Ecnomorphus) nigricans* Grouvelle, 1897, *C. (Eidocolastus) bosschae* Grouvelle, 1892, *C. (Myothorax) vittiger* var. *limbalis* Murray, 1864, *C. (M.) luridus* Murray, 1864, *C. (M.) maculatus* Murray, 1864, *C. (M.) vittiger* var. *nigritus* Murray, 1864, *C. (M.) nepos* Murray, 1864, *C. (M.) notatus* Murray, 1864, *C. (M.) pallescens* Murray, 1864, *C. (M.) vittiger* var. *robustus* Murray, 1864, *C. (M.) schioedtei* Murray, 1864, *C. (M.) vittiger* var. *testaceus* Murray, 1864, *C. (M.) vittiger* Murray, 1864, *Colastus dilutus* Motschulsky, 1858, non *Carpophilus (Myothorax) vittiger* var. *dilutus* Murray, 1864, *Colastus plagiatipennis* Motschulsky, 1858, *Nitidula contegens* Walker, 1858, *Nitidula hemiptera* Fabricius, 1792, non *Dermestes hemipterus* Linnaeus, 1758. Название *Carpophilus (Myothorax) robustus* Murray, 1864, **stat. n.**, которое первоначально было предложено для обозначения разновидности *C. (M.) vittiger*, целесообразно использовать как валидное для отдельного вида, а последнее, согласно изученным лектотипам, следует признавать младшим синонимом *C. (M.) contegens*.

Ключевые слова: метод множественных параллелизмов, строение эдеагуса, синонимия, индивидуальное развитие, палинофагия, опыление.

Introduction

The necessity for this paper appeared in connection with the preparation of chapters for the catalogue of beetles of the Russian Far East (families Kateretidae Kirby, 1837 and Nitidulidae Latreille, 1802 (Kirejtshuk, in prep.)), in particular the definition of the composition of species included in these families and the adopted system for the supraspecific taxa. The last analogous catalogue devoted to the modern Palaearctic fauna of Coleoptera was published in 2007 and repeated in 2013 [Jelínek, 2007; Jelínek, Audisio, 2007]. Within nearly twenty years some additional important publications appeared. Besides, some misprints, missing taxa or some errors in the interpretation and other errors found in these published catalogues require corrections and explanations. Due to favorable circumstances in the last decades of the last century I managed to study representatives of almost all generic taxa of the kateretids and nitidulids, as well as type series of most species deposited in main world collections. This allowed me to find features for dividing these families and to propose a number of changes in their systems, a precis of which with some comments was published in 2008 [Kirejtshuk, 2008]. Some wrong subfamily and generic attributions published in the mentioned catalogues were already corrected [Kirejtshuk, 2008]. Incorrect type designations and erroneous synonymy of the cillaeine taxa were recently corrected by Kirejtshuk and Kovalev [2022]. Initially, this paper was intended only as an explanation of the catalogues being prepared, including additions and corrections related to the coleopterofauna of the Russian Far East, including explanations of the inaccuracies and deficiencies of the 2007's catalogues. In recent years, colleagues from Asian countries (X. Chen, Y. Chen, N. Hayashi, S. Hisamatsu, S.-T. Hisamatsu, M. Liu, T. Nakane and others) have contributed a lot to study the fauna of the cucujoid beetles in the area along the Pacific coast, including the Russian Far East. However, within many important recent contributions not all new systematic and taxonomic proposals have been successful enough, and therefore they are a subject of consideration in this paper.

Significant proposals have also been published to change the present system and hypotheses of phylogenetic relationship of the nitidulid-group of families [Audisio et al., 2009; Cline et al., 2014; Lee et al., 2020; Powell et al., 2020; Peris et al., 2024a, b and some others], which in one way or another concern the classification adopted in the submitted Russian Far East catalogue of the Coleoptera. These new concepts were put forward without taking into account some general proposals for the system of the nitidulid-group of families and their generic composition, developed on the basis of studying extant and extinct representatives performed over the past decades [Kirejtshuk, 1982, 1986a, 2008; Kirejtshuk et al., 2023, etc.]. The main feature of all these changes was the rather limited information on taxonomy and phylogeny used by their authors, who apparently considered many areas of knowledge to be redundant for "phylogenetic" reconstructions. Meanwhile, in all cases, the "redundant" areas included the most fundamental data necessary for combining genera into suprageneric groups, including families. This feature is most clearly formulated in the chapter of one handbook by Jelínek et al. [2010], although the theoretical basis for such an approach to taxonomy and phylogenetics of the group under consideration and the most vivid expression can be read in the Leschen's revision [Leschen, 1999]. In this connection it was once again necessary to define the general basic principles of the accepted system and hypothesis of phylogenetic relationships in this group of families in order to compare them with those proposed recently and to analyze their differences from the previous ones. Studies on the nitidulid-group of families has intensified in the last years and resulted in numerous valuable achievements, but some researches have been conducted using new methods that are not yet sufficiently developed in their proper use. Particularly it concerns the molecular researches of DNA sequences, which sometimes use for wide extrapolation even in the past of modern and fossil groups. Herein the main differences associated with certain taxonomic interpretations and classifications are analyzed, including the ground for different approaches in studies of the nitidulid-group of families.

The brief analysis of the methodological peculiarities of different approaches is given. The recently introduced proposals for the structure of suprageneric taxa are criticized. The situation in the generic taxonomy of the subfamily Meligethinae is considered (reflected in the greatest fullness in the paper by Audisio et al. [2009], as well as other publications by P. Audisio with co-authors). Because of many misidentifications of species of the subgenus *Myothorax* Murray, 1864 of the genus *Carpophilus* Stephens, 1830 published in the applied works devoted to pests of stored products, a key to species of the *dimidiatus*-group of the subgenus *Myothorax*, cosmopolitan and mostly known from the Palearctic and Indo-Malayan regions, from where many species can be expected in the Russian Far East, is elaborated and illustrated with the description of some new species. The present paper also touches upon the issues of the development of feeding and life on male gymnosperm strobiles and angiosperm flowers in the families of the nitidulid-group and especially upon the problem of pollination of plants by ancient representatives of these families. This aspect of interactions between insects and plants is of considerable significance for systematics of these families and their phylogenetic reconstructions.

Structure of the paper

Taking into account the large volume of the paper, we consider it necessary to provide its structure to facilitate orientation in the text:

Historical and methodological comments

Depositories

Classification and supraspecific taxa

The nitidulid-group of families or the superfamily Nitiduloidea Latreille, 1802?

Position of the family Apophisandridae Molino-Olmedo, 2017

Position of the genera *Baltoraea* Kurochkin et Kirejtshuk, 2010, *Cornuturates* Peris, Jelínek et Audisio, 2024, *Cretabaltoraea* Peris, Jelínek et Audisio, 2024, *Diopsiretes* Peris, Jelínek et Audisio, 2024, *Protokateretes* Zhao, Huang and Cai, 2023 and *Vetunitidula* Zhao, Engel, Huang et Cai, 2025 (Apophisandridae)

Subfamily Vetunitidulinae Kirejtshuk, subfam. n. (Apophisandridae)

Notes on *Boreades* Parsons, 1943 (Kateretidae)

Genus *Mesohelotopsis* Kirejtshuk, gen. n. (Helotidae)

On the family Cybocephalidae sensu Cline et al. [2014] and subfamily Prometopiinae sensu [Cline et al., 2014]

Notes on "reclassification" of the subfamily Carpophilinae by Powell et al. [2020]

Notes on "re-examination" of the subfamily Meligethinae by Audisio et al. [2009]

Tribe Plesiogethini Kirejtshuk et Kurochkin, trib. n. (Cybocephalinae)

Draft of a possible phylogenetic hypothesis for the nitidulid-group of families

Review of species of the *dimidiatus*-group of the subgenus *Myothorax* (Nitidulidae, Carpophilinae: *Carpophilus*) mainly from the Palearctic and Indo-Malayan regions

Definition of the *dimidiatus*-group of the subgenus *Myothorax*

Key to males of the *dimidiatus*-group of species of the subgenus *Myothorax* mainly from the Palearctic and Indo-Malayan regions

Carpophilus (*Myothorax*) *assignatus* Kirejtshuk, sp. n.

Carpophilus (*Myothorax*) *brunneus* Chen, Hui et Nuang, 2020

Carpophilus (*Myothorax*) *contegens* (Walker, 1858)

Carpophilus (*Myothorax*) *dimidiatus* (Fabricius, 1792)

Carpophilus (*Myothorax*) *fumatooides* Kirejtshuk, sp. n.

Carpophilus (*Myothorax*) *fumatus* Boheman, 1851

Carpophilus (*Myothorax*) *generosus* Kirejtshuk, sp. n.

Carpophilus (*Myothorax*) *languescens* Kirejtshuk, sp. n.

Carpophilus (*Myothorax*) *mutilatus* Erichson, 1843

Carpophilus (*Myothorax*) *nepos* Murray, 1864

Carpophilus (*Myothorax*) *notatus* Murray, 1864

Carpophilus (*Myothorax*) *pilipennis* Macleay, 1873

Carpophilus (*Myothorax*) *pilosellus* Motschulsky, 1858

Carpophilus (*Myothorax*) *robustus* Murray, 1864, stat. n.

Carpophilus (*Myothorax*) *schioedtei* Murray, 1864

Carpophilus (*Myothorax*) *timorensis* Dobson, 1993

Carpophilus (*Myothorax*) *truncatus* Murray, 1864

Carpophilus (*Myothorax*) *zeaphilus* Dobson, 1969

Species synonymy, notes on species taxonomy and distribution

Synonymy of *Eपुरaea* (*Eपुरaea*) *biguttata* (Thunberg, 1784)

Notes on *Eपुरaea* (*Eपुरaea*) *longipennis* Sjöberg, 1939 and synonymy of *E. (E.) excisicollis* Reitter, 1872

Notes on *Eपुरaea* (*Eपुरaea*) *hilleri* Duftschmid, 1825

Distribution of *Eपुरaea* (*Micruria*) *auripubens* Reitter, 1901

Synonymy of *Carpophilus* (*Ecnomorphus*) *plagiaticollis* (Motschulsky, 1858)

Synonymy of *Carpophilus* (*Myothorax*) *lewisi* Reitter, 1884

Corrections in the list of *Carpophilus* species recorded in China published by Hui and Huang [2019]

Synonymy of *Aethina* (*Aethina*) *aeneipennis* Reitter, 1873

On the designation of the lectotype of *Aethina* (*Circopes*) *suturalis* Reitter, 1884 and notes on *A. (C.) miniata* Hisamatsu, 2014

Synonymy of *Atarphia quadripunctata* Reitter, 1884

Synonymy of *Nitidula carnaria* (Schaller, 1783)

Synonymy of *Physoronia* (*Pocadioides*) *wajdelota* (Wankowicz, 1869)

Synonymy of *Pocadius nobilis* Reitter, 1873

Synonymy of *Meligethes* (*Clypeogethes*) *tenebrosus* Förster, 1849

The subgenus *Glischrochilus* Reitter, 1873 sensu stricto in the Palearctic Region

Synonymy of *Cybocephalus bicinctus* Kirejtshuk, 1988

Probability of pollinophagy and pollination by Apophisandridae and other groups of the nitidulid-group of families

Historical and methodological comments

The phylogenetic reconstructions in the nitidulid-group of families appeared when the attention of the world biological community was focused on the W. Hennig's contribution to the methods of these reconstructions [Mayr, 1974; Platnick, 1979; Hoffmann, Rief, 1988; Crowson, 1991a, etc.]. Taxonomists were actively involved in debating the problems of cladogenetic and anagenetic events, ways of estimation of homoplastic evolutionary processes, significance of numerical phenetics and so on, i.e. it was before the appearance of "hand" cladism and farther uprise of modern cladism and formal methods of computer determination for probable expectations of phylogenetic events, interpreted as true phenomena that do not need proof. It was then revealed that the genital structures and particularly the aedeagus have most strong and very stable differences, which made it possible to regard these three large groups among the considered beetle families and subfamilies (I – Kateretidae with closely related groups,

Ila and Ilb – Nitidulidae with closely related groups) clearly divided into two distinct subgroups: nitiduline-lineage of the Nitidulidae and other families and carpophiline-lineage of Nitidulidae [Kirejtshuk, 1982, 1986a, b, 2000, etc.]. It was done in accordance with the Hennig's methodology [Hennig, 1950].

Later the most attention was given to the multiple structural parallelisms in different nitidulid groups concerning peculiar and partly parallel structural specializations of some organs, regularities and particular differences in the lifestyles of active stages (adults and larvae), to clarify coincidences in genital features with other peculiarities [Kirejtshuk, 1989a, 1991, 1994a, etc.]. It turned out that all these peculiarities are scarcely possible to put (at least at that time) in a matrix and find any software for its adequate processing. Nevertheless, different combining of structural transformations and different trends in evolutionary changes in life strategy in larval and imaginal stages of ontogenetic development allowed to define and formalize some evolutionary regularities (see above lastly cited).

Taxonomic interpretation of the Nitidulidae used by Grouvelle [1913] was regarded as the generally accepted during the end of the 19th and more than three-fourths of 20th century. However, the new studies on morphological structures, peculiarities of bionomics and trophic characteristics of larvae and adults clarified that each of the Grouvelle's subfamilies, Meligethinae Thomson, 1859, Carpophilinae Erichson, 1842 and Nitidulinae, are polyphyletic and should be greatly re-arranged according to current achievements [Kirejtshuk, 2008]. During these studies, independent origins of different anthophagous nitidulid groups, which were put together before, was first proved [Kirejtshuk, 1989a, 1991, 1994a; Kirejtshuk et al., 2023, etc.]. It appears important that the above-mentioned three Grouvelle's subfamilies included specialized anthophagous genera, which, after the conducted researches, were arranged in a new composition in the subfamilies Epuraeinae, Carpophilinae, Cillaeinae Kirejtshuk et Audisio in Kirejtshuk, 1986, in the tribe Mystropini Murray, 1864 (Nitidulinae) sensu Kirejtshuk [2008], according to evident diagnostic differences in male genitalia but also other body structures. The paradox of the situation in the morphological study and determination of antho- or strobilophagous beetles by external structure is that the adults associated with strobiles and flowers often have not pronounced structural adaptations, but the antho- or strobilophagous larvae usually bear pronounced characters in the integument, reduction of processes on various sclerites of the body, and sometimes in the mouth parts. It is strange that Peris et al. [2024a], who declared the considerable archaism (plesiotypy) of the anthophagous nitidulids, did not even mention this fundamental feature.

Other interpretations of the nitidulid-group of families assume a consideration of mosaic of unsorted facts for combining on base separate trace of relationship or for drawing up a matrix, which can, after some computer processing, give a probable order in simulation of phylogenetic process and classification without a long lasting search of ground for each of the considered groups. Such points of view are clearly demonstrated in few recent proposals of "phylogenetic" hypotheses

by some researchers for the nitidulid-group of families produced by computer sorting of characters instead a very thorough analysis of all the facts, taking into account principal patterns from different aspects of consideration with seeking of pattern similarities in each of these aspects [Leschen, 1999; Cline et al., 2014; Powell et al., 2020]. Some enthusiasts of nucleotide sequence studies use the results of comparisons of a few representatives from rather disparate groups for the computer reconstruction or creation of phylogeny thanks to the special software, which could provide, in their opinion, with a probability of reliable reflection of phylogeny going during millions years, the key to understanding the evolutionary processes in all their manifestations.

The chapter by Jelínek et al. [2010] on Nitidulidae in the Handbook of Zoology included many very important and interesting facts but without a certain order in their significance and clear interdependance, even subfamilies and tribes are listed as proposed without a morphological ground and phylogenetic relationships, including in the subsection "Phylogeny and Classification". The first sentence of the latter division is: "Nitidulidae remains one of the most taxonomically intractable families of cucujoids insofar as internal taxonomy is concerned" [Jelínek et al., 2010: 401]. A look at this chapter shows that for its authors this was really undoubtedly the case, although the first author had spent many years very successfully studying various groups of this family and had published several rather important contributions. Unfortunately, despite the significant and successful experience of research of the family, J. Jelínek preferred contrary to the real situation to support the ideas of mosaic and absence of order and knowledge in the structures of adults and the evolution of the family Nitidulidae as a whole. The morphological part of this chapter appears as description of mixture of structural characters, also it was mentioned about two types of nitidulid aedeagus, corresponding ones called here as the TYPE 2a and TYPE 2b (see below). Despite of many correct morphological details in this part Jelínek et al. [2010: 398] wrote a principal mistake that the nitidulid "tegmen" involves both "phallobase + parameres", however nitidulid aedeagus as apparently other families of the nitidulid-subgroup never has trace of articulated paramera, i.e. the dorsal flat unilobed sclerite of aedeagus should be more correctly named as dorsal part of phallobase or tegmen of the ring-like cucujid aedeagus without paramera, and therefore the further examples of aedeagi in this chapter represent mixtures of aedeagi of the TYPE 2a and TYPE 2b. It is important to note that the cucujoid ring-like aedeagus despite of its frequent some similarity in various families needs a very serious revision to understand and explain this similarity in each concrete group. Nevertheless, the authors of this chapter declared that the previous morphological studies including those by A.G. Kirejtshuk as well as their logic interpretation in terms of phylogeny (in W. Hennig's sense) should be considered as "narrative and quantitative analyses" [Jelínek et al., 2010: 403] and they stated that "subfamily relationships were offered by A.G. Kirejtshuk (1982, 1995), and are represented by hand-drawn diagrams based on relatively few characters and his intuition about the distribution of these characters for

a few exemplar taxa within some but not all subfamilies” [Jelínek et al., 2010: 403]. As in other analogous cases, these authors gave no example for their statement neither in the mentioned publication nor later. Indeed, the situation with declarations of these conclusions not supported by facts is completely opposite and many conclusions by these co-authors are lacking real factual ground (not only in the considered chapter but also in some other publications, discussed herein). It should probably be recalled that our division into subfamilies and other supraspecific taxa was made on the basis of studying the male and female genitalia of all available representatives, which was invariably confirmed by all subsequent studies in which the morphological interpretations were made correctly. On the contrary, studying the structure of the genitalia of both sexes helped to solve the problems of the systematic position of some supraspecific taxa for which many structural parallelisms are manifested in the structure of other organs. For example, the taxon *Trimenus* Murray, 1864 was considered as a subgenus of the genus *Tetrisus* Murray, 1864, including in the catalogue of Palaearctic Coleoptera [Jelínek, Audisio, 2007], since only the female of the latter were available for the original description of their species. Further studies of males helped to establish that these supraspecific taxa should not only be considered as separate genera, but should be attributed to different subfamilies (Epurinae vs Nitidulinae) [Kirejtshuk, 2008].

In the chapter under consideration there is no information on the known fossil nitidulids at all. Consideration on probable relations between the published paleontological data and the proposed classification about the structural fundamental differences between the groups of the Recent fauna, are also missing. The preimaginal stages in their chapter are also formally characterised without attention to their features for systematics and phylogeny of nitidulids. However, trophics and mode of life are usually markedly better expressed in differences of larval than imaginal structures. As a result, the chapter of Jelínek et al. [2010] contains many questionable conclusions and ignores of morphological base in the nitidulid system, including genital structures. Thus, this chapter clearly shows the problem with producing of “phylogeny” using a computer software with mathematic estimations of abstract expectations rather than the traditional logic (“hand-drawn”) analysis of available real facts and further their proof. These misinterpretations of Jelínek et al. [2010] gave the readers the impression that before their work no attempt had been made to put the family Nitidulidae in order in terms of morphology, systematics and to provide hypotheses on the phylogeny of the group as a whole. In this considered publication Jelínek et al. [2010] limited themselves to few promising examples of published cladograms for very small taxa [Endrödy-Younga, 1978; Audisio, Jelínek, 1993; Leschen, 1999], which are related to the analysis of very few structural characters of a restricted number of representatives of the Recent fauna having no inner principal differences in structures and having only a very unclear relation to the phylogeny of the family Nitidulidae as a whole. Neither of these publications even covers a single suprageneric taxon of the Recent fauna with large number of representatives (maybe except Leschen

[1999]) and therefore the extrapolations proposed by these authors are hardly appropriate. It seems impossible to compare the mentioned attempts to establish phylogenetic relations of the family with a phylogenetic concept based on examination of about two thousand species a balanced family system [Kirejtshuk, 2008]. The authors of this chapter manifested: “The most comprehensive published cladistics revision of any nitidulid lineage was on Cyllodini (Leschen 1999)” [Jelínek et al., 2010: 404]. It is very easy to estimate the level of this comprehensiveness in the title, content, conclusions and particularly the chosen characters for phylogenetic reconstructions (nitidulid “phylogenetic relationships, convexity, and the origin of phallolophagy” among nitidulids (see below). Examples of this kind fill most of the paragraphs of the chapter under consideration. This feature of it as a whole makes one doubt how familiar the co-authors are with the literature on the subject they were describing. Nevertheless some readers could regard that the researchers who wrote this chapter are enough competent in the knowledge of this subject. These readers took this chapter as a base for their research efforts and therefore applied to use the methods of quick sorting of morphological characters and statistic estimation of probability of an order after comparison of few facts from the nature, instead to apply to other accessible publications of previous researchers, and proposed some taxonomic changes [Cline et al., 2014; Powell et al., 2020, etc.]. These contradict the already known and accessible factual data and above defined principles elaborated after many years of extensive research. This also concerns chaotic presentation of ecological and bionomical features of nitidulid groups in the publication [Jelínek et al., 2010] which indeed are, appositely, in more or less accordance with the systematic position of each groups. These important circumstances forced the preparation of this review of some recent systematic and phylogenetic proposals after appearance of the above-mentioned chapter [Jelínek et al., 2010] and further continuation of systematic and phylogenetic misinterpretations. Thus, this here considered chapter with doubtful and ungrounded statements became essentially a strong call for crucial reform of the system and phylogenetic reconstructions of the family, to which some taxonomists responded without paying any attention to what had been done before publication of this chapter.

To understand the significance of the chapter of Jelínek et al. [2010] and criticism addressed here, it is very important to consider the paper by Leschen [1999], especially strongly recommended in this chapter published by J. Jelínek etc., co-authored by R.A.B. Leschen, as the most “comprehensive” contribution to the future systematics and phylogenetics of the family Nitidulidae. This publication is especially important for understanding the source of the negative attitude towards prior knowledge and the saturation with ideas about its mosaic distribution, which permeate the above analysed chapter [Jelínek et al., 2010]. The title and text of R.A.B. Leschen’s paper express strong claims as being the first comprehensive contribution in this matter. This kind of phylogenetic and systematic challenge became later rather popular among some researchers. The lastly mentioned author wanted to strongly revise the tribe Cyllodini in context of the family phylogeny and,

probably, in accordance with the achievements of modern methodology. It is very important in order to understand all further less complete attempts (recommended as example to follow by Jelínek et al. [2010] and some others up to “re-examination” by Audisio et al. [2009] with refusing of characters for taxonomic discrimination). This paper by R.A.B. Leschen covers a relatively complete number of genera of the tribe Cyllodini Everts, 1898 (with some notes like “unpublished generic catalogue by A.G. Kirejtshuk” or “listed in A.G. Kirejtshuk’s unpublished catalogue”, etc.) and in this respect is somehow unique among the examples of “successful” cladograms given in the chapter under above consideration [Jelínek et al., 2010]. Instead of a comparative morphological analysis for phylogenetic reconstruction, individual and not connected characters were taken as more preferable than organs or blocks of structures united by function, including the structure of the genitalia of both sexes. This author did not use in his paper the majority of suprageneric nitidulid taxa and principal characters for their discrimination, which were elaborated particularly as base of these taxa [Kirejtshuk, 1982, 1986a, b, etc.]. He particularly ignored significance of interdependent characters of the structures of male and female genitalia and others (almost missing even in his list of coded characters for computer creation of “phylogeny”). R.A.B. Leschen prepared a key to the cyllodin genera with some restriction in use because he applied only to one or few members from large genera (as a result, the diagnostic characters of these genera indeed sometimes represent the diagnostic characters rather for the species examined by him for creation of the key, but not for genera as taxa separated from all other generic taxa, i.e. without care on available variability in the genera with many species). Besides, R.A.B. Leschen took some cyllodin generic and only eight not-cyllodin taxa and proceeded a dendrogram. All selected genera (cyllodin and non-cyllodin ones) according to the coded characters allocated for cyllodins were applied for preparation of his matrix. It is precisely in the definition of characters and the correctness of their coding and, to a lesser extent, in the defects of computer software that the main strange peculiarities of the obtained cladograms of this Leschen’s paper consist. Only some of which are shown below. Hardly anyone could doubt that with such a choice the cladogram could show non-“monophyly” of cyllodins, but the relationships of non-cyllodin genera in this cladogram can scarcely coincide with the family system by Kirejtshuk [2008], which is also not surprising given the mentioned specified feature of character selection. It can be supposed that Leschen regarded that it has no sense to conduct a long comparative morphological analysis to find reasons for taxonomic structure of the family. He decided that this aim can be done much faster and better by a computer with the appropriate software, giving an expected equally reliable results.

The considered cladistic analysis is quite impressive to find its shortcomings, showing all irresistible peculiarities of the methodology restricting its application to reconstruct phylogeny as it was understood previously. Some defects can be mentioned after comparison of differences of phylogenetic hypotheses proposed by Kirejtshuk [1982, 1986a, etc.] and Leschen [1999]. In the former works,

the results of a complete analysis of main structural, developmental, ecological, and bionomical regularities are presented, separating them according to their systematic and phylogenetic importance with taking into account the principal significance of genital structures of both sexes in almost all taxa of the considered groups (much more than 2000 species from more than 200 genera). In the latter work there was used only a very small species diversity (separate representatives of 26 genera) for analysis without comparison of most diagnostic suprageneric peculiarities, including principal differences in genital structures. At least R.A.B. Leschen did not show that he knew the peculiar characters in the male and female genitalia of Cyllodini under his revision, which are useful for comparison with those in other nitidulid tribes, or he did not regard these differences as important for phylogeny in proper sense.

R.A.B. Leschen preferred the matrix method considering all characters in the arbitrary list (mosaic) but not in blocks of interdependent structures. This peculiarity determines principal difference between family systems proposed by me and him. It also explains why mosaic viewpoint dominated in the chapter by Jelínek et al. [2010], prepared together with R.A.B. Leschen. In the list of coded characters proposed by R.A.B. Leschen, the followings are prevalent: “anterior margin of labrum” “frontoclypeal suture”, “number of mandibular incisor lobes of right mandible”, “antennal grooves”, “antennal carinae”, ciliation of the sides of the pronotum and elytra, etc., i.e. the characters with very small or unclear phylogenetic significance because the coded conditions of these characters occur in many other coleopterous groups as adaptive homoplasy. He applied to technical methods when creating the cladogram and the “characters were optimised onto weighted trees, unless otherwise specified, using standard ACCTRAN and DELTRAN optimisations” [Leschen, 1999: 852]. Therefore, my and Leschen’s dendrograms could not be similar because in model proposed by me [Kirejtshuk, 1982, 1986a, etc.] the characters with unclear or doubtful phylogenetic meaning were mostly not considered. It has no sense to mention here all mistakes and contradictions included by Leschen [1999] in his revision, particularly in coding of characters and the matrix of them prepared for the cladogram. Some corrections of his proposals were already published before [Kirejtshuk, 2008].

R.A.B. Leschen also got used to mix morphological reasons and consequences with ecological or bionimical ones. In one of his with co-authors paper [Lee et al., 2020] he also published as a conclusion, the hypothesis of a polyphyletic origin of nitidulids in general and their separate groups partly based on the comparison of differences in their diet. It is very significant that for a group, many of whose representatives are somehow related to flowers (imaginal or complete anthophagy), this diet is not even indicated in the text of his paper of 1999, although later R.A.B. Leschen participated in a publication devoted to the origin of anthophagy in nitidulids [Lee et al., 2020]. He noted that the species of the genus *Camptodes* Erichson, 1843 are “phytophagous”: “larvae are known to develop in rotting cacti while adults occur on flowers” [Leschen, 1999: 872]. Adults of introduced species of *Camptodes* introduced to Australia are very common on flowers while the larvae feed

on succulent stems of *Opuntia* cacti (Cactaceae) [Pimienta-Barrios, del Castillo, 2002; Lawrence, Kirejtshuk, 2019, etc.], although larvae were collected in rotten flowers as well (see also below on saprocantharophy). It should be noted that feeding on decaying cacti should rather be called mycetophagy, not phytophagy (as R.A.B. Leschen did).

The Leschen's nomenclature of trophic regimes has some original ideas but seems to be scarcely useful because of many contradictions in different parts of his paper. He did not pay attention on quite regular differences in diets of larvae and adults of many beetles and most holometabolans. With this, he proposed nomenclature based mostly on external circumstances but not on essential ones connected with particular digestion. Particularly his term "polymorphic" diet for two types of feedings, larval mycetophagy and imaginal anthophagy, when wanted coding *Cychramus* Kugelann, 1794 (Cychramini Gistel, 1848), while his intention in coding the similar types of feeding in *Camptodes* (Cylodini), is unclear. Despite of particular consideration of diets of *Cychramus* and *Camptodes* these are coded in this paper, in the matrix, "sap flows" (character 62) without explanation. Besides, this author used for coding mycetophagous forms only as "sap flows" and "mycetophagous" (included their coded associations only with "epigeal fungi", "hypogean fungi", "Phallales", "Gasteromycetes" and "subcortical fungi"). This researcher did not consider and even mention many other mycetophagous nitidulid groups associated with different kinds of organic matter decomposing with the participation of bacteria and fungi. It is difficult to expect that arbitrary coding of ecological and bionomic features could improve or correct the already arbitrary coding of morphological features. These methodological defects are making it scarcely realistic to achieve anything like phylogenetic reconstruction in proper sense at all.

R.A.B. Leschen put in his matrix some characters of genital structures (58–61), but all of them have not principal differences in the types of structures (described by Kirejtshuk [1982] and many times later). The character 58 is rather unclear: "Cross section of gonocoxites. (0) round (Fig. 21); (1) flat (Figs 23–27). The gonocoxites of nitidulids may either be rounded or flat in cross section" [Leschen, 1999: 881]. This researcher even did not show what means "round" cross section in this case because the figure 21 demonstrates gonocoxites of "*Camptodes* sp." of the usual nitidulid shape with membranous window at the ovipositor apex, usually bearing a stylus. If we have a look at this character in the matrix, we found that the "*Cybocephalus*" has the condition "1" according the Leschen's explanation "flat" condition of the gonocoxites. Many females of this genus were dissected by me during last forty years from all zoogeographical regions and all of them had normal ovipositor (i.e., as that in *Camptodes* in the Leschen's figure). In case that this researcher could not explain what he meant when he proposed different conditions of the ovipositor apex, according to the allocation of the 58th character in his matrix it seems that this structure scarcely has an essential phylogenetic significance. As to other genital characters (59–61), their significance for supraspecific taxa and creation of cladograms seems to be rather restricted. Indeed many nitidulid tribes have some

diagnostic specificity, which would be reasonable for the tribal systematics to include it at least in the diagnosis of the tribe. The above notes show that the "phylogenetic" analysis proposed by Leschen [1999] is not such and should be considered a special sorting of random characters. As a result, for example, in the Leschen's cladograms the genus *Epuraea* Erichson, 1843 of the carpophilin-lineage has a position between certainly not closely related genera of the nitidulin-lineage (*Cychramus* (Cychramini), on the one hand, and, on the other, *Thalycra* Erichson, 1843 and *Pocadius* Erichson, 1843 (Nitidulini)). Among other things, it is also the important that, for example, the genital differences and similarities in the nitidulid-group of families are related as with their origin as well as with their functionality. According to usual cladistic processing the independent consideration of interdependable characters produces a rather high weighting and unwanted noise in cladograms. It should be noted that other attempts to change the system after Leschen [1999] turned out to be even further from the data that can be obtained from studying nature. The proposals of Audisio et al. [2009] of change taxonomy of the subfamily Meligethinae have a very peculiar place, as the latter authors demonstrate their preference of branches in cladograms with generic names instead of diagnosis in proper sense or keys. However, in order to introduce such a procedure into research practice, it would be necessary to indicate the names of the used programmes and apparently include their developers as co-authors of the proposed taxa. In cases of using new software it is necessary to change all authorship (to replace the names of colleagues who prepared old software with the creators of the new software) because branches of new cladograms could become different. Unfortunately, P. Audisio et al. did not include in their paper of 2009 either the designations of the software for identification of their taxa, the characters included in their matrices, or the names of the people responsible for developing these software to identify taxa.

R.A.B. Leschen was a pioneer and founder of the fashion to unconventionally change the systematics and create new "phylogenetic" models. The some researchers after his proposal made some more radical innovations apparently considering these new proposals as a further development of the Leschen's concept clearly formulated in his next publication together with Jelínek and other co-authors [Jelínek et al., 2010]. Therefore, this publication aims to reply on these challenges from the traditional viewpoint taking into account that previous achievements of the studies of the groups here considered in the nitidulid-group of families still has a rather great matter.

Cline et al. [2014] made a first attempt to get few DNA sequences of some nitidulids and some beetles of other families and also obtained new data probably useful in future research for understanding of phylogeny of this group, although their conclusions are certainly too premature and need a further critical analysis taking into account different aspects of evolutionary process of this group. The paper by Cline et al. [2014] following the research recommendations by Jelínek et al. [2010] systematics and phylogenetics has no trace of the co-authors' attention to publications of the previous researchers. In the Abstract

of this paper the authors clearly wrote that: “We present a molecular phylogeny of Nitidulidae based on thirty ingroup taxa representing eight of the ten currently recognised subfamilies. Approximately 10K base pairs from seven loci (12S, 16S, 18S, 28S, COI, COII and H3) were used for the phylogenetic reconstruction”. These sentences really present a key to the whole paper and, probably, show the peculiar co-authors scientific opinion. They treated structural and diagnostic features as a kind of tradition that is permissible in cases where apparently no sequencing is given. That is, in their own sequencing and their own use of a computer with some software, they believe that they reach the truth, even without admitting that others may do sequencing of another set of genes, use another computer with other software and get a different result.

A.R. Cline et al. decided that the dendrogram after DNA comparison completely reflects the real phylogeny and can give a reliable ground for many changes in systematic position of nitidulid groups (in the title of their paper: “assessment of subfamilial and tribal classification”). As a result, the nitidulid Cybocephalinae was transferred as a separate family to the “Cerylonid-series”, because they fall in a branch of the mentioned dendrogram together with Endomychidae and Coccinellidae. Cline et al. [2014] also published the morphological diagnoses not only for Cybocephalidae sensu Cline et al., but also for Prometopiinae sensu Cline et al. These diagnoses are very useful to understand what these authors considered in both cases. Almost all diagnostic characters of Cybocephalidae sensu Cline et al. fit with the corresponding nitidulid characters? It is also impossible to distinguish at all the Prometopiinae sensu Cline et al. from the tribe Nitidulini sensu stricto [Kirejtshuk, Mantič, 2015]. Besides, Cline et al. [2014] changed the ranks of some other suprageneric taxa, in particular, they joined the tribes Nitidulini and Cychramini in accordance with branches of their dendrogram, and listed many changes without sufficient explanation and discussion (except their reference to “our results”). However, it can be supposed that the software currently used for creation of a “new” classification of the family is not enough perfect. Another possible thing, which could happen, is occasional appearance of an error in the primary data, which could completely change dendrogram based on small number of data and also conclusions based on it. The research progress of studies on structure of DNA, interdependence and interactions between different molecular blocks during ontogenesis are going so quickly that every year brings new unexpected achievements. The same concerns computer technologies and mathematical statistics.

Therefore, it is impossible to be sure that the results of Cline et al. [2014] will be regarded as adequate to the level of scientific development in a short future, quite the contrary. If we prefer the results of DNA comparison of data under consideration, expressed in terms of probability as absolutely true, and admit that morphological structures bear obviously less reliable evidence for phylogeny, then we are forced to recognise as questionable the position of any modern taxon for which sequencing of DNA has not yet been obtained. With this, all fossil taxa should be recognised incertae sedis with a very small probability to

be reliably determined in future. At the same time, having obtained by traditional methods rather reliable data not on few species (as in the case of molecular research) but on more than 3000 species from the nitidulid-group of families divided in accordance with many features, studied for about 300 years. Thus, if a serious conflict between the system based mainly on structures with many hundreds or thousands of examined species and that based on DNA sequences with few examined species appears, the best way is to estimate a probable reason of this conflict in detail, but not to automatically choose every conclusion after few examination of nucleotides. The extremely paradoxal case of usage of the DNA data for testing of phylogenetic relationship is known for coleopterous suborder Archostemata represented only by about 30 modern species, while some hundred fossil species have already been described. The problem is that only one modern species of *Micromalthus* LeConte, 1878 with abnormal DNA sequences is known in the Recent fauna and it completely ruins all other probable phylogenetic models, and some entomologists still now prefer to believe in the obtained results of comparison of DNA sequences of one modern species rather than a rational argumentation received from the fossil record [Kirejtshuk, 2021].

Having followed the research programme by Jelínek et al. [2010] the co-authors of the paper of Cline et al. [2014] used the supraspecific taxa without proper diagnosis, i.e. unexplained and ungrounded by the authors of both teams. The “Cybocephalidae sensu Cline et al.” and “Prometopiinae sensu Cline et al.” were, for example, used at least in some papers or supplementary files to them [Jelínek, Hájek, 2020; Smith, Szawaryn, 2024; Peris et al., 2024a] and so on. True, one co-author of the paper of Cline et al. [2014] who transferred Cybocephalinae as a separate family to the “cerylonid series”, maybe T.R. Smith, after the critics by Kirejtshuk and Mantič [2015] who suggested that this nitidulid group cannot be regarded in composition of “Coccinelloidea”, published a clear reply where the differences between families Cybocephalidae and Nitidulidae were defined as: “Cybocephalidae possesses five functional abdominal spiracles, and all tarsi have four tarsomeres, while in Nitidulidae, there are six spiracles and five tarsomeres on each leg” [Smith, Szawaryn, 2024: 448]. The use of reductions in traditional systematic research was not considered as a sufficiently significant argument for separation such groups as families (including the opinion of Hennig [1950]). The situation with tarsomeres of cybocephalines will be considered and discussed in a separate paper, which is now in preparation by A.S. Kurochkin and A.G. Kirejtshuk. Therefore the proposed diagnostic characters seems to be very strange for a group which is regarded as a member of another “superfamily”. The variability in the number of abdominal spiracles among cybocephalines needs to be studied. Even if these characters of structural reduction were to be true, can they be used as a sufficient hiatus to separate families at all? The assumption about the age of cybocephalins seems even more unfounded, since it is based solely on indirect assumptions: “Cybocephalids most likely evolved earlier along with their sternorrhynchan prey... Whiteflies (Aleyrodidae) evolved in the Jurassic... and scale insects

(Coccidae) in Early Cretaceous... Molecular dating based on 95 nuclear protein-coding sequences places the origin of the family Cybocephalidae in the Early Cretaceous around 112–128 Ma” [Smith, Szawaryn, 2024: 448–449]. In other words there is no evidence of existence of cybocephalines before the Cenozoic in the mentioned facts, although it can be expected a finding of evidence of their existence in the Mesozoic. In addition to the above mentioned support to a probability of the pre-Cenozoic origin of cybocephalins, serious argument seems to be a wide current range of the genus *Cybocephalus* Erichson, 1844 spreading through almost all zoogeographic regions, excepting the Antarctic one [Smith, 2021].

It seems that a very effective way of checking all innovations and concepts can be the methodology of multiple parallelisms, which I always used. I will discuss it below. This principle harmoniously complements the concept of integrated taxonomy and phylogenomics, providing the latter with an objective basis and a method of verification. It is difficult to imagine another way of reliable verification at present and in the past (as in Darwin’s time) [Kirejtshuk, 2021], which means that it is necessary to find a possibility to solve many problems of phylogenetic interrelations due to reconstructions based on coincidence of patterns of changes (series of interconnected facts) traced in different aspects of evolutionary processes. This principle (method) originates in the ideas of J. Agassiz and E. Haeckel, defined by the former of the two as the principle of triple parallelism, which was successfully developed by Severtsov [1912, 1914, etc.] and his followers. This principle can be extrapolated to the multiple (multidimensional) parallelism (including molecular, geographic (space) and ecological aspects). The range of applicability of this method can be essentially expanded. In accordance with the integrity of all biological systems, other aspects of their evolution can be added to the morphology, embryology, and paleontology initially included in this method. The reconstruction of relationships can be considered as “proven” (meaning most probable under the current knowledge) in case of finding in them independent congruence between morphological analysis, results of comparison of nucleotide sequences and in the fossil record. Each aspect of the phylogenetic process has its own specific limitations for interpretation and extrapolation. However, if only some concrete facts are used for calibration of any tree based on facts and regularities of another aspect (series of facts), there is a considerable risk to make a very probably mistakable result. It is precise that comparison of independent analyses of different aspects of phylogeny that, when they become in coincidence, can be regarded as some supported evidence the plausibility of phylogenetic constructions (main feature of this principle). There are many mistakes connected with usage of the method of calibrations and statistic establishment of phylogenetic branches [Toussaint et al., 2017; Cai et al., 2022, etc.] and, therefore, significance of calibration should be regarded as more or less restricted. Unfortunately, the principle of multiple (multidimensional) parallelism cannot be used to the full extent of its power, but it is necessary to choose the paleontological method of phylogenetic reconstruction as an important source of information for groups that are well-documented through

very diverse fossils, and as for which only few of its relict remnants reached the modern epoch. It can even be argued that this principle cannot be completely implemented, because there is no objective chances for a complete reconstruction of the paleontological record. However, on the other hand, the more complete the filling of all possible aspects of the consideration of phylogenesis with facts and the fewer contradictions there are between them (i.e. all conflicts between facts of different aspects that arose in the process of studies will be resolved), the more substantiated the hypothesis of genuine phylogenesis can be developed (“proven”). Thus, despite all the difficulties in using this methodology, it seems to be the only available way to get a chance to reach a more or less correct interpretation of phylogenetic relations. It seems that maximum attention should be paid to each of the available aspects during the construction of phylogenetic hypothesis. Preference for one of the aspects inevitably leads to errors in interpretation, even if calibrations are used. If the separate results based on different aspects in consideration coincide to each other, the phylogenetic reconstruction can be accepted as probable. When some results demonstrate discrepancies, it is necessary to analyze contradictions seeking ways to solve them.

By now, quite a lot of data on DNA sequencing of various groups of the considered families has been accumulated, however, the contradictions that have arisen between the hypothetical molecular “phylogenies” published in recent decades with phylogenetic data from other fields of knowledge are still only increasing. They can be resolved using the method of multiple parallelisms. Until this is done, it is better to limit comparative and evolutionary molecular studies of DNA to careful preliminary hypotheses on “molecular systematics” and “molecular phylogenetics”, as was done in correct molecular studies on the genus *Carpophilus* and other nitidulids [Brown, 2009; Brown et al., 2012, etc.], *Xenostromylus variegatus* Fairmaire, 1891 [Zhan et al., 2021] and on others without radical changes in the system and supraspecific taxonomy making other phylogenetic data phylogenetic supposedly useless and unnecessary. The latter papers on data with DNA sequences are very different not only in their conclusions, but also in their content from those proposed in the publications by Audisio with co-authors [Audisio et al., 1999, 2009; Trizzino et al., 2009, etc.], Cline et al. [2014], Lee et al. [2020], Powell et al. [2020], here analysed in detail and many others, depriving other phylogenetic data of the possibility of explaining and understanding the history of the biota by few data on random DNA sequences. The results of “molecular phylogenetics” can be recognised as really phylogenetical when they obtain some parallel concordances with other aspects of evolutionary process (but not only with correction by random calibrations).

With that the data obtained by Cline et al. [2014] should deserve a considerable attention of other researchers to estimate their due importance. It can be expected that a future comparison of this dendrogram with other computer “trees” will give more reasonable results for some concepts when new data will be filled by data from other genes, new samples of DNA from other genera, and when available software will be better

elaborated our knowledge on interactions between genes in an organism and in many successive generations will become clearer. Nevertheless, one preliminary hypothesis can be cautiously proposed based also on the published dendrogram and taking into consideration other above-mentioned aspects. According to the traditional viewpoint the nitidulid dorsal part of phallobase (“tegmen”) without deep median excision represents the remains of enlarged phallobase, but the segmented paramera irrevocably disappeared in common ancestor before divergences of the helotids, monotomids and nitidulids and apparently never appeared again. It possible to trace gradual reduction of the paramera in the modern members of the Boganiidae Sen Gupta et Crowson, 1966 [Sen Gupta, Crowson, 1966; Crowson, 1990; Kirejtshuk, 2000; Escalona et al., 2015, etc.]. The probable divergence of the family group into the families with articulated paramera (kateretid-subgroup: Apophisandridae Molino-Olmedo, 2017, Kateretidae, Smicripidae Horn, 1880, ? Parandrexidae Kirejtshuk, 1994 (this family at present is only confirmed by structure of ovipositor similar to that in apophisandrids and kateretids, but not the aedeagus), and probably Boganiidae) and the families with the dorsal part of phallobase (“tegmen”), i.e. without traces of paramera (nitidulid-subgroup: Helotidae Chapuis, 1876, Monotomidae Laporte, 1840, and Nitidulidae) is partly confirmed by the molecular data [Cline et al., 2014; Cai et al., 2022, etc.]. The next important block of very useful data suggests that the carpophiline-lineage is apparently markedly younger not only than a common ancestor of the helotid-monotomid-nitidulid block, but even probably younger than the diversification of the most of modern suprageneric groups of the nitiduline-lineage. Another valuable fact was found by Lee et al. [2020] who made the DNA sequencing for the genus *Calonecrus* Thomson, 1857, which could be not an archaic member of this nitidulid lineage, but rather a derivative one. One of the co-authors of this paper is R.A.B. Leschen who, following the peculiar research program already discussed above and published before 2020 [Leschen, 1999; Jelínek et al., 2010, etc.], kept the peculiar perception of the own targets and research results without relying on or comparing them with the results of other researchers. Although sometimes Lee et al. [2020] refer to previous publications and include them in the list of references, but do not always even check their content. For example, the authors write in their paper [Lee et al., 2020: 919] that “recently (Kirejtshuk, 2008) considered calonecrines, as well as Maynipeplinae, as separate families from Nitidulidae” although in this paper by Kirejtshuk only the possibility of isolating these groups from the nitidulids is considered (“these small groups are so distinct that they could be excluded from this family as two taxa with the family rank” [Kirejtshuk, 2008: 109]). On the base of few abstract and frequently not quite correct statements (mostly not original) Lee et al. [2020] published the divisions “Evolution of food preference”, “Evolution of diet”, “Paraphyly of Nitidulinae” and other subjects with many extraordinary but not grounded conclusions which scarcely have chances to be grounded by facts and processes in the nature and mostly followed from the conviction that the comparative conclusions obtained by Cline and his co-authors [2014] with the assistance

of computer software already available now are, in the opinion of these co-authors, absolutely reliable and true as well as these co-authors, according to their viewpoint, were used the best and most reliable DNA sequences, while everything else hardly deserves serious attention.

However, it is reasonable to assume that it will be able to make correct phylogenetic judgments based on DNA comparison dendrograms only when a set of markers will be selected in a truly intelligent way (rather than largely randomly, as is often done now). The cases discussed below show that molecular studies of nitidulids are currently far from providing a sound selection of markers (although it is possible that till now a true sound selection can only be made experimentally). It can be expected that further development of molecular research and accumulation of more reliable data will provide this selection less occasional. Each aspect of consideration of the phylogenetic process (morphological, molecular, palaeontological, ontogenetic, and others) has its own specific limitations for interpretation and extrapolation, and therefore each separate aspect scarcely can reflect phylogeny in sufficient completeness. Specific peculiarity of molecular aspect apparently mostly consists in its possibility to track sequence of divergences in the considered group. However despite difficulties, the method of multiple parallelism was used to elaborate and test the system, and further to propose the phylogenetic scenario for the nitidulid-group of families and probably will be efficient in future on systematic and phylogenetic research.

Depositories

The used material is stored in the following depositories:

AMNY – American Museum of Natural History (New York, USA);

AMS – Australian Museum (Sydney, Australia);

ANIC – Australian National Insect Collection, CSIRO (Canberra, Australia);

CMN – Canadian Museum of Nature (Ottawa, Canada);

FMNH – Field Museum of Natural History (Chicago, USA);

MCNG – Museo Civico di Storia Naturale Giacomo Doria (Genova, Italy);

MNHN – Muséum National d'Histoire Naturelle (Paris, France);

MRAC – Musée royal de l'Afrique centrale (Tervuren, Belgium);

NHML – Natural History Museum (London, UK);

NMB – Naturhistorisches Museum (Basel, Switzerland);

NME – Naturkundemuseum (Erfurt, Germany);

NMP – Národní Museum v Praze (Prague, Czech Republic);

NRS – Naturhistoriska Riksmuseet (Stockholm, Sweden);

RNHL – Rijksmuseum van Natuurlijke Historia (Leiden, Netherlands);

QMB – Queensland Museum (Brisbane, Australia);

SAM – South Australian Museum (Adelaide, Australia);

SMNS – Staatliches Museum für Naturkunde (Stuttgart, Germany);

TMB – Magyar Természettudományi Múzeum (Budapest, Hungary);

ZIN – Zoological Institute of the Russian Academy of Sciences (St Petersburg, Russia);

ZMB – Museum für Naturkunde an der Humboldt-Universität zu Berlin (Berlin, Germany);

ZMKU – Zoological Museum of Kiel University (Germany);

ZMUC – Zoologisk Museum (Copenhagen, Denmark);

ZML – Zoologiska Museet, Lunds Universitet (Lund, Sweden);

ZMMU – Zoological Museum of Moscow State University (Moscow, Russia);

ZSI – Zoological Survey of India (Calcutta);

ZSM – Zoologische Staatssammlung (Munich, Germany).

Classification and supraspecific taxa

The nitidulid-group of families or the superfamily Nitiduloidea Latreille, 1802?

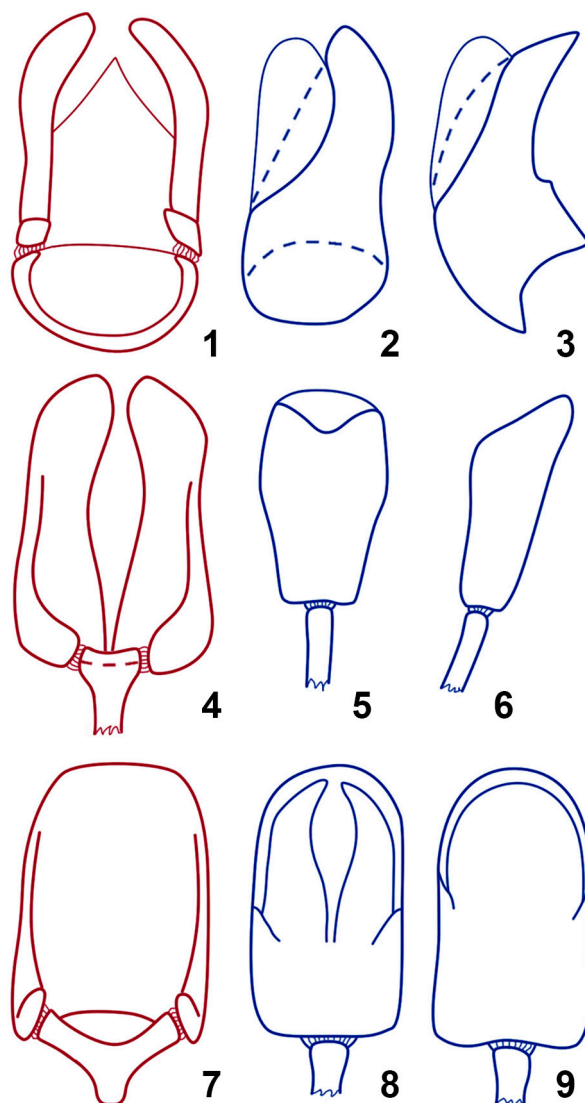
The genera currently treated as a separate family Kateretidae were traditionally long interpreted as a nitidulid subfamily (although Kirby [1837] used the incorrect taxon spelling as family “Catheretidae” (stem Kater-) and Lacordaire [1854] proposed the junior synonym “Brachyptérides”, further used by Murray [1864] and few others as Brachypteridae). Kirejtshuk [1986a] showed that these genera have the genitalia of both sexes with structure completely different from those in other nitidulids, particularly their aedeagus has somewhat expressed asymmetry (Figs 1–3) and consists of (1) phallobase with dorsally articulated paramera and ventral part of phallobase (or fork-sclerite), and also (2) penis trunk looking like a sclerotised tube (TYPE 1), while the true nitidulid aedeagus (Figs 1–9) consists of the united dorsal part of phallobase (“tegmen”) with the fork-sclerite and usually dorsoventally compressed penis trunk. The nitidulids are split into two large groups: (1) the nitiduline-lineage (Figs 7–9) with the plate-like dorsal part of phallobase (“tegmen”) not incised or somewhat incised apically and more or less sclerotised penis trunk (TYPE 2a), and also (2) the carpophiline-lineage (Figs 4–6) with the dorsal part of phallobase (“tegmen”) with a deep or frequently complete median incision (only somewhat similar to the dorsal part of phallobase with paramera in the kateretids) and more or less membranous penis trunk (TYPE 2b). In this publication [Kirejtshuk, 1986a] it was also indicated that the Kateretidae could be related more closely to Boganiidae than to the nitidulid subfamilies, as it is impossible to find a reasonable argumentation of structural transition between kateretid and nitidulid aedeagi, but some similarity of the kateretid aedeagus and that of the nitidulid carpophiline-lineage can be explained as a subsequence of similar functionality of aedeagal sclerites easier than by closer relationship. In contrast to that in the bilobed aedeagus of the nitiduline-lineage, the penis trunk in the kateretid-subgroup of families and nitidulid carpophiline-lineage exduces out of abdomen with passing between the

paramera in the first case and between separate lateral lobes of phallobase (“tegmen”) in the second one (Figs 10, 11). The nitiduline-lineage aedeagus opens by moving apart the apical parts of the two plates (dorsal part of phallobase and subflattened penis trunk), which allows the internal sac of the penis to evert into the female’s ovipositor (Figs 12, 13).

There are some interpretations on the structure of the coleopterous aedeagus and its evolutionary transformations, although two viewpoints on origin of the cucujoid ring-like aedeagus are more or less widely recognised. Crowson [1955, 1981] and later Lawrence et al. [2011] wrote that phallobase (“basal piece”) initially was only beneath the penis trunk and the dorsal tegmen with articulated paramera appeared subsequently. With this the widely spread opinion is that the tegmen consists of the phallobase with paramera or without them, and also that the paramera can disappear and appear again. This opinion is wrong at least for the families of the nitidulid-group because all families of the kateretid-subgroup almost always (except many boganiids) have paramera laterally articulated with a weakly sclerotised median tegminal lobe, while the families of the nitidulid-subgroup never have articulated paramera or lateral lobes similar to them at sides of median tegminal lobe [Kirejtshuk, 1986a], because “lateral lobes” in the latter subgroup looking like the deeply medially incised median tegminal lobe. Structure of modern boganiid aedeagus shows a trend to reduction, but scarcely restoration, while both modern and fossil members of other families of the kateretid-subgroup with known aedeagus apparently maintain an archaic tegmen or phallobase with articulated paramera. Crowson [1967] synonymised “parameron” and tegminal “lateral lobe” and this interpretation became rather popular (see above on opinion of Jelínek et al. [2010] and including in many publications devoted to the nitidulid-group of families (already here cited Audisio et al. [2008, 2014a, etc.], Peris et al. [2024a] and so on)). Even more, Crowson [1967: 16] published that the “inverted” type of the “histeroid” aedeagus with the dorsal plate without articulated appendages but with deep a median excision and processes on either side of it called him “parameres” (figure 11) that is somewhat similar to the aedeagus of the carpophiline-lineage and dorsal view of the “cucujoid” aedeagus with articulated appendages (“parameres”) [Crowson, 1967: 17, fig. 13a] that, on the other hand, is rather different from that in the kateretid-subgroup of families. Both the mentioned illustrations could be an additional reason of the further confusion in homologisation of the true paramera and the lateral lobes of dorsal part of phallobase (tegmen). There is a rather serious discrepancy consisting in the fact that all representatives on the nitidulid-group of families with the studied structure of the male genitalia, in contrast to Crowson’s indication of the probable inversion of the histeroid aedeagus, have a non-inverted aedeagus, and therefore this morphological contradiction requires a special comparative studies of genitalia in different coleopterous groups. Another hypothesis on phallobase as derivatives of abdominal segment X presents in Crowson [1981] who wrote on sternal origin of the “tegminal apodeme” (= “tegminal strut” by Sharp and Muir [1912] = “fork-sclerite” by Kirejtshuk [1998a]) which can be

the ventral part of the “phallobase” and homologised with derivatives of the sternite of the abdominal segment X, while the dorsal part of the phallobase (“tegmen”) – tergite of the abdominal segment X. However, it is difficult to be sure that this scheme of structure and transformation for the ring-like aedeagus of the nitidulid-group of families can be extrapolated on most other cucujoids or even on other coleopterous groups. As a result, there are two distinct groups of families which could be preliminarily recognised as related, although this relation remains unproved.

Despite this, Audisio [1993] proposed to unite these families back into a separate superfamily Nitiduloidea including the families Cybocephalidae, Kateretidae, Nitidulidae, and Smicripidae (mentioned in the original superfamily “diagnosis”), with incomplete and vague comparison of it with other cucujoid families (even with Boganiidae and Rhizophagidae). This author did not explain a syndrome of this taxon (complex of synapomorphies) making it possible to distinguish this taxon members of this superfamily from other cucujoid groups did not show how his proposal can correspond with rules of creation of hierarchic system at all. R.A. Crowson together with the author of this paper were going to find any argumentation for this “superfamily” in the structures of larvae and adults, but they could not do it. Till now the situation with this taxon remains almost without principal changes. Later Kirejtshuk [2000] again demonstrated that the family Kateretidae more similar to Boganiidae and Smicripidae by their genitalia, and Nitidulidae – to Helotidae and Monotomidae. As a result, the phyletic roots of these two groups of families even still now cannot be regarded as well definite. Nevertheless, parallelisms in structural transformations of pollinophagous groups closely related to Kateretidae and those closely related to Nitidulidae can be also considered as those appeared in consequence of homoplasy originated in more related groups [Kirejtshuk, 2021]. Both these groups of families are frequently united into one group of related families (superfamily Nitiduloidea), although such a combination can be recognised still as preliminary because of the above reasons and also necessity of elaboration of a true diagnostic “syndrome” to discriminate them from other cucujoids sensu lato. The list of some characters of separate groups in the paper of Cai et al. [2022] is called by these authors as the “Diagnosis” for the Nitiduloidea but it can scarcely be recognised and used as such. With this, the latter co-authors put in the superfamily Nitiduloidea also the families Protocucujidae Crowson, 1954 and Sphindidae Jacquelin du Val, 1860, but they treated as the separate superfamily Eroteyoidea with two families Boganiidae and Erotylidae Latreille, 1802, while the first seems to be closely related to nitidulid-group of families rather than any other cucujoids sensu lato. Both subgroups of families here united should be regarded as preliminary, because, despite many similarities between these subgroups, their common origin cannot yet be considered as proven and requires further careful research into many other groups of cucujoid groups (not only Protocucujidae and Sphindidae). Other models of phylogenetic relationships in the superfamily Cucujoidea sensu lato are mostly being developed through extensive comparison and analysis of DNA sequences [Robertson et al., 2015; McKenna et al., 2019; Liu et al., 2023, etc.].



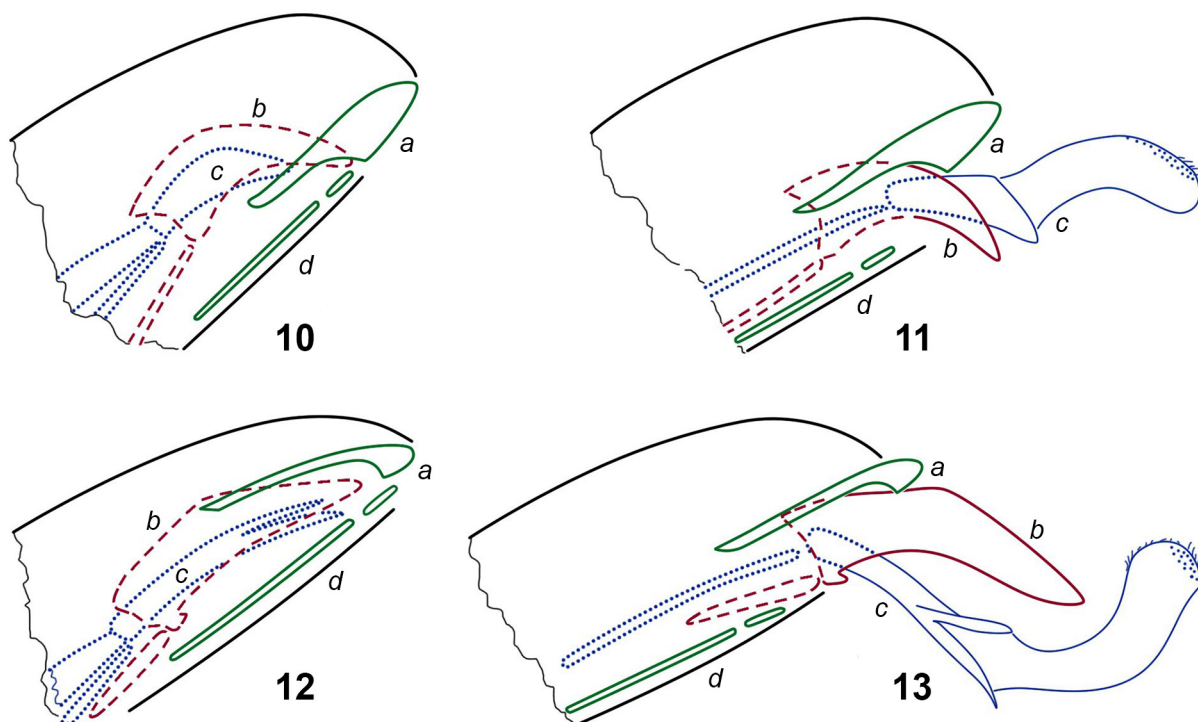
Figs 1–9. Types of aedeagal structure in nitidulid-group of families (after Kirejtshuk [1986a], with changes).

1–3 – TYPE 1: Kateretidae (and also Apophisandridae и Smicripidae); 4–6 – TYPE 2b: Nitidulidae, carpophilinae-lineage: Calonecrinae, Epuraeinae, Carpophilinae, Amphicrossinae; 7–9 – TYPE 2a: Nitidulidae, nitidulinae-lineage: Cillaeinae, Cryptarchinae, Cybocephalinae, Meligethinae, Maynipeplinae, Nitidulinae (and also Helotidae, Monotomidae). 1 – dorsal part of phallobase and paramera, ventral view; 2, 5, 8–9 – penis trunk, dorsal view; 3, 6 – same, lateral view; 4, 7 – dorsal part of phallobase (“tegmen”), ventral view.

Рис. 1–9. Типы строения эдеагуса в группе семейств, близких к Nitidulidae (по [Kirejtshuk, 1986a], с изменениями).

1–3 – ТИП 1: Kateretidae (а также Apophisandridae и Smicripidae); 4–6 – ТИП 2b: Nitidulidae, карпофилиновая линия – Calonecrinae, Epuraeinae, Carpophilinae, Amphicrossinae; 7–9 – ТИП 2a: Nitidulidae, нитидулиновая линия – Cillaeinae, Cryptarchinae, Cybocephalinae, Meligethinae, Maynipeplinae, Nitidulinae (а также Helotidae, Monotomidae). 1 – дорсальная часть фаллобазы и параметры, снизу; 2, 5, 8–9 – ствол пениса, сверху; 3, 6 – то же, сбоку; 4, 7 – дорсальная часть фаллобазы («тегмен»), снизу.

So far, they have little correspondence in position of families under present consideration with the concepts developed here and require a further thorough study of the contradictions of both considered approaches and the search for ways to resolve them. At the same time, the models proposed to date based on molecular differences also do



Figs 10–13. Sagittal section of abdominal apex: mechanism of work of aedeagus in the nitidulid-group of families (after Kirejtshuk [1986a], with changes).

10–11 – TYPE 2: Nitidulidae, carpophiline-lineage – Amphicrossinae, Calonecrinae, Carpophilinae, Epuraeinae (similar mechanism in the kateretid-subgroup of families: Apophisandridae, Kateretidae and Smicripidae); 12–13 – Nitidulidae, nitiduline-lineage – Cillaeinae, Cryptarchinae, Cybocephalinae, Meligethinae, Maynipeplinae and Nitidulinae (and also other families of the nitidulid-subgroup close to Nitidulidae: Helotidae и Monotomidae). 10, 12 – aedeagus retracted into the abdomen; 11, 13 – protruding aedeagus with inner sac of penis turned out. Designations: *a* – male anal sclerite (green); *b* – dorsal part of phallobase (“tegmen”) (red); *c* – penis trunk and its inner sac (blue); *d* – ventral plate and spiculum gastrale (green).

Рис. 10–13. Сагитальный разрез вершины брюшка самца: механизм работы эдеагуса в группе семейств, близких к Nitidulidae (по [Kirejtshuk, 1986a], с изменениями).

10–11 – ТИП 2а: Nitidulidae, карпофилиновая линия – Amphicrossinae, Calonecrinae, Carpophilinae, Epuraeinae (а также сходный механизм в подгруппе семейств, близких к Kateretidae: Apophisandridae, Kateretidae и Smicripidae); 12–13 – Nitidulidae, нитидулиновая линия – Cillaeinae, Cryptarchinae, Cybocephalinae, Meligethinae, Maynipeplinae и Nitidulinae (а также другие семейства подгруппы, близкие к семейству Nitidulidae: Helotidae и Monotomidae). 10, 12 – втянутый в брюшко эдеагус; 11, 13 – выдвинутый наружу эдеагус с вывернутым внутренним мешком пениса. Обозначения: *a* – анальный склерит самца (зеленый); *b* – дорсальная часть фаллобазы («тегмен») (красный); *c* – ствол пениса и внутренний мешок пениса (синий); *d* – вентральная пластинка и гастральная спикула (зеленый).

not appear to be entirely consistent with each other and should therefore be considered preliminary until they are reliably tested, including by comparison with other aspects of evolutionary process in accordance with the principle of multiple parallelisms. Another important thing is to find a reasonable place for this “superfamily” (Nitiduloidea) in the infraorder Cucujiformia obtained balanced relations with other superfamilies included in this infraorder (Clerioidea, Cucujoidea *sensu stricto*, Tenebrionidea etc.) by a logic way thanks to searching of enough actual diagnoses expressed in natural characters for discrimination of taxa, but not by any sort of splitting of branches of dendrograms with nodes of probabilistic branchings obtained thank to computer software.

Position of the family Apophisandridae Molino-Olmedo, 2017

During about ten years it was not clear what a position should have some genera from the Cretaceous Burmese amber with some similarity with both kateretids and nitidulids. When Poinar and Brown [2018] decided

to describe one of these genera they applied to me for an advice. I informed them that it is more likely a kateretid because a parameron was observable from under abdominal apex of the specimen examined (this is mentioned in the Acknowledgement of the Poinar and Brown’s paper). After this description with the attribution of this fossil to Kateretidae many researchers described some related genera also as kateretids [Peris, Jelínek, 2019, 2020; Tihelka et al., 2021; Zhao et al., 2023a, b, etc.]. However, Molino-Olmedo [2017] decided to put one of the considered related genera in the cerambycids and proposed for it a suprageneric name of tribal rank (Apophisandrini) of the subfamily Parandrinae Blanchard, 1845. The original description is not perfect and with the only picture of not good quality. Vitali [2019], specialist on cerambycids, established some reasons to bring this tribe together with Parandrexidae. Recently the ovipositors of the Parandrexidae (*Cretoparacucujus* Cai, Escalona, Li, Huang et Engel, 2018 [Cai et al., 2018]) and genus closely related to *Apophisandra* Molino-Olmedo, 2017 [Molino-Olmedo, 2017] (*Protonitidula* Zhao, Huang and Cai, 2022 [Zhao et al., 2022]) and the “puzzle” of characters in the

genital structures was at last collected and made it possible to erect a separate family Apophisandridae as distinct from both Kateretidae and Nitidulidae but with more similarities shared with the former than the latter [Kirejtshuk et al., 2023].

Recently, Peris et al. [2024a] published one more time a support of a strong similarity of the apophisandrid and kateretid aedeagi, but, unfortunately, with some serious misinterpretations and errors in the text of this paper. It concerns a reconstruction of the dorsoventrally posthumously compressed phallobase with clearly articulated paramera and tube-shaped penis trunk with strongly oblique basal orifice [Peris et al., 2024a: figs 2E, F]. With that these co-authors did not discuss this matter in the main text of their paper, but they wrote in the supplementary file ("Table 2") that the "parameres with articulated mobile and rather weak distal portion; median lobe of the aedeagus much wider proximad". This sentence explains the certainly wrong interpretation of these authors. They regarded that the paramera like those of kateretids (= "mobile and rather weak distal portion") are homologous to lateral lobes of the nitidulid phallobase ("tegmen") because of their some similarities. Perhaps, Peris et al. [2024a] named the dorsal part of phallobase by "parameres". The penis trunk in this paper is called as "median lobe" (the term from the nomenclature by Sharp and Muir [1912]). It is a mixture of incorrect usage of morphological terms making impossible to fulfil any correct comparison by definition but gives a key to understand the entire paper under consideration and its inadequate conclusions. The title of this "Table 2" declares: "Synoptic table of the main diagnostic morphological characters and character states for purported members of the superfamily Nitiduloidea. Refer to Audisio (1993), Audisio et al. (2015) and to Figs 1–24 in Audisio et al. (2017) for complete drawings of anatomical parts and/or morphological explanations". By the way, these authors selected strange characters to distinguish the Nitiduloidea groups (without mention of important characters of thorax, abdomen, and legs), which make them difficult to identify considered taxa, and also they included "Cybocephalidae/Cybocephalinae" in this superfamily, which one of the co-authors (P. Audisio) had previously already transferred to the "cerylonid series" [Cline et al., 2014]. It can be thought that the diagnostic characters were taken by the co-authors mostly from meligethines and some other modern Palaearctic groups known to them. As it was mentioned by Kirejtshuk and Mantič [2015], this group (Cybocephalinae) has not enough serious structural characters to approach it not only to so called the superfamily Coccinelloidea, but also to regard it separately from the family Nitidulidae. Though it would be quite reasonable to take the diagnostic characters from the detailed comparison in the paper Kirejtshuk et al. [2023] with many new characters for discrimination of all families of the nitidulid-group in connection of the proposal of the family Apophisandridae. In this case, it would be possible to discuss every of the characters but not as Peris et al. [2024a] did, discussing the characters that they did not look at the original paper, and the characters that belong to other groups. With this, Kirejtshuk et al. [2023: 20] wrote: "The strict indication on the distinctness of both groups

represents the genitalia of their both sexes: paramera apparently articulated with phallobase in apophisandrids ([26]: Figure 4A) and tegmen in nitidulids; and almost evenly membranous ovipositor without clearly separated inner and outer lobes of gonocoxites in apophisandrids ([35]: Figure 1), while the nitidulid ovipositor usually has the traced sclerotized elements and separated inner and outer lobes of the gonocoxites". So one of the main discoveries of Peris et al. [2024a] was described in detail in the original paper with proposal of the family state (Apophisandridae) and they did not notice it but wrote inappropriate criticism of the latter. These two families (Apophisandridae and Nitidulidae) in most cases are rather different in the thoracic sclerites, structure of legs and abdomen from those in meligethines, but after examination of about 2500 nitidulid species and about 100 apophisandrid ones, it was found that in some cases, exceptions were present that did not allow these structural features to definitely include in the diagnosis (as, apparently, in the case of *Baltoraea* Kurochkin et Kirejtshuk, 2010).

Nevertheless, the principal differences in the genitalia in both sexes of the considered families demonstrate the clearer evidence of a rather ancient divergence, which could happened during the Jurassic. The family Apophisandridae in terms of the level of variability of many structures, is somewhat similar to Nitidulidae, which is, however, known to have much greater number of members and wider variability in many structures in representatives of both recent and fossil faunas. Thus, the present paper is a second attempt to show that apparent evidence often turns out to be false and needs to be verified in accordance with the principle of multiple parallelisms to find independent true evidence. Thus, it became clear, why Peris et al. [2024a: 598], summarizing their conclusions, declared: "We justify that this group of fossils [Apophisandridae] species should be better placed within an extinct basal subfamily of Nitidulidae, with some plesiomorphic character states shared either with Kateretidae and with some basal Nitidulidae lineages (Epuraeinae, Calonecrinae and Mayniplinae)" (note that the indicated groups have three types of aedeagal structure and are probably not closely related). This circumstance was the reason why I spent about 10 years collecting material for more reliable judgments. Only when it became clear that enthusiasts of quick descriptions and conclusions had described several species of this group in three families (kateretids and nitidulids from the nitidulid-group and also cerambycids from the superfamily Chrysomeloidea, and also in manuscripts there were ideas to classify them even as predators) had to look for ways to counteract development of this misunderstanding. It should be noticed that most enthusiasts of hasty publications followed the advice [Poinar, Brown, 2018] to classify apophisandrids as members of the Kateretidae (it was close to a correct attributions) with doubtful attributing pollination to them, but when there was a desire of others to classify them as other families, it was necessary to write down the considerations that had developed during many years [Kirejtshuk et al., 2023].

It is important to mention once again that possible transformation of the cucujoid ring-type aedeagus of the TYPE 1 in the kateretid-subgroup of families into TYPE 2

in the nitidulid-subgroup, is apparently going only in one direction, as it can be traced among modern boganiids [Sen Gupta, Crowson, 1966; Crowson, 1990; Kirejtshuk, 2000; Escalona et al., 2015, etc.] till the enlarged dorsal part of phallobase (“tegmen”) with very small remnants of paramera before complete reduction of the latter and no case of an appearance of paramera after their previous complete disappearing is known. Thus, how is it possible to explain the presence of the aedeagus of the TYPE 1 only in the kateretid-subgroup of families and the aedeagus of the TYPE 2 only in the nitidulid-subgroup of families, except phylogenetic divergence of these subgroups? It is necessary to take into account also that the structure of ovipositor of Kateretidae and Apophisandridae is different from that in Nitidulidae, which was included in “Table 2” in the paper of Peris et al. [2024a]. Probably, in this case it would be reasonable to join with Nitidulidae not only Apophisandridae, also Kateretidae with the same aedeagus, and so on. But Peris et al. [2024a] ignored these principal important aedeagal and also ovipositor similarities.

Suchwide, the kateretids as well as apophisandrids have clearly primary paramera and each parameron articulated to lateral sclerotised part of the phallobase, while its median part extended far from places of parameran articulations (Figs 1–3). The nitidulid phallobasa = “tegmen” has no trace of primary articulated paramera, its median plate is frequently excised at apex and this excision can reach phallobasal (“tegminal”) base forming so called “tegminal” = phallobasal lateral lobes (not lateral lobes of the aedeagus in the sense of Sharp and Muir [1912]) in the carpophiline lineage (Figs 4–9), but sometimes the phallobasa = “tegminal” sides bear small processes. Nevertheless, the nitidulid lateral lobes and lateral processes of phallobase are certainly secondary (not homologous) in relation to primary paramera and their similarity with true paramera show no transitions in structures and it is impossible to interpret them as homology. The origin of their structural similarity is conditioned with similar functionality (Figs 10–13). According to the last studies the apophisandrid aedeagus completely fits the kateretid one (more correct reconstruction of this aedeagus and that of another apophisandrid genus will be published soon (Kirejtshuk et al., in prep.), although a preliminarily reconstruction of the later is accessible in the slide 15 of the presentation [Kirejtshuk, 2024: https://www.zin.ru/animalia/coleoptera/rus/KIR_2024_PPT.HTM]. This principal aspect of considerations is one of the main ones for systematics and phylogenetics of the nitidulid-group of families and the papers of devoted to this matter [Kirejtshuk, 1982, 1986a, b; Kirejtshuk et al., 2023, etc.] are frequently cited but without enough attention to the contents. As the above argumentation shows that the structure of male genitalia made it possible to separate not only families close to Kateretidae (including also Apophisandridae, Boganiidae and Parandrexidae), and also subfamilies of the nitidulid carpophiline-lineage (Amphicrossinae Kirejtshuk, 1986, Calonecrinae Kirejtshuk, 1982, Carpophilinae and Epuraeinae Kirejtshuk, 1986) as well as nitiduline-lineage (Cillaeinae, Cryptarchinae Thomson, 1959, Cybocephalinae, Meligethinae, Nitidulinae (including tribe

Mystropini Murray, 1864) and Maynipeplinae Kirejtshuk, 1998). It can be regarded that the genital structures are an “Ariadne’s thread” to follow traces of the phylogeny of not only three distinct clades in the nitidulid-group of families having joined to the mentioned families also the Helotidae and Monotomidae with the bilobed aedeagus (Figs 4–6), although it is possible to make the same phylogenetic reconstructions even without this “thread” thanks to a correct analysis of other morphological characters and application to the method of multiple parallelisms to explain independent evidence of phylogenetic changes.

It may be important to note that the problem of appearance of considerable similarity within not quite closely related groups in similar conditions draw due attention of many researchers (for example, as adaptive homoplasy), but not, unfortunately, attention of Peris et al. [2024a] and some other researchers. Precisely external structural similarities of anthophagous kateretids and some nitidulids (Epuraeinae and Carpophilinae (carpophiline-lineage), Mystropini and Meligethinae (nitiduline-lineage)) with very different genital structures gave reasons for Peris et al. [2024a] to unite them into one nitidulid group or closely related groups. Besides, study of changes of throphic regime in related groups gives evidence to suppose an independent origin of anthophagy, carpophagy and phyllophagy from initial mycetophagy [Kirejtshuk, 1989a, 1997a; Kirejtshuk et al., 2023, etc.], but apparently never in into opposite direction (and this regularity seems to be characteristic of beetles, and probably of many other insects). Peris et al. [2024a: 594] in the Abstract of their paper wrote: “We attempt to demonstrate their placement in an extinct basal subfamily in Nitidulidae (Apophisandrinae stat. nov.), with some partially shared plesiomorphic characters of both Kateretidae and Nitidulidae: Epuraeinae, and with a series of convergent morphological characters also shared with other extant anthophagous nitidulids including Nitidulinae: Mystropini and Meligethinae”. After excluding Kateretidae as separate family, there is no nitidulid known with the aedeagus of the TYPE 1 (Figs 1–3) and, therefore, such a proposal of Peris et al. [2024a] needs serious explanations. In the text of the lastly cited paper the authors many times repeated that the mentioned groups and also Mystropini (Nitidulinae) have plesiomorphic or symplesiomorphic characters without mention of other anthophagous groups from Carpophilinae, Nitidulini, Cychramini, Cyllodini etc. and never indicating what characters can be treated as plesiomorphic. However, if these authors put the subfamilies Carpophilinae and Cillaeinae back into one subfamily (having specialised anthophagous groups with similar structures), and taking into account of close relations between apophisandrids and kateretids, their taxonomic interpretation of the groups under consideration became surprisingly reminiscent of that is presented in the Junk’s catalogue on the Nitidulidae [Grouvelle, 1913] and other publications appeared before studies on genitalia and other organs of the latter, i.e. the system of the nitidulids was somehow returned to the state that it had about 100 years ago, where many anthophagous groups were joined into three taxonomic units (Kateretinae, Carpophaginae and Meligethinae).

The causes and regularities of structural transformations during (antho-)phyllophagization of nitidulids and other beetles were discussed in detail by Kirejtshuk and co-authors [Kirejtshuk, 1989a, 1997a; Kirejtshuk et al., 2023, etc.]. All the above-mentioned subfamilies belong to different lineages, on the one hand, and have principal differences in their aedeagus, which is an evident trace of their phylogenetic divergence. Their similarities seemed to appear partly as similar adaptations or partly as consequence of shortening of ontogenetic development in such ephemeral substrate as flowers with restricted by flowering period. Therefore, some similarities, regarded as “plesiomorphic” by Peris et al. [2024a], indeed should be interpreted as secondary features as result of short larval development. The latter can be supposed because many structural similarities showing different epuraeines, carpophilines, cillaeines and some tribes nitidulines (but not mystropins), some of which are mycetophagous in larval and imaginal stages, i.e. living and developing in ephemeral substrate, like fermented tree sap and different decaying matter of plant origin. This is another principal aspect, which is very important for understanding of probable phylogeny and structural parallelisms in beetles of the nitidulid-group of families and which was ignored by Peris et al. [2024a]. Besides, it is important to note that the family Parandrexidae, closely related to apophisandrids, kateretids and probably boganiids, is known from the Middle Jurassic [Kirejtshuk, 1994b; Lu et al., 2015, etc.] and Crowson [1981] put forward a very productive hypothesis on relations between Boganiidae, Nitidulidae and Parandriidae recently obtained a new support [Kirejtshuk et al., 2023], but this hypothesis even is not mentioned at all by Peris et al. [2024a, b]. Thus these two publications express the research program defined by Jelínek et al. [2010] with ignoring of the principal significance of genital structures of both sexes in the considered group of families, and also with ignoring of similar structural and bionomical regularities in parallel changes in phylogeny of related groups.

Thus, as the research program for studies declared by Jelínek et al. [2010] found a complete expression in the publication of Peris et al. [2024a], it is quite clear why the Apophisandridae found a position as a subfamily among nitidulids. Nevertheless, the argumentation of it should be regarded as mostly erroneous, because based on misinterpretation of some principal characters, wrong homologisation and misinterpretation of some important things from morphology, paleontology and phylogenetic methodology.

Position of the genera

***Baltoraea* Kurochkin et Kirejtshuk, 2010,
Cornuturetes Peris, Jelínek et Audisio, 2024,
Cretabaltoraea Peris, Jelínek et Audisio, 2024,
Diopsiretes Peris, Jelínek et Audisio, 2024,
Protokateretes Zhao, Huang and Cai, 2023,
 and *Vetunitidula* Zhao, Engel, Huang et Cai, 2025
 (Apophisandridae)**

These genera were initially proposed in the composition of different families: *Baltoraea*, *Cornuturetes*, *Cretabaltoraea* and *Diopsiretes* as members of Nitidulidae,

while *Protokateretes* as a member of Kateretidae. The tomographic scanning and reconstruction of the external surface of *Baltoraea simillima* Kurochkin et Kirejtshuk, 2010 [Peris et al., 2024b] made it possible to observe its underside with clearly visible outline of thoracic sclerites (particularly posterior edge of metaventricle deeply excised as characteristic of apophisandrids but rare among nitidulids, which was not visible before during preparation of its original description), also the recent re-examination its previous imagines [Kirejtshuk, 2015: https://www.zin.ru/animalia/coleoptera/rus/baltor_g.htm] allow to conclude that its tarsomere 4 looks like scarcely cylindrical. Besides, the structure of anterior part of the front and mandibles are more or less different from those characteristic of nitidulids and somewhat similar to those in some apophisandrids. The same can be supposed about strong thorns, characteristic of apophisandrids, but not most known anthophagous nitidulids. Oppositely, the absence of visible crenellation along the posterior edge of pygidium and hypopygidium of *Baltoraea* species is characteristic of nitidulids rather than apophisandrids. Nevertheless, the opinion of D. Peris et al. in approaching *Baltoraea* looks like admissible because there is no (pollino-)anthophagous member among nitidulids having seriate elytral punctation. At the same time, such an attribution is still questional and needs further support (tomography of the genitalia would be best). Although the increasing similarity of species of this genus (the youngest of the known apophisandrids) with some nitidulid groups and not with other members of the apophisandrids, it can be assumed that it is connected with the peculiarity of the expression of the tendency in structural transformation simplifying some structures in groups with short larval development and/or special host plant.

As to other above-mentioned genera, all they are very clearly apophisandrids in many characters mentioned by Kirejtshuk et al. [2023] in legs, head and its appendages, thoracic sclerites, abdomen and legs, which are quite discriminative in cases when they were illustrated in the pictures published in these papers. Peris et al. [2024a, b] put them to Kateretidae or Nitidulidae apparently without attentive application to the original family diagnosis of the apophisandrids and detailed comparison of them with other nitidulid-group families and important diagnostic characters are missing in the text of original descriptions of the type species of the above-mentioned genera. As for the Peris' et al. remarks that the species of the genus *Protokateretes* have cylindrical tarsomere 4 like that in the kateretids, it can be recommended that they look closely at the photographs of the species described by them and other photographs of this genus, especially the legs of its type species [Zhao et al., 2023a, b, 2024; Peris et al., 2024a, b], and compare their remarks with the re-description of this taxon (Apophisandridae) in paper of Kirejtshuk et al. [2023]. Of course, determining whether the ends of a very small cylinder or cone are cut off (crosswise or beveled), and also presence of small setae on its lower surface in a small beetle in amber are a rather delicate problem and should be supplemented by other more reliable accompanying characters.

**Subfamily Vetunitidulinae Kirejtshuk, subfam. n.
(Apophisandridae)**

Type genus *Vetunitidula* Zhao, Engel, Huang et Cai, 2025.

Diagnosis. The new subfamily is rather distinct from another subfamily (Apophisandrinae sensu stricto) in the shape and structure of the abdominal apex in male: last abdominal segment much longer than wide, and subrectilinearly narrowing apically, pygidial apex rather narrow, subtruncate and without trace of serration, hypopygidium with clear laterosternites.

Notes. The type species of this genus has an extraordinary structure of its rather narrow abdominal apex, unique among more than a hundred of fossils having studied by the author of this paper and clearly visible in the original description [Zhao et al., 2025], which is considered as a good reason to propose a new subfamily. Representatives of the nominative subfamily have the last abdominal segment wider than long, with moderately narrow to rather wide apex, which is usually distinctly serrate apice of pygidium and/or hypopygidium along their posterior edge.

Notes on *Boreades* Parsons, 1943

This generic name was proposed for one Nearctic species originally described as *Cercus abdominalis* Erichson, 1843, synonymised by Audisio [1993] with *Heterhelus* Jacquelin du Val, 1858, but Hisamatsu and Lee [2007] decided that it is possible to regard together in a separate "subgenus" *Boreades* with two species: *Heterhelus* (*Boreades*) *abdominalis* and *H. (B.) solani* (Heer, 1841). Indeed, the determination of two most common Palaeartic species (*H. scutellaris* (Heer, 1841) and *H. solani*) sometimes is very complicated because of their great variability in many external characters. On the other hand, the distinctness of the body of *Boreades abdominalis* from all true Palaeartic and Nearctic members of the *Heterhelus* sensu stricto and *Taiwanoheterhelus* Hisamatsu et Lee, 2007 in the peculiarities of body colouration and the sculpture of integument, and also some characters of the underside demonstrate that *Boreades abdominalis* is very distinct from all members of *Heterhelus*. The proper taxonomic rank of *Boreades* and its relations within kateretids require a further revision.

Genus *Mesohelotopsis* Kirejtshuk, gen. n. (Helotidae)

Type species *Metahelotella monochromata* Liu, Ślipiński, Ren et Pang, 2019.

Notes. One helotid species from the Cretaceous Burmese amber described by Liu et al. [2019] as a member of the genus *Metahelotella* Kirejtshuk, 2000 is really somewhat similar to modern species of this genus, but rather distinct from them in the shape of pronotum and structure of its basal border, elytral basal border, and also very peculiar elytral sculpture, and, therefore, it needs to be considered as a new genus. Characters of the underside of the Mesozoic "congener" are not clearly visible. Other fossil helotids were described in publications [Liu et al., 2019; Tihelka et al., 2020; Li et al., 2023].

Diagnosis. Body elongate elliptical, moderately convex both dorsally and ventrally; head slightly longer than wide; long pronotum with archuate anterior edge strongly projecting anteriorly and with scarcely expressed anterior angles, posterior edge thickly bordered and distinctly bisinuate, posterior angles very sharply acute; elytra widest at anterior fourth, with base strongly thickly bordered and looking like sharply convex transverse stripe laterally, projecting as acute process; elytral integument basally and along suture alutaceous and covered with very shallow, coarse and greatly interspaced punctures showing slight trace of longitudinal rows and interspace between them with diffuse and very fine punctures; oppositely, lateral part of elytral integument in distal four-fifths smooth and covered only with coarse deep and greatly interspaced punctures arranged in regular rows; legs rather long and narrow.

Comparison. In contrast to all recent helotids, *Mesohelotopsis monochromata* **comb. n.** has (1) the rather convex and very long pronotum with archuate anterior edge strongly projecting anteriorly and with scarcely expressed anterior angles, but posterior angles very sharply acute; (2) elytral base strongly thickly bordered and looking like a sharply convex stripe laterally projecting as acute process; (3) elytral integument basally and along suture alutaceous and covered with very shallow, coarse and greatly interspaced punctures with slight trace of longitudinal rows and interspace between them with diffuse and very fine punctures, oppositely, the lateral part of elytral integument in the distal four-fifths smooth and covered only with coarse deep and greatly interspaced punctures arranged in regular rows.

All known fossil members of the family are characterised of the rather long pronotum. Representatives of *Mesohelotopsis* **gen. n.** have the somewhat wider body, very strongly vaulted borders along pronotal and elytral base distinctly separated from the remaining integuments of the pronotum and elytra, extremely characteristic sculpture and punctuation of its integument, in particular on elytra, very distinct from those of other fossil genera, although character of elytral punctuation is somewhat similar to that in *Burmahelota* Liu, Ślipiński, Ren et Pang, 2019. Besides, the new genus differs from:

– *Burmahelota* in the distinctly and deeply bi-sinuate pronotal base with median process only slightly projecting posteriorly, pronotum as arcuately narrowing to apex as to base (not widest at anterior edge);

– *Lobatihelota* Li, Liu et Cai, 2023 in the much larger and not strongly projecting laterally eyes, pronotum gently arcuate at sides (not subquadrate) and absence of elytral costae;

– *Palaeohelota* Liu, Ślipiński, Ren et Pang, 2019 in the markedly shorter head (particularly frons), distinctly and deeply bi-sinuate pronotal base with median process slightly projecting posteriorly (not gradually convex), pronotum distinctly convex and more arcuate at sides, absence of elytral costae;

– *Trihelota* Tihelka, Huang et Cai, 2020 in the pronotum gently arcuate at sides (not subquadrate), elytra without spots with completely smooth and coloured integument.

Etymology. “*Meso-*” from Mesozoic, “*heloto-*” from *Helota* and “*-opsis*” (“οψις”) meaning “resembling a (specified) thing”. Gender feminine.

The corrected combination of the type species should be *Mesohelotopsis monochromata* (Liu, Ślipiński, Ren et Pang, 2019), **comb. n.**

On the family Cybocephalidae sensu Cline et al. [2014] and subfamily Prometopiinae sensu Cline et al. [2014]

Cline et al. [2014] proposed the transfer of one nitidulid group of genera usually regarded as the subfamily Cybocephalinae into another place corresponding that in their cladogram, i.e. within “Cerylonid series”, erected a subfamily rank among nitidulids for many members of the *Megauchenia*-complex of the genera (Prometopiinae Böving et Craighead, 1931: *Axyra* Erichson, 1843, *Megauchenia* Macleay, 1825, *Megaucheniodes* Audisio et Jelínek, 1993, *Palaeometopia* Kirejtshuk, 2007, *Prometopia* Erichson, 1843 (including the subgenus *Parametopia* Reitter, 1884), *Pseudoplatychora* Grouvelle, 1890, and *Taraphia* Audisio et Jelínek, 1993), and also proposed some strange grouping of other nitidulids, based only on comparison of sequences of some nucleotids. Many these innovations strongly contradict the previous taxonomic classification of the family [Kirejtshuk, 2008] and have no real support beyond the dendrogram, created by a computer after comparison of DNA sequences. The authors of this publication regarded that the systematic position of taxa can be defined only its placement in their dendrogram created by computer software. Kirejtshuk and Mantič [2015] demonstrated that the diagnoses of Cybocephalidae sensu Cline et al. [2014] and the subfamily Prometopiinae sensu Cline et al. [2014] are not applicable. The Cybocephalinae were returned to the nitidulids, while the Prometopiinae without any character for discrimination of the above-mentioned genera from the remaining genera of the tribe Nitidulini sensu stricto was returned to the nominotypical tribe. Some corrections in the dendrogram of Cline et al. [2014] were made also by Lee et al. [2020] after involving in this dendrogram new DNA sequences, but the lastly mentioned coleopterists tried to find a base of their “phylogenetic” constructions exceptionally on comparison of molecular data and without any other support, particularly with ignoring data on real phylogeny in past. Therefore the conclusions of both these papers need a serious critical revision with use of the method of multiple parallelisms.

Notes on “reclassification” of the subfamily Carpophilinae by Powell et al. [2020]

Some interesting ideas were included in the paper by Powell et al. [2020] devoted to generalizations after very few sequencing of some carpophilines. However, these authors not always strictly adhered to the International Code of Zoological Nomenclature [1999] and, therefore, their conclusions need to be revised and supported by facts used in any logic classification. It is necessary to explain why the “new” proposed “reclassification” is preferable to place the previous one, developed by many scientists beginning

from C. Linnaeus. In the Abstract of this “reclassification” is declared: “The most complete molecular phylogeny of Carpophilinae to date, based on 37 ingroup taxa, covering four of the six recognised genera, is presented... These data were generated using a novel method discussed here” [Powell et al., 2020: 1359]. The authors of this publication as well as before Cline et al. [2014] regarded that the systematic position of taxa can be defined only its placement in their dendrogram created by computer software. In contrast to other above considered [Leschen, 1999; Cline et al., 2014], these authors informed about number of species taken by them for their “comprehensive” contribution in the systematics and the present discussion with them can be much simpler than with two other groups of co-authors. In the section “Systematics”, Powell et al. [2020] cited many papers but no publication concerned the matter of their “reclassification”, except Cline et al. [2014], i.e. one of the co-authors of the paper under consideration considered in detail above, although some brief information was included in the text of their paper as “Taxon sampling”. Thus, this “reclassification” strictly follows recommendations by Jelínek et al. [2010] and founder of this fashion of the systematic research of nitidulids [Leschen, 1999] in regarding the efforts of previous researchers mostly as the “narrative and quantitative analyses” which can be generally neglected and take only the things necessary for the concept of these authors themselves. As it can be understood the “novel method” by Powell et al. [2020] consist in their usage the standard tools and methods of molecular studies, quite fashionable fragments of DNA mostly borrowed from GenBank and apparently commonly used software. As their sampling, these authors took mostly representatives of the Nearctic fauna without clarification subgeneric position of them and use arbitrary attribution for some of them and other without. Because their new concept is out the logical construction summarized in the classification published by Kirejtshuk [2008] and also without any other one, the proposed new hypothesis can not be discussed. In these notes it seems to be enough to mention only the main short shortcomings showing that this concept and “reclassification” are rather premature to consider it for replacement of the classification elaborated by previous researchers nearly during two hundred years. They concern many contradictions to the knowledge on the subfamily Carpophilinae, main of which can be formulated in the following:

A. The genus *Carpophilus* Stephens, 1830 is divided into nine subgenera [Kirejtshuk, 2008]. It means that every species should have a place in one of these nine subgenera. The “reclassification” by Powell et al. proposes a dendrogram obtained after comparison of DNA sequences and includes as well the species with subgeneric attribution as those without it. These authors in their dendrogram joined, for example, in one branch “*Carpophilus tempestivus*” (belonging to the subgenus *Ecnomorphus* Motschulsky, 1858), “*Carpophilus nepos*” (belonging to the subgenus *Myothorax*), “*Ctilodes clinei*” and “*Carpophilus fumatus*” (belonging to the subgenus *Myothorax*) and, as a result, showing a paraphily of the *Myothorax*, and, even more, this branch with four species from different genera and subgenera has a position aside from other members of

the subgenera *Ecnomorphus* and *Myothorax*. At the same time, Powell et al. [2020] put all species of one branch into one genus *Caplothorax* sensu Powell et al., although indeed they belong to the following subgenera of the genus *Carpophilus*:

1) *Caplothorax* Kirejtshuk, 1997: *C. (C.) melanopterus* Erichson, 1843 and *C. (C.) rufus* Murray, 1864;

2) *Megacarpolus* Reitter, 1919: *C. (M.) brevipennis* (Blanchard, 1842) represented by one specimen (female) in very bad condition and should be interpreted as *incertae sedis*, *C. (M.) californicus* (Schaeffer, 1911), *C. (M.) funebris* Sharp, 1889, *C. (M.) lugubris* Murray, 1864, *C. (M.) sayi* Parsons, 1843 (= *niger* Say, 1823, non Seidlitz, 1888), *C. (M.) similis* Sharp, 1889, *C. (M.) viduatus* Sharp, 1889;

3) *Plapennipolus* Kirejtshuk, 1997: *C. (P.) rufiventris* Schaeffer, 1911 and *C. (P.) yuccae* (Crotch, 1874).

It is important to note also that the type series of both *Carpophilus melanopterus* and *C. rufus* are each represented only by one female, which seem to be conspecific (according to the A.G. Kirejtshuk's preliminary examination, yet not published). However, in the dendrogram these two probably conspecific species were put in the different branches of the proposed "phylogenetic" tree.

B. The taxon *Megacarpolus* Reitter, 1919 was initially proposed for the alone Asian species (by monotypy) [Kirejtshuk, 2019] and the subsequent proposal to transfer its New World relatives to another taxon of the genus group (*Caplothorax* sensu Powell et al. [2020]) contradicts the nomenclatural procedure to not divide members of the same taxon only because of geographical isolation. Such a practice in systematic research completely contradicts all the rules of constructing hierarchical systems in principle. Besides, not only the above-mentioned species belong to this subgenus, but also the following American members: *C. (Megacarpolus) deflexus* Sharp, 1889, *C. (M.) rufitarsis* Murray, 1864, *C. (M.) transitans* Sharp, 1889, and *C. (M.) tristis* Erichson, 1843. Kirejtshuk [1997a] introduced *Caplothorax* and *Plapennipolus* only with lists of distinguishing characters for them (as differentiated diagnoses) and the formal requirements of the code are met, although a detailed revision of both subgenera and their proper diagnoses remained still needed. Powell et al. [2020] probably wanted to eliminate this gap but not successfully, because these researchers used for this purpose DNA sequences instead examination of morphological structures of each members under their consideration (their "Diagnosis" proposed by G.S. Power et al. has almost no characters which make it possible to distinguish these subgenera).

C. Only five species of *Megacarpolus* are known from the Eastern Hemisphere [Kirejtshuk, 2019]: *C. (M.) annae* Kirejtshuk, 2019, *C. (M.) funereus* Murray, 1864, *C. (M.) grandis* Motschulsky, 1860, *C. (M.) triton* Murray, 1864 (= *titanus* Reitter, 1884), and *C. (M.) variolosus* Murray, 1864, while Powell et al. [2020: 1365] believed that "many Old World taxa remain in subgenus *Megacarpolus*."

In the considered publication, the co-authors, without mentioning that the connections of the nitidulids with the generative organs of plants are known and have been studied for at least 200 years, conducted an analysis of some data and obtained that "the parsimony-based

ancestral state reconstruction recovered three independent origins of anthophily within *Carpophilinae*" [Powell et al., 2020: 1366]. These origins are, in the co-authors' opinion, happened in the genera *Caplothorax*, *Carpophilus* and *Nitops* Murray, 1864. Peculiar co-authors' interpretations of the carpophiline genera are shown in the previous paragraphs and it is not mentioned what they meant under the origin in, for example, *Carpophilus*, in which adults of many unrelated congeners certainly independently became anthophilous and anthophagous (even specialised with imaginal or complete anthophagy). At the same year another opinion with attempt to decide "evolution of feeding habits of sap beetles" by applying to comparison of DNA sequences [Lee et al., 2020] appeared which produced an opposite result. Unfortunately, the co-authors of both these papers did not indicate how one could check the conformity of their conclusions with the facts in nature and, accordingly, their applicability in biology. Therefore, as in the previous case, the conclusions of Powell et al. [2020] and Lee et al. [2020] need a serious critical revision with use of the method of multiple parallelisms.

Notes on "re-examination" of the subfamily *Meligethinae* by Audisio et al. [2009]

This subfamily was partly revised during the 20th century by Easton [1956, 1957a, b, 1959, 1960, 1964, 1968, etc.], Endrödy-Younga [1978], Jelínek [1975, 2000a, b, etc.] and Kirejtshuk [1979, 1981, 1989b, 1992, etc.] and other colleagues following to the traditional classification procedure and most its genera and subgenera were described in accordance with traditional diagnostic characters mostly in the structure of antennae, ultimate abdominal segment, meso- and metatibiae. However, the publication of Audisio et al. [2009] completely stopped these studies because these co-authors introduced in this large paper 22 new genera in addition to formerly recognized ones, and all of them were treated without proper diagnoses or comparison with other supraspecific taxa, but only with division "Generic description and diagnosis" for every of both new or former "genus". Thus, a very strange situation appeared in the group including about 400 species and after this proposal divided into more than 40 genera, which are impossible to identify without checking every description of all "generic" taxa included in the "re-examination". Almost the only available way to establish the genus membership is to consult P. Audisio, since he was the only one of the co-authors who had experience of studying this group before the publication of this "revision" and is probably responsible for the separation of all the species included. The paragraph 13 of the currently valid version of International Code of Zoological Nomenclature [1999] allows to accept a taxon as valid if its description includes the characters distinguished it from other taxa of this higher taxon. Audisio et al. [2009: 347] explained their approach by the following phrases: "Short differential diagnoses were not included herein for each described genus, because most treated genera are only characterised by peculiar combinations of several different morphological characters (listed in descriptions/redescriptions), and only rarely by single autoapomorphic traits". It is not clear how such

explanations can be acceptable for systematic research as taxonomic argumentation. In the end of the publication [Audisio et al., 2009: 490] these authors wrote only one paragraph with a dendrogram having the caption: “Fig. 43. Cladogram of hypothetical phylogenetic relationships between the 43 recognised genera of Meligethinae, as inferred from an exploratory and preliminary cladistic analysis based on 72 morphological characters”. With this, P. Audisio et al. did not publish any list of these 72 characters, which could illustrate probable relations of these “genera”. However, it is important for the continued possibility of using the proposed taxa in research practice to ensure their recognition through the formulation of a distinct syndrome for each of them. These authors also presented the main movements of the continents (albeit its simplified and outdated interpretation) starting from the Jurassic, as if this explains the “scenario” of the differentiation of modern meligethine “genera” accepted in this “re-examination” (in their opinion this “scenario fits well with available data about the origin, phylogenetic position, dispersion and present-day distributions” [Audisio et al., 2009: 491]). Thus, as a result, one of most important nitidulid subfamily became without a possibility to use its generic structure and find either generic or species attribution because its previous system greatly conflicts with new one which remain ungrounded. This is a rather paradoxical situation never happened before. Biologists and scientific community till now can not determinate any of genera sensu Audisio et al. as these taxa remain without proper generic diagnoses, key to genera, matrix of the characters necessary for generic discrimination and even without name of the software which can be used for the find place in the cladogram published by Audisio et al. [2009] without explanation. Considering papers of Cline et al. [2014] and Powell et al. [2020] readers can get some impression of the authors’ viewpoint and some discussion can be possible. Even proposal of the superfamily Nitiduloidea can be discussed. But the paper by Audisio et al. [2009] is unique because in many cases it gives no chance for it. For example, the probably most archaic genus of the subfamily, *Pria* Stephens, 1830 with the most number of plesiomorphies is placed not at base in the cladogram of this paper and this is not explained in the text, although the most important diagnostic character is mentioned in its “Generic redescription and diagnosis”. This question involuntarily arises in any reader of this paper who knows this subfamily at least a little and such disappointment appears in many places of it. In the references for the “re-examination” Audisio et al. [2009] included also “Audisio P. et al. in press: Preliminary cladistic analysis of pollen-beetles of the subfamily Meligethinae (Coleoptera, Nitidulidae). *Fragmenta Entomologica*” where the list of the characters for discrimination of the “genera” accepted in this re-examination could be expected. However this cited paper, unfortunately, remains still in press. Another important peculiarity of the situation with this generic classification of the subfamily Meligethinae should be noted for readers who wants to understand its hopeless dramatic. In the text of the published paper under this consideration, Audisio and co-authors [2009] make several references to another paper on the molecular

systematics of the subfamily Meligethinae [Trizzino et al., 2009], arguing for its proposed group division. However, in the paper by Trizzino et al., the following is literally written in the Conclusions: “several slippage-derived motifs in the expansion segments provided preliminary genetic support for newly proposed taxonomic arrangements of several genera and subgenera of Meligethinae, which is in direct support of morphological and ecological data”. Thus, one paper relies on another, and the other on the first, but it is not explained to readers how to get out of this circle. In addition, Audisio and co-authors [2009] substantiate many times their classification conclusions with their own unpublished materials and the content of still unpublished data from student works (F. Lomanna and S. Strika).

For further development and discussion of the subfamily system, it was expected that the co-authors would present at least the list of characters used to create the already published cladogram, so that it would be possible to discuss the phylogeny within the framework of logical deductive methods based on established patterns, rather than statistical-probabilistic expectations based on facts formalized in matrices, which in turn still remain unknown. Some times it was published that both true diagnosis and comparison are missing in the paper of Audisio et al. [2009] and, therefore, it is no possibility to discriminate all taxa and particularly new taxa proposed in it [Kirejtshuk 2011a, b; A. Kirejtshuk, P. Kirejtshuk, 2012; Kirejtshuk, Mantič, 2015, etc.]. Nevertheless, during over 15 years passed after appearance of the paper of Audisio et al. [2009], no paper has appeared with diagnoses or comparison of the “genera” recognised by P. Audisio or his co-authors. It was not made even for “genus” *Meligethes* sensu Audisio et al. [2009] revised by Audisio et al. [2014a] without any diagnosis, comparison and key to species. As a result, it is not clear how it is possible to distinguish it from *Odontogethes* Reitter, 1871, proposed as a subgenus to separate some species from the nominotypical taxon by dentate tarsal claws. Indeed, it was later discovered that sometimes closely related species can have dentate or not dentate claws or even specimens of the same species have this character so variable that some individuals can have distinctly dentate but other simple claws. The latter two names were synonymised by Kirejtshuk [1988], but P. Audisio in some his publications recognised this synonymization and not in others (always without explanations), as well as he sometimes used the writing of *Odontogethes* (as proposed Reitter [1871] but usually “*Odonthogethes*” (probably corrected or with a misprint). In the revision of *Meligethes* Audisio et al. [2014a: 28] it is written that “available molecular and morphological datasets provide strong and concordant evidence of the robustness of a relatively large clade that includes *Meligethes*, *Brassicogethes*, *Meligethinus* Grouvelle, 1906, and likely also *Micropria* Grouvelle, 1899 (Strika 2004; Trizzino et al. 2009; Audisio et al. 2008, 2009, 2014, and unpublished data)”. However, all cited papers, which were published, have not data mentioned by Audisio et al. It can be thought that these data remain in the still unpublished “thesis” of S. Strika (2004) many times cited in publications of Audisio et al. or in other “unpublished data”. This paper has no diagnosis for the “genus” *Meligethes* sensu Audisio et al. [2014a] but has four

characters for discrimination of its subgenera sensu Audisio et al. [2014a: 29] and "*Odonthogethes*" sensu Audisio et al. [2014a: 72]: (1) "always simple (never markedly toothed or at least obtusely toothed) tarsal claws" in "*Meligethes*" and "always toothed (sharply toothed or at least obtusely toothed) tarsal claws" in "*Odonthogethes*"; (2) "microsetae of middle portion of the posterior edge of pronotum... more distinctly visible" in "*Meligethes*" and "microsetae of middle portion of the posterior edge of pronotum (in front of scutellum) less distinctly visible" in "*Odonthogethes*"; (3) "temples behind eyes (postero-lateral view) on each side always with a deep subcircular pit placed at the end of antennal grooves" in "*Meligethes*" and "postocular subcircular pit placed immediately under the posterior ventrolateral edge of each eye" in "*Odonthogethes*" (indeed this pit sometimes distinctly expressed, sometimes very slightly expressed and in other cases not expressed at all); (4) "tegmen frequently with more or less distinct projections along the distal inner edge of the paramera" in "*Meligethes*" and "tegmen always without projections along the distal inner edge of the paramera" in "*Odonthogethes*". Thus, the above-mentioned characters clearly show that a hiatus between these "taxa" was also not defined at all. Among other things, it should be noted that here the apical parts of the tegmen, separated by the apical medial excision, are called there by the co-authors as "paramera" (see also above for the understanding of consequence of the erroneous use of these morphological terms).

Finally, everybody who has looked through some representatives of the above-mentioned "genera" sensu Audisio et al. [2009] (for example, "*Meligethes*", "*Brassicogethes*", "*Meligethinus*" Grouvelle, 1906, and likely also "*Micropria*" – see above the phrase from Audisio et al. [2014a: 28]), he will be very surprised that their relations can be represented as a phylogenetic unity. Another thing is a proposal such "genus" as "*Afrogethes*" Audisio et Cline in Audisio et al. [2009] including many so different species that it is impossible to understand what reason was used to unite them. Audisio et al. [2014b] published also some remarks with information on the DNA samples of meligethines available in GenBank and proposed an interpretation of these and other data obtained from the Bayesian analysis in phylogenetic terms and expressed in a dendrogram ("phylogram"). However, the matching of dendrogram "based on molecular data" with a certain classification can have a sense and be only possible if the species involved in it are included in the groups (taxa) defined by proper diagnoses. Besides, in this case the methodology of multiple parallelism for proving of a hypothesis proposed for so integrated objects as living organisms having a common phylogenetic background can also be applied as desirable and optimal thanks to independence of supporting evidence.

Similar situations occur in species taxonomy. For example, Audisio and Spornraft [1990] described "*Meligethes matronalis*", which was subsequently synonymised with "*Meligethes subaeneus*" Sturm, 1845 [Kirejtshuk, 1997b]. After that, two more papers were published by Audisio et al. [2001, 2002] on the morphometry of the three sympatric species (two above-mentioned ones and "*Meligethes coracinus*" Sturm, 1845), their differences in

allozymes, as well as an indication that these species differ in mitochondrial DNA sequencing (as far as known last remains not published). These papers, however, showed not so much the distinctness of the three "species" as the variability of a single species with three species synonyms, i.e. cast doubt on the distinctness of the three "species". In some cases, when P. Audisio proposed new species based on DNA sequencing [Audisio et al., 1999; Trizzino et al., 2009, etc.], accompanied by a morphological diagnosis, subsequent comparison of the type specimens of these "species" showed that these studied type specimens were in their morphological structures hardly different from those of previously described species. A fairly simple way to check whether the three groups of specimens examined are one or three species would be to rear the larvae to get adults and offer them flowers of different plant species for feeding (similar to the laboratory experiments that allowed to prove the synonymy of "*Epuraea biguttata*"). This is the most reliable way to prove species separation and it is much simpler than P. Audisio used. Meligethine specimens are easy to breed because this breeding do not need any complex equipment in addition to flowering plants. By the by, these experiments can also show the true food plants of the meligethine species but not only list of plant species where the adults of beetles were collected. On the other hand, studies of larval structures will certainly give reliable data not only on real trophic interconnections between beetles and flowers but they also could bring very important facts for discrimination as of species as of groups of meligethines.

Recently some young coleopterists published dendrograms for few "genera" sensu Audisio et al. [Liu et al., 2017, 2018, 2020a, b, etc.]. These recent publications contain the all necessary data for the taxa considered in the lastly mentioned papers, including diagnostic characters, dendrograms created after studies morphological characters and comparison of DNA sequences only few "genera" and conclusions on these with initial incorrect interpretation originated from publication by Audisio et al. [2009] and also probably under the personal supervising by P. Audisio. Thus, the new coleopterists were forced to use as a base for their research only the "re-examination" by Audisio and his co-authors with correspondent unwanted defects in their conclusions. The corrections in this "re-examination" can be done only by somebody who can test the subfamily in a wide score of the whole world fauna (not local one) to estimate the "conclusions" by Audisio et al. [2009] taking into consideration the comments stated in the above. This circumstance is a serious as at the moment the conclusions of Audisio et al. [2009] and their followers have rather restricted scientific significance because of their essential taxonomic defects. Is it possible to obtain plausible results from vague premises? Such a revision is urgent in order to start an adequate research of the subfamily Meligethinae. The subfamily is extremely complicated group for systematics because of many similar structural adaptations and parallelisms, known in members of this group, even in the genital structures. Finally, it would be desirable to carry on studies of development and larval structures which will bring also new important data not only for determination of reliable food preference and species

isolation but also even for systematics and phylogeny. Probably it is reasonable to use a way of arrangement of supraspecific taxa, which was applied by Murray [1864] and Kirejtshuk [1997a, b, 1998b, etc.] in the subfamilies Epuraeinae and Carpophilinae, i.e. splitting large genera into many subgenera rather than into many genera with very weak to vanishing hiati. This re-arrangement with grounding by proper diagnostic characters will give a good base for true progress in study of this subfamily.

The above argumentation makes it impossible to use taxonomic composition of the subfamily Meligethinae proposed by Audisio et al. [2009] not only for the catalogue of insects of the Far East, but also in the taxonomy of this subfamily because many “genera” in it still remain mysterious. The only case of wrong use of species name was needed obvious correction by the correct senior synonym in the catalogue of the insects of the Russian Far East (Kirejtshuk, in prep.). The use of the Audisio’s interpretation of meligethine system apparently has led and will lead to permanent misunderstandings, uncertainties and false conclusions. The system of this subfamily preliminarily here regarded as currently admissible as a beginning to further research and improvement with addition of other taxa defined by clear diagnoses was published by Kirejtshuk [2008]. P. Audisio could at least publish the list of characters and the matrix compiled by him and his co-authors, which he used to create the “cladogram of hypothetical phylogenetic relationships” and prepare the publication of 16 years ago [Audisio et al., 2009]. If it becomes known how this cladogram was created and what computer programs were used, this will greatly facilitate the corrections and improvements of the taxonomy of the subfamily Meligethinae because this will make it possible to discuss taxonomic problems. The publication of the matrix for this cladogram will make it possible to check contradictions in coding, independence of chosen characters and probably understand why the cladogram has so peculiar branching. It can be expected that in this case some new characters will provide this matrix with very important information and current new software can produce different cladograms. These corrections could help to overcome the deep crisis in which the systematics of this important subfamily found itself 16 years ago and essentially stopped the development of taxonomy of it, becoming one of the reasons for further publications with similar shortcomings.

Tribe Plesiogethini Kirejtshuk et Kurochkin, trib. n. (Cybocephalinae)

Type genus *Plesiogethes* Zaitsev, Vasilenko et Perkovsky, 2025 (Eocene Rovno amber).

Notes and comparison. The larva obtained the name *Plesiogethes mali* Zaitsev, Vasilenko et Perkovsky, 2025 is characterised with some very unusual features: heavily sclerotised body integument, very long thoracic segments and elongate head with anterior part of epicranium rather projecting anteriorly and bisinuate anterior edge of labrum, very long ultimate maxillary and labial palpomeres and long lateral processes on abdominal segments I–VIII. However other its characters completely fit nitidulid ones: including characteristic body shape, head and its visible

parts of mouthparts (except ultimate palpomeres), types of setae in characteristic localization on body sclerites and pretarsus bearing a single simple microseta as well as single long capitate adhesive seta. All these features are more or less similar to those in nitidulid larvae of different groups, having free-living mode of life, and completely fit those in cybocephalines. Therefore its assignment to the subfamily Cybocephalinae, as preliminarily supposed in Zaitsev et al. [2025], is quite reasonable. Besides, it looks like reasonable to extrapolate on its lifestyle also the cybocephaline predaceous one, although the fossil larva seemed to feed different prey than those in modern cybocephaline members because rather long head, thoracic segments and legs are somehow reminiscent those in some carabids and indicate that this larva moved rather quickly and feeding on rather mobile prey. However, the lateral processes on abdominal segments could be different from the “spiracular tubes” homologous with those in other nitidulid larvae, as the very similar processes on last abdominal segments of larvae in modern cybocephalines bear apical pore (not spiracle) producing silk thread during making by prepupal larva a pupal cradle (chamber).

Diagnosis. Body with heavily sclerotised body integument, comparatively long thoracic segments (about as twice long as abdominal segments) and elongate head with anterior part of epicranium rather projecting anteriorly and bisinuate anterior edge of labrum, very long ultimate maxillary and labial palpomeres, long lateral processes on abdominal segments I–VIII and comparatively long legs.

Draft of a possible phylogenetic hypothesis for the nitidulid-group of families

All of the above in this section, as well as the provisions of previous publications [Kirejtshuk, 1982, 1986a, b, 1998a, 2000; Kirejtshuk et al., 2023, etc.] and discussed also above, can be presented as a preliminary draft of the hypothesis of phylogenetic relationship and is expressed in the following form for two subgroups that are apparently closely related, characterised by fundamental differences in the structure of the genitalia in both sexes and are partly commented on below as a key to the groups according to some pronounced features that require further study and verification:

1. Kateretid-subgroup of families: Boganiidae + + ((Smicripinae + Kateretidae) + (Apophisandridae + Parandrexidae)).

2. Nitidulid-subgroup of families: (Helotidae + + Monotomidae) + (Cybocephalinae + (Cryptarchinae + + (Nitidulinae + Cillaeinae + Meligethinae)) + (Calonecrinae + + (Amphicrossinae + (Epuraeinae + Carpophilinae))).

Comments to the preliminary hypothesis of phylogenetic relationships in the nitidulid-group of families:

1) Boganiidae and other families of the kateretid-subgroup: aedeagus including phallobase with dorsally articulated paramera and penis trunk looking like a sclerotised tube with two basal struts in Boganiidae and with one basal strut in Apophisandridae – Kateretidae – Smicripidae; ovipositor without differentiation of gonocoxites into inner and outer lobes.

2) Pair of Smicripidae and Kateretidae: posterior edge of metaventre between widely separated metacoxal

cavities subrectilinear; tarsomeres 1–3 deeply bilobed and small tarsomere 4 subcylindrical.

3) Pair of Apophisandridae and Parandrexidae: posterior edge of metaventricle between narrowly separated metacoxal cavities more or less angularly excised; tarsomeres 1–4 oblique and usually unilobed or frequently slightly unilobed and small tarsomere 4 more or less lobed.

4) Pair of Helotidae and Monotomidae with many characters similar to those in Nitidulidae, including structure of genitalia of both sexes very similar to those in nitidulids could become isolated from the latter, could be separately and could be before the main divergences of nitidulids.

5) Divergences of the carpophiline-lineage (Amphicrossinae, Calonecrinae, Carpophilinae, Epuraeinae) and nitiduline-lineage (Cillaeinae, Cryptarchinae, Cybocephalinae, Maynipeplinae, Meligethinae, Nitidulinae) were considered by Kirejtshuk [1982, 1986a, b, 1998a].

Review of species of the *dimidiatus*-group of the subgenus *Myothorax* (Nitidulidae: Carpophilinae: *Carpophilus*) mainly from the Palaearctic and Indo-Malayan regions

Definition of the *dimidiatus*-group of the subgenus *Myothorax*

Murray [1864: 372] proposed this subgenus and defined it as: “Body subcylindrically convex, oblong. Thorax subquadrate”. This diagnosis was rather good at that time, but the increased variability of it with increasing number of included species and particularly of more variable subgenera *Ecnomorphus* with five synonyms, and later proposed *Caplothorax* and *Plapennipolus* made it insufficient. It is important addition to the original diagnosis that the subquadrate pronotum has rounded and not projecting both anterior and posterior angles, and also more or less subquadrate elytra. True, some Australian, Central and South American species of *Ecnomorphus* have similar shape of the pronotum and elytra, but the body of the latter species are not so convex as in members of *Myothorax*. Nevertheless, the subgenera need a further comprehensive revision to elaborate more adequate diagnoses for all subgenera.

The subgenus *Myothorax* is composed of many rather distinct species, while few consubgenera are characterised by very great variability of features usually considered in other species as diagnostic and, therefore, the species diagnostics in some cases is almost impossible by testing of individual specimen (particularly if only females accessible). Two groups of this subgenus are represented by closely related species distributed mostly in the Indo-Malayan members, one of these group (*dimidiatus*-group) includes also many species with the (sub)cosmopolitan ranges thanks to their inhabitation in stored products over the world. Taking into consideration the importance of the latter group for human economic activity, a key to its species, descriptions of new species and also general information of type series and synonymy of the members of this group are given below. Most characters of this group are rather variable and need

a great attention for reliable determination, although the complex of external characters combined with structural features of the male genitalia can provide an exact species identification (structure of female ultimate abdominal segment and ovipositor can be sometimes rather distinct, although they are frequently more or less similar in more than one species).

The *dimidiatus*-group is composed of species with the more subparallel-sided and more convex body, less distinct and denser punctation as well as usually with the more contrasting sculpture of integument, more developed pubescence, simple female pygidium and, as a rule, not arrow like lateral lobes of the dorsal part of phallobase (“tegmen”): *C. (M.) assignatus* sp. n., *C. (M.) brunneus* Chen, Hui et Nuang, 2020, *C. (M.) contegens* (Walker, 1958), *C. (M.) dimidiatus* (Fabricius, 1792), *C. (M.) fumatoides* sp. n., *C. (M.) fumatus* (Boheman, 1851), *C. (M.) generosus* sp. n., *C. (M.) languescens* sp. n., *C. (M.) mutilatus* Erichson, 1843, *C. (M.) nepos* Murray, 1864, *C. (M.) notatus* Murray, 1864, *C. (M.) pilipennis* Macleay, 1873, *C. (M.) pilosellus* Motschulsky, 1858, *C. (M.) robustus* Murray, 1864, stat. n., *C. (M.) schioedtei* Murray, 1864, *C. (M.) timorensis* Dobson, 1993, *C. (M.) truncatus* Murray, 1864, ? *C. (M.) xanthopterus* Murray, 1864, and *C. (M.) zeaphilus* Dobson, 1969. The holotype of *C. (M.) xanthopterus* (female, NHML, labelled with “*xanthopterus*”) described from Indonesia (Sumatra) was re-examined. However, it has only the characters allowing to attribute it with a comparable probability to a pair of *C. (M.) dimidiatus* and *C. (M.) pilosellus* because of absence of features secondary sexual dimorphism. In the Southern Hemisphere many populations were found including specimens similar to those of *C. (M.) pilosellus* which can be regarded as separate species, *C. (M.) imitatus* Semeraro, Blanck, Rako et Cunningham, 2023 and *C. (M.) truncatus*, whose discrimination, however, is so complicated that even species isolation of them remains questionable (see below).

Another *lewisi*-group of *Myothorax* units the species with the more robust, elongate oval and moderately convex body, very distinct and sparser punctation as well as with the more smoothed sculpture of integument, less conspicuous pubescence, modified female pygidium and usually with more or less arrow-like lateral lobes of phallobase (“tegmen”): *C. (M.) araucariae* Dobson, 1993, *C. (M.) lewisi* Reitter, 1884 and *C. (M.) pygidialis* Grouvelle, 1897.

The species of the *lewisi*-group are somewhat similar to *C. (M.) joliveti* Kirejtshuk, 2001 and *C. (M.) mimicus* Kirejtshuk, 2001 from the Equatorial Africa in the comparatively wide and less pubescent body with less convex dorsum, although other characters (including in structure of genitalia of both sexes) seem to give evidence that close relations between African and mentioned Asian species are scarcely probable. *Carpophilus (Myothorax) gaveni* Dobson, 1964 and *C. (M.) kusheli* Dobson, 1993 from Australia, Norfolk and New Zealand should be also regarded as members of this subgenus. Besides the last mentioned species, this subgenus includes also *C. (M.) angustatus* Murray, 1864 and *C. (M.) piceus* Grouvelle, 1906 from Madagascar; *C. (M.) australis* Murray,

1864 from Australia; *C. (M.) constrictus* Grouvelle, 1908 from Kenya; *C. (M.) fusciceps* Grouvelle, 1913 (= *C. scotti* Grouvelle, 1913, **syn. n.**, proposed on base of re-examination of the holotypes of both deposited in NHML (holotype of *C. (M.) fusciceps*, female – “Sithouette, 9 (or G)”, “Seychelle Islands, Percy Sladen, Trust Expedition”, “*Carpophilus fusciceps* Grouv.” (written by A. Grouvelle), formerly designated in the collection as lectotype by S. Endrödy-Younga in 1968; holotype of *C. (M.) scotti*, female – “Sithouette, 9 (or G)”, “Seychelle Islands, Percy Sladen, Trust Expedition”, “*Carpophilus scotti* Grouv.” (written by A. Grouvelle), formerly designated in the collection as lectotype by S. Endrödy-Younga in 1968, from Seychelles)); *C. (M.) kollerii* Grouvelle, 1912 from Democratic Republic of the Congo (Zaire); *C. (M.) mutabilis* Fairmaire, 1849 from Polynesia and New Caledonia; *C. (M.) mycetophagus* Lesne, 1938 from Equatorial and East Africa; *C. (M.) oculatus* Murray, 1864 (including *C. (M.) oculatus gilloglyi* Dobson, 1993 and *C. (M.) oculatus cheesmani* Dobson, 1993) from Polynesia; *C. (M.) piceus* Grouvelle, 1906 and *C. (M.) truncatus* from Madagascar and the latter is known also from Seychelles and some areas of Africa. One female of *C. (M.) australis* received from NHML (“Type”, “Melbourne”, “*australis*”) with length 4.5 and breadth 1.7 mm has pressed and destroyed head, pronotum, one elytron and abdominal apex and therefore its characters are not easy to interpret. This specimen is authentic and could potentially be designated as a lectotype if another authentic one with better preserved condition is not found. The original description of the last species definitely says about the peculiar shape of the pronotum and the safe elytron somewhat shorter than usually in other species of *Myothorax*.

Many references on (sub)cosmopolitan species of *Myothorax* associated with stored products were included in the very useful publication of Williams et al. [1983] and later publications on these species are too numerous and not reliable in species determination, and they can be taken from Internet and reference publications, although it is necessary to take into account that determinations of them frequently can be not enough precious. Most records of the *Myothorax* species from stored products in the catalogue of the Palearctic Coleoptera should be treated with some caution, although many of them are rather probable for appearance in Eurasia due to their importation. At the same time there are many publications on these topic which can be scarcely used because their authors do not mention or show the characters important for species identification.

**Key to males of the *dimidiatus*-group of species
of the subgenus *Myothorax*
mainly from the Palearctic and Indo-Malayan regions**

Females have the same external characters, differing from males mostly in the narrower protrarsi, lack of exposed anal sclerite and outlines of posterior edges of the sclerites of ultimate abdominal segment, which are usually rounded to subtruncate or subangular, rarely additionally transversely subcarinate along subcarinate posterior edge (*C. (M.) timorensis*) or excised to emarginate

(*C. (M.) robustus* **stat. n.**, *C. (M.) schioedtei*). Almost each species in the below key are provided also with a drawing of ovipositor.

- 1a. Inner edge of metatibia (usually both meso- and metatibiae) more or less distinctly convex to almost angularly widened in distal half (if convex outline of unner edge nor clear, antennomere 3 markedly longer than antennomere 2); dorsal pubescence rather dense, very conspicuous and subrecumbent 2
- 1b. Inner edge of meso- and metatibiae nearly straight or very slightly curved at the middle; dorsal pubescence variable, but usually sparser, less conspicuous and recumbent (only very rarely in *C. (M.) pilipennis* inner edge of meso- and metatibiae somewhat convex) 3
- 2(1)a. Submesocoxal line less curving at anterior angle of metaventrete; antennomere 3 markedly longer than antennomere 2; last labial palpomere about 1.5 times as long as wide; metafemur with moderately convex posterior edge; metatibia less widened along inner edge; prohypomera with deeper punctures clearly margined posteriorly; body subparallel-sided, usually brownish to dark brown or blackish with lighter elytra, part of underside and appendages. 1.9–3.3 mm. Figs 38–45, 155, see below also *C. (M.) dimidiatus* and Figs 46, 47. Subosmopolitous, in stored products and under natural conditions subpantropical (more common in Africa, Madagascar and Australia) *C. (M.) dimidiatus*
- 2(1)b. Submesocoxal line more curving at anterior angle of metaventrete; last labial palpomere about twice as long as wide; antennomeres 2 and 3 subequal in length; metafemur with emarginate, straight or only slightly convex posterior edge; metatibia more widened along inner edge; prohypomera with shallower punctures less distinctly margined posteriorly; body somewhat more oval, with similar colouration, although in the territory under consideration often comparatively lighter. 1.5–2.9 mm. Figs 49, 50, 122–126, 156. Subcosmopolitan, in stored products and in natural localities subpantropical (more characteristic of the Indo-Malayan Region) *C. (M.) pilosellus*
- 3(2)a. Body dark brownish with one bright yellowish elongate stripe or elongate oval spot on elytral disk along the middle of suture, although rarely body (sub) unicolourous 4
- 3(2)b. Body subunicolourous with unicolourous elytra (yellowish to dark brown) (only some *C. (M.) robustus* **stat. n.** and *C. (M.) schioedtei* with dark elytra or lightened their base and subsutural stripes) 6
- 4(3)a. Disk of each elytron in the middle or in distal two-thirds with yellowish or reddish elongate oval spot indistinctly outlined; body nearly unicolourous chestnut brown to blackish, but ventral surface of head and appendages reddish, sometimes also edges of dorsal sclerites and abdomen somewhat lighter; prosternal process with a well raised median carina reaching its apex; interspaces between punctures on elytra about as great as puncture diameter; mesoventrite with rather coarse sculpture; lateral

- lobes of phallobase ("tegmen") very long and narrow, with dense brush of hairs at midlength. 2.3–4.7 mm. Figs 114–117. Madagascar *C. (M.) notatus*
- 4(3)b. Each elytron with more or less distinctly outlined yellowish elongate stripe along suture and usually along base; prosternal process with weak median carina becoming obsolete at apex; interspaces between punctures on elytra markedly broader than puncture diameter; lateral lobes of phallobase ("tegmen") moderately long and moderately narrow, only with subapical sparse hairs 5
- 5(4)a. Dorsum with very contrasting microreticulation; dorsal punctation finer and denser; distance between punctures on pronotum at most one puncture diameter; mesoventrite with more or less distinct punctures; prosternal process not smoothed and with subtruncate posterior edge; submesocoxal line more curved at anterior angle of metaventrite; pubescence on dorsum rather suberect than subrecumbent; posterior ends of antennal grooves joined through more or less clear transverse concavity. Female unknown. 3.6–4.2 mm. Figs 64–73. Indonesia, Bali *C. (M.) generosus* **sp. n.**
- 5(4)b. Dorsum with somewhat smoothed microreticulation, sometimes almost alutaceous; dorsal punctation coarser and sparser; distance between punctures on pronotum 2–4 puncture diameters; mesoventrite with very coarse sculpture and indistinct punctures; prosternal process smoothed and with arcuate posterior edge; submesocoxal line less curved at anterior angle of metaventrite; pubescence on dorsum rather subrecumbent than suberect; surface behind mentum and between posterior ends of antennal grooves slightly and evenly excavate. 2.3–3.9 mm. Figs 27–37. Subcosmopolitan in stored products; in natural localities in Nepal, India (Andaman Islands), Myanmar, Malaysia ("P. Tioman, Tekek"), Kalimantan, Singapore, Sri Lanka, Indonesia (Java, Sumatra, Moluccas), Philippines (Leyte, Mindanao), Papua New Guinea, Japan, Mexico; Afro-Madagascan, Australian and Polynesian regions *C. (M.) contegens*
- 6(3)a. Lateral lobes of phallobase ("tegmen") very narrow and long, at least 4 times as long as width of base of each lobe 7
- 6(3)b. Lateral lobes of phallobase ("tegmen") not more than 3.5 times as long as width of base of each lobe, usually wider and shorter 8
- 7(6)a. Prosternum with obsolete punctation at anterior edge; metafemur never with tubercle at base of posterior edge; body very dark brown to black with somewhat lighter elytra, ventral surface of head, prohypomera, legs and antennal flagella; pronotum subunicolourous. 2.6–4.8 mm. Figs 51–57. India (Karnataka), Laos *C. (M.) fumatoides* **sp. n.**
- 7(6)b. Prosternum with distinct punctation at anterior edge, reduced only at the middle; metafemur frequently with a tubercle at base of posterior edge; body usually reddish to brown (rarely dark brown to blackish) with much lighter elytra, antennal flagella, legs and usually most underside; pronotum often blackish in the middle and light along periphery. 2.1–4.6 mm. Figs 58–63. Probably subcosmopolitan under artificial conditions and with initial range in natural localities in Africa *C. (M.) fumatus*
- 8(6)a. Lateral lobes of phallobase ("tegmen") flattened and disposed almost in one plane; antennomeres 2 and 3 subequal in length; last labial palpomere clearly widened apically, nearly as long as wide or only 1.5 times as long as wide at apex; body with more or less uniform colouration, with reddish to brownish dorsum; body comparatively small, wide and subparallel-sided 9
- 8(6)b. Lateral lobes of phallobase ("tegmen") moderately or strongly curved posteriorly and laterally; combination of other characters different 10
- 9(8)a. Body almost inconspicuous pubescent and more robust; last labial palpomere only slightly longer than wide at apex; elytra shorter than their width combined and with more arcuate sides; meso- and metatibiae widest as apical fifth; metafemur less than 2.5 times as long as wide; lateral lobes of phallobase ("tegmen") heavily sclerotised, with lateral lobes shorter and rounded at apex. 2.4 mm. Figs 86–94. Cambodia *C. (M.) languescens* **sp. n.**
- 9(8)b. Body clearly pubescent and usually more slender; last labial palpomere about 1.5 times as long as wide at apex; elytra subequal to or somewhat longer than their width combined and with less arcuate sides; meso- and metatibiae widest just at apex; metafemur about or more than 2.5 times as long as wide; lateral lobes of phallobase ("tegmen") slightly sclerotised, with lateral lobes longer and obliquely truncate at apex. 1.7–3.2 mm. Figs 106–113. Subcosmopolitan in stored products and subpantropical in natural localities *C. (M.) nepos*
- 10(8)a. Lateral lobes of phallobase ("tegmen") almost angularly inclined ventrally; anterior part of prosternum and apex of its process with obsolete punctation; posterior edge of prosternal process subtruncate rather than arcuate; body comparatively large: 3.1–5.6 mm; unicolourous straw yellow to brownish or blackish, with lighter basal and subsutural parts of elytra as well as underside, legs and antennal flagella. Figs 127–132. Indonesia (Maluku), Papua New Guinea *C. (M.) robustus* **stat. n.**
- 10(8)b. Lateral lobes of phallobase ("tegmen") gently and arcuately inclined ventrally; combination of other characters usually different 11
- 11(10)a. Lateral lobes of phallobase ("tegmen") with very long and dense hairs or hyaline process at the middle of sides, widened at the middle and rather narrowed apically; last labial palpomere not longer or slightly longer than its width at apex; body usually darker (brownish to dark brown with lighter elytra and appendages) and in general smaller: 2–3.1 mm 12
- 11(10)b. Lateral lobes of phallobase ("tegmen") only with some short subapical hairs, gently narrowed to obliquely truncate or blunt apices, if hyaline process developed, it located at base of lateral lobes of phallobase ("tegmen"); last labial palpomere at least 1.5 times longer than its width at apex; body usually lighter and in general larger: 2–4.8 mm 13

- 12(10)a. Antennomere 3 markedly longer than antennomere 2 and more than twice as long as its width at apex; lateral lobes of phallobase ("tegmen") strongly haired at the middle and without hyaline process, their apices not sharply pointed and gently curved dorsoventrally; last labial palpomere clearly widened to oblique apex; anterior part of prosternum with quite distinct punctation; prosternal process with apex rather widely rounded to subtruncate; body somewhat lighter and, as a rule, larger: 2.2–3.1 mm. Figs 148–154. Subcosmopolitan in stored products and, perhaps, with initial range in Africa *C. (M.) zeaphilus*
- 12(10)b. Antennomere 3 usually not longer than antennomere 2 and much less than twice as long as its width at apex; lateral lobes of phallobase ("tegmen") without distinct hair at the middle, but with a long hyaline process, their apices sharply pointed and strongly curved dorsoventrally; last labial palpomere rather subquadrate; anterior part of prosternum with very reduced punctation or impunctate; prosternal process with apex rounded to subangular; body somewhat darker and, as a rule, smaller: 2–2.6 mm. Figs 74–85. Probably potentially subcosmopolitan in stored products; in natural conditions in China (Shaanxi, Yunnan), India (Kerala), Thailand, Togo, Gambia, Equatorial Guinea *C. (M.) brunneus*
- 13(12)a. Prosternum with distinct punctation and very smoothed sculpture at anterior edge, apex of its process subsemicircular; metafemur considerably more than 2.5 times as long as wide; antennomeres 2 and 3 comparable in length; body in general comparatively more slender and often with darkened pronotum (disk to entire sclerite), elytral apices, metaventrite and sometimes abdomen. 2–4.1 mm. Figs 95–105. Subcosmopolitan in stored products and in natural localities subpantropical; probably with its initial range in the Eastern Hemisphere (most likely in the Indo-Malayan Region) *C. (M.) mutilatus*
- 13(12)b. Prosternum with obsolete punctation and sculpture at anterior edge; metafemur usually not more than 2.5 times as long as wide (in *C. (M.) schioedtei* metafemur sometimes longer); body in general larger: 2.4–4.8 mm; usually colouration different 14
- 14(13)a. Antennomere 3 slightly longer than wide at apex and distinctly shorter than antennomere 2; pronotum somewhat wider at anterior edge than at posterior edge and with slightly arcuate sides; pronotum and elytra with sparse and coarse punctures, interspaces between them about two puncture diameters or broader; tibiae somewhat narrower than antennal club and mesotibia with prominent two teeth in distal fourth; body unicolourous straw reddish, comparatively more slender and smaller: 2.4–2.6 mm. Figs 140–147. Timor *C. (M.) timorensis*
- 14(13)b. Antennomere 3 markedly more than twice (2.5–3.5 times) as long as wide at apex and at least about as long or longer than antennomere 2; medioanterior part of prosternum rectilinear from side; body in general larger: 2.4–4.8 mm; combination of other characters different 15
- 15(14)a. Body more convex, with lateral edges of pronotum invisible or nearly invisible from above; pronotum with subrectilinear sides at basal two-thirds and narrowed markedly more strongly anteriorly than posteriorly; prosternal process distinctly truncate at apex; body variable in colouration: usually unicolourous reddish to dark brown, sometimes with darkened elytra or with lighter part of underside and appendages; elytra comparatively shorter (about 5/6 as long as wide combined); lateral lobes of phallobase ("tegmen") with wider apices. 2.4–4.6 mm. Figs 118–121. Australia (Queensland, New South Wales, Australian Capital Territory, South Australia), New Zealand *C. (M.) pilipennis*
- 15(14)b. Body less convex with lateral edges of pronotum clearly visible from above; pronotum with not vertically sloping and subrectilinear sides, comparably narrowed as anteriorly as posteriorly; prosternal process subsemicircular at apex; elytra comparatively longer 16
- 16(15)a. Antennomeres 2 and 3 comparable in length; body chestnut brown to blackish pronotal disk, but elytra, ventral surface of head, prohypomera, ventrite 1 and appendages considerably lighter or sometimes unicolourous bright reddish with somewhat darkened pronotal disk; lateral lobes of phallobase ("tegmen" longer) less dorsoventrally curved and with wider apices. 2.7–3.3 mm. Figs 14–26. Malaysia (Kalimantan, Sabah), Indonesia (Sulawesi) *C. (M.) assignatus* **sp. n.**
- 16(15)b. Antennomere 3 markedly longer than antennomere 2; colouration different: usually body unicolourous light reddish or with straw yellowish elytra, although sometimes to unicolourous brown (very rarely with infusate pronotal disk and elytral apices); lateral lobes of phallobase ("tegmen") comparatively short, strongly dorsoventrally curved and with narrower apices. 2.4–4.8 mm. Figs 133–139. Vietnam, Laos, Thailand, India (Andaman and Nicobar Islands), Malaysia (Kalimantan), Indonesia (Sumatra, Lombok, Irian Jaya, "Nancorvi", "Sumbawa"), Philippines (Leyte, Luzon, Mindanao), USA (Hawaii) *C. (M.) schioedtei*

Carpophilus (Myothorax) assignatus Kirejtshuk, **sp. n.**
(Figs 14–26)

Type material. Holotype, ♂ (SMNS): Malaysia, "Borneo: Sabah, Crocker Range N.P., NW Keningau, 900–1200 m, 16–20.XI.1996, W. Schawaller". Paratypes: 1♂, 2♀ (SMNS, ZIN), Malaysia, "Borneo: Sabah, Crocker Range N.P., NW Keningau, 900–1200 m, 17.XI.1996, W. Schawaller".

Additional material. 1♀ (NHML), Indonesia, "Sulawesi Utara, Danau Moot, 1 200 m, nr. Kotamobagu, Aug. 1985", "tray 2", "Fog 18, 1 100 m, coffee, I.viii.85", "R. Ent. Soc Lond., Project Wallace, B.M. 1985–10".

Description. Male (holotype). Length 3, breadth 1.2, height 0.7 mm. Body rather convex dorsally and ventrally; chestnut-brown, with darkened disk of pronotum and lighter (reddish) elytra, ventral surface of head, legs, prohypomera and appendages, but slightly darker prosternal disk; dorsum with oily lustre and underside moderately shining; dorsum with recumbent, weakly conspicuous yellowish hairs, somewhat longer than distance between their insertions; underside with shorter and less conspicuous pubescence.

Head surface with not quite distinct punctures, about 1.5 times greater than eye facets in diameter, interspaces between them about half of puncture diameter, with dense and fine, well conspicuous cellular microreticulation. Pronotal surface about as that on head, but punctures at least twice as coarse as eye facets and interspaces between them slightly less than puncture diameter. Elytra with punctures similar to those on pronotum, but finer and with interspaces between them slightly broader than puncture diameter. Uncovered tergites almost as punctured and sculptured as elytral apices, although with sparser punctures. Surface of prosternum with obsolete punctation and rather smooth, but before prosternal process appearing indistinct punctures and smoothed microreticulation. Mesoventrite with very coarse sculpture, submicrogranular. Metaventrte nearly as punctured as elytra, but interspaces between punctures somewhat broader and with smoothed microreticulation. Ventrites with very shallower and finer punctures in comparison with those on the rest surface, interspaces between them with dense and fine cellular microreticulation.

Head about three-fourths as long as distance between eyes, moderately convex and with moderately raised temples. Mandibles moderately strongly developed. Antennae about two-thirds as long as width of head, their club elongate oval (about 1.5 times as long as wide) and comprising about two-sevenths of total antennal length, antennomere 2 about as long as antennomere 3. Antennal grooves deepened at mentum and distinctly outlined, with a rather deep depression between their posterior ends. Mentum about 3 times as wide as long. Last labial palpomere somewhat widened to truncate apex, about 1.5 times as long as wide.

Pronotum rather convex, with subtruncate anterior edge and shallowly emarginate base, sides very slightly arcuate, anterior and posterior angles widely rounded. Elytra about nine-tenth as long as wide combined, sides steeply sloping to lateral edges. Pygidium with nearly transverse apex.

Distance between mesocoxae about one and half and that between metacoxae – one and third as that between procoxae. Prosternal process slightly curved along coxae and moderately widened before arcuately convex apex, which is somewhat narrower than antennal club. Metaventrte slightly convex, with somewhat deepened median suture. Submesocoxal line slightly deviating from posterior edge of coxal cavities at anterior angle of metaventrte and reaching metepisternum at anterior fourth of inner edge. Ventrte 1 as long as hypopygidium and little longer than ventrite 4. Epipleura at base somewhat narrower than antennal club.

Protibia somewhat wider, but meso- and metatibia more or less narrower than antennal club, with nearly straight inner edge, outer edge of meso- and metatibiae with sparse rows of short and stout spines. Profemur about one and third, mesofemur – one and two-thirds, metafemur slightly more than twice as wide as corresponding tibiae. Protarsus about two-thirds as wide as protibia, claws long and narrow, somewhat toothed at base.

Lateral lobes of phallobase (“tegmen”) heavily sclerotised.

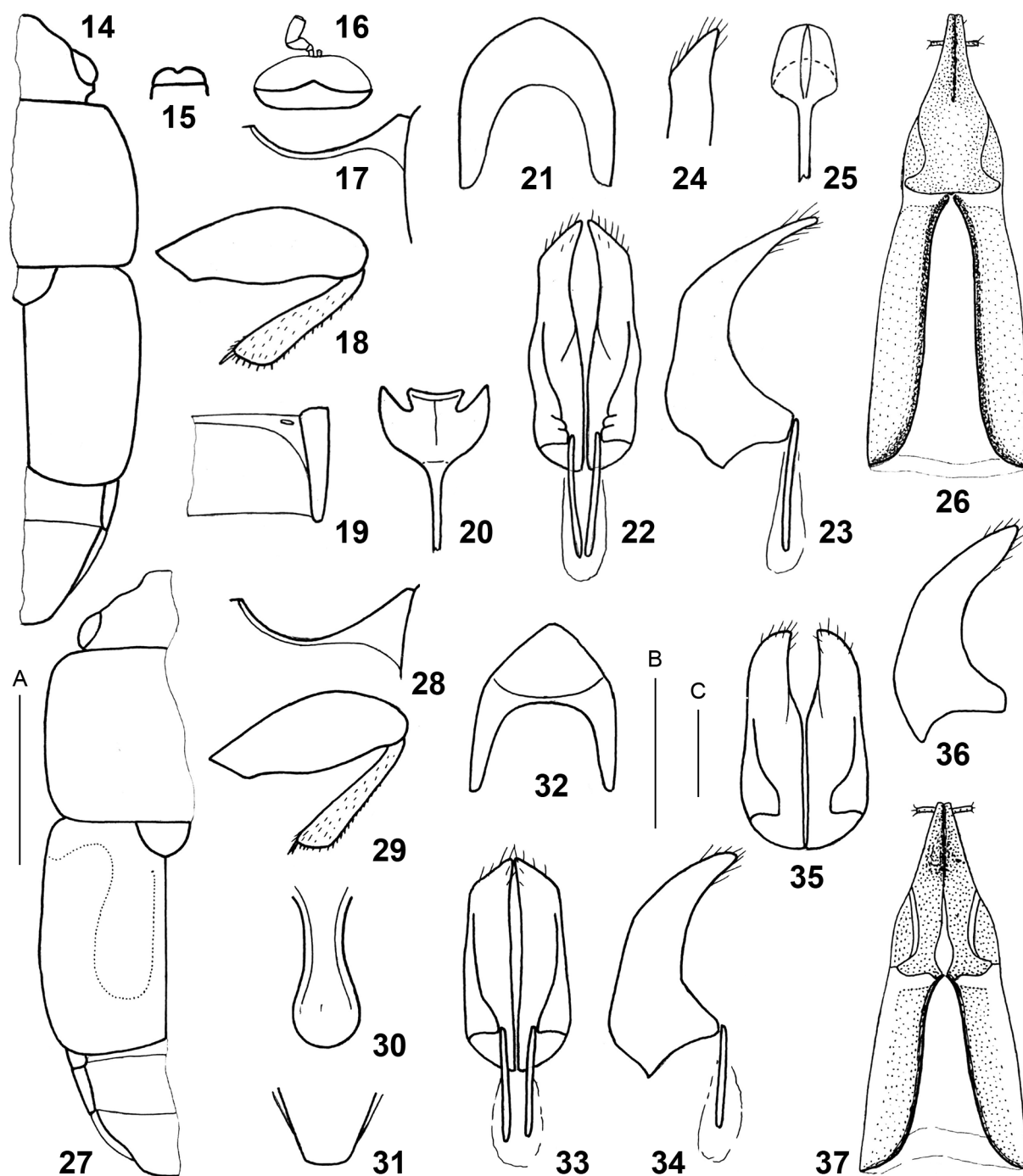
Female. Differs from male in narrower protarsus (about half as wide as protibia) and longer last abdominal segment with pygidium markedly longer than metafemur and widely rounded at apex. Ovipositor well sclerotised.

Variability. Length 2.7–3.3, breadth 1.1–1.3 mm; additional female: length 3.5, breadth 1.7, height 0.9 mm. Largest specimen in the type series (female) with pronotum slightly narrowed anteriorly from base. Punctuation of some paratypes somewhat coarser and microreticulation (particularly on pronotum) more contrasting. The additional specimen (female), in contrast to the holotype and paratypes, has much more robust and subunicolourous bright reddish body with slightly darkened pronotal disk, less conspicuous pubescence, much denser punctures on head and pronotum (interspaces between punctures on pronotum fourth to third of puncture diameter), shallower and indistinct punctures on

elytra, rather coarse punctures on prosternum behind smoothed medioanterior part without visible punctation, apex of prosternal process markedly wider than antennal club, submesocoxal line less deviating from posterior edge of cavity, somewhat wider apices of sclerites of last abdominal segment and somewhat narrower ovipositor.

Diagnosis. This new species has an appearance rather similar to that in *C. (M.) mutilatus* and *C. (M.) pilipennis* (*dimidiatus*-group), although its shape of lateral lobes of phallobase (“tegmen”) resembles *C. (M.) lewisi* (*lewisi*-group) rather than any other members of the subgenus. The differences of the new species from both representatives of the *dimidiatus*-group are given in the key above, however, the darkened pronotal disk and lighter elytra of *C. (M.) assignatus* **sp. n.** make it more similar to *C. (M.) mutilatus*. In addition to the mentioned characters, the new species differs from both species of the *dimidiatus*-group in the deeper antennal grooves and more or less distinct depression between their posterior ends as well as in the structure of apex of its ovipositor and from *C. (M.) mutilatus* also in less distinct punctation of dorsum, outline of submesocoxal line, more deepened median line of metaventrte and wider metatibia with peculiar outline, and from *C. (M.) pilipennis* in narrower tibiae, less distinct punctation and more raised sculpture of dorsum.

Carpophilus (Myothorax) assignatus **sp. n.** has a characteristic shape of lateral lobes of phallobase (“tegmen”) which allows easily to recognise it among other related consubgenera from the Palaearctic and Indo-Malayan regions. The body size and other external characters of this new species can be compared in the first turn with *C. (M.) fumatus* and *C. (M.) fumatoides* **sp. n.** It differs from both of them in the mainly lighter colouration, less distinct punctation of dorsum (particularly on head), subequal length of antennomeres 2 and 3, less distinct punctation and coarser sculpture of mesoventrite, much shorter lateral lobes of phallobase (“tegmen”) and different shape of ovipositor apex. This new species differs from the African *C. (M.) congoensis* Kirejtshuk, 2001 from Equatorial Africa (probably related to both lastly mentioned species) in lighter colouration, less distinct punctation of dorsum (particularly on head), less distinct punctation and more coarse sculpture of mesoventrite, much shorter lateral lobes of phallobase (“tegmen”), but also in the more conspicuous pubescence and light elytra without any spot or patch along suture. The new species under consideration has also some resemblance to the Indo-Malayan *C. (M.) contegens*, *C. (M.) robustus* **stat. n.** and *C. (M.) schioedtei*, but differs from all of them in its not so wide and not strongly dorsoventrally curved lateral lobes of phallobase (“tegmen”), less distinct punctation of dorsum (particularly on head), rather smoothed surface of anterior part of prosternum, narrower and more convex apex of prosternal process, peculiar outline of submesocoxal line, characteristic structure of ovipositor; and also differs from the first in its more subcylindrical body with more subquadrangular pronotum, lighter elytra and appendages, usual shape of male metafemur; from the second in its light colouration with nearly unicolourous elytra, less conspicuous pubescence; from both the first and third of lastly mentioned species in its usually finer body size, subequal length of antennomeres 2 and 3, shorter and



Figs 14–37. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

14–26 – *C. (M.) assignatus* sp. n.; 27–37 – *C. (M.) contegens*. 14 – female body, dorsal view; 15 – anterior part of frons and labrum, dorsal view; 16 – mentum and labial palpus, ventral view; 17, 28 – submesocoxal line of metaventre, ventral view; 18, 29 – male metafemur and tibia, ventral view; 19 – right half of abdominal segment 6 with spiracle, dorsal view; 20 – male ventral plate and spiculum gastrale; 21, 32 – male anal sclerite, ventral view; 22–23, 33–34 – lateral lobes of phallobase (“tegmen”); 22, 33 – ventral view, 23, 34 – lateral view; 24 – apex of lateral lobe of phallobase (“tegmen”), dorsocaudal view; 25 – penis trunk, dorsal view; 26, 37 – ovipositor, ventral view; 27 – male body with dotted outline of lighter part of elytron, dorsal view; 30 – prosternal process, ventral view; 31 – apex of female pygidium, dorsal; 35–36 – (?) extreme in variability of lateral lobes of phallobase (“tegmen”): 35 – ventral view, 36 – lateral view. Scale bars: A – 1 mm (to Figs 14, 27), B – 0.5 mm (to Figs 15–19, 21, 27–32), C – 0.25 mm (to Figs 10, 22, 23–26, 33–37).

Рис. 14–37. Виды подрода *Myothorax* рода *Carpophilus*.

14–26 – *C. (M.) assignatus* sp. n.; 27–37 – *C. (M.) contegens*. 14 – тело самки, сверху; 15 – передний край лба и лабрум, сверху; 16 – ментум и лабиальный щупик, снизу; 17, 28 – заатриковая линия метавентрита, снизу; 18, 29 – задние бедро и голень самца, снизу; 19 – правая половина брюшного сегмента 6 с духальцем, сверху; 20 – вентральная пластинка самца и гастральная спикула; 21, 32 – анальный склерит самца, снизу; 22–23, 33–34 – латеральные доли фаллобазы («тегмен»); 22, 33 – снизу, 23, 34 – сбоку; 24 – вершина латеральной лопасти фаллобазы («тегмена»), дорсокаудально; 25 – ствол пениса, сверху; 26, 37 – яйцеклад, снизу; 27 – тело самца с пунктированным очертанием осветленной части надкрылья, сверху; 30 – отросток переднегруди, снизу; 31 – вершина пигидия самки, сверху; 35–36 – (?) латеральные доли фаллобазы («тегмен») в наиболее изменчивой степени: 35 – снизу, 36 – сбоку. Масштабные линейки: А – 1 мм (к рисункам 14, 27), В – 0.5 мм (к рисункам 15–19, 21, 27–32), С – 0.25 мм (к рисункам 10, 22, 23–26, 33–37).

wider mentum, shorter last labial palpomere. Besides, from *C. (M.) oculatus* from Polynesia this new species differs in the character of its body colouration, subequal length of antennomeres 2 and 3, more dense and more distinct punctation of both dorsum and underside, more contrasting sculpture of integument, narrowly rounded apex of female pygidium, structure genitalia of both sexes. This new species is easily diagnosed from the species of the *lewisi*-group due to its subparallel-sided body, subquadrangular pronotum, dense and not quite clear punctation and rather contrasting sculpture.

Etymology. The epithet of this new species means “assigned”, “appointed”, “determined”.

Carpophilus (Myothorax) brunneus
Chen, Hui et Nuang 2020
(Figs 74–85)

Carpophilus (Myothorax) brunneus Chen, Hui et Huang, 2020: 435 (China: Shaanxi, Yunnan; holotype and paratypes).

Material. India. 4 ex. (NMB, ZIN), “Kerala, 1350 m, 15 km SW Munnar, 1–9.V.1997, 10.02N 76.58E, Kabar Valley, Demlický & Pachlátka”. Thailand. 1 ex. (NMB), “9–14.V.1991, Chiang DAO, 350 m, 19°22N 98°57E, Vit Kubán”, “Thanon Thong Chai, D. Král & V. Kubán”.

Gambia. 5 ex. (ZIN, ZML), “6 km N Kartung in cropped *Borassus* fruit, 20.XI.1977, UTM 28 PCK 851, Loc. 41”, “Cederholm-Danielsson-Hammerstedt-Hedqvist-Samuelsson”.

Guinea-Bissau. 1 ex. (ZIN), “Portug. Guinea, Bissau, 9.III.97, E. Hintz”. Togo. 1 ex. (ZMB), “Bismarckburg, 17.XI.1892, Conradt”.

Diagnosis. This species is very similar to *C. (M.) zeaphilus*, differing from it only in the characters listed in the above key to species. The most peculiar differences of this species from *C. (M.) zeaphilus* consists in the shape of lateral lobes of phallobase (“tegmen”) with a hyaline process on the lateral side of each, subtruncate apex of prosternal process and subtruncate apex of female pygidium. Almost all studied specimens of this species are certainly darker and with sparser punctation than all specimens of *C. (M.) zeaphilus* collected in different part of Africa and examined during this study.

Both mentioned species have a clear feature very distinct among the members of the subgenus: developed hairs or an hyaline process at the middle of each lateral lobe of phallobase (“tegmen”), which have a little reminiscence only of that in *C. (M.) mimicus* from the Equatorial Africa, and *C. (M.) notatus* from Madagascar, although both last-mentioned species are much larger and dorsally somewhat subflattened and with much larger, wider and well sclerotised gonocoxites of ovipositor than those in *C. (M.) brunneus* and *C. (M.) zeaphilus*; besides, the first has the sparser and finer punctation of both dorsum and underside, smoothed integument, slightly conspicuous pubescence, strongly widened and flattened apex of prosternal process, antennomere 3 much longer than antennomere 2, lateral lobes with quite different outline and also with shorter and not so dense hairs, while the second is different in its darker colouration with a light spot on each elytron, much denser and coarser punctation, more raised microreticulation of integument, carinate prosternal process and very long lateral lobes of phallobase (“tegmen”). Among other members of the subgenus, the considered pair of species significantly resemble *C. (M.) nepos*, differing from it not only in the structure of genitalia of

both sexes, but also in the comparatively denser and more conspicuous pubescence, narrower femora and tibiae. It is important to notice that *C. (M.) nepos* not infrequently has nearly unicolourous body and always with punctation on anterior part of prosternum.

This species and *C. (M.) zeaphilus* are more or less similar to some small species or species with very variable body size of the *dimidiatus*-group, namely *C. (M.) contegens*, *C. (M.) dimidiatus*, *C. (M.) languescens* **sp. n.**, *C. (M.) mutilatus*, *C. (M.) pilosellus*, *C. (M.) timorensis* and *C. (M.) truncatus*, but, except differences in the structure of genitalia and much coarser and sparser punctation as well as the differences, which are diagnosed both from one another, these species differs:

– from *C. (M.) contegens* in their pattern of body colouration, usually more arcuate pronotal sides, shorter last labial palpomere, outline of submesocoxal line, narrower tibiae;

– from *C. (M.) dimidiatus* and probably *C. (M.) truncatus* in their usually slightly lighter body, less raised and not so conspicuous pubescence, more arcuate pronotal sides, nearly straight inner edge of meso- and metatibiae, subtruncate apex of female pygidium;

– from *C. (M.) languescens* **sp. n.** in their darker and more subparallel-sided body, last labial palpomere not widened apically, much narrower tibiae, different shape of mesotibia, longer metafemur;

– from *C. (M.) mutilatus* in their darker body with unicolourous pronotum, usually more arcuate pronotal sides, narrower tibiae, subtruncate apex of female pygidium;

– from *C. (M.) pilosellus* in their markedly less pubescent dorsum, outline of submesocoxal line, usually more contrasting sculpture of integument, nearly straight inner edge of meso- and metatibiae;

– from *C. (M.) timorensis* in their more developed pubescence, antennomere 3 not shorter than antennomere 2, more distinct dorsal punctation, medioanterior part of prosternum rectilinear viewing from side, submesocoxal line more deviating from anterior angles of metaventre and simple apex of female pygidium.

Carpophilus (Myothorax) contegens (Walker, 1858)
(Figs 27–37)

Nitidula contegens Walker, 1858: 206 (Sri Lanka, syntypes) = *Carpophilus contegens* Olliff, 1885: 69; *Carpophilus (Myothorax) maculatus* Murray, 1864: 372 (Oahu; syntypes), **syn. n.** = *C. (M.) vittiger* Murray, 1864: 373 (“in India orientali et insulis Waigiou, Aru, Morty, Dorey & c.”; syntypes) = *C. (M.) vittiger* var. *nigritus* Murray, 1864: 373 (Waigiou; syntypes), **syn. n.** = *C. (M.) vittiger* var. *testaceus* Murray, 1864: 273 (Waigiou; syntypes), **syn. n.** = *C. (M.) vittiger* var. *dilutus* Murray, 1864: 373 (Macassar; syntypes), **syn. n.**, non *Colastus dilutus* Motschulsky, 1858.

In total, more than 500 specimens, including type specimens.

Type material. Sri Lanka. 1♂, lectotype of *C. (M.) contegens* (NHML), here designated, “Type”, “Ceylon”, “*contegens*”, “*contigens* Walker (type)”.

Indonesia. 1♂, lectotype of *C. (M.) vittiger* var. *testaceus* (NHML), here designated, and 2♂, 1♀, paralectotypes of *C. (M.) vittiger* var. *testaceus* (NHML), “N. Guin., Wagiu”, “Wag.”, “Wallace”, “ex Mus. Murray”, “Fry Coll. 1905-100”; 1♀, (?) paralectotype of *C. (M.) vittiger* var. *testaceus* (NHML), “Molucas, Morty”, “Wallace”, “M.”, “Ex Mus. Murray”, “*C. vittiger* var. *testaceus* Murr.”; 1♂, lectotype of *C. (M.) vittiger* var. *nigritus* (NHML), here designated, “Wag”, “*vittiger* var.”, “*vittiger* var. *nigritus* Waigou”,

"68.106", "*Carpophilus maculatus nigritus* R.M. Dobson Det., Sept. 1984"; 1♂, (?) paralectotype of *C. (M.) vittiger* var. *nigritus* (NHML), "Moluccas", "Type", "Ex Mus. Murray", "*vittiger* var.", "Fry Coll., 1905-100", "*Carpophilus maculatus nigritus* R.M. Dobson Det., Sept. 1984"; 1♀, (?) syntype of *C. (M.) vittiger dilutus* (NHML), "Moluccas, Jilolo", "Wallace", "Fry Coll., 1905-100"; 1♀, (?) syntype of *C. (M.) vittiger* var. *dilutus* (NHML), "ex Mus. Murray", "N. Guin. Wagiu", "*vittiger* var.", "Wallace", "Fry Coll., 1905-100", "*Carpophilus maculatus dilutus* R.M. Dobson Det., lectotype"; 1♀, lectotype of *C. (M.) vittiger* (NHML), here designated, (?) Indonesia, "Type", "Murr.", "2.64.9", "68.106", "*vittiger*".

USA, Hawaii: 1♂, lectotype of *C. (M.) maculatus* (NHML), here designated (marked as lectotype in the collection by S. Endrödy-Younga in 1964), "68.106", "Type", "*maculatus*"; 1♂, 1♀, paralectotypes of *C. (M.) maculatus* (NHML), "Pacific, Sandw. I.", "ex Mus. Murray", and one of them also "51853", "Type", "Oahu", "*maculatus*, Brit. Mus. Oahu".

Additional material (some selected specimens). Liberia. 1 ex. (ZMB), "Monrovia, ?".

Cameroon. 1 ex. (ZMB), "von Coffea liberica, Botaa, 23.3.1938, Buhr".

Democratic Republic of Congo (Zaire). 1 ex. (MRAC), "Basoko, 18.I.1921, L. Ghesquière".

Tanzania. 1 ex. (ZMB), "zwischen Massa und Tanga, über Magila und Pangan", "14.7-6.8.1891, Conradt".

Seychelles. 15 ex. (ZIN, ZMB), "Mahé, Schultess-Merian"; 1 ex. (ZIN), Poire, 6-8.08.84, Seichel. Soviet Exped. (in Russian).

India. 5 ex. (NMB, ZIN), "Andaman Is., Havelock I., env. of village, N 7, 11°59'N 92°58'E, 22-IV-14.V.1998, Karel & Simon Majer".

Nepal. 1 ex. (SMNS), "Gorkha Distr., Darondi, Khola zw. Motar u. Naya Sangu, 700-1100, Kulturland, 14 Aug. 83, Martens & Schawaller".

Myanmar. 1 ex. (NRS), "Kokee, Kava, Feb. 1919", "J.A. Kusche"; 1 ex. (NRS), "S. SHAN States, 1500 m, Taunggyi, I.VIII-22.IX.34, Malaise"; 1 ex. (NMB), "N. Shan S., 10-15 km N Usipaw, 600-700 m, 22.02.1996, S. Kazantzev".

Singapore. 1 ex. (MSNG), "Singapore, 1894, Modigliani".

Malaysia. 1 ex. (ZMB), "N. Borneo, Kina-Balu"; 2 ex. (ZIN), "Malaysia, Tioman, Tekek, 22.3.1987, T.-E. Leiler".

Indonesia. 1 ex. (TMB), "Sumatra"; 3 ex. (TMB), "Java, Xántus"; 1 ex. (RNHL), "Kerckhoven, Breanger, W. Java"; 1 ex. (RNHL), "Dr. R. Hagen, Tandjong, Morawa, Serdang (N.O. Sumatra)"; 1 ex. (SAM), "Aru Is., H. Elgner"; 1 ex. (ZMB), "N.O. Sumatra, Prov. Langkat, 1906, E. Heinze"; 1 ex. (ZMB), "W. Sumatra, Padang, 23.XII.08, Schoede S.G."; 1 ex. (NRS), "Medan, Mjób"; 2 ex. (RNHL), "Java, Seneng M., (Sem.) Sds, 797, 10-2-32, L.G.E. Kalshoven"; 1 ex. (RNHL), "Getasan, 1100 m, Java, Dec. 33, v. Doesburg"; "van Doesburg"; 2 ex. (AMNY), "Marotai, Moluccas, March, 1945, Gilbert Banner".

Malaysia or Indonesia. 2 ex. (ZMB), "S.O. Borneo, Grabowsky"; 6 ex. (ZMB), "Borneo, Dr. Scheidt".

Japan. 5 ex. (ZMB), "Japan, 1905, E. Kaiser".

Philippines. 1 ex. (SMNS), "Mindanao, 1-3 May 1996, Misamis occ. 1700 m, Don Victoriana, Bolm"; 1 ex. (SMNS), "Mindanao, 30 km E of Malaybalay, Busoi, 5-9 May 1996, Bolm, 1000 m"; 4 ex. (SMNS), "Mindanao, 30 km NW of Maramag, 13-17 May 1996, Bagomingsilang, 1700 m, Bolm"; 1 ex. (SMNS), "Leyte, Lake Danao, forest edge, 500 m, 19.2-8.3.1991, Schawaller & al.".

Papua New Guinea. 3 ex. (TMB), "N. Guinea, Biry, 96", "Friderich-Wilh-hafen" (named by O. Sjöberg as "*mutilatus* Er."); 1 ex. (TMB), "Stephansort, Astrolabe Bai", "N. Guinea, Biry, 1898"; 1 ex. (TMB), "N. Guinea, Biró, 1901", "Friderich-Wilh-hafen" (named by O. Sjöberg as "*mutilatus* Er.").

Polynesia. About 30 ex. (ZIN, ZMUC), "Cook Is., "Friderich-Wilh-hafen" (named by O. Sjöberg as "*mutilatus* Er."); 2 ex. (ZIN, ZMUC), "Tahiti, paa en raad, Appelsin, Galatea"; 1 ex. (ZMUC), "C. fairmarei Deyr., Tahiti"; 2 ex. (ZIN, ZMUC), "Society Is., Huahine, Fare, XI.1985, N.L.H. Krauss".

USA. 33 ex. (ZIN, ZMUC), Hawaii, "Oahu (paa Nordsiden), *Pandanus frugter*, Galatea".

Mexico. 1 ex. (ZIN), "Saltillo Coahuila, Bajío UAAAN, 25°25'23" N 101°00'19" E, 1592 m; collected in dried fruits (orange, apple and lemon), may 15.V.2016 and 01-05.VI.2016, H. Hernandez"; 2 ex. (ZIN), "Chiapas, Angel Albino Corzo, 15° 52' N y 92° 43' E. 640 m, collected in dried fruits (orange, apple and banana), 24.XII.2016, H. Hernandez".

Diagnosis. This species is a member of the *dimidiatus*-group and easily diagnosed due to its characteristic colouration, shape of apex of female pygidium, and genitalia. Among the considered species it has some similarity in colouration to *C. (M.) generosus* **sp. n.**, *C. (M.) notatus*, *C. (M.) robustus* **stat. n.** and *C. (M.) schioedtei*, although the intensity and pattern of its colouration usually are comparatively more stable than

in the mentioned relatives. The genitalia of both sexes are quite distinct, although aedeagus of it is somewhat similar to that in *C. (M.) schioedtei*. Despite the certain variability in external characters, *C. (M.) contegens* differs:

– from *C. (M.) generosus* **sp. n.** in its lightened base of elytra, markedly less developed temples, subequal length of antennomeres 2 and 3, sparser and coarser punctures on most sclerites, more contrasting sculpture on all sclerites (particularly on mesoventrite), shape of prosternal process, outline of submesocoxal lines;

– from *C. (M.) notatus* in its usually larger body, lighter general body colouration, lightened base of elytra, never subcarinate prosternal process, markedly finer punctuation of mesoventrite, female pygidium widely rounded at not explanate apex;

– from *C. (M.) robustus* **stat. n.** and *C. (M.) schioedtei* in its usually smaller and more slender body, comparatively smaller head with, as a rule, moderately raised temples, subequal length of antennomeres 2 and 3, more distinct punctuation on uncovered tergites, usually contrastingly punctured and sculptured prosternum, not emarginate apex of female pygidium.

Light and small specimens of the species under consideration is rather similar and reminiscent of those of *C. (M.) robustus* **stat. n.** and *C. (M.) schioedtei*, although they are clearly distinguished only by structure of their ovipositor apex and, as a rule, proportions in length of antennomeres 2 and 3. The typical specimens of *C. (M.) contegens* differ from those of *C. (M.) schioedtei* in the pattern of body colouration, shape of pronotum, outline of posterior edge of male metafemur and female pygidium, curvature of inner edge of lateral lobes of phallobase ("tegmen"), shape of ovipositor apex, but smallest specimens of both rather similar and only structure of ovipositor remains quite distinct. Finally, some specimens of the considered species are also rather similar to the Polynesian specimens of *C. (M.) oculatus*, but differ from the latter mostly in the character of body colouration, distinct punctuation of prosternum and structure of genitalia of both sexes, although some differences are traced in shape of pronotum and width of basal antennomeres. *Carpophilus (Myothorax) contegens* can be compared also with some species of the *dimidiatus*-group with medium body sizes than with smaller members of the group. Nevertheless, the species under consideration is different from them not only in its peculiar colouration, shape of female pygidium and genitalia of both sexes, but also:

– from *C. (M.) assignatus* **sp. n.** in its usually sparser punctuation of dorsum, markedly different punctuation and sculpture of prosternum, meso- and metaventrite, shorter male metafemur;

– from *C. (M.) fumatoides* **sp. n.** and *C. (M.) fumatus* in its usually finer and sparser punctuation as well as in the less contrasting sculpture of integument, more conspicuous pubescence, never raised tubercle at base of posterior edge of metafemur;

– from *C. (M.) mutilatus* in the outline of its submesocoxal lines, clearer punctuation on uncovered tergites, sparser and finer punctuation and distinct cellular microreticulation on prosternum, meso- and metaventrite, somewhat wider metatibia;

– from *C. (M.) pilipennis* in more subquadrangular shape of its pronotum, usually sparser and finer punctuation of integument (but more distinct punctuation on prosternum), less contrasting cellular microreticulation on dorsum, less medially curved prosternal process with rather subarcuate apex, slightly deepened median part of male metaventrite and longer male metafemur.

Notes. Walker [1858: 206] in his description of *Nitidula contegens* gave quite reliable diagnosis of this species: “nigra, elytris basi (margine excepto) et apud suturum (triente apicali excepta) testaceus”. Nevertheless, Murray [1864] missed this indication, described *C. (M.) maculatus* and *C. (M.) vittiger* having provided it with rather similar diagnoses. Later, Gemminger and de Harold [1868] erroneously synonymised *Ecnomorphus biguttatus* Motschulsky, 1858 (which is regarded in the subfamily Cryptarchinae) and *C. (M.) vittiger* with the varieties proposed to the latter by A. Murray and, finally, Grouvelle [1908] first synonymized *C. (M.) contegens* and *C. (M.) vittiger* as the same variety of *C. (M.) dimidiatus*. The last synonymy supplemented by the Murray’s varieties entered into the Junk’s catalogue [Grouvelle, 1913] and succeeding publications [Blackwelder, 1957; Plaza, 1977, etc.]. Indeed, the type specimens of the varieties proposed by A. Murray for *C. (M.) vittiger* belong to three different species: *C. (M.) contegens*, *C. (M.) robustus* **stat. n.** and *C. (M.) schioedtei*. Unfortunately, Murray [1864] did not write in the original description an exact designation of the specimens examined, their origin and their depositories, particularly for the varieties proposed by him. It seems that the identificational labels were written by him or somebody else later the preparation of the manuscript of his monograph and without proper accuracy. All the specimens from the type series of *C. (M.) vittiger* deposited in NHML were examined, and some disagreement between the text of the Murray’s monograph and labels was made out. This circumstance does not allow to be sure in attribution of part of specimens to the concrete variety, although all of them can be interpreted as the syntypes of *C. (M.) vittiger* in general.

The type specimens of *Nitidula contegens*, *Carpophilus (Myothorax) maculatus*, *C. (M.) vittiger*, and *C. (M.) vittiger* var. *nigritus* used for fixation of these names correspond with the text of the original description and represent the mature specimens of the same species. The lectotype and paralectotypes of *C. (M.) vittiger* var. *testaceus* are immature, but without doubts conspecific with the specimens mentioned above. The labels of the specimens indicated as *C. (M.) vittiger* var. *dilutus* are different from that which can be interpreted as suited to the text of the description and, therefore, these specimens are designated here as questional syntypes. One of specimen from the type series of *C. (M.) vittiger* var. *testaceus* is conspecific with the specimens of *C. (M.) vittiger* var. *robustus* (see below). The synonymy of *C. (M.) maculatus* and *C. (M.) vittiger* was established by Hinton [1945], probably after his re-examination of the types listed above.

Carpophilus (Myothorax) dimidiatus (Fabricius, 1792)
(Figs 38–45, 153)

Nitidula dimidiata Fabricius, 1792: 261 (“Indie Occidentali”; syntypes), non *Cateretes dimidiatus* Heer, 1841 = *Carpophilus pusillus* Stephens, 1830: 51 (East Indies; syntypes) = *C. auropilosus* Wollaston, 1854: 117 (Madeira; ? holotype).

In total, some hundred specimens from different zoogeographical regions (mostly from the Afro-Madagascan Region) represented in almost each collection, type specimens of *Nitidula dimidiata* and others from many of all zoogeographic regions, except Antarctic one.

Type material. 1♀, lectotype of *N. dimidiata* (ZMUC), designated by Dobson [1956], “*Carpophilus dimidiatus* (F.), Lectotype, R.M. Dobson Det., January 1956”; 1♂, paralectotype of *N. dimidiata* (ZMUC), “ex Am. mer. – Schmidt”, “AlloTYPE des. Dobson 1956”; 11 ex., (?) paralectotypes of *N. dimidiata* (ZMB), “8378”, “*dimidiata* Fab., Ld., Am. Ins., Lund” (with additional labels under different specimens: 1 ex. – “Demerary”, 1 ex. – “Cuba, Otto”, 1 ex. – “Latjunjoa”, 1 ex. – “Am. spt., Dej”, 1 ex. – “Carot. m., Zimm.” – the specimens with these labels could apparently be added to *N. dimidiata* after description by J.C. Fabricius or somebody else).

Additional material (some selected specimens). India. 1 ex. (ZSI), “Ja. 2, Tommu, 25.5.72, on Mango leaf, T. Sengupta”.

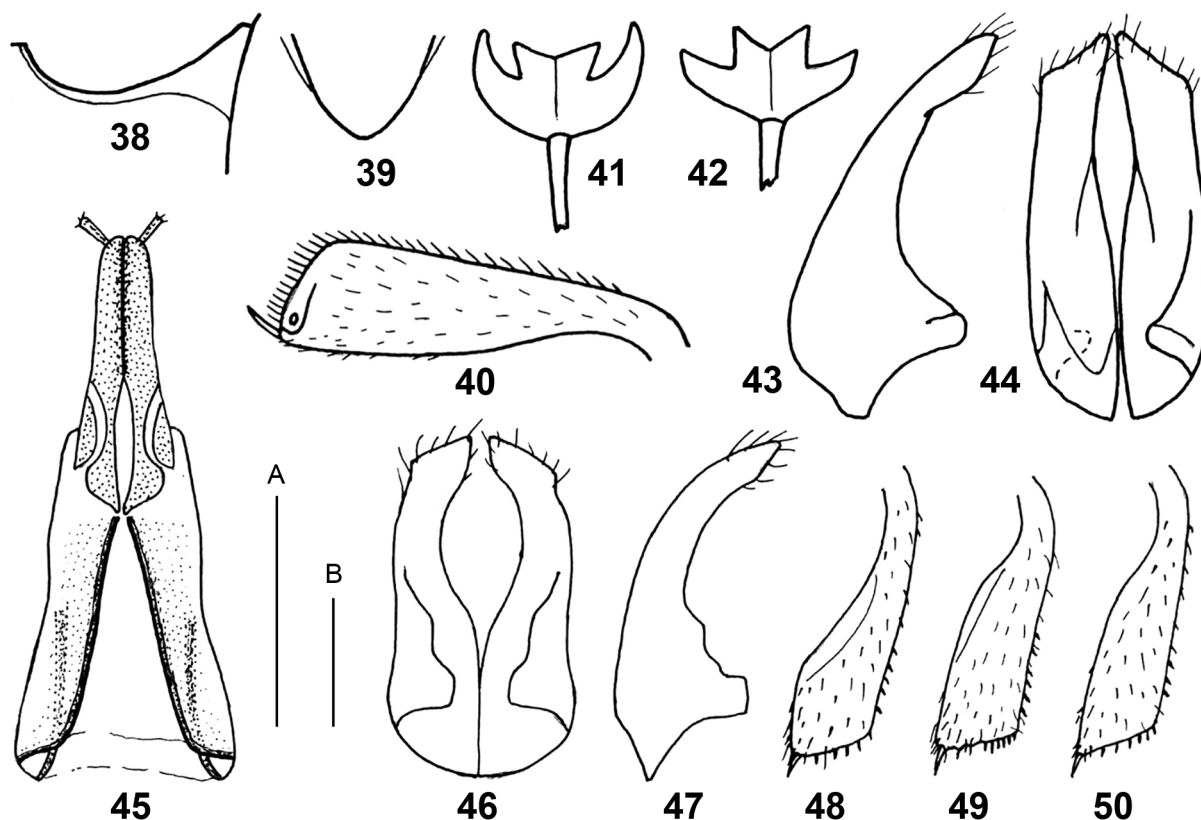
Nepal. 1 ex. (NMW), “E-Nepal, Arun Valley, Sultibari, 500 m, 11–14.6.1988, Probst”.

Indonesia. 16 ex. (RNHL, ZIN), “In old fruits of native castanea on the ground”, “Buitenzorg, 10-II-1924, Dr. Kalshoven L. – 19”; 2 ex. (RNHL), “Java, Seneng M., (Sem.) Sds, 797, 10-2-32, L.G.E. Kalshoven”; 1 ex. (RNHL), “Getasan, 1100 m, Java, Dec. 33, v. Doesburg”; some hundred specimens (ZIN, ZMB), mostly from Afro-Madagascan Region, North Africa, Madeira, Europe, Ukraine (Kharkov), Russia (Leningrad Region, St Petersburg, Krasnodar Region), etc.

Diagnosis. This species is characterised by comparatively small and usually dark body, comparatively short elytra, comparatively narrow protibia and rather short lateral lobes of phallobase (“tegmen”), although identification of this species in some cases is very difficult because of a great scope of variability of some characters. Among small members of the *dimidiatus*-group with subparallel-sided and convex body (*C. (M.) brunneus*, *C. (M.) languescens* **sp. n.**, *C. (M.) nepos*, *C. (M.) pilosellus*, *C. (M.) timorensis*, *C. (M.) truncatus*, *C. (M.) zeaphilus*) it can be diagnosed due to not only its peculiar structure of lateral lobes of phallobase (“tegmen”), but also due to the following characters:

– from *C. (M.) languescens* **sp. n.** and *C. (M.) nepos* due to its more slender, usually darker and not unicolourous body, denser and more conspicuous pubescence, usually more subquadrangular pronotum, much denser and usually significantly finer punctuation of dorsum, not quite subovoid antennal club, different length of antennomeres 2 and 3, more distinct punctuation and sculpture of anterior part of prosternum, outline of submesocoxal line and more curved inner edge of metatibia, different structure of ovipositor; and from *C. (M.) languescens* **sp. n.** also due to its wider prosternal process, narrower legs with oblique apex of meso- and metatibiae;

– from *C. (M.) brunneus* and *C. (M.) zeaphilus* due to its more slender and usually darker body, denser and more conspicuous pubescence, more subquadrangular pronotum, denser and coarser punctuation on dorsum, longer last labial palpomere, outline of submesocoxal line and more curved inner edge of metatibia; and from the first of them also due to its different length of antennomeres 2 and 3;



Figs 38–50. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

38–45 – *C. (M.) dimidiatus*; 46–48 – *C. (M.) truncatus*; 49–50 – *C. (M.) pilosellus*. 38 – submesocoxal line of metaventre, ventral view; 39 – apex of female pygidium, dorsal view; 40 – male metatibia, dorsal view; 41 – characteristic ventral plate and spiculum gastrale; 42 – aberrant ventral plate and spiculum gastrale of specimen from the West Caucasus; 43–44 – lateral lobes of phallobase (“tegmen”) of usual structure: 43 – lateral view, 44 – ventral view; 45 – ovipositor, ventral view; 46–47 – lateral lobes of phallobase (“tegmen”) of paralectotype (NHML): 46 – ventral view, 47 – lateral view; 48–50 – male metatibia, dorsal view: 48 – specimen from Seychelles (ZIN), 49 – lectotype (ZMMU), 50 – specimen from Japan (ZIN). Scale bars: A – 0.5 mm (to Figs 38–40, 48–50), B – 0.25 mm (to Figs 41–47).

Рис. 38–50. Виды подрода *Myothorax* рода *Carpophilus*.

38–45 – *C. (M.) dimidiatus*; 46–48 – *C. (M.) truncatus*; 49–50 – *C. (M.) pilosellus*. 38 – затазиковая линия метавентрита, снизу; 39 – вершина пигидия самки, сверху; 40 – задняя голень самца, сверху; 41 – ventральная пластинка и гастральная спикула самца характерного строения, снизу; 42 – ventральная пластинка и гастральная спикула самца aberrантного строения с Западного Кавказа, снизу; 43–44 – латеральные доли фаллобазы («тегмен») обычного строения: 43 – сбоку, 44 – снизу; 45 – яйцеклад, снизу; 46–47 – латеральные доли фаллобазы («тегмен») паралектотипа (NHML): 46 – снизу, 47 – сбоку; 48–50 – задняя голень самца, сверху: 48 – экземпляр с Сейшельских островов (ZIN), 49 – лектотип (ZMMU), 50 – экземпляр из Японии (ZIN). Масштабные линейки: A – 0.5 мм (к рисункам 38–40, 48–50), B – 0.25 мм (к рисункам 41–47).

– from *C. (M.) pilosellus* due to the peculiarities listed in the above key;

– from *C. (M.) timorensis* due to the antennomere 2 distinctly longer than antennomere 3, usually darker colouration, distinct and denser punctures on prosternum, more distinct dorsal punctation, medioanterior part of prosternum rectilinear from side, outline of submesocoxal line, wider metatibia with convex inner edge, simple apex of female pygidium;

– from *C. (M.) truncatus* mostly due to the different shape of metatibiae and somewhat shorter antennomere 3.

The species under consideration is also similar to *C. (M.) mutilatus*, which has an intermediate position between larger and smaller members of the *dimidiatus*-group, however, *C. (M.) dimidiatus* differs from it not only due to its somewhat smaller, convex and more slender body, but also due to its peculiar character of body colouration, unicolourous pronotum, more raised and more conspicuous pubescence on dorsum, difference in the

length of antennomeres 2 and 3, outline of submesocoxal line, somewhat wider meso- and metatibiae, which are more curved along inner edge, longer lateral lobes of phallobase (“tegmen”) and peculiar ovipositor.

Notes. R.M. Dobson examined the type series of *Nitidula dimidiata* in 1956 and designated two specimens as mentioned above in the “Type material”. Two other paralectotypes, deposited in ZMUC were identified by him as “*Carpophilus languidus* Er.” (although they cannot be regarded as the latter as well). The designated lectotype of *Nitidula dimidiata* has 2.8 mm in length, dark brown body with lightened elytra and distinctly convex outer edge of metatibia. The type series of *Carpophilus (Myothorax) pusillus* and *C. (M.) auropilosus* should be deposited in NHML.

Sometimes specimens, which are rather similar to one another, can be attributed to one of the related species, usually interpreted as *C. (M.) dimidiatus* and *C. (M.) pilosellus*. In some rare cases it is quite problematical

to find a correct decision to identify specimens with partly intermediate state of characters (including characters in shape of lateral lobes of phallobase ("tegmen")). The species distinctness of these consubgenera needs a further study. Most African specimens (particularly from South Africa) are dark to completely blackish with the coarser and somewhat sparser punctation (with very distinct punctures on pygidium, nearly as large as those on other sclerites of dorsum), while most Indo-Malayan, Palearctic and Nearctic specimens examined are comparatively lighter or with darkened pronotum and thoracic underside, although the Australian, Central and South American specimens are not infrequently completely black. Besides, the African representatives (particularly from South Africa) are usually rather shining from below (with smoothed interspaces on thoracic underside), while specimens from other areas have more or less clearly microsculptured interspaces on thoracic underside. This difficulties in distinction of these species become even more than shown above, if representatives from Madagascar and Seychelles (as well as from some African areas) are included into consideration, where there is another form traditionally as *C. truncatus*, namely *C. (M.) imitatus*, described from Australia. The latter is very similar to dark variety of *C. (M.) dimidiatus*, but with the male metatibia rather like that in *C. (M.) pilosellus* than that in *C. (M.) dimidiatus*. Alone external difference of *C. (M.) truncatus* from other mentioned species is a stripe along inner edge of metatibia, which is widened in the anterior half of tibia, although among the representatives of *C. (M.) pilosellus* from the Indo-Malayan Region some have metatibia rather similar to that in typical *C. (M.) truncatus*. Finally, the lateral lobes of phallobase ("tegmen") in *C. (M.) dimidiatus* usually are markedly shorter and wider than in most specimens of *C. (M.) pilosellus*, but these lateral lobes in *C. (M.) truncatus* and *C. (M.) imitatus* are somehow characterised by the intermediate length and width of the lateral lobes and sometimes *C. (M.) pilosellus* also has the shorter lateral lobes than those in characteristic specimens.

In connection with the fact that representatives of the subgenus *Myothorax* have been very frequently named as "*dimidiatus*", there are a lot of misusage of this name in literature. At least over than 200 years this species was increasing its range to subcosmopolitan one. At present it is difficult to be sure in opinion on an initial range of this species before it was distributed by human activity, however, it could be supposed an initial palaeotropical distribution of it. It seems to be rather common in natural localities in the Afro-Madagascan and Australian regions, in particular, in South Africa, as well as Central and South America than in other regions of the globe. The type locality of *Nitidula dimidiata* is Central America, that of *Carpophilus pusillus* – the East Indies and that of *C. auropillosus* – Madeira.

Carpophilus (Myothorax) fumatoides Kirejtshuk, **sp. n.**
(Figs 51–57)

Material. Holotype, ♂ (NMP): Laos, "6–11.5.1997, 20 km NW Louang, Namtha, 21°09'N 101°18'E, 800–1000 m, Jendek & Šuaša". Paratypes: 1♂ (ZIN), Laos, "6–11.5.1997, 20 km NW Louang, Namtha, N 21°09.2, E 101°18.7 al., 800–1000 m, J. Jendek & O. Šuaša"; 9 ex. (♂♂, ♀♀) (TMB, ZIN), India, "Karnataka, Shimoga, Jog Falls, 500 m, leg. Gy. Topál", "singled near river Sharavati, 2.III.1980".

Description. Male (holotype). Length 4.7, breadth 1.7, height 0.8 mm. Body rather convex dorsally and moderately ventrally; blackish to black with brown reddish base and anterior part of head, edges of pronotum, proximal four-fifths of elytra, apical ventrites, antennal flagella and legs; dorsum with an oily lustre and underside moderately shining, dorsum with moderately dense and long, recumbent, rather conspicuous yellowish hairs, about 2.5 times as long as distance between their insertions.

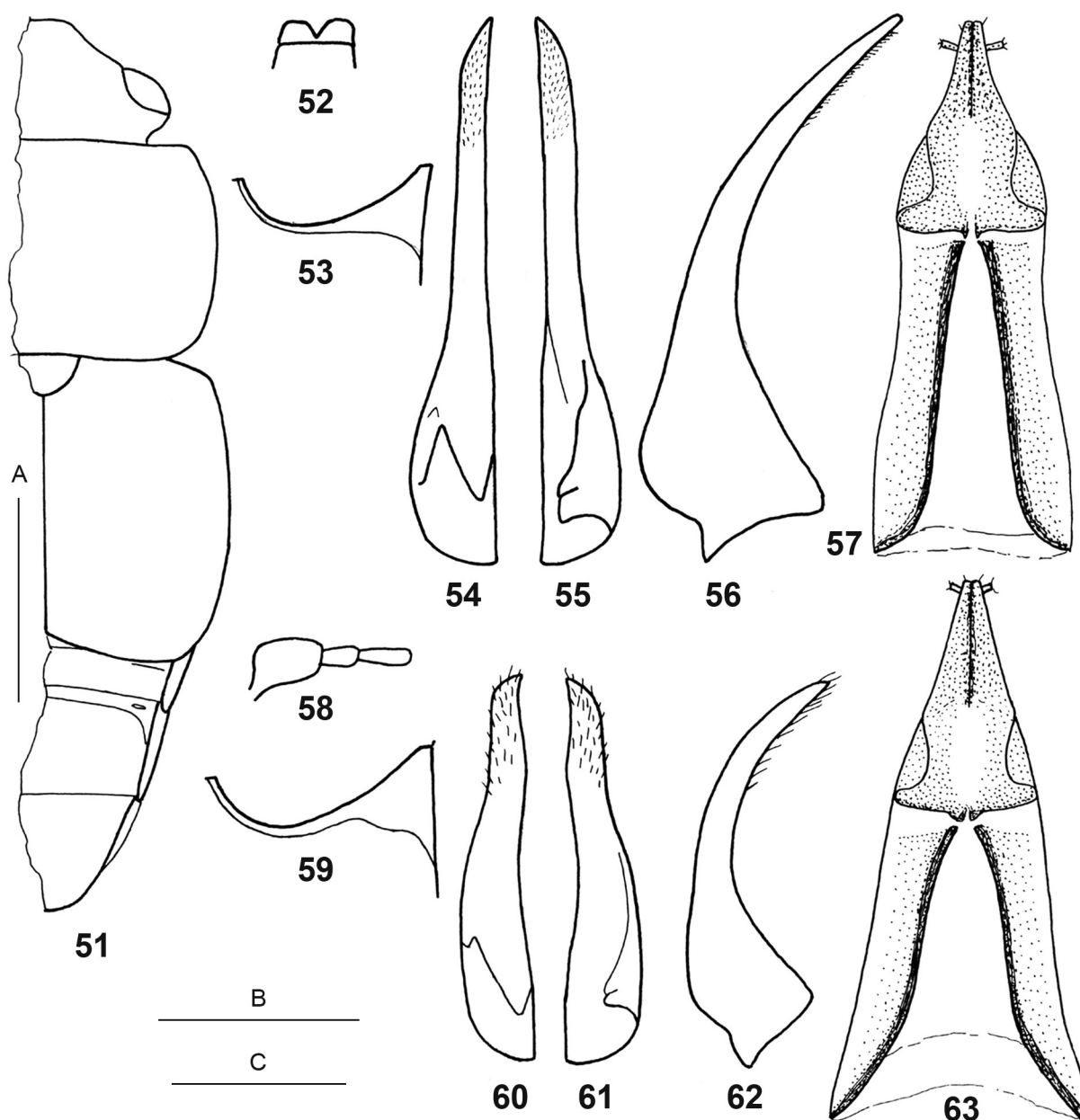
Head surface with distinct deep (sometimes contiguous) punctures, 2–2.5 times as coarse as eye facets in diameter, interspaces between them at most fourth of puncture diameter, with dense cellular microreticulation. Pronotum with similar punctation and microreticulation, but punctures somewhat coarser and sparser, with interspaces fourth to third of puncture diameter, although at sides punctures rather dense and mostly contiguous. Elytra with similar, but somewhat elongate and markedly shallower punctures than those on head and pronotum and interspaces between them about third of puncture diameter and very contrastingly cellularly microreticulated, at apices punctures becoming finer. Uncovered tergites with deep and somewhat elongate punctures with cross-section about twice as coarse as those of eye facets, interspaces between them about half puncture cross-section and with very contrasting microreticulation. Apical ventrites with fine punctures, as coarse as eye facets, interspaces between them about one puncture diameter and with contrasting microreticulation. Prosternum with obsolete punctation and rather smoothed at anterior edge, but with distinct and shallow punctures at coxae and on intercoxal process (about 1.5 times larger than facets), interspaces between them about third of puncture diameter and narrower, with dense cellular microreticulation. Mesoventrite with quite distinct irregular punctures (as coarse as on head and pronotum) and very coarse sculpture. Metaventrite with regular punctures, somewhat finer than on those on head and pronotum, interspaces between them about as great as one puncture diameter and with somewhat smoothed microreticulation. Ventrite 1 with fine and sparse punctures, interspaces between them smoothly microreticulated.

Head slightly shorter than distance between eyes, weakly convex and with well developed temples. Antennae about three-fourths as long as width of head, their club suboval (about one and third as long as wide and with widest antennomere 10) and comprising about two-sevenths of total antennal length, antennomere 3 slightly longer than antennomere 2. Pronotum subquadrangular, moderately convex and only at sides rather steeply convex, its anterior and posterior angles widely rounded. Elytra about five-sixths as long as combined width, at sides steeply sloping to lateral edges. Pygidium rather subtruncate than subarcuate at apex, about two-thirds as long as metatibia.

Antennal grooves moderately deepened at mentum, their posterior ends joined by transverse shallow depression. Mentum about 3 times as wide as long. Last labial palpomere nearly subcylindrical to scarcely widened to truncate apex, about twice as long as wide at apex.

Distance between mesocoxae as great as that between metacoxae, almost 1.5 times as great as that between procoxae. Prosternal process very slightly curved along coxae and rather widened before subtruncate apex, its sides rounded, where it is somewhat wider than antennal club. Metaventrite subflattened, with slightly deepened median suture. Submesocoxal line slightly arcuately deviating from the posterior edge of coxal cavities at outer angle of metaventrite and reaching metepisternum at anterior fourth of its inner edge. Ventrite 1 about as long as hypopygidium and somewhat longer than ventrite 4. Hypopygidium about two-thirds as long as metatibia. Epipleura at base about as wide as antennal club.

Tibiae comparatively short, protibia markedly wider, meso- and metatibiae subequal to width to antennal club, with nearly straight inner edge (or slightly concave in metatibia), outer edge of meso- and metatibiae with sparse rows of short and rather stout



Figs 51–63. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

51–57 – *C. (M.) fumatoides* sp. n.; 58–63 – *C. (M.) fumatus*. 51 – male body with spiracles of abdominal segments 5 and 6, dorsal view; 52 – anterior part of frons and labrum, dorsal view; 53, 59 – submesocoxal line of metaventricle, ventral view; 54–56, 60–62 – lateral lobes of phallobase (“tegmen”): 54, 60 – dorsal view, 55, 61 – ventral view, 56, 62 – lateral view; 57, 63 – ovipositor, ventral view; 58 – antennomeres 1–3. Scale bars: A – 1 mm (to Fig. 51), B – 0.5 mm (to Figs 52–53, 58, 59), C – 0.25 mm (to Figs 54–57, 60–63).

Рис. 51–63. Виды подрода *Myothorax* рода *Carpophilus*.

51–57 – *C. (M.) fumatoides* sp. n.; 58–63 – *C. (M.) fumatus*. 51 – тело самца с дыхальцами на брюшных сегментах 5 и 6, сверху; 52 – передняя часть лба и лабрум, сверху; 53, 59 – субмезококсовая линия метавентрита, снизу; 54–56, 60–62 – латеральные доли фаллобазы («тегмен»): 54, 60 – сверху, 55, 61 – снизу, 56, 62 – сбоку; 57, 63 – яйцеклад, снизу. 58 – антенномы 1–3. Масштабные линейки: А – 1 мм (к рисунку 51), В – 0.5 мм (к рисункам 52–53, 58, 59), С – 0.25 мм (к рисункам 54–57, 60–63).

spines. Pro- and mesofemora about 1.7 and metafemur 2.5 times as wide as corresponding tibiae, metafemur 2.5 times as long as wide and slightly convex at posterior edge. Protarsus about half as wide as protibia, claws long and narrow, somewhat toothed at base.

Lateral lobes of phallobase (“tegmen”) heavily sclerotised.

Female. Differs from male in subflattened metaventricle along midline, narrower protarsus (two-fifths as wide as protibia), longer last abdominal segment with subrounded-subangular and slightly subexplanate apex of pygidium (both pygidium and hypopygidium slightly longer than metatibia). Ovipositor well sclerotised.

Variability. Length 2.6–4.8, breadth 1.1–1.7, height 0.6–0.8 mm. The paratypes from India are smaller and with more subquadrate pronotum. The males from this series have protarsus about two-thirds as wide as protibia. This species is extremely variable in body size and colouration, but in general the body of the studied specimens is rather dark to nearly unicolourous dark brown (including appendages).

Diagnosis. This new species is similar to *C. (M.) fumatus*, although differs from it in the more widely reduced punctation at the middle of anterior part

of prosternum, more or less clear transverse depression between the posterior ends of antennal grooves, metafemur never with tubercle at base of its posterior edge, also in general darker body and shape of the ovipositor apex. The lateral lobes of phallobase ("tegmen") of both these species has a rather similar structure, but somewhat differs in length and thickness of lateral lobes. Also, lateral lobes of phallobase ("tegmen") of the new species in contrast to that of *C. (M.) fumatus* is rather heavily sclerotised.

From other species of the *dimidiatus*-group this new species is clearly distinguished in its long lateral lobes of phallobase ("tegmen"). The body size and colouration of this new species are similar to those in *C. (M.) assignatus* sp. n., *C. (M.) generosus* sp. n., *C. (M.) mutilatus*, *C. (M.) schioedtei*, *C. (M.) pilipennis* and in particular to the darkest specimens of *C. (M.) robustus* stat. n. The characters of punctuation and sculpture of sclerites on underside as well as the structure of ovipositor and many other external structural peculiarities of this new species in general resemble those of *C. (M.) assignatus* sp. n. rather than other above listed species. Identification of their representatives in some cases presents a certain difficulty because of variability of characters of these species. Nevertheless, in addition to the peculiar feature in structure of lateral lobes of phallobase ("tegmen"), *C. (M.) fumatoides* sp. n. differs:

- from *C. (M.) assignatus* sp. n. in its antennal club markedly darker than flagellum, difference in length of antennomeres 2 and 3; from *C. (M.) contegens* in its somewhat larger body, pattern of body colouration, shape of gonocoxites;
- from *C. (M.) generosus* sp. n. in its less contrasting sculpture of dorsum, lack of clear antennal grooves behind the middle of mentum, not truncate or subtruncate apex of prosternal process and different outline of submesocoxal line;
- from *C. (M.) mutilatus* in the smoothed anterior part of prosternum, difference in length of antennomeres 2 and 3, darkened antennal club, disposition of styli on ovipositor;
- from *C. (M.) robustus* stat. n. and *C. (M.) schioedtei* in its not so great difference in length of antennomeres 2 and 3, and shape of gonocoxites;
- from *C. (M.) pilipennis* in its more slender and much less convex body (particularly pronotum), usually much darker body, antennal club darker than flagellum, not so deepened midline of metaventricle and shape of gonocoxites.

The new species under consideration has a certain similarity to *C. (M.) congoensis* from Equatorial Africa, but it is clearly distinct from it in the peculiarities of body colouration, denser punctuation and not very smooth integument, antennomere 3 longer than antennomere 2, shape of gonocoxites.

Etymology. The name of this species is formed from the name of the related species "*fumatus*" (blacken, smocked) and "*ideus*" (from Greek "*eidos*" – idea, species, kind).

Carpophilus (Myothorax) fumatus Boheman, 1851
(Figs 58–63)

Carpophilus fumatus Boheman, 1851: 564 ("Caffraria"; syntypes) = *C. ochropterus* Klug, 1862: 209 (Mozambique; syntypes).

In total, about a thousand specimens from Africa and Madagascar, deposited in many collections, including type specimens below and others mostly in the Afro-Madagascan Region (MRAC, NRS, ZMB, ZIN, ZMB, ZML, etc.).

Type material. South Africa. 1 ex., lectotype of *C. (M.) fumatus* (NRS), designated by Kirejtshuk [1996], "Caffraria J. Wahlb."; 1 ex., paralectotype of *C. (M.) fumatus* (NRS), "Cap. B. Spei., J. Wahlb."

Mozambique. 1 ex., lectotype, here designated, and 1 ex., paralectotype of *C. (M.) ochropterus* (ZMB) (marked as lectotype in the collection by S. Endrödy-Younga), "Mosambik, Peters", "*ochropterus* Kl., Madag., Goud."; 9 ex., at least partly probably paralectotype(s) of *C. (M.) ochropterus* (ZMB), "cotypes" *ochropterus* – "53763", "*fumatus* Boh., Gerst.", Ugono v.d. mont. Deck" (under one of specimens also "Mosambik, Peters").

Additional material (some selected specimens). Portugal. 5 ex. (ZML), Madeira.

Algeria. 4 ex. (FMNH).

Tunisia. 5 ex. (ZML).

USA. 2 ex. (ZML), "USA, Hawaii: W. Waihee".

Notes. This species is very similar to the previous one (see above and data in Kirejtshuk [1996]).

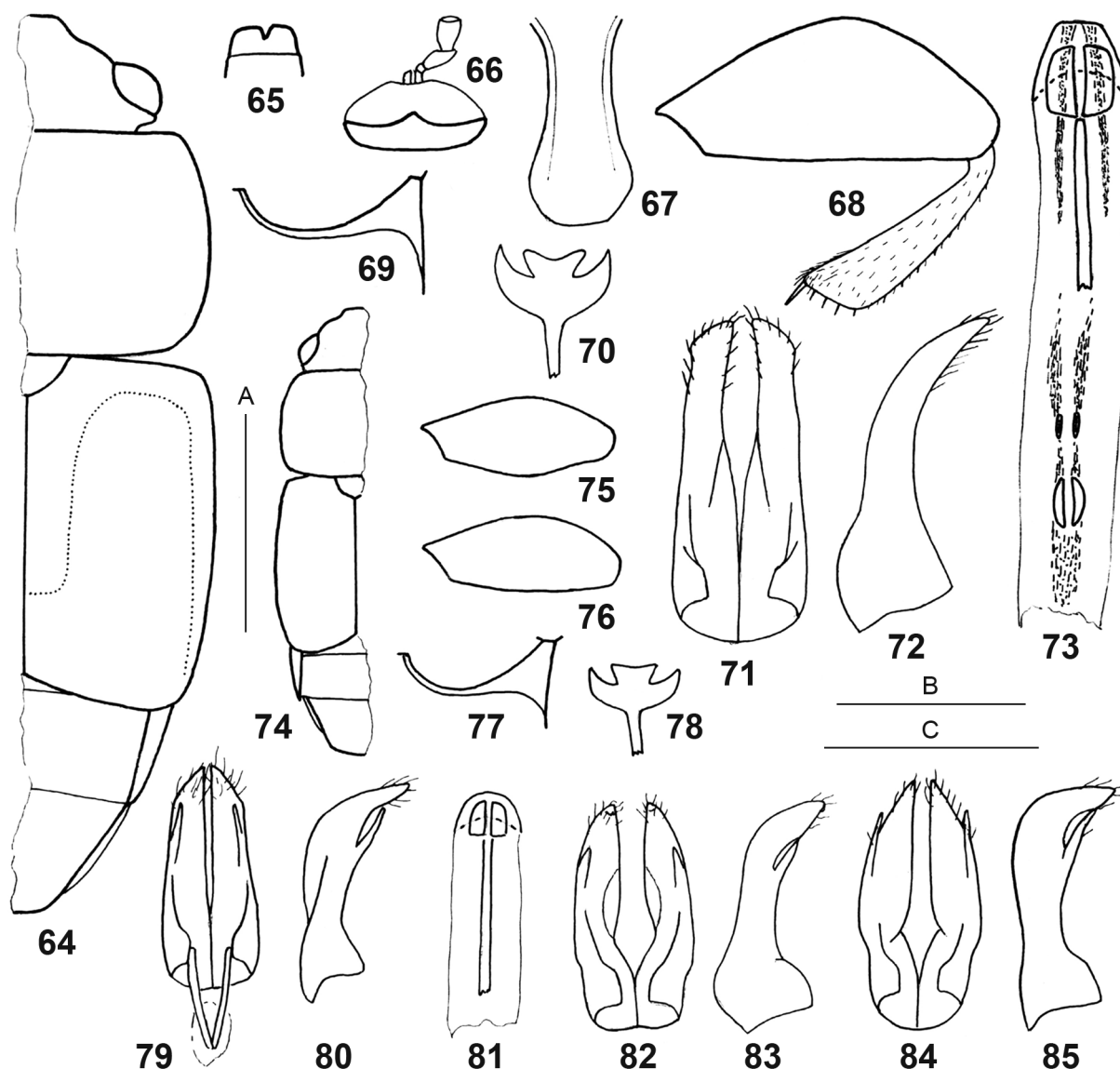
Carpophilus (Myothorax) generosus Kirejtshuk, sp. n.
(Figs 64–73)

Material. Holotype, ♂ (SMNS): Indonesia, "Bali, Danau Buyan, 1300 m, 19–21.2.1994, Bolm". Paratype: 1♂ (RNHL), Indonesia, "Getasan, 1100 m, Java, Dec. 33, v. Doesburg".

Description. Male (holotype). Length 4.2, breadth 1.3, height 0.8 mm. Body rather convex ventrally and dorsally; black with bright brown reddish base and anterior part of head, base and subsutural places of elytra, abdominal apex, prohypomera, mouthparts, antennal flagella and legs; dorsum almost dull and underside with a faint oily lustre; dorsum with moderately dense and long, subrecumbent (forming clear arc to plane of integument), rather conspicuous yellowish hairs, about twice and more longer than distance between their insertions.

Head surface with quite distinct, very dense (subcontiguous) and deep regular punctures, about twice as coarse as eye facets in diameter, interspaces between them with dense and extremely contrasting cellular microreticulation. Pronotum with similar punctuation, but punctures somewhat coarser and much sparser, interspaces between them about two-thirds of puncture diameter, with somewhat smoothed, dense cellular microreticulation, but at sides punctures subcontiguous. Elytra with punctures markedly finer and rather shallower than those on head and pronotum (slightly coarser than eye facets) and with interspaces between them markedly broader than one puncture diameter and rather contrastingly microreticulated, at apices punctures becoming finer. Uncovered tergites and ventrites with punctures very similar to those on elytra, but interspaces between them about one puncture diameter or smaller and with very contrasting microsculpture. Prosternum with distinct punctures only at coxae and at sides (about as those on uncovered tergites and apical ventrites), narrow interspaces between them and space at sides of anterior part with more or less distinct cellular microreticulation, space at the middle of anterior edge completely smooth. Mesoventricle as coarsely punctured as head and sides of pronotum, but finer and slightly shallower punctures, very narrow interspaces between them contrastingly microreticulated. Metaventricle with very dense and distinct punctures, as coarse as those on head and pronotum, but clearly shallower, interspaces between them about third of puncture diameter and with dense and very contrasting microreticulation.

Head about four-fifths as long as distance between eyes, weakly convex and with well developed temples. Mandibles rather well developed. Antennae about three-fourths as long as width of head, their club rather subovoid (about 1.5 times as long as wide and with antennomere 10 widest) and comprising almost fourth of total antennal length, antennomere 3 slightly longer than antennomere 2. Pronotum with somewhat arcuate sides,



Figs 64–85. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

64–73 – *C. (M.) generosus* sp. n., male, holotype; 74–85 – *C. (M.) brunneus*. 64 – body with dotted outline of lighter part of elytron, dorsal view; 65 – anterior part of frons and labrum, dorsal view; 66 – mentum and labial palpus, ventral view; 67 – prosternal process, ventral view; 68 – metafemur and tibia, ventral view; 69 – submesocoxal line of metaventrite, ventral view; 70 – ventral plate and spiculum gastrale; 71–72 – lateral lobes of phallobase ("tegmen"): 71 – ventral view, 72 – lateral view; 73 – penis trunk with armature of inner sac, dorsal; 74 – body of male from India (Kerala) (ZIN), dorsal view; 75 – mesofemur of the same male, ventral view; 76 – metafemur of male from Thailand (NMB), ventral view; 77 – submesocoxal line of metaventrite of specimen from India (Kerala) (ZIN), ventral view; 78 – ventral plate and spiculum gastrale of the same male; 79–80 – lateral lobes of phallobase ("tegmen") of the same specimen: 79 – ventral view, 80 – lateral view; 81 – penis trunk of the same specimen, dorsal view; 82–83 – lateral lobes of phallobase ("tegmen") of specimen from Thailand (NMB): 82 – ventral view, 83 – lateral view; 84–85 – lateral lobes of phallobase ("tegmen") of specimen from the Gambia (ZIN): 84 – ventral view, 85 – lateral view. Scale bars: A – 1 mm (to Figs 64, 74), B – 0.5 mm (to Figs 65–69, 75–77), C – 0.25 mm (to Figs 70–73, 78–85).

Рис. 64–85. Виды подрода *Myothorax* рода *Carpophilus*.

64–73 – *C. (M.) generosus* sp. n., самец, голотип; 74–85 – *C. (M.) brunneus*. 64 – тело с пунктированным очертанием осветленной части надкрылья, сверху; 65 – передняя часть лба и лабрум, сверху; 66 – ментум и лабиальный щупик, снизу; 67 – отросток переднегруды, снизу; 68 – задние бедро и голень, снизу; 69 – субмезококсовая линия метавентрита, снизу; 70 – вентральная пластинка и гастральная спикула; 71–72 – латеральные доли фаллобазы («тегмен»): 71 – снизу, 72 – сбоку; 73 – ствол пениса и вооружение его внутреннего мешка, сверху; 74 – тело самца из Индии (Керала) (ZIN), сверху; 75 – среднее бедро этого же самца, снизу; 76 – заднее бедро самца из Таиланда (NMB), снизу; 77 – субмезококсовая линия метавентрита экземпляра из Индии (Керала) (ZIN), снизу; 78 – вентральная пластинка и гастральная спикула этого же самца; 79–80 – латеральные доли фаллобазы («тегмен») этого же экземпляра: 79 – снизу, 80 – сбоку; 81 – ствол пениса этого же экземпляра, сверху; 82–83 – латеральные доли фаллобазы («тегмен») экземпляра из Таиланда (NMB): 82 – снизу, 83 – сбоку; 84–85 – латеральные доли фаллобазы («тегмен») экземпляра из Гамбии (ZIN): 84 – снизу, 85 – сбоку. Машштабные линейки: A – 1 мм (к рисункам 64, 74), B – 0.5 мм (к рисункам 65–69, 75–77), C – 0.25 мм (к рисункам 70–73, 78–85).

moderately convex and only at sides rather steeply convex, its anterior angles subangular and posterior angles widely rounded. Elytra slightly longer than wide combined, subflattened on disk and at sides steeply sloping to lateral edges. Pygidium about two-thirds as long as metafemur and widely rounded at apex. Antennal grooves rather deep, distinctly outlined in both inner and outer edges, strongly and subrectilinearly convergent, their posterior ends joined through more or less clear transverse concavity. Mentum about 2.5 times as wide as long. Last labial palpomere nearly slightly widened to truncate apex, about 1.5 times as long as wide.

Distance between mesocoxae and that between metacoxae about 1.5 times as great as that between procoxae. Prosternal process scarcely curved along coxae and slightly widened before subtruncate apex, subangular at sides, where somewhat wider than antennal club. Submesocoxal line slightly arcuately deviating from posterior edge of coxal cavities at outer angle of metaventrite and reaching metepisternum at anterior fifth of inner edge. Ventrite 1 much shorter than hypopygidium and somewhat longer than ventrite 4. Hypopygidium about two-thirds as long as metafemur. Epipleura at base somewhat wider than antennal club.

Tibiae comparatively short and subequal in width, but markedly wider than antennal club, with nearly straight inner edge, outer edge of meso- and metatibiae with rather dense rows of short and moderately stout spines. Pro- and mesofemora about 1.5 times, metafemur twice as wide as corresponding tibiae, metafemur about 2.5 times as long as wide and of usual outline. Protarsus about three-fourths as wide as protibia, claws long and narrow.

Lateral lobes of phallobase ("tegmen") well sclerotised.

Variability. The paratype is smaller (3.6 mm), lighter (basal two-thirds of elytra and last abdominal segments brownish, subsutural elongate stripes, prohypomera and legs bright reddish) and with more subrecumbent dorsal pubescence (but not recumbent).

Diagnosis. This new species is more similar to the species of the *dimidiatus*-group with the medium body size listed as probable relatives to *C. (M.) assignatus* sp. n. (see above), although well characterised by very dense punctation of both dorsum and underside, very contrasting microreticulation of integument, comparatively small and narrow antennal club, rather conspicuous and subrecumbent (not completely recumbent) dorsal pubescence, outline of submesocoxal line. Besides, *C. (M.) generosus* sp. n. has quite distinct in the structure of the lateral lobes of phallobase ("tegmen").

Etymology. The name of this species means "pedigree", "thoroughbred".

Carpophilus (Myothorax) languescens Kirejtshuk, sp. n.
(Figs 86–94)

Material. Holotype, ♂ (NMB): Cambodia, "4.1.1998, Siem Reap, town area".

Description. Male (holotype). Length 2.4, breadth 1.1, height 0.6 mm. Body rather convex ventrally and dorsally; almost unicolourous reddish with somewhat darkened metaventrite and abdominal apex; dorsum and underside with a faint oily lustre; dorsum with moderately dense and rather short, recumbent, scarcely conspicuous yellowish hairs, shorter or about as long as distance between their insertions; underside with slightly more conspicuously pubescent.

Head surface with quite distinct and deep regular punctures, about 1.5 times as coarse as eye facets in diameter, interspaces between them somewhat narrower than a puncture diameter, with dense and moderately contrasting cellular microreticulation. Pronotum with punctures markedly coarser and much

sparser than those on head, interspaces between them slightly narrower than a puncture diameter, with somewhat smoothed, dense cellular microreticulation, but punctures becoming coarser and denser at sides, and sculpture more contrasting. Elytra at basal half with very similar punctation and sculpture to those on disk of pronotum, but interspaces between punctures broader than one puncture diameter, at apices punctures becoming finer. Uncovered tergites with very shallow, not quite distinct and sometimes elongate punctures, about as coarse as those on rest of dorsal sclerites, but interspaces between them about half puncture diameter or narrower and with very contrasting microsculpture. Ventrites with very small, shallow but mostly well outlined punctures, about as coarse as eye facets, but interspaces between them about a puncture diameter or narrower and with partly smoothed microsculpture (on hypopygidium punctures denser and interspaces with more contrasting sculpture). Prosternum with quite distinct and deep punctures on most part (about as coarse as those on dorsal sclerites), very narrow interspaces between them with rather smoothed microreticulation, space along anterior edge not punctured and completely smooth. Mesoventrite with very coarse and rather shallow punctures, interspaces between them contrastingly microreticulated. Metaventrite with very dense and distinct punctures, as coarse as those on dorsal sclerites and prosternum, interspaces between them third to half of puncture diameter and with dense and slightly smoothed microreticulation.

Head about fourth-fifths as long as distance between eyes, weakly convex and with well developed temples. Mandibles moderately developed. Antennae about six-sevenths as long as width of head, their club rather subovoid (about one and thirds as long as wide and with antennomere 10 widest) and comprising almost two-sevenths of total antennal length, antennomeres 2 and 3 subequal in length. Pronotum with somewhat arcuate sides, moderately convex and only at sides rather steeply convex, its anterior and posterior angles widely rounded. Elytra about 1.1 times as long as wide combined, at sides steeply sloping to lateral edges. Pygidium about three-fourths as long as metafemur and widely rounded at apex. Antennal grooves rather deepened, without clear transverse depression between posterior ends of antennal grooves. Mentum about 2.5 times as wide as long. Last labial palpomere nearly slightly widened to truncate apex, about 1.5 times as long as wide.

Distance between mesocoxae and that between metacoxae about 1.5 times as great as that between procoxae. Prosternal process scarcely curved along coxae and slightly widened before subtruncate apex, subangular at sides, where it somewhat wider than antennal club. Submesocoxal line slightly arcuately deviating from posterior edge of coxal cavities at outer angle of metaventrite and reaching metepisternum at anterior fourth of its inner edge. Ventrite 1 scarcely shorter than hypopygidium and somewhat longer than ventrite 4. Hypopygidium about three-fourths as long as metafemur. Epipleura at base somewhat wider than antennal club.

Tibiae subequal in width, slightly narrower than antennal club, with almost straight inner edge, outer edge of mesotibia with rather dense rows of short and stout spines. Pro- and mesofemora about one and two-thirds, metafemur 2.5 times as wide as corresponding tibiae, metafemur much less than 2.5 times as long as wide and of usual outline. Protarsus about four-fifths as wide as protibia, claws narrow.

Lateral lobes of phallobase ("tegmen") heavily sclerotised.

Diagnosis. This new species is very similar to *C. (M.) nepos*, externally differing from it only in subunicolourous body, almost inconspicuous pubescence, shape of meso- and metatibiae as well as in the shape of heavily sclerotised phallobase ("tegmen") (*C. (M.) nepos* has a characteristic weakly sclerotised lateral lobes of phallobase ("tegmen") with much longer lateral lobes and with different apices of them). Besides these characters

and others mentioned in the above key, the anterior part of prosternum of *C. (M.) languescens* **sp. n.** is markedly smoother than that of *C. (M.) nepos*. This new species and *C. (M.) nepos* have a comparatively small body, comparable with that of *C. (M.) dimidiatus*, *C. (M.) brunneus*, *C. (M.) pilosellus*, *C. (M.) timorensis* and *C. (M.) zeaphilus*, however, the lateral lobes of phallobase ("tegmen") of the first two species are different from that of all the species compared with them. The shape of meso- and metatibiae of the new species under consideration are quite distinct from those of all species lastly mentioned. Except peculiar structure of the lateral lobes of phallobase ("tegmen"), *C. (M.) languescens* **sp. n.** and *C. (M.) nepos* are also characterised by their rather robust body with arcuate pronotal and elytral sides, comparatively sparse and distinct punctation of dorsum, usually somewhat smoothed integument and very weak pubescence, characteristic outline of submesocoxal line. They differ from *C. (M.) dimidiatus*, *C. (M.) pilosellus* and *C. (M.) truncatus* in their more robust and lighter body, much less developed pubescence, character of punctation and sculpture (including those on prosternum), nearly straight inner edge of meso- and metatibiae; and also from *C. (M.) dimidiatus* in their subequal length of antennomeres 2 and 3; and also from *C. (M.) pilosellus* in their shorter last labial palpomere. *Carpophilus (Myothorax) languescens* **sp. n.** and *C. (M.) nepos* differ from *C. (M.) brunneus* and *C. (M.) zeaphilus* in their much less developed pubescence, character of punctation and sculpture (including those on prosternum), shape of prosternal process. Finally, *C. (M.) languescens* **sp. n.** and *C. (M.) nepos* differ from *C. (M.) timorensis* in their more robust body, antennomere 3 not shorter than antennomere 2, more distinct dorsal punctation, medioanterior part of prosternum rectilinear from side, submesocoxal line more deviating from anterior angles of metaventricle wider meso- and metatibiae.

Etymology. The name of this species means "weakened", "relaxed".

Carpophilus (Myothorax) mutilatus Erichson, 1843
(Figs 95–105)

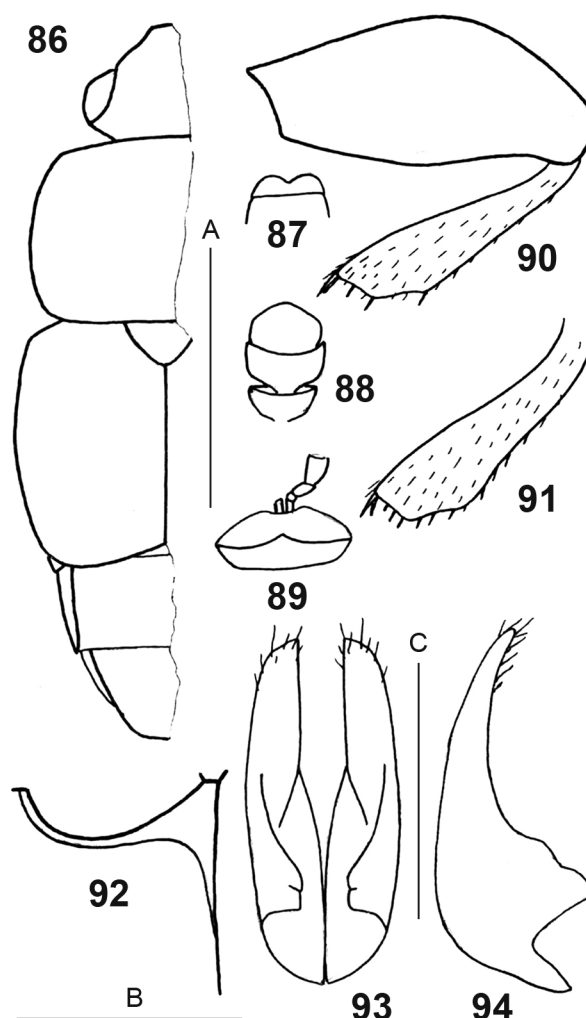
Nitidula hemiptera Fabricius, 1792: 261 (America; syntypes), non *Dermestes hemipterus* Linnaeus, 1758 = *Carpophilus mutilatus* Erichson, 1843: 258 (Sicilia; syntypes) = ? *Carpophilus tempestivus* Jacquelin du Val, 1856: 42 (? Cuba), non *C. tempestivus* Erichson, 1843 = ? *Ips bimaculatus* Montrouzier, 1860: 262 (New Caledonia), non *Silpha bimaculata* Marsham, 1802 = ? *Ips puberulus* Montrouzier, 1860: 263 (New Caledonia, Lifu) = *Carpophilus (Myothorax) luridus* Murray, 1864: 377 ("Europa, America boreali, America meridionali, India orientali & c.", syntypes).

In total, over than one thousand specimens were examined, including type specimens below and others, deposited in different collections from all zoogeographical regions, except Antarctic one.

Type material. Italy. 1♂, lectotype of *C. mutilatus* (ZMB), designated by Dobson [1960], and 4 paralectotypes (ZMB), "8376", "mutilata N., Lusit., Sicil".

Sri Lanka. 1♂, lectotype of *C. (M.) luridus* (NHML), here designated, "Ceylon", "ex Mus. Murray", "Fry Coll. 1905-100", "luridus (Dej.), Murr. D.M. Cat., Ceylon".

America. 1♀, paralectotype of *C. (M.) luridus* (NHML), "TYPE", "ex Mus. Murray", "Am. Bor.", "luridus, n. Am.", "68.106"; 1♂, lectotype of *Nitidula hemiptera* Fabricius, non Linnaeus (ZMKU), here designated, and



Figs 86–94. *Carpophilus (Myothorax) languescens* **sp. n.**, male, holotype.

86 – body, dorsal view; 87 – anterior part of frons and labrum, dorsal view; 88 – antennal club; 89 – mentum and labial palpus, ventral view; 90 – metafemur and tibia, ventral view; 91 – mesotibia, ventral view; 92 – submesocoxal line of metaventricle, ventral view; 93–94 – lateral lobes of phallobase ("tegmen"): 93 – ventral view, 94 – lateral view. Scale bars: A – 1 mm (to Fig. 86), B – 0.5 mm (to Figs 87–92), C – 0.25 mm (to Figs 93–94).

Рис. 86–94. *Carpophilus (Myothorax) languescens* **sp. n.**, самец, голотип.

86 – тело, сверху; 87 – передний край лба и лабрум, сверху; 88 – булава усиков; 89 – ментум и лабиальный щупик, снизу; 90 – задние бедро и голень, снизу; 91 – средняя голень, снизу; 92 – субмезококкальная линия метавентрита, снизу; 93–94 – латеральные доли фаллобазы («тегмен»): 93 – снизу, 94 – сбоку. Машштабные линейки: А – 1 мм (к рисунку 86), В – 0.5 мм (к рисункам 87–92), С – 0.25 мм (к рисункам 93–94).

1 ex., paralectotype of *N. hemiptera* Fabricius, non Linnaeus (ZMKU) – two specimens (including one labelled by Kirejtshuk as the lectotype) in a separate tray "353 – 30", "TYPE"; 11 ex., (?) paralectotypes of *N. hemiptera* Fabricius, non Linnaeus (ZMB), "8375", "hemiptera Fab., Lund, Am. Ins., Lund" (with additional labels under different specimens: 1 ex. – "Cuba, Otto", 1 ex. – "St. Thom., Moritz", 1 ex. – "Brasil. Sell." – the specimens with these labels apparently added to *N. dimidiata* after description by J.C. Fabricius or somebody else).

Additional material (some selected specimens). Russia. About 100 ex. (ZIN), St Petersburg, Leningrad Region, Krasnodar Region, Primorskiy Region.

Afghanistan. 2 ex. (ZIN), Nuristan, Kamdeš, 1300 m, 11.9.1971, O. Kabakov (in Russian).

India. 2 ex. (NHML), "Mothronwala, Dehra Dun, H.G.C.", "flowers of *Hedydium*", "H.G. Champion Coll."; 1 ex. (NHML), "Lachiwala, Dehra Dun, H.G.C.", "H.G. Champion Coll."; 1 ex. (NHML), "Haldwani Distr., Kumaon, H.G.C.", "H.G. Champion Coll."; 1 ex. (NHML), "Kheri Forest, U.P., Jan' 16, H.G.C.", "H.G. Champion Coll."; 9 ex. (NHML, ZIN), "Dehra Dun, H.G.C.", "14.12.25", "H.G. Champion. Coll."; 17 ex. (NHML), "Fraserpet, Coorg., F.R.I. Sandal Insect Survey"; 2 ex. (NHML), "Jalgaon, Maharashtra", "banana florets"; 15 ex. (TMB, ZIN), "W Bengal, Darjeeling, North Point, 1000-1300 m, Gy. Topál"; 5 ex. (TMB, ZIN), "Karnataka, Shimoga Distr., Jog Falls, 500 m, near river Sharawati, 1.III.1980, Gy. Topál"; 1 ex. (TMB), "Aligarh, Bot Gard of Guslim Univ., swept in grass and bushes", "12.I.1982, J. Papp"; 2 ex. (SMNS), "Rajasthan: Bharatpur, 12.8.1989, A. Riedel"; 5 ex. (ZIN), "Rajasthan, Cazri Farm, 9.X.1989, fruit trap, A. Kompantzev"; 4 ex. (NMB, ZIN), "Andaman Is., Havelok I., env. of village N7, 11°59'N, 92°58'E, 22.IV-14.V.1998, Karel & Simon Majer".

Nepal. 1 ex. (TMB), "Piple, IX-X.1969, Woyanovich".

Sri Lanka. 1 ex. (AMNY), "Western Prov., Nugegoda, May 3-10, 1969, P.B. Karunaratne (from rotten fruits)"; 1 ex. (AMNY), "Central Prov., Katugastota, 1600 ft, May 26, 1969, P.B. Karunaratne".

China. 1 ex. (ZMB), "Taiwan, Formosa, H. Sauter".

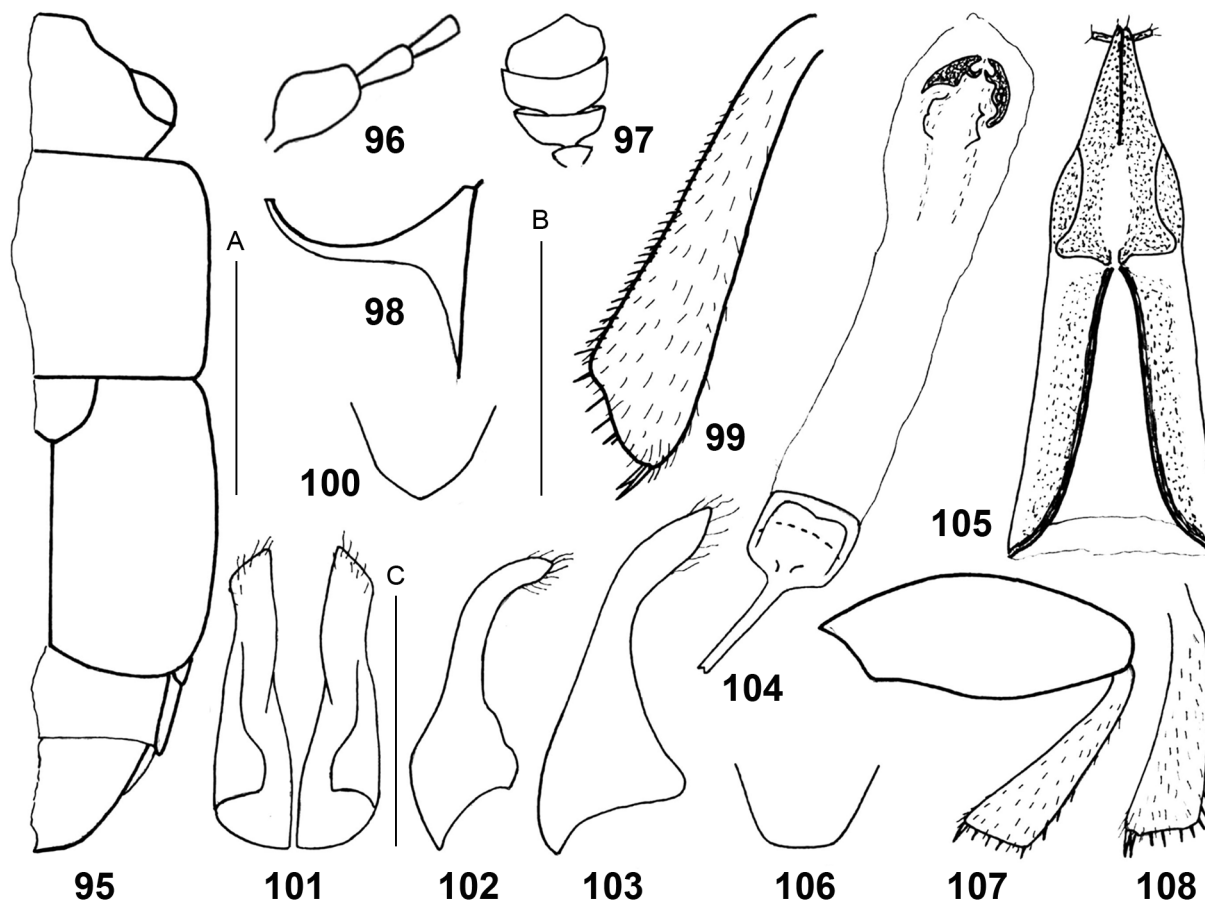
Thailand. 1 ex. (TMB), "Khon Kaen, Im Zoo, ad lucen", "26.I.1978, Sunanta, Aumphantiri"; 4 ex. (ZML), "...Pattaya, 1979, T. Palm"; 2 ex. (ZIN,

ZMUC), "Chieng Mai Province, 300 m, 30.ix.1981, Zool. Mus. Copenhagen"; 1 ex. (MNG), "NE Bangkok, Khao Yai Nat. Park, 750-850 m, 26.XI-3.XII.85, Burckhart-Löbl".

Vietnam. 2 ex. (TMB), "Yen so, SE of Hanoi, 19-23.IV.1966, Gy. Topál, beaten from trees"; 5 ex. (TMB, ZIN), "Xuan dinh, NW of Hanoi, 26-29.IV.1966, Gy. Topál", "netted in grasses"; 3 ex. (TMB, ZIN), "Hanoi, Hotel Kim lien, 1-2.V.1966, Gy. Topál", "from decaying banana tree"; 3 ex. (NMP, ZIN), "Hoa Binh, 4-7.6.1986, Ha Son Binh prov., Jan Horák".

Malaysia. 87 ex. (MMUE, ZIN), "Penang, Universiti Sains, 1.6.76, Mangka trap, R.A. Beaver" (and "...3.6.76, Banana trap..."); 4 ex. (SMNS, ZIN), "Pahang, 30 km S Pekan, 20.2.1994, Grimm & Rachinsky"; 1 ex. (SMNS), "Borneo: Sabah, Kinabalu N.P.: Headquarters, 1500-1600 m, 11-15.XI.1996, W. Schawaller"; 29 ex. (SMNS, ZIN), "Borneo: Sabah, Crocker Range N.P., NW Keningau, 900-1200 m, at light, 18.XI.1996, D. Grimm"; 1 ex. (SMNS), "Borneo: Sabah, Gaya Island, 22-23.XI.1996, W. Schawaller".

Indonesia. 1 ex. (RNHL), "Sumatra, Manna, M. Knappert", "*Carpophilus vittiger* det. Murr."; 2 ex. (RNHL), "P.H. v. Doesburg, Java, Samarang"; 3 ex. (NRS), "Sumatra, Medan, Mjöb"; 5 ex. (RNHL, ZIN), "L.G.E. Kalshoven, Java, 250 m, Buitezorg, 11-I-1926" (and "X-1919", "3-5-1927"); 5 ex. (RNHL, ZIN), "Dr. J. v.d. Vecht, Tjiomas, Buitezorg, 1 Oct. 1936"; 1 ex. (NHML), "Sulawesi Utara, Dumoga-Bone N.P., May 1985", "trap Flight intercept", "Plot A, ca. 200 m, Lowland forest", "R. Ent. Soc Lond., Project Wallace, B.M. 1985-10".



Figs 95-108. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

95-105 - *C. (M.) mutilatus*; 106-108 - *C. (M.) nepos*. 95 - male body, dorsal view; 96 - antennomeres 1-3; 97 - antennal club; 98 - submesocoxal line of metaventrite, ventral view; 99 - male pygidium, dorsal view; 101-102 - lateral lobes of phallobase ("tegmen"): 101 - ventral view, 102 - lateral view; 103 - aberrant lateral lobes of phallobase ("tegmen") of specimen from Vietnam (Hoa binh) (ZIN), lateral view; 104 - penis trunk with extracted inner sac, dorsal view; 105 - ovipositor, ventral view; 106 - apex of female pygidium, dorsal view; 107 - male metafemur and tibia, ventral view; 108 - male mesotibia, ventral view. Scale bars: A - 1 mm (to Fig. 95), B - 0.5 mm (to Figs 96-100, 106-108), C - 0.25 mm (to Figs 101-105).

Рис. 95-108. Виды подрода *Myothorax* рода *Carpophilus*.

95-105 - *C. (M.) mutilatus*; 106-108 - *C. (M.) nepos*. 95 - тело самца, сверху; 96 - антенномеры 1-3; 97 - булава усиков; 98 - субмезококсовая линия метавентрита, снизу; 99 - задняя голень самца, снизу; 100 - вершина пигидия самки, сверху; 101-102 - латеральные доли фаллобазы («тегмен»): 101 - снизу, 102 - сбоку; 103 - aberrantные латеральные доли фаллобазы («тегмен») экземпляра из Вьетнама (Хоабинь) (ZIN), сбоку; 104 - ствол пениса с вывернутым внутренним мешком, сверху; 105 - яйцеклад, снизу; 106 - вершина пигидия самки, сверху; 107 - задние бедро и голень самца, снизу; 108 - задняя голень самца, снизу. Масштабные линейки: A - 0.5 мм (к рисунку 95), B - 0.5 мм (к рисункам 96-100, 106-108), C - 0.25 мм (к рисункам 101-105).

Philippines. 1 ex. (ZMB), "Insel Negros, Dumaguete, leg. Böttcher, 29.2.1914"; 9 ex. (ZIN, ZMB), "Ilaga, 3 Februar 1915, Böttcher"; 1 ex. (SMNS), "Leyte Visca, N Baybay, cultiv. land, 1991, Schawaller et al."; 1 ex. (NMB), "15.VII.1995, Philipp., Palawan, Prov. Narra: Tigman", "Wolfgang Ulrich".

Mexico. 3 ex. (ZIN), "Saltillo Coahuila, Bajío UAAAN, 25°25'23" N 101°00'19" E, 1592 m; collected in dried fruits (orange, apple and lemon), may 15.V.2016 and 01–05.VI.2016, H. Hernandez"; 7 ex. (ZIN), "Chiapas, Angel Albino Corzo, 15° 52' N y 92° 43' E. 640 m, collected in dried fruits (orange, apple and banana), 24.XII.2016, H. Hernandez".

Diagnosis. This species seems to be the most variable among members of the *dimidiatus*-group and due to its comparatively slender body and nearly straight inner edge of meso- and metatibiae it is more similar to *C. (M.) assignatus* **sp. n.**, *C. (M.) contengens*, *C. (M.) fumatoides* **sp. n.**, *C. (M.) fumatus*, *C. (M.) generosus* **sp. n.**, *C. (M.) notatus*, *C. (M.) pilipennis*, *C. (M.) robustus* **stat. n.**, *C. (M.) schioedtei* and *C. (M.) timorensis*. The species under consideration has a peculiar dorsoventral curvature of lateral lobes of phallobase ("tegmen") and peculiar female gonocoxites with characteristic disposition of styli at simple apex as well as characteristic submesocoxal line. Besides, it differs:

- from *C. (M.) assignatus* **sp. n.** and *C. (M.) pilipennis* also in the characters listed in the above key: distinct punctation on entire surface and very smoothed sculpture at anterior edge of prosternum, subsemicircular apex of its process; metafemur considerably more than 2.5 times as long as wide; in general smaller body (although the scopes of body size are considerably overlapping), comparatively more slender and often with darkened pronotum;

- from *C. (M.) contengens* also in its pattern of body colouration, usually less raised pubescence, frequently less distinct punctation on uncovered tergites, denser and coarser punctation and somewhat smoothed cellular microreticulation on prosternum, meso- and metaventrete, somewhat narrower metatibia and not truncate apex of female pygidium;

- from *C. (M.) fumatoides* **sp. n.** and *C. (M.) fumatus* also in its usually smaller and much lighter body, distinctly punctured and microreticulated anterior part of prosternum, subequal length of antennomeres 2 and 3, light antennal club;

- from *C. (M.) generosus* **sp. n.** also in its lighter body with different pattern of infuscation; much less dense punctation and less contrasting sculpture of integument (but with raised punctures and usually microreticulation on anterior part of prosternum), clearly recumbent dorsal pubescence, light antennal club, flattened surface behind mentum between posterior ends of antennal grooves;

- from *C. (M.) notatus* also in its much lighter body, distinct punctation on anterior part of prosternum, but not so coarse punctation and somewhat smoothed microreticulation on mesoventrite, comparatively narrower metafemur and tibiae;

- from *C. (M.) robustus* **stat. n.**, *C. (M.) schioedtei* as well as Polynesian *C. (M.) mutabilis* and *C. (M.) oculatus* also in its more developed punctation of underside (rather dense on prosternum and metaventrete), prosternal process with apex somewhat curved along coxae and subtruncate at posterior edge, usually more distinctly microreticulate prosternal and mesoventral surface, comparatively smaller antennal club, somewhat narrower tibiae and simple apex of female pygidium;

- from *C. (M.) timorensis* also in its generally larger body, antennomere 3 not shorter than antennomere 2, more distinct punctation, including that on medioanterior part of pronotum, medioanterior part of prosternum rectilinear from side, submesocoxal line more deviating from anterior angles of metaventrete and simple apex of female pygidium.

Finally, it differs from the species with more or less convex outer edge of metatibiae (*C. (M.) dimidiatus*, *C. (M.) pilosellus* and *C. (M.) truncatus*) in not only the peculiar structures of genitalia of both sexes, but also in its usually larger body, more distinct punctation of integument, less developed and less conspicuous dorsal pubescence, peculiar outline of the submesocoxal line.

Notes. The references to this species in the Western Hemisphere should be corroborated by a further study. Dobson [1960] supported that the holotype of *C. (M.) luridus* (type series deposited in NHML) is conspecific with the lectotype of *C. (M.) mutilatus*. Some of references to *C. (M.) dimidiatus* seem to concern the species under consideration as well as *C. (M.) nepos* or *C. (M.) pilosellus*. In the collection of ZMB the specimens of this species are labelled as the following: 1♂ – "Thio", "76995", "*biguttatus* Motsch."; 1♀ – "Kanala", "76995", "*biguttatus* Motsch.". Probably this misidentification referred to the species described by Motschulsky [1858], which indeed belongs to the subfamily Cryptarchinae. This situation apparently is connected with the error in the catalogue by Gemminger and de Harold [1868: 810]. The depositories of the series of *C. (M.) bimaculatus* Montrouzier (not Marsham) and *C. (M.) puberulus* remain unknown, although that of *C. (M.) tempestivus* Jacquelin du Val (non Erichson) should be deposited in MNHN.

This species was first described from Central America (type locality of *Nitidula hemiptera* Fabricius (non Linnaeus)) and later from Europe (*Carpophilus mutilatus* – Sicily). Murray [1864] thought that this species was originated from the West Indies and added to it the cosmopolitan variety "*luridus*", however, Reitter [1919: 55] pointed out that it spreads in "Europa und über den ganzen südöstlichen Teil der Erde". After study of collections of many museums it became possible to suppose that this species is cosmopolitan, but more common in the Indo-Malayan Region.

Carpophilus (Myothorax) nepos Murray, 1864
(Figs 106–113)

Carpophilus (Myothorax) nepos Murray, 1864: 381 (Brazil; syntypes) = *Carpophilus freemani* Dobson, 1956: 37 (USA: Iowa; Brazil: Manaus; (?) Bolivia).

In total, more than a hundred specimens were examined, including the types as well as others mostly from the Indo-Malayan Region, and also from the other areas of Eurasia, Africa and both North and South America (AMNY, MSNG, NHML, NMB, NMP, SMNS, ZIN, ZMB, ZSI).

Type material. Brazil. 1♂, lectotype of *C. (M.) nepos* (NRS), here designated, "Rio Jan", "F. Sahlb."; 1♂, paralectotype (NRS), "Rio Jan", "Fry"; 6 paratypes of *C. freemani* (NHML), "Brazil nuts at Hull, Dec. 1954", "Brit. Mus. 1956-26".

Additional material (some selected specimens). Tanzania. 1 ex. (ZMB), "D.O. Afrika, Daressalam, Methner"; 1 ex. (ZMB), "D.O. Afrika, Dereina, 19.XI.1905, Schröder".

India. 1 ex. (ZMB), "India or., Nagpore", "Coll. G. Hauser"; 1 ex. (NHML), "W. Almora, Kumaon, India, H.G.C."; 1 ex. (NHML), "Sarda, Bengal, P.W.C."; 1 ex. (ZSI), "Ja 2, Tammu, 25.5.72, on Mango leaf, T. Sengupta"; 1 ex. (ZIN), "Grarakhpur Peach, 10.6.73, T. Sengupta"; 1 ex. (ZSI), "Calcutta, Lichu, 10.5.76, T. Sengupta"; 2 ex. (TMB, ZIN), "W Bengal, Nagarkanda, sifted gargage-heap", "3-14.I.1980, leg. Gy. Topál"; 2 ex. (ZIN), "Rajasthan, Jodhpur, 10-12.IX.1989, A. Kompantzev".

Sri Lanka. 10 ex. (AMNY, ZIN), "Western Prov., Nugegoda, May 3-10, 1969, P.B. Karunaratne (from rotten fruits)"; 2 ex. (TMB, ZIN), "SW, Dodanduwa, 15 km NW of Galle, 3-20.3.1988, T. Munk".

Thailand. 1 ex. (NMB), "...23-25.II.1993, Ranong prov., 9°56' 98'40", Ranong Hot Spring, K. Majer"; 4 ex. (ZIN, ZML), "Pattaya, 1979, T. Palm"; 1 ex. (ZMUC), "Chieng Mai Province, 325 m, 15-30.x.1984, Karsholt, Lomholdt & Nielsen"; 4 ex. (MSNG, ZIN), "Mae Hong Son, Tom Lok, 8 km N Mae Lang, 700 m, 11, 13.XI.1985, Burckhardt-Löbl"; 2 ex. (SMNS), "Changwat Chiang Mai, Chiang Mai, Dez. 1988, leg. Trautner & Geigenmüller"; 14 ex. (NMB, ZIN), "1-21.iii.1996, Chumphon prov., Pha To env., 9°48' 98'47", K. Majer".

Vietnam. 1 ex. (TMB), "Prov. Ha-Tinh, forêtière Hũong-sôn, 150 m, forêt trop. pluv.", "à la lumière, 19.VIII.1963, T. Pócs"; 1 ex. (TMB), "Hanoi, Hotel Kim-lien, 1-2.V.1966, Gy. Topál, from decaying banana tree"; 2 ex. (NMB, ZIN), "21.35N 106.30E, 52 km SW of Lang Son, 27.iv-6.v.1996, 370 m, Pacholátko & Demlický".

Malaysia. 1 ex. (ZIN), "Johor, Lombong, 15 km N Kota Tinggi, 27-30.7.1992, R. Schuh".

Philippines. 2 ex. (ZMB), "Mindanao, Kalambugan b. Lanao, Böttcher"; 3 ex. (ZMB, ZIN), "Luzon, Manila, 27.10.1914, leg. Böttcher".

Mexico. 5 ex. (ZIN), "Saltillo Coahuila, Bajío UAAAN, 25°25'23" N 101°00'19" E, 1592 m; collected in dried fruits (orange, apple and lemon), may 15.V.2016 and 01-05.VI.2016, H. Hernandez"; 3 ex. (ZIN), "Chiapas, Angel Albino Corzo, 15° 52' N y 92° 43' E. 640 m, collected in dried fruits (orange, apple and banana), 24.XII.2016, H. Hernandez".

Addition to description. This species is very similar to *C. (M.) languescens* sp. n. (see description of the latter). Length 1.7-3.2, breadth 0.8-1.2, height 0.5-0.7 mm. Rather convex ventrally and dorsally; general colouration of dorsal surface of head, pronotum, abdominal tergites, metaventrite and often elytral apices usually about brownish to dark brown, but the remainder markedly lighter (elytra especially lighter); dorsum and underside with faint oily lustre; dorsum with moderately dense and short, subrecumbent, moderately conspicuous yellowish hairs, 1.5-2 times as long as distance between their insertions; underside with less conspicuously pubescence. Lateral lobes of phallobase ("tegmen") and ovipositor weakly sclerotised.

Diagnosis. This species differs from *C. (M.) languescens* sp. n. only in the almost always lighter elytra, more conspicuous pubescence, shape of meso- and metatibiae as well as in the shape of weakly sclerotised lateral lobes of phallobase ("tegmen") with much longer and different apices of lateral lobes (see above the key to species). Besides the considered characters, this species in contrast to *C. (M.) languescens* sp. n. has shorter elytra, which are 6/7-7/8 as long as wide combined.

Notes. The type specimens of *C. (M.) freemani* are deposited in the collection of NHML. Some of references to *C. (M.) dimidiatus* seem to concern the species under consideration as well as *C. (M.) mutilatus* or *C. (M.) pilosellus*. The author of this paper published the synonymy of *C. (M.) nepos* and *C. (M.) freemani* without explanation [Kirejtshuk, 1996], although his opinion was grounded on study of the type series of the first. Both synonyms of this species were proposed for the specimens originated from Brazil (type locality) or the type locality of *C. (M.) freemani* can be in Bolivia (its holotype taken from Brazil nuts originated from Brazil or Bolivia), although this species has the world-wide range under artificial conditions and is known from natural localities of many areas with a warm climate.

Carpophilus (Myothorax) notatus Murray, 1864 (Figs 114-117)

Carpophilus (Myothorax) notatus Murray, 1864: 380 (Madagascar; syntypes).

In total, some dozens of specimens were examined, including types below and others from Madagascar (MRAC, NHML, NMNH, ZIN).

Type material. Madagascar. 1♂, lectotype of *C. (M.) notatus* (ZMB), here designated, and 2 ex., paralectotypes (ZMB), with the same labels: "*binotatus* Kl., Madag., Goud.", "8364"; 4 ex., paralectotypes of *C. (M.) notatus* (ZMB) (marked as lectotype in the collection by S. Endrödy-Younga in 1964), "Madagascar, Goud.", "8364".

Additional material (some selected specimens). Madagascar. 1 ex. (NMHN), "Region de l'Androy, Ambovombe, Dr J. Decorse, 1901"; 2 ex. (ZIN), "Maroansetra, VII-XI.1946"; 6 ex. (MRAC, ZIN), "Madagascar Est: Ambodivoangy, VI.1960, J. Vadon"; 1 ex. (ZMB), "Antanarivivo, Ambodrona, 3-5.1.1995, J. Janák".

Notes. This species is included in this review because it is useful to be compared with its relatives from the Indo-Malayan Region. It is quite distinct from all the species of the *dimidiatus*-group of species thanks to the very characteristic body colouration with bright yellow oval spot on each elytron, and particularly long and narrow lateral lobes of its phallobase ("tegmen").

Carpophilus (Myothorax) pilipennis Macleay, 1873 (Figs 118-121)

Carpophilus pilipennis Macleay, 1873: 160 (Australia: Gayndah; type (? types)) = *C. davidsoni* Dobson, 1952: 256 (Australia, New Zealand), **syn. n.**

In total, several hundred of specimens were examined, including types below as well as specimens from Australia and other territories (AMS, ANIC, MVM, QMB, ZIN).

Type material. Australia. 1♀, syntype of *C. (M.) pilipennis* (AMS), "K 26 893", "*Carpophilus pilipennis*, Gayndah"; 1 ex., paratype of *C. (M.) davidsoni* (NHML), "Dubba, New South Wales, 22/12/48"; 2 ex., paratypes of *C. (M.) davidsoni* (AMS), "Leeton, NSW, 1/2/49, E.L. Jones".

Additional material (some selected specimens). Australia. 13 ex., (QMB, ZIN), Queensland; 2 ex. (NHML), "N.S.W. Nowra, 30-iii-1934, F.A. Rodway"; 1 ex. (NHML), "Pozières R., 15-I-1970, J. Heaton".

New Zealand. 16 ex. (NHM, ZIN), "AK: Auckland, Mt. Eden, garden, 80 m, I.1984", "P.M. Hammond".

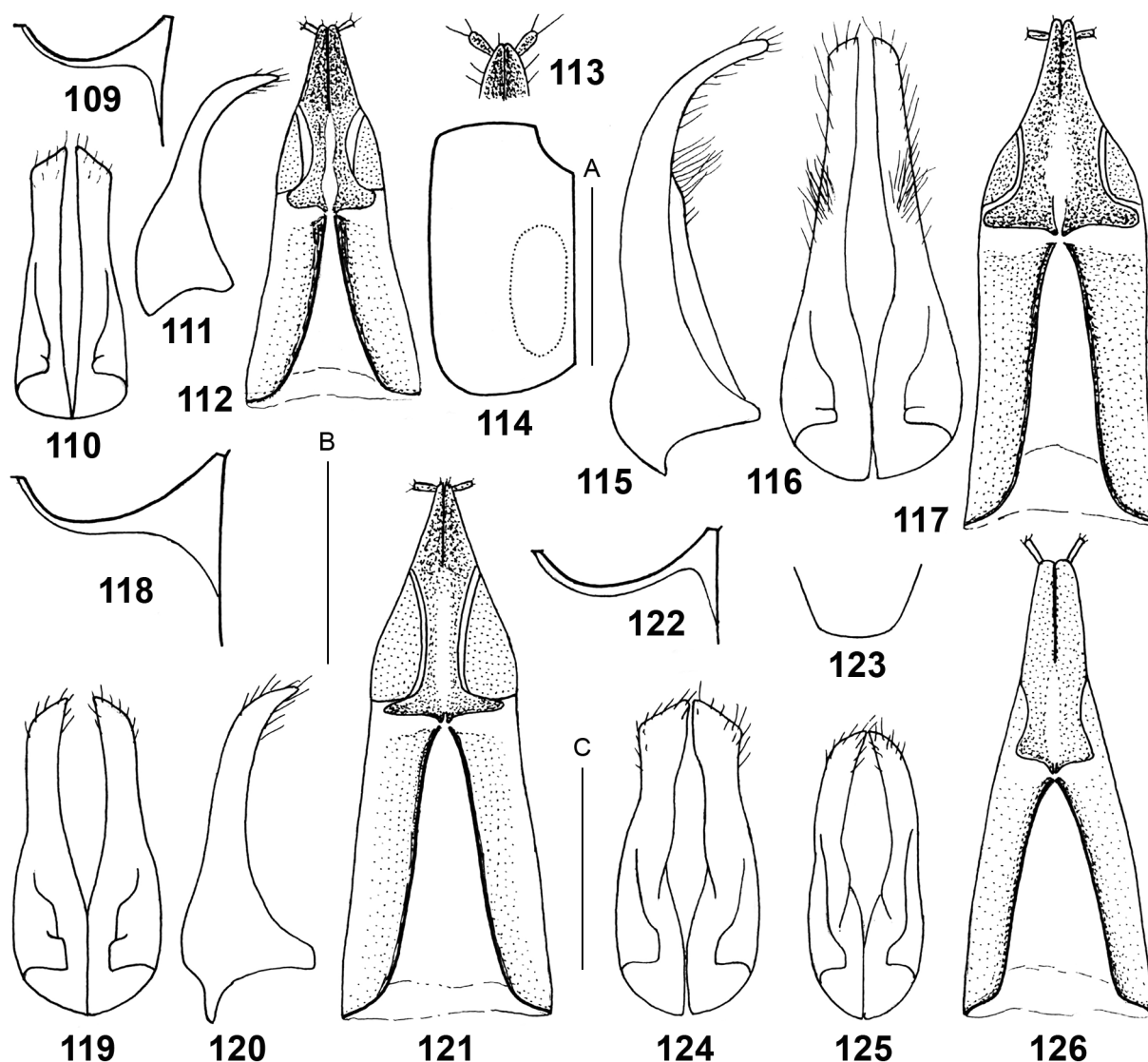
Polynesia. About 200 ex. (FMNH), Marianas (Guam, Saipan etc.).

Notes. The re-examination of one syntype of *C. (M.) pilipennis* showed that this female seems to be conspecific with two paratypes of *C. (M.) davidsoni*, other studied specimens from different parts of East Australia as well as they fit the illustrations by Dobson [1952]. The records of this species from Polynesia [Gillooly, 1962] and Philippines [Gillooly, 1969] should be reverified, although some Polynesian specimens examined in the collection of FMHN are really conspecific with *C. (M.) pilipennis*.

Carpophilus (Myothorax) pilosellus Motschulsky, 1858 (Figs 122-126, 156)

Carpophilus pilosellus Motschulsky, 1858: 41 (East Indies; syntypes) = *C. floridanus* Fall, 1910: 122 (USA; syntypes) = *C. halli* Dobson, 1954: 299 (Nigeria, Sierra Leone, Honduras).

In total, more than 250 specimens were examined, including type specimens below and others mostly from the Himalayas, Indochina and adjacent territories, but also from different territories of the globe (NMB, NME, NMP, TMB, ZIN, ZMB).



Figs 109–126. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

109–113 – *C. (M.) nepos*; 114–117 – *C. (M.) notatus*; 118–121 – *C. (M.) pilipennis*; 122–126 – *C. (M.) pilosellus*. 109, 118, 122 – submesocoxal line of metaventrite, ventral view; 110–111, 115–116, 119–120 – lateral lobes of phallobase ("tegmen"): 110, 115, 119 – ventral view, 111, 116, 120 – lateral view; 112, 117, 121, 126 – ovipositor, ventral view; 113 – apex of ovipositor, ventral view; 114 – elytron with dotted outline of light spot, dorsal view; 123 – apex of female pygidium, dorsal view; 124 – lateral lobes of phallobase ("tegmen") of the lectotype of *C. (M.) pilosellus*, ventral view; 125 – lateral lobes of phallobase ("tegmen") of specimen from Japan, ventral view. Scale bars: A – 1 mm (to Fig. 114), B – 0.5 mm (to Figs 109, 118, 122–123), C – 0.5 mm (to Figs 110–113, 115–117, 119–121, 124–126).

Рис. 109–126. Виды подрода *Myothorax* рода *Carpophilus*.

109–113 – *C. (M.) nepos*; 114–117 – *C. (M.) notatus*; 118–121 – *C. (M.) pilipennis*; 122–126 – *C. (M.) pilosellus*. 109, 118, 122 – субмезококсовая линия метавентрита, снизу; 110–111, 115–116, 119–120 – латеральные доли фаллобазы («тегмен»): 110, 115, 119 – снизу, 111, 116, 120 – сбоку; 112, 117, 121, 126 – яйцеклад, снизу; 113 – вершина яйцеклада, снизу; 114 – надкрылье с пунктированным очертанием осветленного пятна, сверху; 123 – вершина пигидия самки, сверху; 124 – латеральные доли фаллобазы («тегмен») лектотипа *C. (M.) pilosellus*, снизу; 125 – латеральные доли фаллобазы («тегмен») экземпляра из Японии, снизу. Масштабные линейки: A – 1 мм (к рисунку 114), B – 0.5 мм (к рисункам 109, 118, 122–123), C – 0.5 мм (к рисункам 110–113, 115–117, 119–121, 124–126).

Type material. (?) India. 1♂, lectotype of *C. pilosellus* (ZMMU), here designated, and 7 ex., paralectotypes (ZMMU), "Ind. or."

Additional material (some selected specimens). Russia. About 50 ex. (ZIN), St Petersburg, Leningrad Region, Samara Region, Primorskiy Region, etc.

Jordanian. 1 ex. (TMB), "N Jordan, J. Klapperich", "Irbid, 600 m, 28.10.0957".

China (including Taiwan). 1 ex. (TMB), "Formosa, Sauter"; 1 ex. (NHML), "Charbin, 20.vi.1952"; 2 ex. (NME, ZIN), "Shaanxi, Qin Ling Shan, 109.16E, 34.20N, Li Shan Mt., nr. Lintong, 31 km E Xian, 1000–1200 m, Div. Meadows & Forest, 26–27.08.1995, A. Pütz".

Cambodia. 1 ex. (NMP), "centr., Phnom ??, 5.XII.84, Frühbauer".

Vietnam. 1 ex. (ZIN), mountains SW Shon Zyong, 20.3.1962, Kabakov (in Russian); 1 ex. (ZIN), mountains SW Shon Zyong, 23.3.1962, Kabakov (in Russian) [Kum-Ranh].

Thailand. 1 ex. (ZML), "Pattaya, 1979, T. Palm"; 5 ex. (NMB, ZIN), "9–14.V.1991, Thiang Dao, 350 m, 19°22'N 98°57'E, Vít Kubán".

Indonesia. 11 ex. (ZIN, ZMB), "S.O. Borneo, Grabowsky".

Philippines. 1 ex. (ZMB), "Calapan, Böttcher, 3.2.1916".

Papua New Guinea. 22 ex. (TMB), "N. Guinea, Biry, 1896" (and 1897, 1898, 1900, 1901); 1 ex. (TMB), "Brit. N. Guinea, Mazalón".

Polynesia. About 100 ex. (FMNH), Marianas (Guam, Saipan etc.).

Diagnosis. This species due to its small dark body and convex inner edge of metatibia (especially convex in male) is very similar to *C. (M.) dimidiatus* and its most closely related consubgenera (*C. (M.) imitatus* and *C. (M.) truncatus* – see below), differing from them in the characters mentioned in the above key to species and below. The lateral lobes of phallobase (“tegmen”) in most cases are much longer and narrower than in *C. (M.) dimidiatus* and different from those of all three mentioned relatives.

Notes. Except the duplicates of the type series of *C. (M.) pilosellus* re-examined by the author, there are some other type specimens deposited in NHML [Gilligly, 1962]. The type series of *C. (M.) floridanus* is deposited in the collection of the Museum of Comparative Zoology at Harvard College in Cambridge (Massachusetts, USA) and that of *C. (M.) halli* – in NHML. The writer used the synonymy proposed for these names by Gilligly [1962] and Connell [1963]. Some of references to *C. (M.) dimidiatus* seem to concern the species under consideration as well as *C. (M.) mutilatus* or *C. (M.) truncatus*. This species together with *C. (M.) dimidiatus* and *C. (M.) truncatus* form a group of very similar and apparently closely related species (see above the “Notes” of *C. (M.) dimidiatus*). Kirejtshuk [1996] pointed out that *C. (M.) truncatus* was mixed with more common *C. (M.) pilosellus* and he also indicated the some diagnostic characters to separate these species. After study of many additional specimens from different collections, it became clear that the distinctness of these forms and their relations with *C. (M.) dimidiatus* need a further more detailed revision. This species seems to have subcosmopolitan range, although it was first described from the East Indies (*C. (M.) pilosellus*), then from Florida (*C. (M.) floridanus*), and last from stored products transported from Nigeria, Sierra Leone, Honduras (*C. (M.) halli* with type series remaining not defined because R.M. Dobson in its description did not mention the origin of the holotype). At present, it seems problematic to conclude on the initial range of this species, but it seems be very likely in the Indo-Malayan Region.

Carpophilus (Myothorax) robustus Murray, 1864, **stat. n.**
(Figs 127–132)

Carpophilus (Myothorax) vittiger var. *robustus* Murray, 1864: 373 (Waigiu; syntypes).

In total, about 50 specimens were examined, including types below and 32 ex. (SMNS, TMB, ZIN).

Type material. Indonesia. 1♂, lectotype of *C. (M.) vittiger* var. *robustus* (NHML), here designated, “Wagiou”, “N. Guin., Waigiu” (Waigeo), “Wallace”, “ex Mus. Murray”, “Fry Coll. 1905-100”, “*Carpophilus maculatus robustus* Murr., R.M. Dobson Det.”; 1♂, paralectotype of *C. (M.) vittiger* var. *robustus* (NHML), “Wagou” (Waigeo), “*vittiger* var.”, “68.106”, “*vittiger* var. *robustus*, Dorey”, with the same Dobson’s label; 1♂, paralectotype of *C. (M.) vittiger* var. *testaceus* (NHML), “Wagiou” (Waigeo), “*vittiger* var.”, “68.106”, “B.M., Type”, “*vittiger* var. *testaceus*”, with the same Dobson’s label.

Additional material (some selected specimens). Indonesia. 1 ex. (SMNS), “Maluku, Is. Halmahera, Tobelo, Mamuya, 12.XI.1999, 20–500 m, A. Riedel”.

Papua New Guinea. 31 ex. (TMB, ZIN), “N Guinea, Biry, 1898”, “Simbang Huon Golf”; 1 ex. (TMB), “N Guinea, Biry, 1900”, “Friedrich-Wilh.-hafen”.

Diagnosis. This species is very similar and, probably, closely related to *C. (M.) schioedtei* as well as to the Polynesian *C. (M.) mutabilis* and *C. (M.) oculatus* (see

below the diagnosis of the *C. (M.) schioedtei* and the above key to species), however, it differs from the first in the denser punctuation and raised microreticulation of the integument on pronotum, difference in length of antennomeres 2 and 3 as well as in its more expressed punctuation and sculpture on prosternum, and in comparison with the second the species under consideration also has the more robust body, usually with very convex and subquadrangular pronotum, never with traces of explanate pronotal sides, subtruncate apex of prosternal process and very distinct shape of the lateral lobes of phallobase (“tegmen”). Besides, this species is very distinct from both *C. (M.) mutabilis* and *C. (M.) oculatus* in the pattern of the body colouration.

Notes. Three type specimens from two “varieties” of *C. (M.) vittiger* belong to the species quite distinct in the structure of the male genitalia. The labels of the one of these specimens corresponds the Murray’s text devoted to *C. (M.) vittiger* var. *robustus* and it was designated as a lectotype of it. The second specimen of *C. (M.) vittiger* var. *robustus* has some inconsistency in the labels (“Wagou” and “*vittiger* var. *robustus*, Dorey”) and it is reasonable to regard it only as a paralectotype, despite that it is more mature, larger and darker. Finally, one of the specimens of *C. (M.) vittiger* var. *testaceus* belongs to this species, but the name *testaceus* in accordance with the lectotype designation should be treated as a synonym of *C. (M.) contegens* (see above). The type locality of *C. (M.) vittiger* var. *robustus* is Waigeo (“Waigiu” – an island in the Raja Ampat Archipelago offshore the Indonesian part of New Guinea). Besides, it is so far known only from the Papuan Province from Simbang Huon Golf (Papua New Guinea) and from a close insular system – Maluku (Halmahera Island: Tobelo, Mamuya).

Carpophilus (Myothorax) schioedtei Murray, 1864
(Figs 133–139)

Carpophilus (Myothorax) schioedtei Murray, 1864: 381 (“Pulo Milu”; syntypes) = *C. (M.) pallescens* Murray, 1864: 380 (“Waigiu”; syntypes), **syn. n.** = *C. (M.) vittiger* var. *limbalis* Murray, 1864: 373 (“Dorey”; syntypes), **syn. n.**

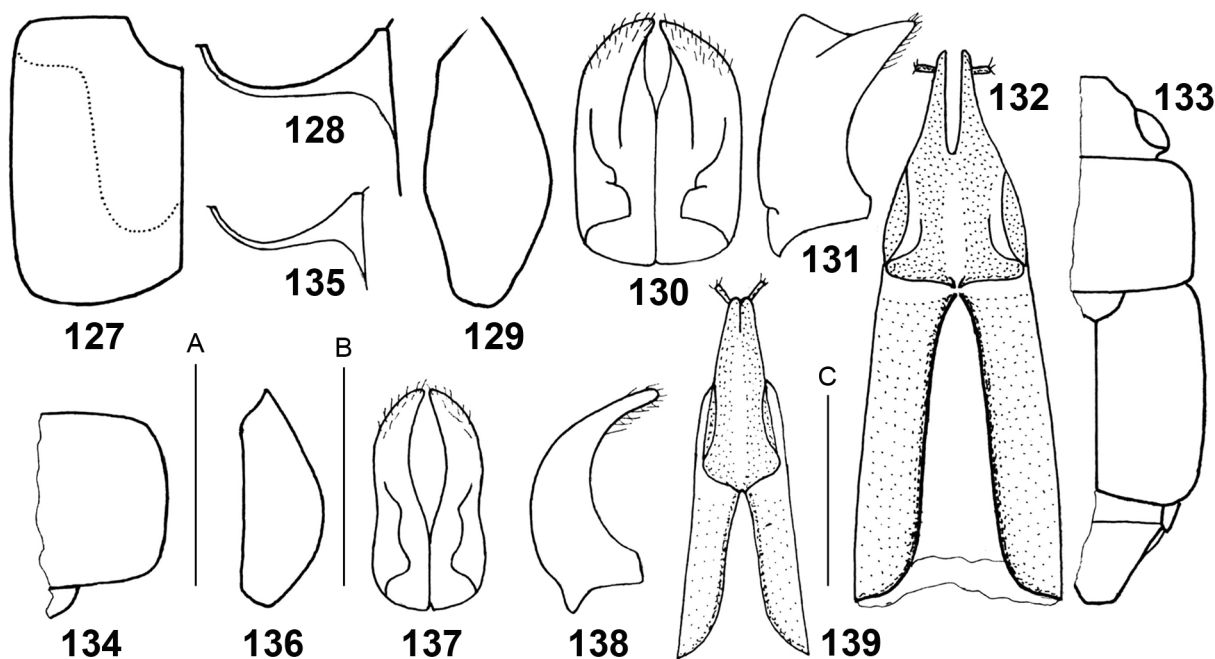
In total, more than 160 specimens were examined, including the types as well as others from different collections (ANIC, NHML, NMB, NMP, RNHL, SMNS, ZIN, ZMB, ZMO, ZMUC).

Type material. India. 1♂, lectotype of *C. (M.) schioedtei* (ZMUC), here designated, “Pulo Milu, Galatea”, “*schiodtei* Murr.”, “holotypus Jelínek 1984”.

Indonesia. 1♀, lectotype of *C. pallescens* (NHML), here designated, and 1♀, paralectotype of *C. (M.) pallescens* (NHML), “Waigiu”, “68.106”; 1♀, lectotype of *C. (M.) vittiger* var. *limbalis* (NHML), here designated, “Wallace”, “ex Mus. Murray”, “Moluccas, Dorey”, “Dor”, “Fry Coll. 1905-100”, “*limbalis*”; 1♀, (?) paralectotype of *C. (M.) vittiger* var. *limbalis* (NHML), “Celebes, Macass”, “ex Mus. Murray”, “Type”, “*vittiger* var.”, “Fry Coll. 1905-100”, “*Carpophilus maculatus limbalis* Murr., R.M. Dobson Det., Lectotype”.

Additional material (some selected specimens). India. 15 ex. (ZIN, ZMUC), “Pulo Milu, Galatea”; 2 ex. (ZMUC), “Nancovri, Galatea”; 1 ex. (NMB), “Andaman Is., Havelok I., env. of village N7, 11°59’N, 92°58’E, 22.IV–14.V.1998, Karel & Simon Majer”.

China. 1 ex. (ZMB), “Tainan, Formosa, 1911, H. Sauter”, “22.VII”, “*Carpophilus dimidiatus* F.”, “det. Grouvelle”; 5 ex. (NHML, ZIN), “Hong Kong, Sai Kung Farm (case 432)”, “in rotten flowers of orange, 16.IV.81, R. Winney, 83/8A”; 2 ex. (NHML, ZIN), “Hong Kong, Tai Po Kau, 7.X.92”, “inside fallen fruit of *Citrus reticulata*”.



Figs 127–139. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

127–132 – *C. (M.) robustus* stat. n.; 133–139 – *C. (M.) schioedtei*. 127 – elytron with dotted outline of lightened part, dorsal view; 128 – submesocoxal line of metaventrite, ventral view; 129 – male metafemur, ventral view; 130–131, 137–138 – lateral lobes of phallobase ("tegmen"); 130, 137 – ventral view, 131, 138 – lateral view; 132, 139 – ovipositor, ventral view; 133 – female body, the holotype, dorsal view; 134 – pronotum of specimen from Vietnam, dorsal view; 135 – submesocoxal line of metaventrite, ventral view; 136 – female metafemur (holotype), ventral view. Scale bars: A – 1 mm (to Figs 127, 133–134), B – 0.5 mm (to Figs 128–129, 135–136), C – 0.5 mm (to Figs 130–132, 137–139).

Рис. 127–139. Виды подрода *Myothorax* рода *Carpophilus*.

127–132 – *C. (M.) robustus* stat. n.; 133–139 – *C. (M.) schioedtei*. 127 – надкрылье с пунктированным очертанием осветленной части, сверху; 128 – субмезококсовая линия метавентрита, снизу; 129 – заднее бедро самца, снизу; 130–131, 137–138 – латеральные доли фаллобазы («тегмен»); 130, 137 – снизу, 131, 138 – сбоку; 132, 139 – яйцеклада, снизу; 133 – тело самки, голотип, сверху; 134 – переднеспинка экземпляра из Вьетнама, сверху; 135 – субмезококсовая линия метавентрита, снизу; 136 – заднее бедро самки (голотип), снизу. Масштабные линейки: А – 1 мм (к рисункам 127, 133–134), В – 0.5 мм (к рисункам 128–129, 135–136), С – 0.5 мм (к рисункам 130–132, 137–139).

Thailand. 5 ex. (NMB, ZIN), "23–25.II.1993, Ranong prov., 9°56' 98'40", Ranong Hot Spring, K. Majer"; 24 ex. (NMB, ZIN), "1–21.iii.1996, Chumphon prov., Pha To env., 9°48' 98'47", K. Majer"; 1 ex. (SMNS), "29.VIII.1996, Nong Khai, 17°52'N 102°44'E, M. Hauser".

Laos. 14 ex. (NMP, ZIN), "5–11.5.1997, 20 km NW Louang Namtha, N 21°09.2 E 101°18.7, Alt. 900 ± 100 m, E. Jendek & O. Šauša".

Vietnam. 11 ex. (ANIC, SMNS, ZIN), 400 m, Son Đòong, Range Tam Đảo, O. Kabakov, 20.02.1962 (in Russian), fruits of *Dillenia*, 24.02.1962 (in Russian); 3 ex. (ZIN), mountains SO Chảo quý, 300 m, 6.02.1963, O. Kabakov (in Russian); 5 ex. (NMP, ZIN), "Hoa Binh, 4–7.6.1986, Jan Horák"; 1 ex. (NMB), "2–12.V, Cuc Phuong N.P., 100 km S Hanoi, J. Jendek, 1991".

Malaysia. 2 ex. (SMNS), "Borneo: Sabah, Crocker Range N.P., NW Keningau, 900–1200 m, at light, 18.XI.1996, D. Grimm".

Malaysia or Indonesia. 1 ex. (ZMB), "N. Borneo, H. v. Tertyen".

Indonesia. 1 ex. (RNHL), "Dr B.H. Hagen, Tandjong, Morawa, Serdang (N.O. Sumatra)"; 1 ex. (RNHL), "Amboina, Ned. India, L. de Vos"; 1 ex. (NHML), "Ternate, 92–20"; 9 ex. (SMNS, ZIN), "Irian Jaya: Jayapura, Sentani, Cyclop-Mts., 5–10.1991, 300 m, A. Riedel"; 1 ex. (SMNS), "NE Sumbawa, 4 km NW of Dompou, 13.II.1994, Bolm"; 2 ex. (SMNS), "Lombok, Crocker Range N.P., NW Keningau, 900–1200 m, at light, 18.XI.1996, Bolm".

Philippines. 6 ex. (ZIN, ZMB), "Insel Leyte, Burauen bei Leyte, Böttcher, 7.5.1915"; 1 ex. (ZMB), "Luzon, Böttcher, II.1918"; 1 ex. (ZMUC), "Palawan, Mantilingajan, Pinigisan, 600 meter, 23 Sept. 1963, Noona Dan Exp. 61–62"; 2 ex. (NMB), "1600 m, Mindanao, 30 km W of Maramag, 28–30 Dec. 1990, Bolm"; 17 ex. (SMNS, ZIN, ZMO), "Mindanao, 30 km E of Malaybalay, Busdi, 5–9 May 1996, Bolm, 1000 m"; 1 ex. (SMNS), "Mindanao, 30 km NW Maramag, 13–17 May 1996, Bagingsilang, 1700 m, Bolm"; 1 ex. (SMNS), "Mindanao, Davao Prov., 29 km NW of New Bataan, 20–22 May 1996, Bolm, 1200 m".

Papua New Guinea. 2 ex. (NHML), "N. Guinea, Kapakapa, Mag-Guigno 1891, L. Loria".

Oceania. 13 ex. (NHML), Solomon I., New Hebrides, Malekula.

USA. 4 ex. (ZIN, ZMUC), Hawaii, "Oahu, Galatea".

Diagnosis. This species is very similar and, probably, closely related to *C. (M.) robustus* stat. n. differing from it mostly in the structure of lateral lobes of phallobase ("tegmen") and the characters listed in the above key to species. It is more or less characteristic that the posterior edge of the prosternal process in this species is more arcuate to subsemicircular, while that in *C. (M.) robustus* stat. n. is subtruncate. The shape of the pronotum in this species often is quite characteristic, but that in smaller specimens is without clear lateral explanations and almost as outlined as that in smallest specimens of *C. (M.) robustus* stat. n. In contrast to *C. (M.) robustus* stat. n., the male pygidium in this species is subtruncate rather than arcuate or angular, antennal grooves are frequently joined behind the mentum by a more or less clear transverse depression. *Carpophilus (Myothorax) schioedtei* is also very similar to the Polynesian *C. (M.) mutabilis* but differs from it in the colouration of its body, outline of pronotum and elytra, denser punctuation and more developed sculpture of integument, more conspicuous pubescence and narrower lateral lobes of its phallobase ("tegmen").

This species has an appearance quite characteristic of many species of the *dimidiatus*-group, however, the structure of the male genitalia allows to suppose a closer relationship between this species and *C. (M.) contegens*. Nevertheless, except peculiar structure of genitalia of both sexes, *C. (M.) schioedtei* differs from the latter in

the usually lighter and larger body, less distinct, denser and finer punctation of its integument, more smoothed surface of the prosternum, greater difference in the length of antennomeres 2 and 3, nearly subtruncate apex of the prosternal process, longer last labial palpomere, somewhat shorter metafemur, rounded to subangular apex of the male pygidium and emarginate apex of the female pygidium.

Carpophilus (Myothorax) schioedtei, except the peculiar genitalia, pronotum and shape of apex of the female pygidium, differs also:

- from *C. (M.) assignatus* **sp. n.** in its comparatively larger and rather subquadrate antennal club, different length of the antennomeres 2 and 3, prosternal process usually less curved along coxae and with more subflattened apex, submesocoxal line more deviating from the edge of coxal cavities;

- from *C. (M.) fumatoides* **sp. n.**, *C. (M.) fumatus* and *C. (M.) generosus* **sp. n.** in its lighter body colouration, a greater difference in length of the antennomeres 2 and 3, prosternal process with more flattened apex, more smoothed prosternal and mesoventral surface, comparatively larger antennal club; and from the latter also in the sparser punctation and less contrasting sculpture of integument, not subtruncate apex of the prosternal process and different outline of the submesocoxal line;

- from *C. (M.) mutilatus* in its less developed punctation of underside (much sparser or reduced on prosternum and metaventrite), prosternal process with more flattened apex and subtruncate posterior edge, more smoothed prosternal and mesoventral surface, comparatively larger antennal club and somewhat wider tibiae;

- from *C. (M.) notatus* in its lighter body with less contrasting spots on elytra, less coarse and not so dense punctation of integument (especially reduced or smoothed punctation and sculpture on prosternum and mesoventrite), subquadrate antennal club, prosternal process less curved along coxae and with subflattened apex;

- from *C. (M.) pilipennis* in its more slender body with not so raised sculpture on dorsum, different length of the antennomeres 2 and 3, prosternal process less curved along coxae and with subflattened apex, somewhat more smoothed surface of mesoventrite, less deepened median line of the metaventrite, submesocoxal line less strongly deviating from the posterior edge of cavities.

Finally, the species under consideration differs from the Polynesian *C. (M.) oculatus* mostly in the pattern of body colouration, characters of punctation and sculpture of integument as well as in the genital structure of both sexes; and also from *C. (M.) timorensis* in its generally larger body, antennomere 3 not shorter than antennomere 2, more distinct punctation, including that on medioanterior part of prosternum, medioanterior part of prosternum rectilinear from side, submesocoxal line more deviating from anterior angles of metaventrite and simple apex of the female pygidium.

Notes. Among the specimens collected during voyage of the Galathea on the island Pulo Milu (Nicobar Islands) one female was studied by A. Murray and for

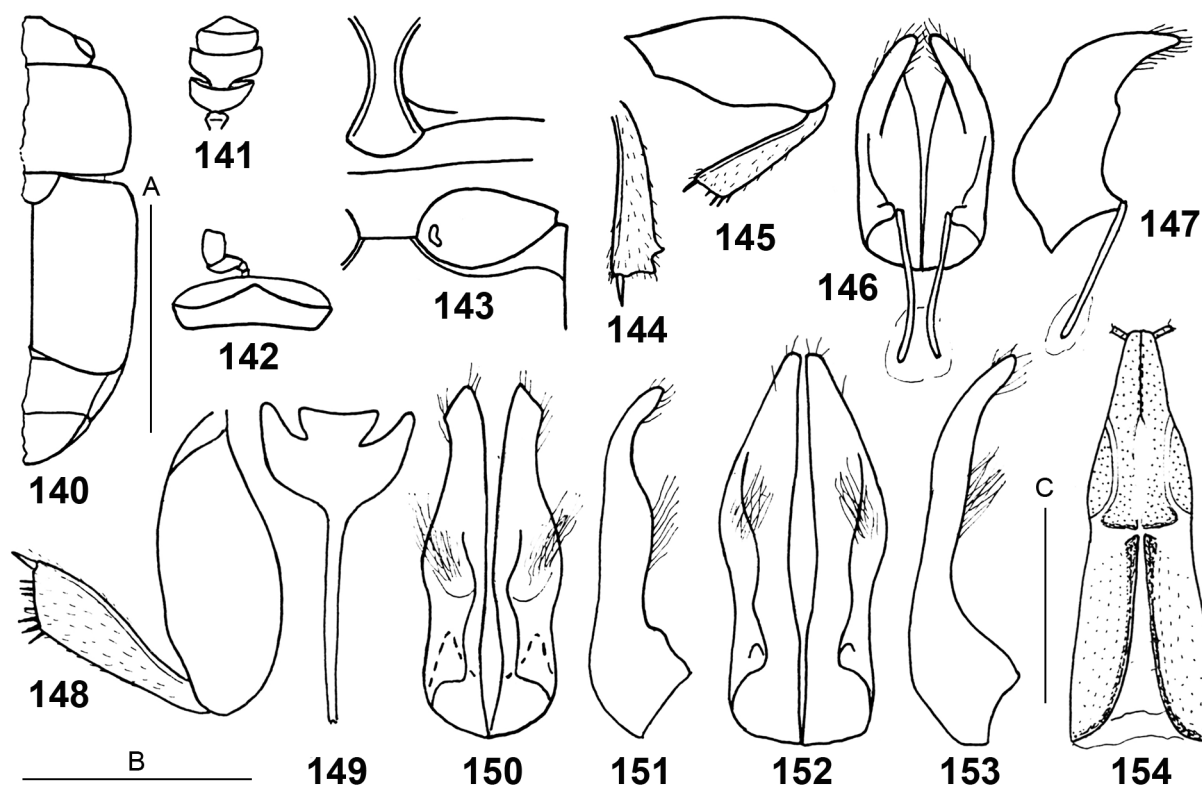
this specimen (small – with body length 2.4 mm – and brownish female with lighter elytra) he proposed the name *C. (M.) schioedtei*. Although the characters of this light and small specimen are not easy to interpret, other specimens originated from the same series are quite mature and include both sexes. It is necessary to note that lateral lobes of phallobase (“tegmen”) of the most males from this series are rather narrow at base. Besides, specimens from the type locality are characterised by darker head, pronotum and uncovered tergites. On the other hand, the studied specimens from Thailand show a great variability in width of the lateral lobes of phallobase (“tegmen”) at base; pattern of the body infuscation as that in *C. (M.) mutilatus* (with blackish pronotal disk) and female pygidium in many cases convex or even subangular. The both type specimens of *C. (M.) pallescens*, lectotype and paralectotype, are small females, which are difficult for a reliable identification, and, therefore, the name *pallescens* is preferable regarded as the second synonym, although it was published above the page with the description of *schioedtei*. The form *C. (M.) vittiger* var. *limbalis* is represented in the collection of NHML by two females. One of the latter, chosen for the lectotype designation, has two geographical labels consistent to the text of the original description (“Dorey”). This specimen is rather small (2.1 mm in length), pale and with slightly darkened elytra apices. Another female of this series is larger (3.6 mm), brownish with slightly darker elytral apices. This specimen has indication on another locality (“Celebes, Macass.”), and therefore, it is designated as questionable paralectotype of this variety (see above the “Notes” to *C. (M.) contegens*), but not as the lectotype, as proposed on label by R.M. Dobson. Moreover, because of similarity in the female genitalia, the small specimens of both *C. (M.) robustus* **stat. n.** and the species under consideration are rather problematical for a reliable separation, the name *limbalis* would be reasonable to regard as not a senior synonym for one of these forms. However, the two females of *C. (M.) limbatus* examined with a more probability are rather conspecific with the specimens of the species under consideration than with those here regarded as *C. (M.) robustus* **stat. n.** Taking into account these circumstances, the author proposes to treat the name *limbalis* as a junior synonym of *schioedtei*, despite the fact that the description of *limbalis* is located in the text of the Murray’s monograph some pages above the latter name.

Carpophilus (Myothorax) timorensis Dobson, 1993
(Figs 140–147)

Carpophilus timorensis Dobson, 1993: 7 (Timor; holotype and paratypes).

Type material. Timor. 1♂, 1♀, paratypes of *C. (M.) timorensis* (BMNL), “Dilli, Timor, 20–22 Jan, Dr. M. Cameron, B.M. 1936–555”, “not *maculatus* Murr. or *freemani* Dobs.”, “*Carpophilus timorensis* Dobson, R.M. Dobson det.”

Notes. This species is included in this review because it is useful to be compared with its other relatives from the Indo-Malayan Region. It can be identified after the above key to species and also “Diagnosis” for *C. (M.) brunneus*, *C. (M.) dimidiatus*, *C. (M.) languescens* **sp. n.**, *C. (M.) mutilatus*, and *C. (M.) schioedtei*.



Figs 140–154. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

140–147 – *C. (M.) timorensis*; 148–154 – *C. (M.) zeaphilus*. 140 – male body, dorsal view; 141 – antennal club; 142 – mentum and labial palpus, ventral view; 143 – prosternal process, mesoventrite, mesocoxal cavity and submesocoxal line of metaventricle, ventral view; 144 – male mesotibia, ventral view; 145, 148 – male metafemur and tibia, ventral view; 146–147 – lateral lobes of phallobase ("tegmen"): 146 – ventral view, 147 – lateral view; 149 – male ventral plate and spiculum gastrale; 150–151, 152–153 – lateral lobes of phallobase ("tegmen") of specimen from the Afrotropical Region: 150, 152 – ventral view, 151, 153 – lateral view; 154 – ovipositor, ventral view. Scale bars: A – 1 mm (to Fig. 140), B – 0.5 mm (to Figs 142–145, 148), C – 0.5 mm (to Figs 146–147, 149–154).

Рис. 140–154. Виды подрода *Myothorax* рода *Carpophilus*.

140–147 – *C. (M.) timorensis*; 148–154 – *C. (M.) zeaphilus*. 140 – тело самца, сверху; 141 – булава усиков; 142 – ментум и лабиальный щупик, снизу; 143 – отросток переднегруди, мезовентрит, мезококсовая впадина, субмезококсовая линия метавентрита, снизу; 144 – средняя голень самца, снизу; 145, 148 – заднее бедро и голень самца, снизу; 146–147 – латеральные доли фаллобазы («тегмен»): 146 – снизу, 147 – сбоку; 149 – вентральная пластинка и гастральная спикула самца; 150–151, 152–153 – латеральные доли фаллобазы («тегмен») экземпляра из Афротропической области: 150, 152 – снизу, 151, 153 – сбоку; 154 – яйцеклад, снизу. Масштабные линейки: A – 1 мм (к рисунку 140), B – 0.5 мм (к рисункам 142–145, 148), C – 0.25 мм (к рисункам 146–147, 149–154).

Carpophilus (Myothorax) truncatus Murray, 1864
(Figs 46–48)

Carpophilus (Myothorax) truncatus Murray, 1864: 381 (Madagascar; syntypes) = *Carpophilus jarijari* Powell et Hamilton, 2019: 193 (Australia: Victoria; holotype and paratypes) = ? *C. floridanus* Fall, 1910 = ? *C. halli* Dobson, 1964.

In total, more than 60 specimens examined, including type specimens.

Type material. Madagascar. 4 ex., syntypes of *C. (M.) truncatus* (ZMB) (marked in the collection by S. Endrödy-Younga in 1964), "Madagascar, Goudot", "8371"; 2 ex., syntypes of *C. (M.) truncatus* (NHML), "Madagascar", "ex Mus. Murray", "Fry Coll. 1905-100."

Additional material (some selected specimens). Morocco. 1 ex. (ZSM), "Marrokko, Agadir, Flugh/faule, Orange, 1.4.85, leg. Spornraft".

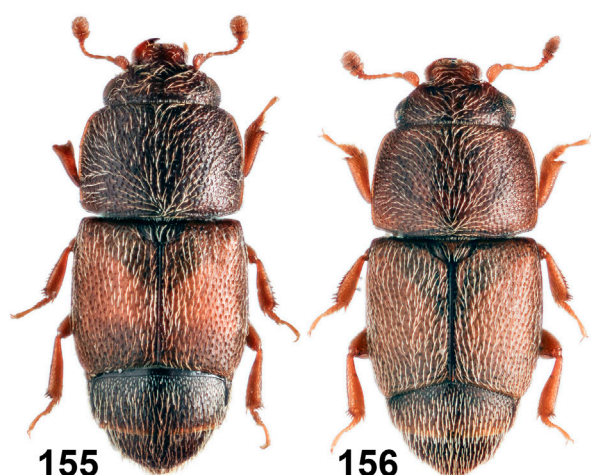
South Africa. 2 ex. (ZSM), "Natal, Durban, 27 August 1980, leg. Spornraft".

Madagascar. 3 ex. (ZIN), "Annanarivo: Sikoro, C. schaufus"; 5 ex. (ZIN, ZMB), "Madagascar Centre, Antananarivo, 3–5.1.1995, J. Jana'k", "1250–1350 m, jardins tamisages".

Seychelles. 2 ex. (ZIN), "S. Seychelles, Farquinar Atoll, 16–19.VIII.1984, USSR Zool. Exp."

Mauritius. 4 ex. (NHML).

Notes. It can be identified after the above key to species and also "Diagnosis" in *C. (M.) dimidiatus*. Semeraro et al. [2023] redescribed this species in detail and described *C. (M.) imitatus* Semeraro, Blacket, Rako et Cunningham, 2023 after study of some series from local populations from Australia (Victoria, New South Wales, South Australia), however the complete examination of large series of these two "species" and also *C. (M.) dimidiatus* and *C. (M.) pilosellus* from different geographical places of the Southern Hemisphere remains rather necessary to define their diagnostic characters and true distribution. Probably, synonymization of the names of the members of *Carpophilus* by Gillogly [1962] and Connell [1963] was quite correct when they put both *Carpophilus floridanus* from Florida and *C. halli* from stored products transported from Nigeria, Sierra Leone, Honduras to junior synonyms of *C. (M.) pilosellus*. However Jelínek and Audisio [2007] transferred both these names to synonyms of *C. (M.) truncatus*. Therefore, it would be reasonable once again to have a look at the antennomeres 2



Figs 155–156. Species of the subgenus *Myothorax* of the genus *Carpophilus*.

155 – *C. (M.) dimidiatus*, beetle length 2.6 mm; 156 – *C. (M.) pilosellus*, beetle length 2.5 mm.

Рис. 155–156. Виды подрода *Myothorax* рода *Carpophilus*.

155 – *C. (M.) dimidiatus*, длина жука 2.6 мм; 156 – *C. (M.) pilosellus*, длина жука 2.5 мм.

and 3 in the type specimens of *C. floridanus* and *C. halli*. At least *C. (M.) pilosellus* seems to be rather usual in stored products of Europe and Palearctic as a whole, while *C. (M.) truncatus* has also lot of chances to come there from areas of the Southern Hemisphere thanks to transportation by men.

Carpophilus (Myothorax) zeaphilus Dobson, 1969
(Figs 148–154)

Carpophilus zeaphilus Dobson, 1969: 99 (Kenya; holotype and paratypes).

Many specimens from Africa and Madagascar were examined, partly listed by Kirejtshuk [1996] and compared with the type specimens in NHML.

Notes. This species is rather similar to *C. (M.) brunneus* and its diagnosis is discussed above in the “Diagnosis” of it. It can be identified after the above key to species and also “Diagnosis” in *C. (M.) dimidiatus* and *C. (M.) languescens* **sp. n.** This species was recorded from other continents, although it seems to be more common in Africa. The type locality of this species is Kiganjo (Kenya) and it is thought that Africa was the continent of its initial range before it started to distribute by men.

Species synonymy, notes on species taxonomy and distribution

**Synonymy of *Epuraea (Epuraea) biguttata*
(Thunberg, 1784)**

The problem of determination of specimens which could be named *Epuraea (Epuraea) biguttata* and *E. (E.) unicolor* (Olivier, 1790) is known to everybody who tried to do it. After examination of some thousand museum specimens, Kurochkin and Kirejtshuk [2006] fulfilled the following some testing experiments in Samara Region

of Russia, which included larvae taken in six localities (different administrative districts) from different ecotopes (fruiting bodies of *Fomes fomentarius* (Fr.) Gill. on *Quercus robur* L. and *Betula pendula* Roth, spore powder, under bark of *Quercus robur*, *Acer platanoides* L. and *Betula pendula* on fermented sap) and bred adults on different substrates (sometimes with change on another and different from that where the larvae were taken, and also on yeast/banana/sugar/water mixture). These experiments showed that there are no reliable diagnostic characters to consider *E. (E.) biguttata* and *E. (E.) unicolor* as separate species and the characters of “*E. (E.) biguttata*” and “*E. (E.) unicolor*” are mostly dependable on the substrate of habit and feeding. Hisamatsu [2016] after a rather wide comparison materials from different places of the Palearctic Region found that the structures (including the armature of the inner sac of penis) formerly treated for separation of these “species” should be recognised as intraspecific variability. Nevertheless, Jelínek and Audisio [2007] in their catalogue mentioned *E. (E.) biguttata* and *E. (E.) unicolor* separately. Later, Booth [2020] regarded that the mentioned names can be used for two separate species, he examined some localities in the United Kingdom and found two forms which could be regarded as two species. However, two types of the armature of inner sac of penis drawn by R. Booth as belong two considered “species” have not been found among examined specimens from different localities of both European and Asian parts of Russia, but the continental specimens showed a great variability of the armature of inner sac of penis. Thus, the opinion of P. Audisio, R. Booth and J. Jelínek on a possibility to divide *E. (E.) biguttata* into two species (“*E. (E.) biguttata*” and “*E. (E.) unicolor*”) should be recognized as unproven.

Notes on *Epuraea (Epuraea) longipennis* Sjöberg, 1939 and synonymy of *E. (E.) excisicollis* Reitter, 1872

The holotype of *Epuraea longipennis* was studied by A.G. Kirejtshuk in the 90s of the last century and after that it was loaned by P. Audisio (Roma University), who was keeping it about at least 20 years. The latter researcher published the synonymy of the name of “*longipennis*” with name *Epuraea (Epuraea) dolosa* Kirejtshuk, 1995 [Audisio et al., 2006] and was asked to send the specimen to the Hungarian Natural History Museum or its pictures to St Petersburg for a next examination. However, he did not find a possibility to return this Sjöberg’s type back to the museum up to 2021 (until the death of O. Merkl, curator of collection of the Hungarian Natural History Museum). According to the first examination, the Sjöberg’s type does not fit the type specimens of *E. (E.) dolosa*. It remains unclear what was the reason for the synonymization of names with completely dissimilar types (*longipennis* and *dolosa*). Therefore, this synonymy is not included in the catalogue of the Far East insects (Kirejtshuk, in prep.). In the same paper, Audisio et al. [2006] designated as a neotype of *E. (E.) excisicollis* Reitter, 1872 the specimen which seems to be a variety of *E. (E.) dolosa* with markedly wider body with comparatively shorter elytra, having also pronotal and elytral sides more widely explanated. Large series of *Epuraea* Erichson, 1843 specimens from West

Siberia (partly published by Kerchev et al. [2022]) showed a great variability of *E. (E.) excisicollis*. The taxonomic situation can be change if the true type specimen is found during further research.

In accordance with the latter designation for this Reitter's name as the senior synonym of this species, the synonymy of it at the moment is following: *Epuraea excisicollis* Reitter, 1872: 18 (Germany) = *E. danica* Sjöberg, 1939: 115 (Denmark) = *E. (Epuraea) dolosa* Kirejtshuk, 1995: 279, **syn. n.** (northern part of the Eastern Europe).

Notes on *Epuraea (Epuraea) hilleri* Duftschmid, 1825

After synonymization of *Epuraea hilleri*, *E. (Epuraea) concurens* Sjöberg, 1939 and *E. (E.) fageticola* Audisio, 1991 (= *Nitidula castanea* Duftschmid, 1825, not C.R. Sahlberg, 1820 et non Melsheimer, 1846) by Kirejtshuk [1997b] establishing that this species has two forms without "subspecific status", Audisio et al. [2006] put forward a hypothesis on splitting of one species into two subspecies (the eastern *E. (E.) hilleri hilleri* and the western *E. (E.) hilleri fageticola*) with difference in body size, which appeared a sequence of the Pliocene/Pleistocene ice-cycle. Additional specimens confirmed the Kirejtshuk's opinion on the irregular distribution of populations of this species with predominance of populations with smaller specimens in eastern, northern and mountainous areas, while the populations in the western and southern areas of the species range include mainly larger specimens, although some specimens in the last-mentioned part of the species range are as small as those in northern or eastern ones. It seems that such a distribution could be resulted by phenological circumstance or having temperature dependence rather than historical which could have a phylogenetic explanation.

Distribution of *Epuraea (Micruria) auripubens* Reitter, 1901

This species was described from Mongolia ("Changai-Gebirge" [Reitter, 1901]). It can be easily distinguished even after its original description, particularly thanks to "tibiis extus apice subdentate-productis" and it is included into the key to *Epuraea* species of the Russian Far East [Kirejtshuk, 1992]. Recently it was found also in China, Altai Mountains, Kuril Islands. As it is common among epuraeines, this species demonstrates a significant level of variability in the width of pronotal explanation and sharpness of penis apex.

Material. 1 ex. (ZIN), Da-Tzin'-Lu, 23.06.1893, Potanin (in Russian); 1 ex. (ZIN), between Tzun' Gor and Tao (ch)guan', 8.08.1893, Potanin (in Russian); 1 ex. (ZIN), Lan'-Chzhou-Fu, 1–8.08.1908, Kozlov (in Russian); 2 ex. (ZIN), Kosh-Agach, Altay, Narchuk, 16.06.1964 (in Russian); 1 ex. (ZIN), Mongolia, Khuvsgul Aimag, Uliy Daba Pass, M. Kozlov, 16–17.07.975 (in Russian); 1 ex. (ZIN), Kuril Islands, Kharimkotan Isl., 8.08.1996, V. Tislenko (in Russian); 3 ex. (ZIN), KH-96-ASI-969, Kharimkotan, A. Lelej, 8.08.98 (in Russian); 2 ex. (ZIN) Racshua Isl., 4.08.1999, A. Lelej, S. Storozhenko (in Russian).

Synonymy of *Carpophilus (Ecnomorphus) plagiatiipennis* (Motschulsky, 1858)

This species is one of the most common and widely distributed consubgener, demonstrating a wide level of

variability in many characters studied in many specimens from the Indo-Malayan Region, including the characters used by Dasgupta and Pal [2019] for distinguishing of *Carpophilus (Ecnomorphus) jahari* Dasgupta et Pal, 2019 and the type specimens of "species" proposed earlier.

Thus, the corrected synonymy of this species is following: *Colastus plagiatiipennis* Motschulsky, 1858: 39 (? syntypes, India orientalis ("des montagnes de Nura-Ellia" (= Nuwara Eliya, Sri Lanka))) = *C. dilutus* Motschulsky, 1858, non *Carpophilus (Myothorax) vittiger* var. *dilutus* Murray, 1864: 373 = *C. (Eidocolastus) bosschae* Grouvelle, 1892: 43 (syntypes, Borneo occidentalis) = *C. (E.) nigricans* Grouvelle, 1897: 356 (syntypes, Sumatra) = *C. (Ecnomorphus) jahari* Dasgupta et Pal, 2019: 24, **syn. n.** (holotype and paratype, India, Arunachal Pradesh).

In total, more than 300 specimens were examined, including type specimens below and others (NHML, NMB, NMP, NMW, NRS, RMNH, SMNS, TMB, ZIN, ZMB, ZMUC).

Type material. Sri Lanka. 1♂, lectotype of *Colastus plagiatiipennis* (ZMMU), here designated (marked as lectotype in the collection by J. Jelinek), and 6 ex., paralectotypes of *C. plagiatiipennis* (ZMMU, ZIN), "Ind. or."; 1♂, lectotype of *C. dilutus* (ZMMU), here designated, and 3 ex., paralectotypes of *C. dilutus* (ZMMU), "Ind. or."; 1 ex., paralectotype of *C. plagiatiipennis* (NRS), "Ceylon", "Motsch."

Malaysia. 1♀, lectotype of *Carpophilus boschai* (RMNH), here designated, "Borneo occ., Sambus, Dr J. Bosscha".

Indonesia. 1♂, lectotype of *Carpophilus (Eidocolastus) nigricans* (MSNG), here designated, "SUMATRA, SI-RAMBÉ, XII.90–III.91, E. Modigliani", "*Carpophilus nigricans* Grouv." (written by A. Grouvelle).

Additional material (some selected specimens). India. 2 ex. (TMB, ZIN), "Karnataka, Shimoga Distr., Jog Falls, 500 m, Gy. Topál", "from decaying jack-fruit and carcasses, 9.III.1980, Gy. Topál"; 1 ex. (NMW), "Kerala, Alleppey, 8–9.10.1991, R. Schuh".

Nepal. 1 ex. (SMNS), "311 Ilam Distr., Modia Khola Valley, N Siwalik Mts., Berlese sample, Shorea mixed forest, 320 m, 6 April 1988, J. Martens & W. Schawaller".

Sri Lanka. 1 ex. (NHML), "Colombo"; 1 ex. (NHML), "Mt. Lavinia, Ceylon, R.N. Parker".

Thailand. 3 ex. (ZIN, ZMUC), "Chiang Mai Province, Doi Inthanon N.P.: Mae Klang, 3–400 m, X.1981, Zool. Museum Copenhagen leg."; 1 ex. (ZMUC), "Chiang Mai Province, Doi Inthanon N.P.: Vajirataru, 750 m, 10.X.1981, Zool. Museum Copenhagen leg."; 2 ex. (NMB, ZIN), "25.V.1991, Fang, 300 m, 19°55'N 99°12'E, Vít Kubán"; 1 ex. (ZMUC), "Satun province, Thale Ban National Park, 6°42'N 100°10'E, 14–16.x.1991, O. Martin"; 31 ex. (ZIN, ZMUC), "Yala province, Bang Lang National Park, 6°04'N 101°11'E, Dead tree, 18–20.x.1991, O. Martin"; 1 ex. (ZMUC), "Trang province, Hat Chao Mai National Park, 7°19'N 99°27'E, 25–27.x.1991, O. Martin"; 1 ex. (NMP), "S. Thailand, 25.4.1992, Betong, S. Bílý"; 1 ex. (NMP), "NW Thailand, 1–7.V.1992, Mae Hong Son, Ben Si Lang, 1000 m, S. Bílý"; 1 ex. (ZIN), "Soppong, 1500 m, 19.27N, 98.20E, V. Kubán, 28–31.5.95"; 1 ex. (NMP), "Mae Hong Son prov., 19°27'N 98°20'E, 1500 m, Soppong, 7–12.V, Vít Kubán".

Laos. 1 ex. (TMB), "Bolikhamsay Prov., Nam Leuk village, 300 m", "from cut logs, N 52, 13.IV.1998, O. Merkl and C. Sorba".

Vietnam. 1 ex. (ZIN), ridge, Tam Dao, Shon-Zuong, lowland valley, 20.2.1962, O. Kabakov (in Russian); 4 ex. (ZIN), mountains, S O Son-Duong, 300 m, 24.2.1962, Kabakov (in Russian); 1 ex. (ZIN), mountains, 40–50 km NO Thai Nguyen, 5.2.1963, O. Kabakov (in Russian); 1 ex. (NMB), "14,10N 108,30E, 40 km NW of An Khe, Buon Luoi, 28–30.V.1966, Pacholátko & Demlický"; 3 ex. (NMB, ZIN), "(Tonkin), pr. Hoang Liin Son, Sapa, 11–15.V.1990, Vít Kubán"; 3 ex. (ZIN), "Mai hou, prov. Ha Son Binh, 31.10–4.11.1990, Belokobylskij".

Malaysia. 16 ex. (NRS, ZIN), "Mt. Tibang, 1,700 m", "O. Borneo, Mjöberg"; 4 ex. (NHML), "Penang, G.F. Bryant. XI.13" (and "X.13"); 1 ex. (NHML), "Mt. Matang, W. Sarawak, G.E. Bryant, XII.1913"; 10 ex. (NHML), "Sabah, Tawai Plat, 1300 ft, 8 m S. Telupid, 8.ix.1977"; 1 ex. (ZIN), "Sarawak, Kapit Distr., Sebung, Baleh riv., 6–21.3.1994, Horák".

Indonesia. 2 ex. (RMNH, ZIN), "Matthes, Palunberg, Sumatra", "Coll. Veth"; 3 ex. (TMB), "Engano, Bua-Bua, V–VI.1891, Modigliani", det. (?) Grouvelle as *Eidocolastus dilutus*; 6 ex. (ZIN, ZMUC), "Mentawai, Sipora, Sereinu, V–VI.94, Modigliani"; 1 ex. (NHML), "ex koffubessen, Avros Medan, 29-I-35" (determined by P. Audisio as "*C. bifenestratus*");

1 ex. (NHML), "Sulawesi Utara, Dumoga-Bone N.P., January 1985", "underground funnel trap with carrion", "lowland forest, ca 200 m", "R. Ent. Soc Lond., Project Wallace, B.M. 1985-10"; 1 ex. (NHML), "Sulawesi Utara, Dumoga-Bone N.P., March 1985", "At light", "Clarke' Camp, Lower montane forest, 1140 m", "R. Ent. Soc Lond., Project Wallace, B.M. 1985-10"; 3 ex. (NHML), "Sulawesi Utara, Dumoga-Bone N.P., 9-16 May 1985", "Malaise trap", "lowland forest, ca 200 m", "R. Ent. Soc Lond., Project Wallace, B.M. 1985-10"; 1 ex. (ZIN), "Sulawesi Utara", "G. Mogogonipa, summit, 1008 m, 25.xi.1985", "R. Ent. Soc Lond., Project Wallace, B.M. 1985-10" (named by J. Jelinek as *C. sinuatus*); 2 ex. (NMB, ZIN), "Sumatra (N), Brastagi, G. Sibayak, 1450-1900 m, 19-23.II.1991, Bocák & Bocáková"; 2 ex. (SMNS, ZMB), "E-Jawa, Ijen. pl. Nat. P., 1800 m, Sodong, 26-27.II.1994, Bolm".

Philippines. 140 ex. (STM, ZIN), "Pt Banao, Mindanao"; 32 ex. (ZIN, ZMB), "Port Bangabei Capis, Insel Panay, Böttcher, 9.I.1915".

Synonymy of *Carpophilus (Myothorax) lewisi* Reitter, 1884

This species is one of commonest and widely distributed consubgenera, demonstrating a wide level of variability in many characters, established after examination of many specimens from the Palaearctic and Indo-Malayan regions, including some type series.

The corrected synonymy of this species is following:
Carpophilus lewisi Reitter, 1884 = *C. signatus* Grouvelle, 1908, **syn. n.** = *C. signatus* var. *ornatus* Grouvelle, 1908, **syn. n.** = *C. subcalvus* Kirejtshuk, 1984, **syn. n.**

In total, about 200 specimens were examined, including type specimens below and other specimens from the Indo-Malayan Region (NHML, NMB, NMW, RMNH, SMNS, TMB, ZIN).

Type material. Russia. 1 ex., holotype, and 2 ex., paratypes of *C. (M.) subcalvus* (ZIN), Vladivostok, Prim. Region, Berger, 13-26.viii.911 (in Russian).

Japan. 1 ♂, lectotype of *C. lewisi* (NHML), here designated, "Jokohama", "Japan, G. Lewis, 1910-320", "*C. lewisi* m. n. sp., Japan".

India. 2 ♀, syntypes of *C. signatus* (MNHN), "Kurseong, P. Braet", "*C. signatus* ty. Grouv." (written by A. Grouvelle); 1 ♀, holotype of *C. ornatus* (MNHN), "Sikkim, Resenzeit, H. Fruhstorfer", "*Carpophilus ornatus* ty. Grouv." (written by A. Grouvelle).

Additional material (some selected specimens). Russia. 4 ex. (ZIN), Primorsky Region, "Ussuriysky District, Gornotaezhnoe, 19.05.989, A. Kirejtshuk" (also "13.05.989" and "11.06.989"); 2 ex. (ZIN), Ussuriysk District, Gornotaezhnoe, 5 km ESE, stream valley, 20.05.1989, A. Kirejtshuk (in Russian); 1 ex. (ZIN), Ussuriysk District, Gornotaezhnoe, stream valley, 3.06.1989, A. Kirejtshuk, flowers of Acer (in Russian); 1 ex. (ZIN), Ussuriysk District, Gornotaezhnoe, felling near village, 7.06.1989, A. Kirejtshuk (in Russian).

China. 1 ex. (ZIN), Yunnan, environs of Biibyan', Daveishan', 1300 m, 23.06.1956, Khuan Ke-Zen etc. (in Russian and Chinese); 1 ex. (ZIN), Salween valley, W Baoshan', 800 m, Yunnan, V.1955, V. Popov (in Russian and Chinese); 31 ex. (NMB, ZIN), "Yunnan, 1500-2500 m, 25.22N 98.49E, 17-24/5.1995, Gaoligong mts., Vít Kubáň".

Pakistan. 3 ex. (NHML), "Punjab, Murree Hills, Camp Thobba", "H. Roberts".

India. 14 ex. (NMB, ZIN), "Darjeeling D., Bhakta B."; 9 ex. (TMB), "Ind. or., Trichinopoly"; 1 ex. (NHML), "Kurseong, Inde, Verschraeghen, 1904"; 1 ex. (NHML), "3079", "Ihoobsering Lebeng, IV.09, H.M.L."; 1 ex. (TMB), "W. Bengal, Darjeeling, below North Point, 650-1300 m, Gy. Topál"; 9 ex. (NMB, ZIN), "Chuba, 11.IV.1979, 670 m", "Darjeeling D., Bhakta B."; 5 ex. (NMB, ZIN), "Ringkabong, 890 m, 16.IV.1979", "Darjeeling D., Bhakta B."; 3 ex. (NMB), "Kalimpang, 1000 m, Upper Bombusti, 5.V.1985", "Darjeeling D., Ch.J. Rai".

Nepal. 1 ex. (SMNS), "185 Ilam Distr., zw. Mai u. Ilam, 1330 m, 1.4.1980, Martens & Ausobsky"; 1 ex. (NHML), "4500', Kathmandu, British Embassy, 20.V-23.VI.1983", "At light", "M.J.D. Brendell"; 1 ex. (ZIN), "303 Kathmandu Distr., Kathmandu Valley, Baneshwar, cultural land, gardens, 30 Mar.-2 Apr. 1988, 1400 m, J. Martens & W. Schawaller"; 4 ex. (SMNS, ZIN), "316 Ilam Distr., Bililate nr. Ilam, 1330 m, remnant trees around spring, moist soil, 1330 m, 8 April 1988, Martens & Schawaller"; 10 ex. (NMB, ZIN), "Kathmandu V., Godavari, 1500 m", "21-27.V.1989, M. Brancucci"; 1 ex. (SMNS), "632, Kathmandu, Baneshwar, 1350 m, 18-24.VI.2000, W. Schawaller".

Thailand. 1 ex. (SMNS), "Amphoe Chiang Dao, Dai Chiang Dao, 9.1.1989, 1500 m, Traitner & Geigenmüller"; 3 ex. (NMB, ZIN), "18-23.IV.1991, Doi Suthep-Pui, 1300-1500 m, P. Pacholátko".

Vietnam. 2 ex. (ZIN), 400 m, Son Duong, range Tam-Dao, onions of Dillenia, O. Kabakov, 24.02.1962 (in Russian); 1 ex. (ZIN), mountains, near Sa-pa, 1600-2000 m, 4.04.1963, O. Kabakov (in Russian); 1 ex. (NMB), "N. Viet Nam (Tonkin, Prov Vinh Phu, 1990, Tam Dao, 17-21.V., Vít Kubáň"; 1 ex. (NMW), "N-Vietnam, 25.V-10.VI, Sapa (Lao Cai), 22°20' S 103°50' E, E. Jendek, 1991"; 1 ex. (NMB), "N. Vietnam, 21.27N 105.39E, 70 km NW Hanoi, Tam Dao, 1-8.VI.1996, 900-1200 m, Pacholátko & Dembicky".

Indonesia. 2 ex. (RMNH), "Dr. Kohlbrugge, Tosari, Java", "*Carpophilus pygidialis* Grouv., var. det. Gr. 1910"; 1 ex. (NMB), "Sumatra (Jambi), Gunung, Kerinki, 1800-2100 m, 6-7.III.1991, Bocák & Bocáková".

Corrections in the list of *Carpophilus* species recorded in China published by Hui and Huang [2019]

In the mentioned paper a review of the species of the genus *Carpophilus* was compiled with addition specimens newly determined by Z. Hui and M. Huang. Unfortunately, among names of the species, which are rather probable in China, there are also mentioned some more or less doubtful or impossible to expect in natural conditions of China:

– *Carpophilus (Carpophilus) flavipes* Murray, 1864 according to the examined type and other specimens is distributed in India, Nepal, Sri Lanka, Myanmar, Thailand, Vietnam, Malaysia (both peninsular and insular parts), Singapore, Indonesia (Java, Kalimantan, Mentawai, Sulawesi etc.), Philippines (Mindanao, Luzon, Mindoro, Leyte, Panay etc.), (NHML, NMB, NMP, ROM, STMD, ZIN, ZMB, ZMMU, ZMUC, ZSM), but no specimen is known from the Palaearctic Region and China (including Taiwan);

– *Carpophilus (Ecnomorphorus) sexpustulatus* (Fabricius, 1792) spreads in the Mediterranean [Jelinek, Audisio, 2007] and can scarcely be expected in China;

– *Carpophilus (Semocarpulus) succisus* Erichson, 1843 is known from the Neotropical Region and also after a rather doubtful record from Azores [Listagem..., 2010; Jelinek et al., 2016];

– *Carpophilus (Myothorax) truncatus* – this name seems to be erroneously used for *C. (M.) pilosellus* (see above).

Synonymy of *Aethina (Aethina) aeneipennis* Reitter, 1873

The characters in description of *Aethina (Aethina) zhizhuaca* Chen et Huang, 2024 completely correspond to those in other specimens of *A. (A.) aeneipennis* [Kirejtshuk, 1986c] and therefore the former [Chen et al., 2024] is certainly an additional junior synonym of the latter.

Thus, the emended synonymy of this species is following: *Aethina aeneipennis* Reitter, 1873 = *Meligethopsis singularis* Rebmman, 1944 = *Aethina (Aethina) zhizhuaca* Chen et Huang, 2024, **syn. n.**

On the designation of the lectotype of *Aethina (Circopes) suturalis* Reitter, 1884 and notes on *A. (C.) miniata* Hisamatsu, 2014

Aethina (Circopes) suturalis (Figs 157, 158) is rather common in the eastern part of the Palaearctic Region (Russia: Primorsky and Khabarovsk regions, Kunashir Island; Japan: Honshu, Shikoku, Kyushu; South-Eastern China; South Korea) [Kirejtshuk, 1986c; Hisamatsu, 2014]

and seems to demonstrate a considerable variability in many characters: general body colouration and colouration of separate body segments or only elytra, punctuation and sculpture of integument and particularly in dorsal pubescence. This species, in contrast to consubgenera, usually has longitudinal rows of hairs on elytra bearing hairs subequal in length, although the subsutural lines on its elytra (another subgeneric diagnostic character) always are rather distinct [Reitter, 1884]. Nevertheless, the conspecific individuals of this species could be easily mixed with specimens of other *Circopes* Reitter, 1873 species or even with small and unicoloured light specimens of *A. (Aethina) inconspicua* Nakane, 1967, and because E. Reitter did not mention depository of type and designate a holotype among many studied specimens [Reitter, 1885: 42]: “Fukushima, Suyama, Vada-togé im Juni und Juli 1881”. In order to avoid any taxonomic problem in future the lectotype designation is proposed for one of specimen deposited in NHML labelled with red round “Type, H.T.”, “Japan, C. Lewis, 1910-320”, “Fukushima, 26.VII.–29.VII.81”, handwritten “*Aethina suturalis* m.n.sp.”, “NHMUK 013664051” and another specimen should be considered as an additional because it was labelled with “Suyama, 20.IV.–22.IV.80”, “Japan, G. Lewis, 1910-320” (the date is different from that published). Many specimens named as “*Aethina suturalis* m.n.sp.” with geographic labels different from that published by Reitter [1885] are deposited in different museums.

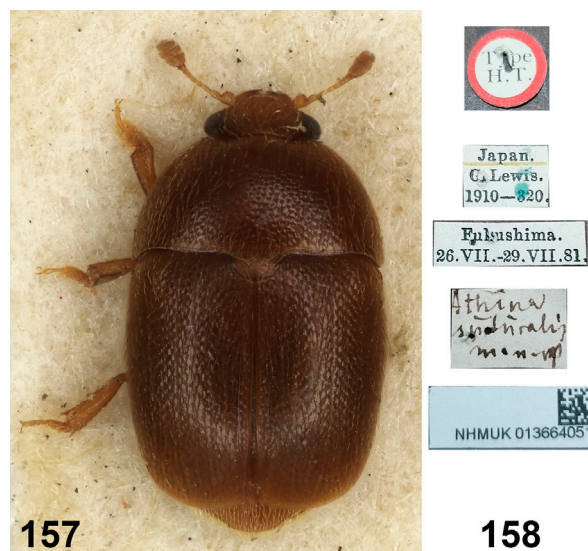
Aethina (Circopes) miniata was described as rather distinct from *A. (Circopes) suturalis* in the characters mentioned by Hisamatsu [2014], but it has also a very considerable resemblance in external as in genital characters with those of *A. (C.) subquadrata* (Motschulsky, 1858). Therefore, it seems that the pictures and description of type specimens of *A. (C.) minuata* in Hisamatsu [2014] and examined specimens of *A. (C.) subquadrata* fit to each other as conspecific ones. On the other hand, *A. (C.) subquadrata*, in contrast to many consubgenera, is known widespread species in many areas of the Indo-Malayan Region showing a great variability in many characters. Therefore the true relation between these taxa (*A. (C.) minuata* and *A. (C.) subquadrata*) needs a further serious revision of specimens from many localities.

Synonymy of *Atarphia quadripunctata* Reitter, 1884

Jelínek et al. [2012] proposed a new species of the genus *Atarphia* Reitter, 1884 from China (*Atarphia cincta*) based on some differences in the coloured spots on dorsal body surface, “length” of metaventrite and proportions of some other sclerites. All these characters are more or less variable, particularly secondary sexual ones, and cannot be used for discrimination of two “species” even among specimens from the same small locality (see below).

Thus, the current synonymy of this species is as following: *Atarphia quadripunctata* Reitter, 1884 = = *A. cincta* Jelínek et Hájek, 2012, **syn. n.**

Material. Russia. 10 ex. (ZIN), Primorskiy Region, Preserve Kedrovaya pad', 1.9.85, Kompantzev A.V. (in Russian) (also “№16, 10.9.85”, “№16, 15.9.85”, “№16, 20.9.85”); 2 ex. (ZIN), Primorskiy Region, Ussuriysk District, Gornotaezhnoe, valley forest, 13.06.1989, A. Kirejtshuk (in Russian).



Figs 157–158. *Aethina (Circopes) suturalis*, lectotype.
157 – lectotype, length of specimen 2.6 mm; 158 – labels pinned under lectotype.

Figs 157–158. *Aethina (Circopes) suturalis*, лектотип.
157 – лектотип, длина экземпляра 2.6 мм; 158 – этикетки, подколотые под лектотипом.

Synonymy of *Nitidula carnaria* (Schaller, 1783)

Lasoń et al. [2021] described a new species of the genus *Nitidula* Fabricius, 1775 from Russia, Kazakhstan, Mongolia and China (*N. obenbergeri* Lasoń, Hájek et Jelínek, 2021) based on the very peculiar structure of the penis trunk and rather small “differences” in some external structures from *N. carnaria* including some morphometric indicators and variation of body colouration. The most distinct of them, which can be used, may be regarded the proportion of antennomeres 4 and 5 ([Lasoń et al. 2021: 510]: *N. obenbergeri*: “Antennae as long as the width of head across eyes, antennomeres IV and V as a rule (safe very small specimens) distinctly longer than wide”; and *N. carnaria*: “Antennae shorter than the width of head across eyes, antennomeres IV and V as long as wide”). Sometimes the similar character is more or less applicable as in *Carpophilus* and other cases, although it can be efficient when difference in proportions of antennomeres is markedly greater (see above), but even in these cases this character is not enough reliable. It is necessary to take into account that length of antennomeres sometimes can be variable because of partial invagination of base of one antennomere in to the (sub)membraneous apex of the preceding one. It can be clearly seen even on the pictures proposed for illustrations in the paper of Lasoń et al. [2021: figs 1, 3]. Other characters proposed by them for discrimination of these two species are formulated in the key to *Nitidula* species. The most problematic matter is the pictures of the penis trunk (figs 1, 3), which look like very different in “*N. carnaria*” and “*N. obenbergeri*”. Dissection of some specimens with smaller body from the same areas (Russia, Kazakhstan, Mongolia and China), in which the co-authors found their “new species”, did not allow to find any specimen with such abnormal structure

of penis trunk. Some level of variability has been found mostly in the outlines of lateral sides of the penis trunk: slightly narrowing in the apical third to subparallel-sided or slightly widening apically, however not to the same extent as shown in figure 6 “*N. obenbergeri*” of Lasoń et al. [2021]. Another very strange thing seen in this figure 6 is that the preapical paramedian processes of penis trunk of *N. obenbergeri* in this picture, and strange overlapping by membranous lobes of apical orifice of the penis trunk. The last mentioned feature of *N. obenbergeri* does not correspond with usual structure of male genitalia in nitidulids. Two more oddities are present in this case: why could an isolated species arise in the center of the range of a transpalearctic and comparatively numerous species, living together with the “new” one in the same biotopes, and what forms are found to the east and west of the range of *N. obenbergeri*, as well as in other zoogeographic regions (Nearctic, Indo-Malayan and Australian regions). Finally, if there are two sympatric species, then it is necessary to find out to which of them the Schaller’s type belongs in order to solve the taxonomic problem that has arisen: which name can be applicable to which species. It is proposed that until at least some of these problems are resolved, these forms (“*N. carnaria*” and “*N. obenbergeri*” sensu Lasoń et al.) be considered as varieties of the same species.

Thus, the current synonymy of this species is as following: *Silpha carnaria* Schaller, 1783 = *Nitidula quadripustulata* Fabricius, 1792 = *N. guttalis* Herbst, 1793 = *N. flavipennis* Heer, 1841 = *N. variata* Stephens, 1830 = ? *N. obenbergeri* Lasoń, Hájek et Jelínek, 2021.

Synonymy of *Physoronia (Pocadioides) wajdelota* (Wankowicz, 1869)

This species was first described as an abnormal member of the genus *Pocadius* from Europe and later three similar “species” were proposed for specimens from Japan. Recently their attribution was some times discussed [Jelínek, 1978, 1999, 2008; Kirejtshuk, 1992, 1997b, 2006, etc.], however this taxonomic problem of their link with genus and subgenus is still under debate because complicated hiatus between generic and subgeneric taxa of the *Pocadius*-complex proposed for the Recent Eurasian fauna [Kirejtshuk, 2008]. The current taxonomic combination and species synonymy of the names previously established for Japanese specimens described as three “species” by Reitter [1873, 1884] was proposed by Kirejtshuk [1997b].

Fresh specimens collected in the West Siberia (Russia: Tyumen Region) (Kirejtshuk et al., in prep.) gave an obvious reason to estimate variability of all morphological characters of these most widely distributed consubgenera and propose the following synonymy: *Pocadius wajdelota* Wankowicz, 1869 = *P. japonica* Reitter, 1873, **syn. n.** = *P. rufimargo* Reitter, 1884 = *P. unicolor* Reitter, 1884.

Synonymy of *Pocadius nobilis* Reitter, 1873

The *Pocadius* species are associated with fungi closely related to the genus *Lycoperdon* Pers. (formerly family Lycoperdaceae) characterised of rather wide species ranges

and, as a result, frequently coleopterous species associated with these fungi also have rather great structural variability and wide ecological distribution (in various biotopes). The names here are present such a case concerning a species, whose north populations consist of specimens more or less uniform in structures, while southern ones have specimens with greater variability. Mostly small or very small series of available specimens from the southern parts of the species range represented by not characteristic specimens due to different variable characters were recognised in two papers as members of separate species [Cline, 2008; Chen, Huang, 2020]. This circumstance forces to propose the following synonymy: *Pocadius nobilis* Reitter, 1873 = *P. yunnanensis* Grouvelle, 1910 = *P. fasciatus* Cline, 2008, **syn. n.** = *P. okinawaensis* Cline, 2008, **syn. n.** = *P. tenebrosus* Chen et Huang, 2020, **syn. n.** = *P. zhangjiajieensis* Chen et Huang, 2020, **syn. n.**

In total, about 300 specimens were examined, including type specimens below and 4 ex. (ZIN) from the series used for description of *P. okinawaensis* and others from the Russian Far East, Indo-Malayan Region (NHML, NMB, NMW, RMNH, SMNS, TMB, ZIN, ZMB).

Type material. Japan. 2 ex., paralectotypes of *P. nobilis* (NHML), round label “Type/HT”, “232” (handwriting), “Japan, G. Lewis, 1910-320”, “*Pocadius nobilis* m.” (handwriting), “NHML”; 1 ex., paralectotype (RNHL), “Japan, leg. Lewis”, “Coll. Reitter / *nobilis*”, “Holotypus 1873”, “*P. nobilis*; m.” (handwriting); 2 ex., paralectotypes of *P. yunnanensis*, which should be regarded as valid paralectotypes, although designated by A.G. Kirejtshuk as the lectotype and paralectotype in the collection about twenty years before the publication of Cline [2008], “Yunnan Mission”, “Ant. Grouvelle, Yunnan”, “*Pocadius yunnanensis* Grouv.”; 17 ex., including 13 ex. (FMNH, type series of *P. okinawaensis*) and 4 ex. (ZIN), “Ryukyu Is.: OKINAWA; Katsudake, XI:28:1945, E. Ray”.

The genus *Pocadius* was preliminarily revised by Cline [2008] after his study of specimens. He examined many museum collections without sufficient attention in observing the traditions of taxonomic research, including the designation of lectotypes among type specimens, and also freely treating the publications of his predecessors. Thus, a further comprehensive revision of this genus remains necessary. For example, Cline [2008] designated as a lectotype of *P. nobilis* one specimen in the collection of RNHL. At the same time, other specimens from the same series were deposited in NHML where the Lewis’ collection initially should be housed were designated as paralectotype or additional specimens. As a result, instead of selecting one specimen from the Lewis’ collection in NHML to designate as the lectotype, A.R. Cline designated as the lectotype one duplicate deposited in RNHL, and the two specimens on the same pin, that have a label “Type/HT” in NHML, were labelled by him as the “paralectotypes”, and, finally, the remaining specimens of the type series in its original location are named by A.R. Cline as “additional” specimens. On contrary, he published deposition of the lectotype and paralectotype of *P. yunnanensis* in NMHN, where should be deposited only duplicates of this type series. Thus, the potential lectotype and paralectotype of the latter type series accordingly with rather logical tradition were designated by A.G. Kirejtshuk in RNHL before the publication of Cline [2008], where they should be deposited, but after the published other designations by A.R. Cline should be recognised as invalid, i.e. lectotype of *P. yunnanensis* designated by A.G. Kirejtshuk should be considered as paralectotype. Even more, the last mentioned

specimens with the correct designations were not included in the Cline's "revision" with false and unrealistic explanations. Apparently, other cases of this type of the Cline's research can be found in this paper [Cline, 2008] and this should be kept in mind. Cline [2008] also considered *P. nobilis* and *P. yunnanensis* synonymized by Kirejtshuk [1984] as two separate species, referring to the characters in the "description and key", however, in his key only evidently variable characters are given and such a character also could not be possible to find in the Cline's descriptions of both *P. nobilis* and *P. yunnanensis*. Unfortunately, the Cline's key to species is based in many cases on variable characters and scarcely possible for reliable identification. Synonymised here *Pocadius fasciatus*, *P. tenebrosus* and *P. zhangjiajieensis* are known to the author only from their sufficiently informative original descriptions.

Synonymy of *Meligethes (Clypeogethes) tenebrosus* Förster, 1849

The situation with the two specimens that claimed to be types of "*Meligethes persicus*" (one in ZMMU and the another in MNHN) was assessed in detail in the paper of Kirejtshuk and Kurochkin [2004], which shows that in both cases neither specimen could be used to describe the species in question, because the both were labelled with a wrong generic attribution, different from that in the original description (!) *Nitidula persica*) and their characters are rather different from those published in the original description of *Nitidula persica* Falderman, 1835. If we accept this obvious fact, then the synonymy of this species should be as follows: *Meligethes tenebrosus* Förster, 1849 = *M. sinuans* Rey, 1889 = *M. pedicularius* auctorum, non *Nitidula pedicularia* Gyllenhal, 1808 = *Meligethes persicus* auctorum, non *Nitidula persica* Faldermann, 1835.

The subgenus *Glischrochilus* Reitter, 1873 sensu stricto in the Palaearctic Region

This subgenus is mostly represented in the modern Western Hemisphere's fauna, while there were only three traditionally recognised species in the Palaearctic Region and regarded to be associated with living under the bark mostly of conifers. They are represented by one mostly and widely spread in the boreal Palaearctic forests, *Glischrochilus (Glischrochilus) quadripunctatus* Linnaeus, 1758, and also by two localized ones, one in the eastern northern part of Asia (Kamchatka), *G. (G.) biguttulus* Motschulsky, 1860, and another in the eastern Asian part with more or less moderate climate (Russian Far East, eastern northern China, Korea, and Japan), *G. (G.) cruciatus* Motschulsky, 1860. The most widely distributed "species" exhibits a clinal variability in body shape and size, while the specimens from northern areas along the eastern range borders are gradually becoming smaller and more slender (somewhat similar to those of *G. (G.) biguttulus*), while those from southern areas are becoming only somewhat smaller (somewhat similar to those of *G. (G.) cruciatus*). Occurrence in the western boundaries of *G. (G.) quadripunctatus* both local "species" specimens with transited pattern of colouration give a reason to suppose that the Palaearctic Region is

inhabited only by one polymorphous species consisted of three subspecies. This idea needs to be properly verified by detailed comparative examination.

Recently, some researchers (T. Clayhills, J. Vilén etc.) found some adults of *Glischrochilus (Glischrochilus)* collected using cross flight interception (window) traps at *Populus tremula* L. in some localities in Finland. They (together with P. Audisio, A.R. Cline etc.) decided that these are representing a new species, but they did not observe these specimens in places where these beetles could live and develop (at living aspen trees), they also did not collect any adult or larva for study and breeding the larvae on different substrate to check if these larvae from these beetles produce the similar specimens in next generation (see more on this method above). These researchers only obtained the DNA sequences of the *Glischrochilus (Glischrochilus)* specimens collected in the flight interception traps nearby aspen trees, compared with the DNA sequences of other *Glischrochilus (Glischrochilus)* specimens which could be associated with conifers and found some differences which, in their opinion, give an enough reason to propose a new species (Clayhills et al. [2016]: *G. (G.) tremulae* Clayhills, Audisio et Cline, 2016). These authors found some slightly expressed morphometric differences between few specimens collected from the flight interception traps nearby aspen and other specimens determined as *G. (G.) quadripunctatus* which are as if noticeable in the outline of the pronotum, the convexity of the upper body surface, expression of the temples, width of the male tarsal plate, small differences in the aedeagal structures. The mentioned co-authors could not find specimens of this "new" species in museum material from Europe, Siberia, Turkey and the Caucasus and this seems to suggest a limited range of "*G. (G.) tremulae*". However, Lasoń [2023] collected some similar specimens under bark and fresh cut trunks of aspen in Poland and decided that this is good support of separation of this "new" species and his observations brought some additional characters, which, in his opinion, are enough for discrimination of two "species". Recent examination of thousands of specimens deposited in the ZIN collection shows that the specimens with complete set of the characters of this "new" species are really mostly rare among mounted museum specimens, although specimens with some structural deviations resembling something intermediate state of each of the characters mentioned by Clayhills et al. [2016], Clayhills [2017] and Lasoń [2023] seem to be more or less frequent at least in the East European localities. A.S. Kurochkin during 2001–2002 got extensive sampling of *G. (G.) quadripunctatus* in Samara Region of the European Russia in different biotopes and under bark of different tree species. It is interesting that adults with an appearance of "*G. (G.) tremulae*" were collected under bark as of *Pinus silvestris* L. as of *Populus tremula* together with typical specimens of *G. (G.) quadripunctatus*. The form "*G. (G.) tremulae*" seems to be becoming less frequent in the Asian part of the Palaearctic Region and eastern from Tyumen Region of Russia remains unrecorded. It is important to note that the observed range of variability of each of all characters (including genital ones) in different populations of *G. (G.) quadripunctatus* is much greater

than that indicated by Clayhills et al. [2016], Clayhills [2017] and Lasoń [2023] as diagnostic one for “two” species. Another important thing is that such two forms of appearance can be traced also in *G. (G.) cruciatus* (one like “typical” *G. (G.) quadripunctatus* and another like “*G. (G.) tremulae*”). This coincidence of two forms can be explained by some similarity of determining ecological circumstances in which their larvae develop rather than inner factors (like molecular differences). As to molecular differences between the typical *G. (G.) quadripunctatus* and “*G. (G.) tremulae*”, it is necessary to continue the studies of DNA sequences and seeking factors determining of them taking into account that the molecular diversity of so variable species as *G. (G.) quadripunctatus* could be even much higher than that in the phyllophagous *Xenostrogylus variegatus* Fairmaire, 1891 having considerably smaller range [Zhan et al., 2021] (see also above). Probably in order to check if *G. (G.) quadripunctatus* can be split into two species it is necessary to test DNA sequences not for specimens from one small local area but from many localities through the whole Eurasia and find any real ground to erect a separate species for a form with something different DNA. It seems to be also scarcely possible to distinguish “species” separated only by few DNA sequences and this proposal can be scarcely possible to regard this taxonomic proposal as reasonable till a wide comparison of some hundred populations and comprehensive analysis of all aspects of their variability.

Thus, the current synonymy of this species is following: *Silpha quadripunctata* Linnaeus, 1758 = *Silpha quadripustulatus* Linnaeus, 1761 = *Ips niger* J.R. Sahlberg, 1889 = *Glischrochilus (Glischrochilus) tremulae* Clayhills, Audisio et Cline, 2016, **syn. n.**

Synonymy of *Cybocephalus bicinctus* Kirejtshuk, 1988

The synonymy of this species is quite evident because the both description include very distinct the same characters in the shape of protibiae and extremely peculiar body colouration [Kirejtshuk, 1988; Hisamatsu, 2013]. Thus, the current synonymy of this species is following: *Cybocephalus bicinctus* Kirejtshuk, 1988 = *C. chlorocapitis* Hisamatsu, 2013, **syn. n.**

Probability of polliphagy and pollination by Apophisandridae and other groups of the nitidulid-group of families

What attracts pollen-bearing beetles to female cones has not yet been certainly established for any species.
R.A. Crowson [1991b: 17]

This epigraph very well conveys the impression that many people have when it comes to the participation of beetles visiting the generative organs of plants in pollination. Pollination of dioecious gymnosperms has always been considered a logical obstacle to any theoretical constructions of the origin of angiosperms, and studies of pollination of modern gymnosperms have not provided convincing grounds for entomophily, both

then and now. Therefore, Crowson [1991b: 16] added “some palaeobotanists suspect that the ancestry of true flowering plants (Angiospermae), an “abominable mystery” to C. Darwin, may have lain among the cycadeoids”. Many researchers of past years shared such opinion and now they do not understand how the popularity of attributing ancient pollination to the extinct species that cannot have direct evidence of participation in pollination arose. In fact, some current researchers have solved the problem by simply abandoning it, i.e. recognising the unprovable and discarding all other arguments. But since this problem especially affects the evolution of many families of the nitidulid-group, it makes sense to dwell on it, since it is essential for understanding not only the latest publications on apophisadrids, but also the phylogeny and system not only of Apophisadrid, but all the families discussed here. Unfortunately, some recent systematic and phylogenetic proposals were done without knowledge about this aspect of evolution of the nitidulid-groups of families (see also above).

The discussion of the participation of insects in pollination of dioecious cycads has been the subject of heated debate for many years. There are supporters of different points of view even now. It is probably correct to think that it does not matter who visits to female generative organs, but the result expressed in pollination itself is important. It can be assumed that it is not important for plants what or who was the pollinator in a particular case: wind, vertebrates or insects. In this sense, all three components can be considered as potential pollinators. Therefore modern pollen-feeding beetles are pollinators of gymnosperms to the extent that they visit male cones and end up after visiting them in female ones. Apparently, disputes on this matter in the literature are not very urgent and frequently not enough convincing. However, it is impossible not to take into account the fact that there is a difference in the composition of visitors to male and female cones and it is very likely that this difference somehow affects participation in pollination. Female cones are more often inhabited by curculionoids, chrysomeloids and other groups, but not by representatives of the nitidulid-group of families. There are probably sufficient grounds that similar situations prevailed in Mesozoic biotas. Botanists do not always pay attention to this, but there is also data that in the cones of both sexes, only sometimes both inhabitants of predominantly male cones, in which they undergo larval development, and inhabitants of female cones are found. Apparently the composition of visitors initially was occasional, although it is possible to suppose that in time some advantages for visiting could appear and be increased due to the natural selection. The situation seemed to resemble that known for modern dioecious palms and the beetles visiting to male and female inflorescences. As a result, even rare visits to female inflorescences by inhabitants of male ones from the tribe Mystropini increases fruiting [Kirejtshuk, Couturier, 2010; Kirejtshuk et al., 2023, etc.]. It is also important that everything that is known about as modern gymnosperm cycads and araucarias as modern angiosperm dioecious palms can be used to somewhat understand the circumstances of the Mesozoic biotas. In these cases, all random visitors of female gymnosperm

cones and angiosperm inflorescences, even those who came from male gymnosperm cones and angiosperm flowers of the same species, can hardly be justified in calling them pollinators, although their participation in pollination cannot be denied (similar to the wind). With this always, it is necessary to take in account that rotting gymnosperm strobiles and angiosperm inflorescences of both sexes could and can be visited and used for larval development by the same species associated with decaying substrates of plant origin as in past as present.

It can be assumed that in the initial stages of the development of considered relationships, insects were rather accidental pollinators supplementing wind pollination, and with the further development of interdependent co-adaptations of beetles and plants, the proportions of pollination by beetles increased in the proportion compared with other factors (wind and vertebrates). But the beetles apparently, as a rule, remained pollen eaters (pollinophagous) both in the imaginal and larval stages (as pollinophagous beetles of the nitidulid-group of families in the Recent fauna). And they become pollinators by chance or peculiar circumstances. Thus pollen-eating was in past and currently is a vital thing for them (beetle adults and larvae), and pollination was and is just a passing coincidence. To call all apophisandrids pollinators is an even more incredibly exaggerated definition, because it is impossible to be sure in pollination for all specimens of the species bearing some trace of morphological adaptations to pollinophagy. It is somehow the same as calling all epuraeines anthophagous (as was done by Peris et al. [2024a]) only because very few known species, in which adults have pronounced adaptations to living in flowers (subgenus *Apria* Grouvelle, 1919 of the genus *Epuraea* and subgenus *Mandipetes* Kirejtshuk, 1997 of the genus *Amystrops* Grouvelle, 1906) and some separate species from many different and sometimes rather large groups. It is interesting that a significant part of apophisandrids have an appearance that really resembles epuraeines (the appearance of a universal generalised inhabitant of decaying plant remains and fungal substrates, including decaying cones of modern gymnosperms and flowers of angiosperms). Such similarity can be explained mainly by the circumstances of accelerated larval development in the ephemeral substrates of their habitat, which determined the removal of the final stages of ontogenetic (preimaginal) differentiations, bearing traces of last phylogenetic innovations (including generic and sometimes suprageneric differences). Thus, habitual appearance of adults of apophisandrids, epuraeines and mystropins has not evidence of their ancient relationship (as Peris et al. [2024a] thought) but they are typical examples of convergence caused by the similarity of changes in ontogenesis (i.e. the most common cases in the phylogeny of not only most coleopterous groups but also holometabolans in general).

As has long been known, plant generative organs always were particularly attractive resource for insect feeding, interconnections between these groups of organisms becoming in time more multiple and diverse and were rather essential in evolution of both, although some crises of various scale (sometime rather serious up to (sub)global) happened. As was discussed above,

feeding on pollen of plant male generative organs does not automatically mean pollination (i.e. transfer pollen from male plant organs to female plant organs), and formation of regular pollination was lasting many millions years up to the time when the angiosperms appeared. During this long period many mutual co-adaptations progressively appeared and progressively evolved in both plants and insects. It is very important to take into account that appearance and development of feeding on pollen happened many times, and different insect groups could use different ways to master such feeding habits. Insects with large body could begin to regularly visit gymnosperm male cones to get pollen for eating and this habit could maintain during long period without changes (i.e. without visiting or occasional visits to gymnosperm female cones). These habits of large insects seemed to provide them a peculiar evolutionary trend and phylogeny [Crowson, 1991b; Bernhardt, 2000; Wang et al., 2013, etc.]. Beetles of the nitidulid-group of families with smaller body had other evolutionary perspectives. They can be traced in some analogous interactions between modern beetles of these families and gymnosperms and dioecious angiosperms and extrapolated on probable interactions between the Mesozoic plants and beetles. Crowson [1991b] noted that all beetles of the nitidulid-group of families were found only in male cones of cycads and araucarias (Boganiid paracucujines, *Conotelus* Erichson, 1843 (nitidulid Conotelini Kirejtshuk et Kovalev, 2022) and *Colopterus* Erichson, 1842 (nitidulid Cillaeini), *Epuraea* (nitidulid Epuraeini), *Carpophilus* (nitidulid Carpophilinae), monotomid *Europs* Wollaston, 1854), often in decaying cycad cones. The male cones of modern cycads (particularly decaying ones) are also visited by many representatives of this group of families [Kirejtshuk, 1994a, b; Escalona et al., 2015; Kirejtshuk, Kovalev, 2022, etc.], but regular association of beetles with gymnosperms is known for Boganiidae demonstrating regular interconnections with cycad male cones [Sen Gupta, Crowson, 1966, 1969; Endrödy-Younga, Crowson, 1986; Crowson, 1990; Endrödy-Younga, 1991; Donaldson et al., 1995; Donaldson, 1997; Suinyuy et al., 2009; Escalona et al., 2015, etc.], although unverified references to possibility of polination without supporting facts have also often been published. Another important aspect is the modern association of nitidulids with male inflorescences of the dioecious palms. In Africa the male inflorescences of *Elaeis* palms are inhabited by some specialised nitidulids from the epuraeines (carpophiline-lineage) and meligethines (nitiduline-lineage) with different types of aedeagus [Jelínek, 1992], while some specialised nitiduline American pollinophagous beetles from the endemic Western Hemispheran tribe Mystropini (Nitidulidae of the nitidulin-lineage) are also associated with *Elaeis* palms [Núñez et al., 2005; Kirejtshuk, Couturier, 2010, etc.]. The habitual appearance of all these palm epuraeines, meligethines and nitidulines is extremely similar. If the opinion of Peris et al. [2024a, b] their structural plesiotypy can be considered as correct, their differences in the genitalia and characters of their external structures should be considered apomorphic. So, according to the opinion of Peris et al. [2024a, b], the coleopterists of the 19th and early 20th century were right in their taxonomic attributions

of nitidulid beetles and all morphological and bionomical studies of the last hundred years were wrong as well as changing of taxonomy and phylogenetic reconstructions after the latter studies. This quite fits in well with the recommendations by Jelínek et al. [2010] and methodology by Leschen [1999] to ignore previous systematic and phylogenetic studies as “narrative and quantitative”, including those of recent decades in new phylogenetic reconstructions.

On the other hand, all the mentioned palm nitidulids live and develop in great number in male palm inflorescences and only single individuals rarely (i.e. probably occasionally) visit to the female palm inflorescences. In general, the male flowers are inhabited and used for larval development by the beetles from the coleopterous groups completely different from those in female flowers. Can these groups be considered pollinators, i.e. carriers of pollen from male flowers to female flowers for pollination of the latter? Besides, many visitors of decaying gymnosperm cones and angiosperm flowers do it because of attraction by fermented substrate but not because of attraction by cones or flowers proper. Finally, the range of diversity of relationships between beetles and angiosperm flowers is apparently much larger than that between beetles and gymnosperm cones. For example, the kateretids of two genera living and developing on *Acorus* spp. (Acoraceae) without close relationship share a trophic base: species of *Platamartus* Reitter, 1892 are more common during male flowering and those of *Sibirhelus* Kirejtshuk, 1989 during seed maturation, and the larvae of the latter seem to be carpophagous rather anthophagous, while adults live throughout the entire period of flowering and fruiting [Sokolov et al., 2024]. Very frequently numerous groups like some epuraeinae genera (carpophilinae-lineage), genera *Carpophilus* (carpophilinae-lineage), *Aethina* Erichson, 1843 (nitidulinae-lineage), *Camptodes* (nitidulinae-lineage) seems to include as completely (larvae and adults) anthophagous as completely (larvae and adults) mycetophagous representatives, and also some representatives of intermediate with anthophagous adults and mycetophagous larvae according to the scheme of ways of changes in trophic associations [Kirejtshuk, 1989a; Kirejtshuk et al., 2023, etc.]. An unusual lifestyle is known with a case of a counter adaptation of plant for regular interaction between *Duguetia cadaverica* Huber (Annonaceae) with foul-smelling flowers to attract a beetle regular pollinator *Pycnocnemus* sp. (Cyllocini) [Teichert et al., 2012], and some mycetophagous *Triacanus* spp. (nitidulinae Cyllocini) associated with fungi of family Fallaceae are recorded as pollinators of *Orchidantha fimbriata* Holttum (Lowiaceae) [Kirejtshuk, 2016] (saprocanthrophily). It is important that appearance of anthophagous adults does not reflect this type of feeding behavior in morphological structures. On contrary, anthophagous larvae always demonstrate more or less expressed structural adaptations to the “open” lifestyle which could be preadaptive for leaf-meaning habit of the larvae of *Xenostromylus* spp. and *Anister* spp. This very important aspect for the phylogenetic interpretation in the nitidulid-group of families is the life habit and structural features of modern anthophagous larvae and this very important aspect is used in phylogenetic and

systematic reconstructions by Kirejtshuk with co-authors [Kirejtshuk, 1989a, 1991, 2000, 2008; Kirejtshuk, Couturier, 2010; Kirejtshuk et al., 2023, etc.], but was ignored by Audisio et al. [2009, etc.] and Peris et al. [2024a, b]. It is easily to trace the main larval features of anthophagous and mycetophagous representatives in the review of Japanese nitidulid larvae of Hayashi [1978] and published separate descriptions [Bondar, 1940; Kurochkin, Kirejtshuk, 2003; Kirejtshuk et al., 2007; Kirejtshuk, Couturier, 2010, etc.]. The mycetophagous larvae have the structures similar to those of other mycetophagous cucujoids from many families, while anthophagous larvae demonstrate quite characteristic features comparable only with larvae associated with more or less open lifestyle and somewhat like those known in phyllophagous nitidulines and parasitoid cybocephalines. This evolutionary trend is displayed in the scheme of changes in trophic associations in Nitidulidae to appearance and development of phyllophagy [Kirejtshuk, 1989a; Kirejtshuk et al., 2023] but can be extrapolated on many groups of cucujiformian families. The appearance of structure of antho- and phyllophagous larvae different from those of mycetophagous ones can be easily understood and explained by comparatively short larval development in ephemeral substrate, while it is scarcely possible to admit that the structure of anthophagous larva could be primary in relation to that of mycetophagous one (this is important to assess the unrealistic plausibility of the hypothesis of Peris et al. [2024a, b]). Another conclusion from the above is that in some fossils it is impossible to know whether the adult beetle is anthophagous or mycetophagous without actualization of data on their modern relatives.

So there is only one way to go – it is to use traditional actualization of the above data from the Recent biota to imagine what could be possible in the Mesozoic. Only five modern anthophagous groups of the subfamily/tribal taxonomic rank from the nitidulid-group of families (epuraeines, kateretines, meligethines, mystropines and paracucujines) having close trophic associations with modern dioecious or “conditionally dioecious” plants (they are from the angiosperm families Acoraceae, Arecaceae, Araceae and gymnosperm Cycadaceae) without obligatory pollination by the beetles under consideration and all of them have a considerable resemblance to fossil apophisandrids. Other anthophagous subfamilies/tribes of this group of families are represented by species less similar or very different from fossil apophisandrids (they are carpophilines, cillaeines, cychramines, cyllocidines and nitidulines) and they have trophic associations mostly with monoecious angiosperm plants, which can be pollinated by the mentioned coleopterous groups. One of interesting peculiarity of the modern mystropin lifestyle is their trophic associations only with dioecious Arecaceae and “conditionally dioecious” Araceae. On the other hand, it is necessary to add the fossil Mesozoic parandrexids also with a great similarity to apophisandrids, which could be associated with gymnosperm male cones and also could be by occasional pollinators [Crowson, 1981, 1991b]. Thus, known available data from representatives of the nitidulid-group of families of the Recent biota demonstrate probably ancient trace of pollinophagy but no trace of certain obligatory pollination. It is important

to mention that the family Parandrexidae, closely related to apophisandrids, kateretids and probably boganiids, is known from the Middle Jurassic [Kirejtshuk, 1994b; Soriano et al., 2006; Lu et al., 2015, etc.]. The hypothesis of Crowson [1981, 1991b] on relations between Boganiidae, Nitidulidae and Jurassic Parandrixidae and that the latter of them could be, in his opinion, pollinophagous and associated with namely gymnosperm male cones, obtained a new strong morphological support [Kirejtshuk et al., 2023], but both this hypothesis and two of the above mentioned coleopterous families also even are not mentioned by Peris et al. [2024a, b].

Audisio et al. [2009], Jelínek et al. [2010] and Peris et al. [2024a, b] regarded mostly only anthophagous meligethines, mistropins, kateretids and “apophisandrids” and “some modern genera of Epuraeinae”. Indeed, the meligethines, mistropins and kateretids are really specialized anthophagous groups (although some kateretids seem to be rather carpophagous than anthophagous), while no epuraeine genus is known as specialised anthophagous (only a couple of small subgenera of two large genera – see above) and fossil apophisandrid includes some genera which apparently could be strobilo- or even anthophagous, but “pollinophagous” habit of others remain hypothetical rather than grounded by real facts. On the other hand, most groups of the nitidulid-group of families have representatives characterised by clear and obligatory association with plant generative organs. Only the family Helotidae and probably Monotomidae, and also nitidulid subfamilies Amphicrossinae, Calonecrinae, Cryptarchinae and Cybocephalinae represent the exception, i.e. they have no clear connection with either gymnosperm male strobiles or angiosperm flowers. Another peculiarity of pollinophagy in the Recent fauna of the nitidulid-groups of families is usual complete or at least imaginal pollinophagy of related representatives in generative organs of plants of rather phylogenetically separated groups. Two closely related Australian members of the subgenus *Circopes* (Nitidulini: *Aethina*) became complete strobilophagous in *Macrozamia riedleri* (Fisch. ex Gaudich.) C.A. Gardner (Zamiaceae) (*A. (C.) unguiculata* Kirejtshuk, 1986) and complete anthophagous in *Cordylina stricta* (Sims) Endl. (Dracenaceae) (*A. (C.) australis* Kirejtshuk, 1986) [Kirejtshuk, 1994a]. Besides, among mostly mycetophagous *Aethina*-complex of genera the complete anthophagy is characteristic of other groups of the subgenera *Circopes*, *Ithyra* Reitter, 1873 (specialised on flowers of Acanthaceae) and *Idaethina* Gemminger et Harold, 1868 (specialised as complete anthophagous in flowers of Malvaceae (mostly from genus *Hibiscus* L.)), and phyllophagy is known for species of the genus *Anister* Grouvelle, 1901 and carpophagy for those of the subgenus *Australaethina* Kirejtshuk et Lawrence, 1999 of the genus *Neopocadius* Grouvelle, 1906 [Kirejtshuk, Lawrence, 1999]. The rather similar situation is found in other nitiduline and cillaeine tribes of the family Nitidulidae (above cited papers by A.G. Kirejtshuk) and in this regard, the question involuntarily arises why Peris et al. [2024a] published as a reliable unproven fact on anthophagy of “some modern genera of Epuraeinae”, but ignored most already long-known facts about other anthophagous (and

also phyllophagous and carpophagous) habits of most nitidulids published in the 20th century or even before.

Thus, it appears unlikely that Mesozoic paradrexids, boganiids and apophisandrids, and many other pollinophagous beetles were specialised pollinators of gymnosperms, i.e. they necessarily transferred pollen from male cones to female cones. However, since they were probably specialised pollen consumers, they could therefore more often than other beetles visit female cones of the same cycad species after visiting male cones and thus realize pollination. Most likely, the first users of pollen of gymnosperms cannot be recognised by their appearance not only as pollinators, but also as visitors of the generative organs of plants (like many currently living specialised complete (both larval and imaginal) anthophagous species). The same applies to nitidulids and boganiids associated with modern gymnosperms (see above). However, this does not mean that all nitidulids and boganiids should be called pollinators. The situation is that if some modern species of *Epuraea* turned out to be an anthophagous, this does not mean at all that all other modern species should be anthophagous (with this most of its congeners are mycetophagous or with other trophic diets up to predation (for example, some its congeners prey on nematodes or scolytine larvae)). Particularly it concerns some other groups with a more or less generalized appearance due to comparatively quick larval development in ephemeral substrates, which does not necessarily have to be “archaic”. And one should not build phylogenetic concepts on this external impression until careful research has been carried out. It should be taken into account that such generalized groups are also known among nitidulid taenioncins, carpophilines, nitidulins, cyllodins, cychramins, cillaeins, conotelins including also specialised strobilo- and anthophagous representatives (in addition to completely anthophagous meligethines and mistropins, and also strobilo- and anthophagous and partly carpophagous boganiids and kateretids). The so global generalizations and many misinterpretations on pollinators proposed by Cai et al. [2018] and Peris et al. (see above lastly cited) and some other paleontologists on feeding and habits of fossils after considering only few occasional and restricted groups of modern anthophagous beetles and rather brief studies of scarce material on fossils seem to be too hurried and superfluous with ignoring of many important points of the problem.

Such a viewpoint on the pollination of Mesozoic members of the kateretid-subgroup of the families should be regarded as rather unilateral to be accepted as plausible and grounded because of the conclusions conflicting data from extinct and modern biotas, while concept of Crowson [1981] on pollinophagy of Jurassic representatives of the kateretid-subgroup obtained during further over than 40 years some important additional supports). However, we must also not forget that in most cases it is impossible to recognise anthophagous or mycetophagous habit by the external appearance of a beetle, and that most of the studied fossils will forever remain with unknown food preferences. It is expected this argumentation will be used by further researchers who would be better to revise all already described apiophisandrid genera to divide them

into those which could be probably pollinophagous and other with other diets, and also to take this circumstances in preparation of future publications. It is as important to do this as it is to remove from use supraspecific taxa without real diagnoses that do not allow for all recognised species to find a systematic position.

The above (in particular, evidence from the fossil record) makes it possible to propose the following scenario for describing the development of pollinophagy within representatives of the nitidulid-group of families in the Mesozoic and Cenozoic. By the middle of the Mesozoic, the kateretid-subgroup of families was already widely represented in the Eastern Hemisphere (Asia [Martynov, 1926; Kirejtshuk, 1994b, etc.] and “Pyrenees” (Iberian plate) [Soriano et al., 2006]), in which not only groups with completely mycetophagous members (boganiids) appeared, but also imaginal and complete pollinophagous representatives (boganiids and paradreids), specialised in male cones of gymnosperms, which apparently became relatively numerous and diverse by the end of the Jurassic and in the Lower Cretaceous [Kirejtshuk, 1994b; Soriano et al., 2006; Lu et al., 2015; Kirejtshuk et al., 2023, etc.]. Paradreids reached the boundary between the Lower and Upper Cretaceous, later probably at the Albian/Cenomanian they seemed to have been gradually replaced by a new family (apophisandrids), i.e. the family, in which pollinophagous members constituted a significant part of the diversity and seemed to survive at least until the late Eocene (*Baltoraea* [Kurochkin, Kirejtshuk, 2010]). Another branch of the kateretid-subgroup of families appears in the known fossil record at the boundary of the Jurassic and Cretaceous with the family Kateretidae (*Lebanorettes* Kirejtshuk et al., 2008), which could be also associated with gymnosperm cones, while all other representatives of this family with known bionomy are associated with flowers and fruits (seeds) of angiosperms on the Recent flora of the most floristic regions (except for the Antarctic Region), although *Antirhelus* Kirejtshuk, 2023 from the Eocene could have a diet different from other kateretids [Kupryjanowicz et al., 2019; Kirejtshuk et al., 2023]. The second family of this branch (Smicripidae) was recorded from Albian/Cenomanian Burmese amber as well as Eocene Baltic and Rovno amber [Kirejtshuk, Nel, 2008; Bukejs, Kirejtshuk, 2015; Kirejtshuk, 2017; Kupryjanowicz et al., 2019; Lyubarsky, Perkovsky, 2023], while all modern species of it has largely retained its association with ancient larval mycetophagy to the present day (stage II according to regular changes in trophic associations [Kirejtshuk, 1989a]).

The appearance of the nitidulid-subgroup of families in the published fossil record is also determined by the early Cretaceous, although there are reasons to assume its actual appearance much earlier. Unfortunately, late Cretaceous outcrops are very poor in fossil beetles in general [Zherikhin, 1978]. As a result, the currently available late Cretaceous fossils do not include reliable pollinophagous beetles and can only be reliably indicated for the Paleogene. Nevertheless, it can be tentatively assumed that the change in the representation of gymnosperms and angiosperms in the Cretaceous floras should have been reflected in changes in the composition of pollinophages. This could

be associated with a decrease in the proportion of fossils found from the kateretid line and the appearance of pollinophages of the nitidulid line, but this assumption also requires paleontological confirmation. It can also be assumed that the period of change in the proportion of pollinophagous beetles on gymnosperms to the pollinophagous beetles on angiosperms followed a change in the proportions of these groups of plants in late Mesozoic floras and was quite long. Therefore, the existing gap in the fossil record is quite explainable by these circumstances. Unfortunately, significant amounts of beetles in the examined fossil record reappear starting from the Eocene, and therefore many researchers have the impression that Eocene outcrops indicate a sharp emergence of Cenozoic fauna after the Mesozoic one. Nevertheless one true boganiid with a great similarity to characteristic pollinophagous apophisandrids and nitidulids having very long antennae will be described soon from the late Cretaceous of China (Kirejtshuk, in prep.). Besides, species-rich materials from the middle of the Paleocene show that even at this time beetles retained Mesozoic groups in their composition [Kirejtshuk et al., 2016; Kirejtshuk, Nel, 2018; Nabozhenko, Kirejtshuk, 2017; Nel et al., 2024, etc.]. It is important to note that the conclusions made without taking this feature into account, including ones by Peris et al. [2024a, b], relate not so much to the available material that they write about, but to the publications that they used to prepare the conclusions for their papers.

At present rather few obvious fossil pollinophagous beetles from the nitidulid subgroup of families have been described. There are only two species of meligethine genus *Melipriopsis* Kirejtshuk, 2011 from Eocene Baltic amber [Kirejtshuk, 2011b; Kirejtshuk, Bukejs, 2023]. These data can be considered combining with the relict range of most archaic meligethine genus *Pria* currently spread mostly in the Afro-Madagascan Region, and also in the Palaearctic and Indo-Malayan regions, and one species is known from Australia (*P. pumilla* Cooper, 1982). This combination supports a concept of the most archaic position of this genus within the subfamily Meligethinae. Other groups consisting only of members with complete (imaginal and larval) pollinophagy and widely distributed can be hypothetically regarded as older ones, while the groups which include species with different lifestyle and trophic regime in terms the scheme proposed by Kirejtshuk [1989a] and repeated by Kirejtshuk et al. [2023] younger. Most data on these groups and observed types of their ontogeny and diet were published in the paper listed in the below references (see below papers of A.G. Kirejtshuk) and some additional data mentioned above. As noted above, it seems to be important that the pollinophagous beetles of different phyletic branches of the nitidulid-group of families associated with dioecious gymnosperm and angiosperm plants (apophisandrids, epuraeines, meligethines and mystripins) demonstrate a considerable secondary similarity in their appearance and structural peculiarities of mouthparts and other appendages (antennae and legs), although their principal structures of their thorax and particularly genitalia of both sexes are similar to those as characteristic (diagnostic) of kateretid-group in apophisandrids and nitidulid-subgroup of families in

others, i.e. manifesting evidence of their true phylogenetic roots and thereby proving their convergent origin of the characters in appearance, mouthparts, antennae and legs. Therefore these convergent (homoplastic) features should be definitely interpreted as certainly younger than the diagnostic group characters in thorax and genitalia. The closest relatives of apophisandrids can be expected among boganiids, generalized appearance pollinophagous epuraeines (tribe Epuraeini) could be more or less initial for the nitidulid carpophiline-lineage, while meligethines seem to have close relations with "Palaeogean" members of the nitidulin *Aethina*-complex of genera, but mystropins could have a American phyletic root from another nitidulin complex of genera (probably from relatives of the *Nitidula*-, *Soronia*-complexes or other complexes closest to them [Kirejtshuk, 2008]; they have been found in the Miocene Dominican amber, but waiting for description). Considering the fossil records and different aspects of phylogenetic processes in the nitidulid-group of families it is scarcely possible to imagine and find argumentation for that the above mentioned similarity of polliniphagous kateretid- and nitidulid-subgroups of families could be maintained from the Jurassic as was supposed by Peris et al. [2024a, b]). Another statement of Peris et al. [2024a: 598] that the apophisandrids "should be better placed within an extinct basal subfamily of Nitidulidae, with some plesiomorphic character states shared either with Kateretidae and with some basal Nitidulidae lineages (Epuraeinae, Calonecrinae and Maynipeplinae)" can be scarcely understood because these authors did not indicate what systematic interpretation was recognised by them (indeed in this statement they join together two subgroups of families (kateretid- and nitidulid-subgroups) and two different nitidulid lineages (carpophiline- and nitiduline-ones).

In addition, it can be noted that the meligethines are distinguished from other subfamilies in some peculiarities which are not always easy to observe and compare in many specimens from different groups. One of such peculiarities is a pair of paramedian deep arcuate impressions along the base of pygidium, characteristic of all meligethine taxa. Something like this there are in the members of the *Aethina*-complex of genera, but, in contrast to meligethines, the transverse row of arcuate impressions vary in number and outline (usually eight). This similarity in both these groups can be preliminarily regarded as an evidence of phyletic relation and both groups are characterised a trend to anthophagy: meligethines consist of members with complete anthophagy, while the members of different genera of the *Aethina*-complex show all three stages of changes in trophic associations from complete mycetophagy (stage I) to complete anthophagy, complete carpophagy, imaginal anthophagy + larval carpophagy or phyllophagy. Thus, the bionomical aspect of evolution coincides the structural one and can be used for grounding a phylogenetic hypothesis.

In this section it was shown how the method of multiple parallelisms can be used to substantiate a phylogenetic hypothesis. The material presented in this paper demonstrates the verification of the correspondence between the paleontological, morphological, ontogenetic, ecological and bionomic aspects of evolution, which

provides grounds for recognising the proposed phylogenetic hypothesis of Kirejtshuk [1982] as sufficiently probable. At present, the development of this hypothesis provides grounds for drawing conclusions on the historical development of the group of families under consideration in general. On its basis, the following conclusions are suggested:

1. The nitidulid-group of families could have a common origin during or somewhat earlier than the Middle Jurassic, although this statement needs further support.

2. The kateretid-subgroup should be considered as mainly Mesozoic with probable dominance of members with at least imaginal pollinophagy on male gymnosperm cones, recorded mostly in the late Mesozoic (Middle Jurassic – Albion/Cenomanian) and reaching the Eocene (Baltic amber); only some its genera are represented in the modern biota: Boganiidae (some members with complete mycetophagy and some with complete pollinophagy on gymnosperms), Kateretidae (mostly complete antho- or caprophagy on angiosperms), Smicripidae (mycetophagy and partly with imaginal anthophagy on angiosperms).

3. The nitidulid-subgroup should be considered, despite the antiquity of its origin (at least early Cretaceous), as mostly prosperous in the Cenozoic, having given rise apparently during the late Cretaceous and Cenozoic to a large number of modern forms with imaginal and complete strobilophagy on gymnosperms and anthophagy on angiosperms from most suprageneric taxa of this subgroup of families, and also with further stages of changes in trophic associations: complete carpophagy, imaginal anthophagy + + larval phylophagy, complete phyllophagy, etc. Only one family of this subgroup (Nitidulidae) reveals numerous independent transitions to feeding on the generative organs of some modern gymnosperms and many families of angiosperms. Representatives of various subfamilies of both nitidulid phyletic lineages (epuraeine- and nitiduline-lineages) got obligate connections with plant flowers as specialized pollinophagous forms in the imaginal and larval stages of their individual development, and some have become even carpophagous or phyllophagous ones.

4. The majority of specialized anthophagous nitidulids differ little from their mycetophagous relatives and these groups apparently had comparatively recent origin (possibly more or less recently or at most during the Neogene). Two groups specialised as completely anthophagous are sufficiently isolated from other nitidulids and are considered as separate suprageneric taxa (subfamily Meligethinae and nitiduline tribe Mystropini). These lastly mentioned groups apparently had more ancient origin than other anthophagous groups (possibly appeared during the Paleogene or near the boundary between the late Cretaceous and Paleocene).

5. Some unrelated groups of specialised strobilophagous and anthophagous of both subgroups of families (Apophisandridae, Kateretidae and Parandrexidae from the kateretid-subgroup, as well as some nitidulid subfamilies from the nitidulid-subgroup of families) acquired a considerable similarity as a result of classic convergence, often approximately parallel in time, and sometimes confined to different time eras (Mesozoic and Cenozoic). In these cases, the appearance of a

generalized appearance was mostly due to accelerated larval development in conditions of habitat in ephemeral substrates, which were and are generative organs during the pollination period of many plants. Convergent similarity often misled some researchers, who considered unrelated groups as closely related before in the 18th–20th centuries and even in this century. For a long time, the groups close related to the genus *Kateretes* Herbst, 1793 were considered as a subfamily within the family Nitidulidae, until it became clear from the study of the structure of the genitalia of both sexes that the similarity of their external appearance is obviously convergent. Recently, initially described as kateretids and other families, Cretaceous genera close to the *Apophisandra* were mistakenly transferred to the family Nitidulidae. In this paper, it was further proven that the latter belong to the kateretid-, but not the nitidulid-group of families, phylogenetically related more to the paradreids than to the kateretids sensu stricto. It was also shown that many Mesozoic apophisandrids, which could be associated to Mesozoic dioecious gymnosperms, exhibit the greatest similarity not only in appearance, but also in many body appendages, with some modern groups of nitidulids (epuraeins, mystropins and meligethines), associated with dioecious palms (i.e. apparently namely dioeciousness of plants can be reflected in the development of peculiar similarity of pollinophagous nitidulids, inhabited on them).

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