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Reclassification of the North Temperate Taxa Associated with *Staphylinus* Sensu Lato, Including Comments on Relevant Subtribes of Staphylinini (Coleoptera: Staphylinidae)

ALEŠ SMETANA[1, 2] AND ANTHONY DAVIES[2]

ABSTRACT

This paper presents a reclassification of the north temperate taxa associated with the genus *Staphylinus* sensu lato, and comments on relevant subtribes of the tribe Staphylinini. The treatment contains the following: (1) a historical introduction to the past and recent classification of these genera; (2) a discussion of the characters used herein, many of them being unconventional and used for the first time, and many of which are illustrated either by SEM photomicrographs or by line drawings; (3) a key to the north temperate subtribes of the tribe Staphylinini; (4) a discussion of the diagnostic characters of each of the five relevant subtribes (Philonthina, Quediina, Anisolinina, Staphylinina, and Xanthopygina); (5) a key to the north temperate generic- and subgeneric-level taxa associated with the genus *Staphylinus* sensu lato; (6) type species information and a discussion of diagnostic characters for each taxon at the generic and subgeneric level; (7) a discussion of reasons for taxonomic and nomenclatural steps taken at both generic and specific levels; (8) a checklist of north temperate taxa; and (9) a list of the references mentioned in the discussions in the text (not including those associated with citations of scientific names).

At the subtribal level, Craspedomerina, originally erected by Bernhauer (1911: 88) as Craspedomeri, is placed in synonymy with Philonthina. Triacrina, originally erected as Triacri by Bernhauer (1931: 84), is placed in synonymy with Xanthopygina (both syn. nov.).

At the generic level, new concepts are presented for *Staphylinus*, *Dinothenarus*, *Parabemus*, *Ocypus*, *Matidus*, *Pseudocypus*, *Tasgius*, and *Rayacheila*.

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New synonymies at the generic level are as follows (synonyms in brackets): *Thoracostrongylus* Bernhauer, 1915 (= *Parontholestes* Coiffait, 1982), *Platydracus* Thomson, 1858 (= *Neotasgius* J. Müller, 1925), *Parabemus* Reitter, 1909 (= *Parocypus* Bernhauer, 1915; *Hypabemus* Scheerpeltz, 1966), *Ocypus* Leach, 1819 (= *Goerius* Westwood, 1827; *Xanthocypus* J. Müller, 1925), *Pseudocypus* Mulsant and Rey, 1876 (= *Protocypus* J. Müller, 1923; *Nudabemus* Coiffait, 1982), *Agelosus* Sharp, 1874 (= *Apecholinus* Bernhauer, 1933), *Tasgius* Stephens, 1829 (= *Pseudotasgius* Seidlitz, 1891; *Paratasgius* Jarrige, 1952), *Rayacheila* Motschulsky, 1845 (= *Anodus* Nordmann, 1837 [nec Spix, 1829]; *Alapsodus* Tottenham, 1939; *Allocypus* Coiffait, 1964; *Metocypus* Coiffait, 1964; *Paralapsodus* Coiffait, 1974).

At the specific level, lectotypes are designated for *Dinothenarus insignis* (J. Müller, 1926), *Ocypus almorensis* (Cameron, 1932), *Ocypus fulvotomentosus* Eppelsheim, 1889, and *Ocypus lewisius* Sharp, 1874. Nine replacement names, 58 new synonymies, 224 new combinations, and numerous new statuses at both generic and specific levels are established; the latter four categories are to be found in the checklist.

INTRODUCTION

The complex of the genera and subgenera associated with the genus *Staphylinus* contains species that are large to very large; some of them are in fact the largest representatives of the family Staphylinidae. One might therefore assume that the group is well known and that its higher taxonomy was worked out in a reasonable way long ago. Nothing could be farther from the truth, however.

Historically, most of the species in the area covered by this paper were described in the genus *Staphylinus*. Then, in the early 1800s, Leach (1819) started splitting the genus *Staphylinus* (by that time already in somewhat restricted sense) by adding the genera *Creophilus*, *Emus*, and *Ocypus*. Shortly thereafter, Westwood (1827) added the genus *Goerius*, Stephens (1829) added the genera *Trichoderma* and *Tasgius*, Mannerheim (1830) added *Physetops*, and Nordmann (1837) added *Anodus* (preoccupied, eventually becoming a synonym of *Rayacheila*). In 1840, in his prodigious work ''Genera et species staphylinorum, insectorum coleopterorum familiae,'' Erichson divided the genus *Staphylinus* into two genera: *Staphylinus* and *Ocypus*, each subdivided into several ''Familiae'' (12 in *Staphylinus* and 4 in *Ocypus*). *Staphylinus* included, in addition to numerous tropical groups, the former genera *Emus* (Fam. I), *Creophilus* (Fam. II), a group of species that eventually became members of the genus *Ontholestes* (Fam. VI), and a large heterogeneous group containing species that were subsequently assigned to *Staphylinus*, *Platydracus*, and *Dinothenarus* (Fam. VIII). *Ocypus* included a heterogeneous group of species that were subsequently assigned to *Goerius* and *Pseudocypus* (Fam. I), as well as the former genera *Physetops* (Fam. II), *Tasgius* (Fam. III), and *Anodus* (Fam. IV). Erichson's concept turned out to be very important and was in principle accepted by most subsequent classical authors, including Ganglbauer (see below). In 1845, Motschulsky established the enigmatic monotypic genus *Rayacheila*, the status of which remained uncertain for a long time but was mostly listed as a synonym of *Goerius* or *Ocypus*; it becomes the valid name for the taxon known until now as *Alapsodus*. In 1857, Kraatz entirely accepted Erichson's concept of the two genera *Staphylinus* and *Ocypus*, with the exclusion of the genera *Emus*, *Creophilus*, *Leistotrophus* Perty, 1830 (actually misidentified; see below), and *Physetops*. In 1858, Thomson erected the genera *Platydracus* and *Dinothenarus* (the latter became the valid name for the preoccupied Stephens' name *Trichoderma*). In 1860, Motschulsky established the monotypic genus *Matidus* that became the valid name for a large group of species that were recently listed mostly under *Ocypus*. In 1874, Fauvel combined *Creophilus* and *Emus* under the former name, continued to use *Leistotrophus* as applied by Kraatz (1857), and combined all previously established taxa under one name, *Staphylinus*, which included four different groups. It is worth mentioning that in his ''Groupe 4'' he included ''*Anodus* Nordm.—*Ocypus* Steph.—*Matidus*, *Rhagochila* Mots.'' This is significant because it shows the difficulties in

interpreting some of the taxa, particularly those described by Motschulsky, a situation that persisted until quite recently. In 1876, Mulsant and Rey recognized all previously described taxa (mentioned above) as separate genera and added the genus *Abemus*. In 1895, Ganglbauer in his classical work ''Die Käfer von Mitteleuropa,'' which became the standard reference and identification aid for a long period, again essentially accepted Erichson's concept, as it was modified by Kraatz (1857), except that he considered the species assigned by Erichson to ''Fam. IV'' (*Anodus*) as members of the subgenus *Ocypus* s. str.; he also recognized Kraatz's misidentification of *Leistotrophus* and established the genus *Ontholestes* for the north temperate species included in *Leistotrophus* by Kraatz. Ganglbauer's treatment, including the erroneous concept of *Ocypus* s. str., was accepted by most subsequent authors, including Reitter (1909) in his ''Fauna Germanica.''

It is apparent at this point that the higher taxonomy of the group this paper deals with was worked out based mostly on European fauna, although some ''exotic'' elements, such as *Agelosus* and *Miobdelus* of Sharp from Japan, or *Naddia* (= *Caranistes* Erichson, 1840) of Fauvel from the northern Oriental region, were also registered. In the early 1920s, J. Müller started to publish his series of papers dealing with *Staphylinus*. This series of nine papers extended over 20 years (J. Müller, 1923, 1924, 1925, 1926a, b, c, d, 1932, 1943), in which he frequently dealt with the east Palearctic fauna. It is significant that Müller's concept was very conservative, as shown by the fact that he recognized only one genus, *Staphylinus*. Since the publication of Müller's papers, most subsequent authors followed a concept of either one genus, *Staphylinus*, or two genera, *Staphylinus* and *Ocypus*. This situation lasted until Coiffait in several papers between 1956 and 1974 not only elevated all previously described taxa to the generic level, but also provided numerous additional generic-level taxa (some based entirely on characters on the aedeagus), particularly in the group that is united here under the name of *Tasgius* (Coiffait, 1956, 1964, 1974). The publication of Coiffait's papers destabilized the higher taxonomy of the group. Some authors continued to use the system of the two genera *Staphylinus* and *Ocypus*, with the other taxa recognized at the subgeneric level (e.g., Szujecki, 1980); some authors accepted Coiffait's concept entirely (e.g., Outerelo and Gamarra, 1985), while others continued to use some of the taxa as subgenera, mostly of the genus *Ocypus* (e.g., Pilon, 1998). Some criticisms of Coiffait's concept appeared, and some of his taxa were placed in synonymy (e.g., *Atlantogoerius* with *Pseudocypus* and *Metocypus* with *Alapsodus* [Dvořák, 1984]), but in general the instability in the higher taxonomy of the group persisted until now.

At the specific level, J. Müller in his series of papers mentioned above, started a trend to split many species (mainly in *Ocypus* and *Pseudocypus*) into subspecies, based mostly on differences in the shape of the aedeagus. While many of the subspecies were valid geographical races, others turned out to be unacceptable, mainly because the variability of the characters on the aedeagus in many species was not known at that time. Unfortunately, the splitting of the species into subspecies was picked up by some modern authors, particularly by Coiffait, who in numerous papers (mainly 1956, 1964, 1970, 1971, 1974) continued to split many species, again mostly in *Ocypus* and *Pseudocypus*, using almost exclusively characters on the aedeagus. This approach was eventually criticized by some authors. For example, Smetana (1965b: 44) demonstrated, using a long series of males of *O. picipennis* collected in one mountain pass in Anatolia, that the shape of the apical area of the aedeagus varied such that at least two ''subspecies'' had to be recognized as occurring in this high pass. Subsequently, some of the ''subspecies'' were synonymized (e.g., Smetana, 1965b, 1967, 1971; Gusarov, 1992; Drugmand, 1998), or at least their validity was questioned (e.g., Pilon, 1998). Many additional new synonymies are presented in this paper (see the checklist).

As indicated above, the group was in need of a new taxonomic revision (both at the generic and specific levels) that would be based on new characters and on the reevaluation of characters already in use, as well as on a large number of specimens of as many taxa

as possible. This paper does exactly that. It is a taxonomic revision, exploring the usefulness of some new, hitherto unused characters. We intentionally do not provide a cladistic analysis, which is almost obligatory these days. This may be objectionable to some researchers, but we feel that a meaningful cladistic analysis of this group must include the instrumental, enormously diversified fauna that is indigenous to the easternmost parts of the Palearctic Region, particularly within the mountainous areas of mainland China. Our knowledge of this fauna is only fragmentary at present, but it is improving steadily thanks to the extensive recent collecting in that area. Once our knowledge becomes comparable to that of the western portions of the Palearctic Region, a cladistic analysis will have a better chance of clarifying the phylogeny of the group. Hopefully, such future study will support, at least in general terms, our findings presented here. At any rate, we hope that the results presented in this paper will be considered a positive step toward the reliable taxonomic treatment of this group, which is quite interesting not only taxonomically, but also zoogeographically.

In the following text, the author and the date of publication are given only for the first mention of the taxa not included in the checklist at the end of the paper.

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DISCUSSION OF CHARACTERS

The following section is not a comprehensive discussion of all characters of higher taxa in Staphylinina. It deals only with those characters that are important for understanding the taxonomic changes that are proposed in this paper and does not attempt to acknowledge and comment on all papers published on the subject. The states of these characters in the other subtribes of Staphylinini, and occasionally in other tribes, are mentioned where it is considered useful. The sexual characters, both male and female, are seldom used and therefore not discussed in this section. There is no doubt that such characters will prove important for the higher taxonomy of the group; however, it is difficult to assess them properly, mainly because our knowledge of the extremely rich eastern Palearctic fauna (particularly that of mainland China), which is instrumental for understanding the evolutionary trends and relationships within the group, is extremely poor (see also above).

Many of the characters used are unconventional and have not been used before. Their appreciation requires careful examination, since they are often inconspicuous. Most of them are on the ventral side of the body. It is therefore recommended that if the European method of mounting the specimens on plates is used, at least one specimen of the series (when available) should be mounted upside down, with the mandibles widely open and the coxae of the legs lifted and pushed aside so that the structures on thoracic sterna are easily observable. The same applies to pinned or pointed specimens, particularly as far as the sternal characters are concerned.

MANDIBULAE (MANDIBLES) AND THEIR

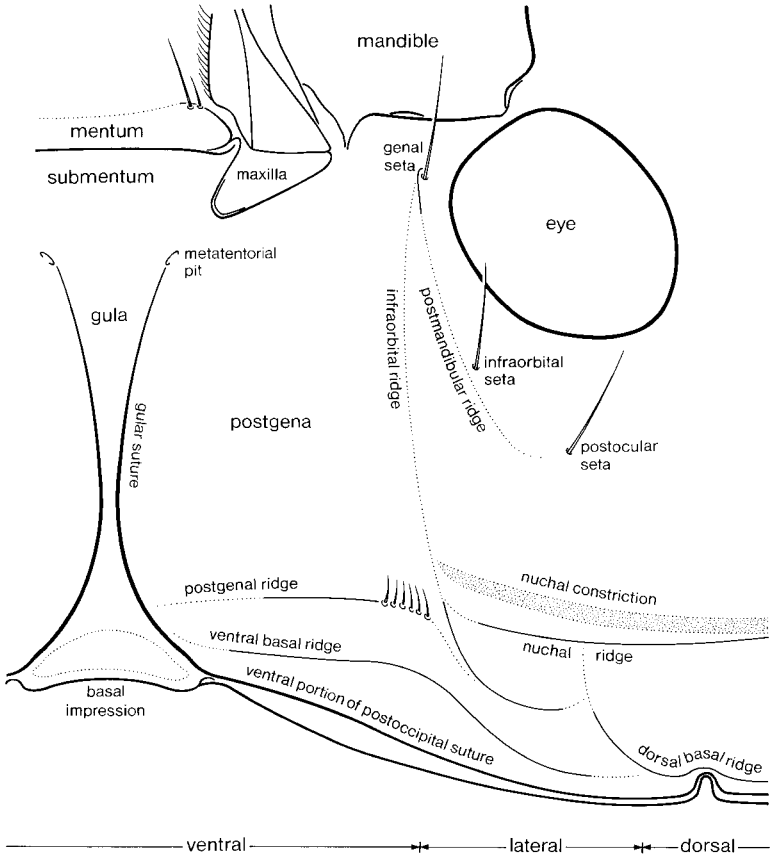

Fig. 1. Cuticular ridges on the surface of the head of a hypothetical member of the tribe Staphylinini.

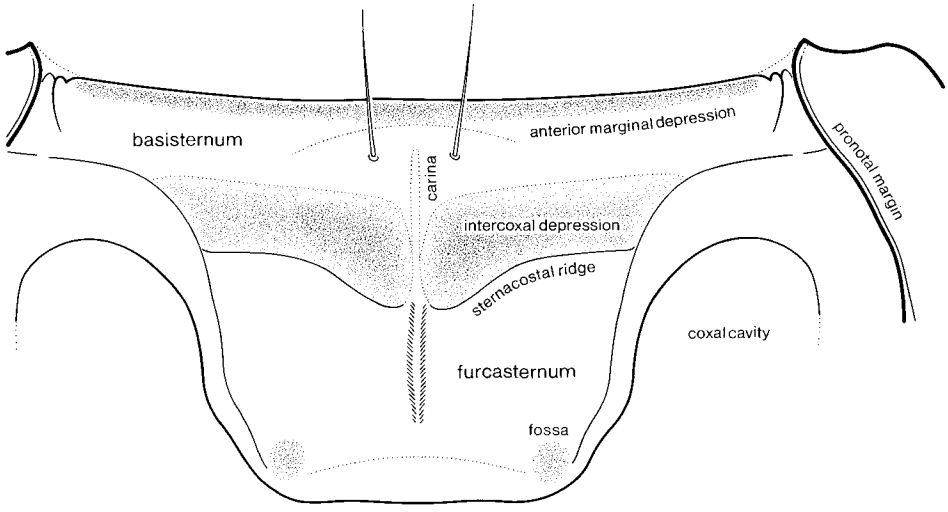

Fig. 2. Prosternum of a hypothetical member of the tribe Staphylinini.

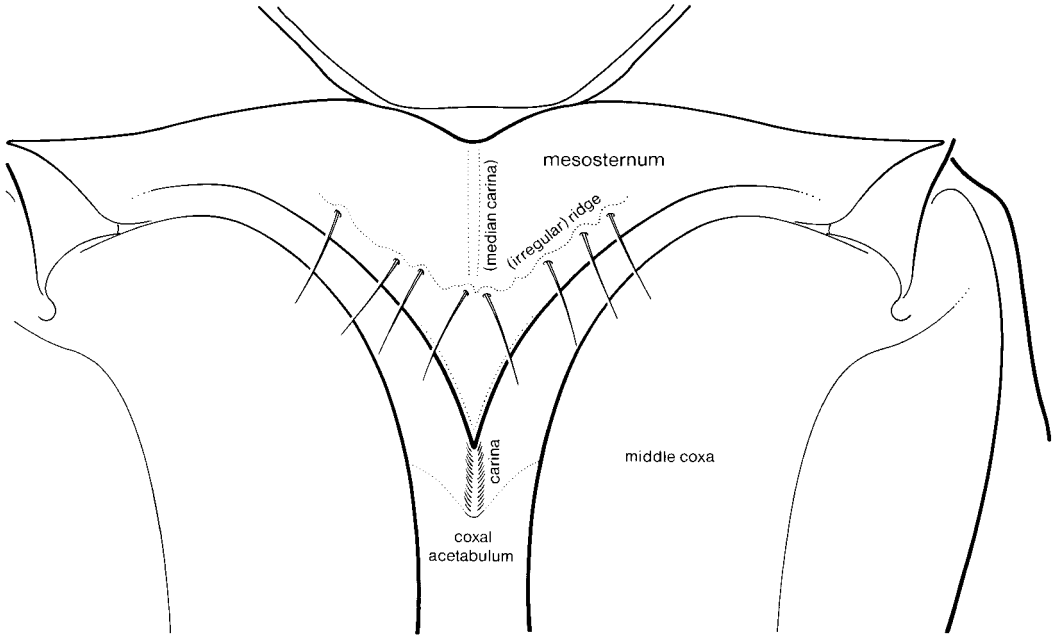

Fig. 3. Mesosternum of a hypothetical member of the tribe Staphylinini.

TEETH: In general, there is a great variation in the shape of the mandibles, as well as in the development of the teeth at their medial edge. The two mandibles are mostly dissimilar in the number and shape of the teeth (there are exceptions to this; e.g., the medial edge of each mandible in *Protogoerius brullei* has one similarly shaped tooth and the same occurs in some species of *Pseudocypus*). The shape of the teeth sometimes varies within one species (e.g., in *Ocypus affinis*). Rarely, each mandible is devoid of teeth (*Tasgius* [*Rayacheila*]) (fig. 4), or there is only one simple, sometimes not clearly differentiated tooth present on each mandible (*Tasgius* [*Tasgius*]) (fig. 5). The teeth are mostly situated in one plane, usually dorsal (e.g., members of *Ocypus*); however, in some cases the teeth appear in two planes, dorsal and ventral, either on both mandibles (e.g., most members of *Platydracus*, particularly the New World species) (figs. 6, 7) or at least on one mandible, usually the left one (e.g., members of *Staphylinus*) (fig. 8). The shape of the mandibles varies considerably and is also in some taxa (e.g., *Creophilus*) subject to sexual dimorphism (with the apical portion longer and sharper in males). In general, the shape varies from short and stout mandibles with short and blunt apices in *Naddia* (fig. 9) through moderately long and robust mandibles in *Staphylinus* or *Ocypus* (figs. 8, 10) to slender, flat mandibles that eventually become sickle-shaped (*Tasgius* [*Rayacheila*]) (fig. 4). The latter type is apparently the most derived state. In the Staphylinina and Xanthopygina the basolateral ridge on the mandible is usually markedly developed, distinctly removed from the lateral margin, and bordered by a deep depression (fig. 124). It is also well developed in Philonthina, but tends to be closer to the lateral margin and not bordered by a deep depression, whereas it is much closer to the lateral margin and poorly developed to absent in almost all Quediina.

MANDIBULAR PROSTHECA: Three states of the mandibular prostheca are present. (1) Medial edge of the prostheca is copiously ciliate along its entire length, with more extensive basal group of ciliae becoming less dense and shorter toward apex, with prostheca often appearing as more or less bilobed, or even multilobed, as in *Platydracus*, *Dinothenarus*, *Abemus*, and others (figs. 11, 12); this type may represent the primitive state and seems to be prevalent in Philonthina and

Xanthopygina (although it is more simple in both). (2) Supporting structure of the prostheca is long and lanceolate, with shorter ciliae along medial margin becoming gradually longer to moderately long near apex, as in *Agelosus*, *Ocypus* (*Pseudocypus*), and *Tasgius* (*Tasgius*) (figs. 13, 14). (3) Supporting structure of prostheca is parallel-sided, narrow, elongate, and sometimes rodlike, with ciliae present only at the apex, as in *Emus*, *Protogoerius*, *Staphylinus*, and *Tasgius* (*Rayacheila*) (figs. 15, 16).

MAXILLA: The chaetotaxy of the maxillary sclerites, as well as the shape and setation of the segments of the maxillary palpus, are taxonomically important. The apex of the palpifer (markedly variable and more useful at the generic level) may bear one strong lateral seta (*Anisolinus* Sharp, 1889; *Erichsonius* Fauvel, 1874; some Xanthopygina [*Plociopterus* Kraatz, 1857]; and all Tachyporinae we examined) (figs. 17, 19), or one strong lateral and one shorter, finer medial seta (most Staphylinina [figs. 121, 156], Xanthopygina, and Philonthina [usually very short to minute; figs. 20, 33], as well as many Paederinae), or one strong subapical and two or three shorter apical setae (e.g., *Physetops*, *Protogoerius*, but none of the Xanthopygina or Quediina we examined [as in fig. 149]); the Quediina have members in almost all of the above categories and some others. The stipes usually bears one strong lateral and one more or less fine medial seta (Philonthina, Anisolinina, Staphylinina, Xanthopygina) (figs. 17–19, 33), or two strong basal setae (Quediina) (fig. 21).

The maxillary palpus, or rather the shape and condition of its last segment as related to those of the penultimate segment, is taxonomically important. In Staphylinina, the last segment is usually narrower, subequal in length to the penultimate segment, and is generally fusiform (figs. 22, 23); sometimes it is variably shorter than the penultimate segment, but is still more or less fusiform (fig. 24) or almost cylindrical (fig. 25); it is rarely as broad at the apex as at the middle (where the last segment of labial palpus is broadly expanded, as in *Agelosus*, *Physetops*, and *Tasgius* [*Rayacheila*]), or the last two segments are broadly expanded (*Naddia*). The last segment always bears modified peglike setae in the glandular openings on the surface (figs. 26, 27), but it is mostly asetose (figs. 22, 28); rarely it is variously setose (as in *Ocypus* [*Matidus*], *Physetops*, and *Tasgius*, all with setae also on the apical segment of the labial palpus) (figs. 25, 29, 30); sometimes it has fine longitudinal furrows at the base (*Ontholestes*, as in *Philonthus* Stephens, 1829) (figs. 31, 32). The character of the setation (or its absence), on the last segment of the maxillary palpus was largely ignored in the past. Although this character was mentioned in some recent publications (e.g., Hayashi, 1993: 285, 299), its importance for the higher taxonomy in Staphylinina was still not properly assessed. Most recently, the absence of the setation on this segment was used by Drugmand (1998: 58) to define the Ophthalmicus group of species in the genus *Ocypus*, but this character state is in fact a synapomorphy of the entire subgenus *Ocypus*. Similarly, the presence and number of setae on the apical segment of the labial palpus vary widely, but in most cases it seems that those with many setae also have the apex dilated to various extents.

LABIUM: The chaetotaxy of the mentum is of importance for distinguishing the subtribes of Staphylinini. In general, the mentum bears either only one long seta (Philonthina [fig. 33] [*Erichsonius* and some *Cafius* Stephens, 1829 have one or more shorter additional setae along or removed from the anterior margin] and all Tachyporinae examined), or one short and one long anterolateral setae (Anisolinina, Staphylinina, Xanthopygina [*Plociopterus* has only one]) (figs. 19, 34). Nearly all genera in the subtribe Staphylinina seem to have two of these setae, except for *Emus* and *Naddia*, in which the conformation of the mentum is unusual. In *Ontholestes* the setae are near the lateral margin, and the lateral seta is minute or absent. However, within Staphylinina this character is not reliable, as the size and number of setae vary considerably, even within a single species (e.g., *Tasgius ater*, *T. pedator*), and most often the setae are broken. The sizes of the setae vary, but the medial seta is usually markedly stronger and longer than the lateral seta (fig. 34) (this seems to be reversed in Paederinae). The mentum itself is fairly consistent in shape, with the anterior margin being fairly

distinct and broadly emarginate (obsolete medially in *Abemus*), and the posterior margin follows the shape of the submentum (except, e.g., in *Dinothenarus*, *Emus*, and *Ocypus* [*Pseudocypus*], which have a semicircular, fine basal carina extending variably between the basolateral angles (figs. 38, 119, 120). The lateral margins are very long in *Agelosus* and *Ocypus* (*Matidus*). The ligula is mostly entirely bilobed (fig. 35) or at least variably emarginate medioapically (figs. 36, 37) in members of Staphylinina, but it may be occasionally virtually nonemarginate (e.g., in almost all *Dinothenarus* [*Dinothenarus*]) (fig. 38). In the past, the shape of the ligula was commonly used to separate the old tribes Philonthini (ligula solid) and Staphylinini (ligula emarginate/bilobed). However, as shown above, this approach is not reliable, particularly since some members of Philonthina have a slightly emarginate ligula, even in some species of *Philonthus* (e.g., in *P. caeruleipennis* [Mannerheim, 1831]) (fig. 20). *Agelosus*, most *Dinothenarus*, *Miobdelus*, *Naddia*, *Ocypus* (*Ocypus*, *Pseudocypus*), *Protogoerius*, and *Wasmannellus* have from a few to many setae on the apical segment of the labial palpus, whereas *Abemus*, *Creophilus*, some *Dinothenarus*, *Emus*, *Hadrotes* Mäklin, 1852, *Ontholestes*, *Platydracus*, *Staphylinus*, *Thinopinus* LeConte, 1852, and *Thoracostrongylus* have no setae on either apical segment.

SUBMENTUM: The anterior margin of the submentum is usually straight or feebly outwardly arcuate, with small lateral lobes. It is broadly outwardly arcuate in *Abemus*, *Creophilus*, *Miobdelus*, and *Tasgius* (*Rayacheila*), and broadly emarginate in *Emus*, *Hadrotes*, *Physetops*, *Staphylinus*, and some *Ocypus* (*Pseudocypus*). It seems to be distinctly, completely beaded only in *Platydracus*, *Ocypus* (*Pseudocypus*), and *Thoracostrongylus*.

CUTICULAR RIDGES ON THE HEAD (fig. 1): In the Staphylinini, there are several taxonomically important ridges—particularly in the postgenal area ventrally, and dorsally behind the nuchal constriction—that are usually consistent in their positions (when present). The *ventral basal ridge* anteriad to the continuous gular/postoccipital suture, which is always present, originates near the base of the gula. The *dorsal basal ridge* is anteriad to the dorsal portion of the postoccipital suture; this character has been largely overlooked because of its position beneath the anterior margin of the pronotum, and it was earlier deemed to be present only in the Xanthopygina (where it is strongest and mostly unobscured by punctures); it is usually extended anteriad toward the nuchal constriction laterally, and it sometimes meets the base of the infraorbital ridge. The *postgenal ridge* is anteriad to the ventral basal ridge at the base of the postgena, which is apparently completely absent only in *Thinopinus* (although it is sometimes confused or obsolete ventrally); it runs parallel to, or is confluent with, the base of the infraorbital ridge laterally. The *infraorbital ridge*, which, when complete (as in most Quediina), begins on the dorsolateral area of the neck, passes ventrally along the lateral portion of the postgenal ridge, to the lateral end of the nuchal ridge (which may join it or become confluent with it, as in most Quediina and *Glenus* Kraatz, 1857 [Xanthopygina]), and then it continues anteriad to near the base of the mandible below the genal puncture. In the Xanthopygina it usually extends some distance in front of the lateral bend of the postgenal ridge (*Elmas* Blackwelder, 1952, some *Eugastus* Sharp, 1876, *Gastrisus* Sharp, 1876), even more than in *Quedionuchus* Sharp, 1884; in most Staphylinina it becomes obsolete just in front of the lateral portion of the postgenal ridge, and in most Philonthina it appears rudimentary, joining the postgenal ridge immediately. The *nuchal ridge* follows immediately behind the line of the nuchal constriction dorsally; as mentioned above, it is very strong in most Quediina and becomes confluent with the infraorbital ridge laterally, whereas in most Staphylinina it reaches, or almost reaches, the base of the infraorbital ridge at various angles and distances from the nuchal constriction (it is notably short laterally in some *Ontholestes* and *Protogoerius*, and it is obsolete medially in *Physetops*, *Creophilus*, *Hadrotes*, and *Thinopinus*); it becomes obsolete laterally near the anterior end of the dorsal basal ridge in Anisolinina, most Philonthina (notably excepting *Erichsonius*), most Xanthopygina, and in all Paederinae studied. The *postmandibular ridge* is the most variable and most difficult to inter-

pret; when complete (as in many Xanthopygina and some Philonthina), it extends from just below the genal puncture behind the base of the mandible posteriad, very near the infraorbital puncture (often intermittently); alternatively, it may be deflected ventrad behind the base of the maxilla (as in many Philonthina). These two types are deemed to be homologous in origin, since they both often occur in one genus (notably *Philonthus*, in which both types and every extent of completeness occur). The postmandibular ridge is also deemed to be distinct from the infraorbital ridge, since the infraorbital ridge originates on the dorsum of the neck, and both ridges are distinct in many Xanthopygina. Interestingly, the postmandibular ridge is the only one present in the Tachyporinae (besides the postoccipital suture); it is complete in all Bolitobiini studied. In all Tachyporini studied, there is a ridge originating behind the mandible that is deflected completely around the base of the maxilla (note that *Leucotachinus* Coiffait and Saiz, 1968 has a separate postocular ridge). This ridge has been interpreted by Stickney (1923: fig. 173) as the remnant of the occipital suture, which may be correct; however, *Xanthopygus* Kraatz, 1857 and some *Philonthus* (e.g., *P. longicornis* Stephens, 1832) have a separate ridge in this orientation beneath the maxilla, and the postmandibular ridge is distinct and distant.

The gular sutures vary considerably, but usually they are moderately separated and most approximate somewhere in the basal half of the postgena, diverging anteriad to the submentum and posteriad to the base (except in *Ocypus* [*Matidus*] and *Physetops*, where they are distinctly more approximate before the middle). At the base of the gula there is usually a transverse impression that is usually distinct but poorly delimited anteriorly (e.g., in *Agelosus*, *Creophilus*, *Hadrotes*, *Thinopinus*, *Wasmannellus*, and most *Platydracus*); it is delimited anteriorly by a narrowly rounded ridge in *Abemus* and *Thoracostrongylus*, and by a distinct transverse ridge in *Emus*, *Naddia*, *Ontholestes*, and most Philonthina. In most of the Quediina, it is visible only along the basal marginal carina.

PUNCTATION ON DORSUM OF NECK: In the Quediina the dorsal disc of the neck bears no visible punctures. In the Philonthina, the disc is virtually impunctate, bearing no more than microscopic micropunctulae (fig. 39). In most Xanthopygina, it is only very finely, sparsely punctate (though never only micropunctulate, as in Philonthina), with only a few moderate punctures at lateral margins. In *Creophilus*, *Hadrotes*, and *Thinopinus*, there is a mixture of fine and moderate punctures, but they are broadly obsolete on the disc. In the rest of Staphylinina, and in Anisolinina, the dorsal disc of the neck is usually densely punctured, ranging from fine punctures (e.g., in *Abemus*, *Emus*, and *Protogoerius*) (fig. 40) to larger umbilicate punctures (*Miobdelus*), as well as rugose punctures (*Naddia*) (fig. 41).

SUPERIOR AND INFERIOR MARGINAL LINES OF PRONOTAL HYPOMERON: Two basically different states are present in these lines: (1) the two lines join at variable distance behind the anterior angles of the pronotum as a result of deflection of the superior line (e.g., *Dinothenarus*, *Tasgius*) (figs. 42, 43) and continue together in a broadly rounded arc along the prosternal margin to the anterior margin of the pronotum (*Ontholestes* is unusual in having the lines distinctly narrowly rounded at the anterolateral margin of the prosternum, as in fig. 44); or (2) the two lines never distinctly join because either the inferior line (Anisolinina, some Philonthina, *Agelosus*, *Ocypus* [*Ocypus*, *Matidus*]) (figs. 45–48) or the superior line (*Creophilus*, *Hadrotes*, *Naddia miniata*, *Thinopinus*, and *Wasmannellus*) (fig. 49) becomes indistinct or obsolete near the anterior angles; in the latter case, the superior line is distinctly deflected under the anterior angle (as in the Philonthina), and the superior line is frequently deflected as a fine line to meet the inferior line near the anterior angle. This deflection is variable between species (especially *Creophilus* and *Naddia*), and sometimes even within a species. However, there is significant variability in the development of the two lines throughout the Staphylinina. They may join in the anterior half of the pronotal hypomeron at variable distances from anterior angles, as in *Staphylinus dimidiaticornis* (fig. 50) or *Miobdelus* sp. (fig. 51); or they may run close to each other anteriorly, appearing as a more or less grooved carina, as in *Platydracus stercorar-*

ius (fig. 52) or *Ocypus tenebricosus* (fig. 48); or they may remain variably widely separated, as described above.

In the Xanthopygina, on the other hand, the inferior line always continues separately and uninterrupted along the prosternal margin, usually to the anterior margin of the pronotum, where it either meets the superior line (most cases), or the superior line becomes obsolete near the anterior angles. This state is considered to be one of the main characters of Xanthopygina (to the best of our knowledge, there are no exceptions), although additional characters need to be applied (see below). *Agelosus* was treated recently as a member of the Xanthopygina (Naomi, 1983: 582), based on the separation of the two lines: however, Hayashi (1991: 179) correctly returned it to Staphylinina, based essentially on arguments presented already by Sharp (1889: 111) when erecting the genus. As noted above, other members of the Staphylinina, Anisolinina, and even the Philonthina (Hayashi, 1994: 127) (some *Bisnius* Stephens, 1829 and *Leptopeltus* Bernhauer, 1906, and many *Philonthus* and *Rabigus* Mulsant and Rey, 1876) also display this separation of the lines, although not so widely. In all of these cases, however, it is the inferior line that becomes indistinct or obsolete near the coxal cavity. As a result of these various conformations, the disc of the pronotum is virtually invisible in ventral view in Xanthopygina (fig. 53) and is scarcely visible around the anterior angles in Anisolinina. In most Philonthina, where the superior line is distinctly deflected under the anterior angle, the deflected portion is visible from about the edge of the coxal insertion. This pattern also exists in Staphylinina (e.g., *Naddia*), or the deflected portion is visible from the posterior edge of the coxal insertion (e.g., *Platydracus* [fig. 52], and *Protogoerius*) or even from closer to the posterior angles of the pronotum (e.g., *Dinothenarus* [fig. 54], and *Thoracostrongylus*).

PRONOTAL EPIMERON: The proepimeron is distinctly developed and highly sclerotized in nearly all Quediina (fig. 55) (as well as in all Tachyporini studied, except the proepimeron is absent in *Cileoporus* Campbell, 1995, with its margin flattened against the venter, and in *Tachinoporus* Cameron, 1928), except where it apparently became fused with the peritreme, as has the episternum (*Acylophorus* Nordmann, 1837, *Anchocerus* Fauvel, 1905); it apparently is absent only in *Heterothops* Stephens, 1829 and is rudimentary in *Haematodes* Laporte, 1835 and *Smilax* Laporte, 1835. On the other hand, the proepimeron is apparently completely absent in the Anisolinina, Philonthina (except *Erichsonius*) (fig. 45), and in the Bolitobiini (the hypomeron is sharply deflected and flattened against the venter). The proepimeron ranges between these two extremes in the Xanthopygina and Staphylinina, being always membranous when present. It varies from moderately developed to absent in the Xanthopygina, and from well developed, broadly triangular (e.g., *Abemus* [fig. 56], *Creophilus*) to poorly developed (e.g., *Thoracostrongylus*) to absent (e.g., *Eucibdelus* Kraatz, 1859, *Physetops*, *Staphylinus* [fig. 57]) in the Staphylinina, and it varies from moderate to absent in *Dinothenarus* and *Tasgius*.

PROSTERNUM (fig. 2): The anteromedial portion of the prosternum varies greatly in the Staphylinina: in *Dinothenarus* (*Dinothenarus*), *Emus*, and *Ontholestes*, it is highly prominent, forming a rounded knob that slopes abruptly anteriad, and it markedly delimits the transverse marginal depression; in *Abemus*, *Dinothenarus* (*Parabemus*), *Naddia*, and *Thoracostrongylus* (as in many Philonthina), it is moderately prominent, with a distinct, but broadly rounded slope anteriad; in *Creophilus*, *Hadrotes*, almost all *Ocypus*, and others, it slopes very gradually so that the marginal depression is defined only by its own posterior margin; it is highly variable in *Platydracus* and *Staphylinus*, although never as prominent as in the first group; the Anisolinina have the whole anterior portion of the prosternum almost flattened (*Eucibdelus* in Staphylinina approaches this state). The prosternal keel is very variable in the Staphylinina, even within the genera, and thus only a few more-or-less consistent features can be described: in *Abemus* and *Ontholestes*, the keel forms a very strong carina, convex in profile, starting between the macrosetae, with no tooth at the intercoxal ridge; in most *Ocypus* (especially *Ocypus* s. str.), *Naddia*, *Thoracostrongylus*, and *Wasmannellus* (and less so in *Platydracus*), the medial

margin of the sternacostal ridge is extended anteriad for some distance along the intercoxal depression, often forming a highly prominent, finlike carina (fig. 58); in *Physetops*, the intercoxal depression is very long, and the furcasternum is abruptly declivous, producing a sharp toothlike process at the sternacostal ridge; in most other genera the carina is weak, confined to the area adjacent to the sternacostal ridge, or it is obsolete, as in *Creophilus*, *Emus*, and *Thinopinus*.

In most genera the sternacostal ridge is slightly oblique and relatively straight; in *Emus*, it is distinctly transverse and much closer to the two macrosetae mesially; in *Dinothenarus* s. str. and *Hadrotes*, it is distinctly arched posteriad near the carina, approaching the posterior furcasternal margin (fig. 54); this pattern also occurs in most *Tasgius* (*Rayacheila*), but the furcasternum is long.

MESOSTERNUM (fig. 3): In all Staphylinini studied, the disc of the mesosternum bears a series of long setae in various positions that are arranged in a subtransverse- to V-shaped pattern. In *Ontholestes*, they are in a subtransverse arrangement on either side of a distinct longitudinal medial carina. The setae are in moderately impressed punctures arranged subtransversely in *Creophilus*, *Emus*, *Staphylinus*, and *Thinopinus*. Setae are on the edge of large, rounded depressions forming an irregular, broadly U-shaped ridge in *Dinothenarus* (fig. 59) and *Physetops*. They are on small elevations in broadly U-shaped patterns in *Naddia* or *Platydracus*, or are roughly parallel to the margins of the projection, as in *Abemus*, or are along or behind an elevated ridge which may be feeble to well elevated, irregular to even, and subtransverse to V-shaped in most other genera of Staphylinina (fig. 60), as well as in *Amichrotus* (fig. 98) and Philonthina (fig. 87). The margins of the mesosternal intercoxal process converge acutely or subacutely in most Staphylinina (figs. 59, 60), with the angle being most variable in *Ocypus* and *Platydracus* (where the apex can be roundly truncate); they converge subrectangularly in *Protogoerius*, *Creophilus*, *Dinothenarus* (*Dinothenarus*), and *Ontholestes*; in *Emus*, the margins are broadly arcuate and broadly truncate apically (fig. 101).

In most genera the acetabulum behind the intercoxal process is slightly to moderately depressed (in *Physetops*, there is a small rounded carina behind it), but it is deeply depressed in *Miobdelus*, *Ocypus*, *Thinopinus*, *Protogoerius*, and some *Dinothenarus* (*Parabemus*), and there are variously shaped carinae behind the projection in *Ascialinus*, *Hadrotes*, *Agelosus*, *Tasgius* (figs. 62, 154), and some *Ocypus* (especially *Pseudocypus*).

METASTERNUM: The anterior metasternal projection is very long in the Anisolinina and in *Ocypus* (*Ocypus*) *weisei* (fig. 63), *Ontholestes*, and *Thoracostrongylus*, with the apex ranging from narrowly to broadly rounded. The margins converge at an angle that is distinctly less than rectangular in *Abemus* and most *Platydracus*, with the apex narrowly to moderately rounded. They converge subrectangularly in *Dinothenarus* (*Dinothenarus*), with the apex broadly rounded (it is more variable in *Dinothenarus* [*Parabemus*]); or they converge rectangularly, with the apex broadly rounded in *Wasmannellus*. In *Miobdelus*, *Physetops*, and almost all *Ocypus*, *Protogoerius* and *Tasgius*, the margins converge quite obtusely, with the apex very broadly rounded (except the apex is more narrowly rounded in some *Ocypus* [*Matidus*] and *Tasgius* [*Tasgius*]). The apical and lateral margins of the projection are obsolete in *Creophilus*, *Emus*, *Hadrotes*, *Platydracus* (*Chaetodracus*), *Staphylinus* (fig. 64), and *Thinopinus*.

APEX OF HIND COXAE: In the Staphylinini the dorsal apicolateral lobe of the hind coxae bears a series of setae that are usually distinctly coarser than the rest of the setae on the surface, frequently aligning along a feeble ridge. The number and size of these setae vary considerably in the Staphylinina, but there are a few notable trends: in most *Dinothenarus* (s. str. in particular), *Emus*, and some *Platydracus*, there are more than three distinctly coarser setae in the apical series (fig. 65); in *Naddia* and *Thoracostrongylus*, there appears to be only one distinct spine, usually located distinctly subapically in *Thoracostrongylus*; in *Creophilus*, *Eucibdelus*, *Hadrotes*, *Leistotrophus*, *Ontholestes*, *Staphylinus*, and *Thinopinus*, they are almost indistinguishable in size from the other setae, or they are completely absent (fig. 66); in

most of the rest of the Staphylinina there are usually two or three coarse spines.

EMPODIAL SETAE: The importance of the presence or absence of the pair of empodial setae between the tarsal claws for subtribal taxonomy was recently published by Schillhammer (1998b). The empodial setae are present in the Anisolinina, Staphylinina, Xanthopygina, and Quediina (figs. 67–69), but not in the Philonthina (including Craspedomerina) (figs. 70, 71). A notable case is the genus *Thinopinus*, in which each claw may bear from 3 to 5 empodial setae.

KEY TO NORTH TEMPERATE SUBTRIBES OF STAPHYLININI

1. Tarsal formula 5, 4, 4. Maxillary and labial palpus each conspicuously slender and elongate. General habitus resembling genus *Tachyporus* of Tachyporinae . . . . . **Tanygnathinina**
– Tarsal formula 5, 5, 5. Maxillary and labial palpus each no more than moderately slender and long. General habitus not resembling genus *Tachyporus* 2
2. Middle portion of disc of neck virtually impunctate, with no more than microscopic micropunctulation (fig. 39) 3
– Middle portion of disc of neck punctate, with coarseness and density of punctation variable, but always ranging above microscopic micropunctulation (figs. 40, 41); if impunctate, then pronotum with roughly punctate pit at each lateral margin in front of basal margin (*Creophilus* of Staphylinina) 4
3. Empodial setae between claws of all tarsi absent (figs. 70, 71). Superior marginal line of pronotal hypomeron deflexed under anterior angle of pronotum before continuing onto anterior margin of pronotum (figs. 72, 73). Pronotal hypomeron no more than moderately inflexed below anterior angle of pronotum, meeting prosternum at a very flat angle, with both sclerites fused, and notosternal suture therefore absent (fig. 73). Head without apparent infraorbital ridge (fig. 74). Neck with dorsal basal ridge (fig. 39) (excluding *Erichsonius*, and *Gabronthus* Tottenham, 1955) . . . . . **Philonthina** (Craspedomerina, **syn. nov.**)
– Empodial setae between claws of all tarsi present (figs. 67–69). Superior marginal line of pronotal hypomeron situated entirely on lateral margin, not deflexed under anterior angle of pronotum before continuing onto anterior margin of pronotum (fig. 75). Pronotal hypomeron strongly inflexed below anterior angle of pronotum, therefore meeting prosternum at a sharp angle (up to 90°), with both sclerites separated by notosternal suture (fig. 76). Head almost always with complete infraorbital ridge, at least extending significantly in front of postgenal ridge (fig. 77). Neck without dorsal basal ridge (fig. 78) . . . . . **Quediina**
4. Superior and inferior marginal lines of pronotal hypomeron variably widely separated throughout, never joined (figs. 46, 48, 53) 5
– Superior and inferior marginal lines of pronotal hypomeron joined at variable distance behind or at anterior angles of pronotum (figs. 42–44, 50, 51) . . . . . **Staphylinina** (pars)
5. Superior marginal line of pronotal hypomeron not deflexed, no part of deflected portion of pronotal disc visible in ventral view (fig. 79). Punctures on disc of neck fine, sparse, with only a few moderate punctures laterally (fig. 80). Head almost always with long postmandibular ridge (fig. 81) . . . . . **Xanthopygina** (Triacrina, **syn. nov.**)
– Superior marginal line of pronotal hypomeron deflexed; deflected portion of pronotal disc visible in ventral view, at least at anterior angles (fig. 73). Punctures on disc of neck dense, moderate to coarse (figs. 40, 41). Head with short to rudimentary postmandibular ridge (fig. 82) 6
6. Superior marginal line of pronotal hypomeron not distinctly deflected under anterior angle of pronotum before continuing onto anterior margin of pronotum (fig. 83). Ventral basal ridge extended anteriad for considerable distance parallel to gular suture, at least as far as postgenal ridge. Second segment of maxillary palpus with medial margin obtusely rounded apically, with insertion of third segment situated entirely in lateral half of apex (fig. 84) . . . . . **Anisolinina**
– Superior marginal line of pronotal hypomeron deflexed under anterior angle of pronotum before continuing onto anterior margin of pronotum (figs. 54, 56). Ventral basal ridge not extended significantly parallel to gular suture, but meeting it transversely or acutely. Second segment of maxillary palpus with apex transversely truncate, with insertion of third segment situated for most part at middle of apex (fig. 85). . . . . **Staphylinina** (pars)

NORTH TEMPERATE SUBTRIBES OF STAPHYLININI

The subtribe Tanygnathinina, containing only the genus *Atanygnathus* Jakobson, 1909, is quite distinctive and is therefore not discussed any further. For the remaining subtribes, some sets of characters that are considered important for distinguishing them, are discussed further. It became apparent during this study that some subtribes and their conventional characters needed to be reassessed, and that new characters needed to be established for a meaningful characterization of these groups. Some of these characters show ranges of variation and apparently developed in a parallel fashion several times in different lineages. This is particularly true for the configuration of the two marginal lines of the pronotal hypomeron (superior and inferior lines), or for the development of the ligula (emarginate/bilobed versus solid). The importance of both characters was undoubtedly overrated until now. On the other hand, the presence of rare exceptions to otherwise reliable characters does not really affect their importance. Such exceptions are in general not rare and are well known to any practising taxonomist, especially where broadly evolved characters are secondarily lost.

SUBTRIBE PHILONTHINA

All members of this subtribe are without empodial setae between the claws of all tarsi (figs. 70, 71). This character state separates them positively from members of any other subtribe. They also share the character states delineated below.

Ligula entire, no more than slightly sinuate medioapically (e.g., in *Philonthus caeruleipennis*) (fig. 20, as in members of Quediina), with sinuation rarely more pronounced. Palpifer with medioapical seta minute to less than half as long as long lateroapical seta (figs. 18, 20). Labial and maxillary palpus with apical segment asetose, elongate fusiform, or shorter and tapering apicad, not broadened apically. Mentum rarely with more than one anterolateral seta on each side (fig. 20). Postmandibular ridge usually present (often obsolete only in males with swollen genae), either deflexed behind maxilla or following line of large punctures around eyes (as in Xanthopygina). Neck with middle portion of disc virtually impunctate, with no more than microscopic micropunctulation (fig. 39). Nuchal ridge present mesially, usually becoming obsolete near apex of dorsal basal ridge (fig. 39). Infraorbital ridge usually rudimentary, extending at most very little in front of postgenal ridge. Dorsal basal ridge rarely absent, with lateral extensions usually directed almost directly anteriad (fig. 39), often weak and ending toward base of rudimentary infraorbital ridge anteriad. Ventral basal ridge usually follows closely along base of gular sutures up to postgena (as in Anisolinina). Gular sutures usually close together or united basally; transverse depression at base of gula usually delimited by anteriorly broadly arcuate ridge from lateral margins of base.

Pronotal hypomeron with superior marginal line distinctly deflexed under anterior angle of pronotum, so that deflexed portion of pronotal disc visible in ventral view (fig. 45), and with inferior marginal line almost always joining it behind or along prosternal lateral margin; both lines continue together below anterior angle and along anterior margin of pronotum; if two lines not joined, inferior line becomes obsolete near lateral margin of procoxal cavity (as in some Staphylinina); hypomeron no more than moderately inflexed before anterior angles of pronotum, meeting prosternum at very flat angle, with both sclerites fused, and notosternal suture therefore absent (fig. 45) (as in Staphylinina and Xanthopygina). Proepimeron absent. Prosternum with basisternum evenly rounded, only moderately convex, without carina medially before sternacostal suture (fig. 86). Mesosternum with series of large setae situated in broadly arcuate pattern, usually just behind well-formed, broadly arcuate transverse ridge near middle of its length (fig. 87); mesosternum without medial carina. Metasternum with margin of anterior projection almost always very broadly rounded, short between middle coxae (fig. 87).

NOTES: Neck without dorsal basal ridge in *Erichsonius* and *Gabronthus*. Proepimeron present, and prosternum with short carina in front of sternacostal ridge in *Erichsonius*. Mesosternum without transverse ridge in *Craspedomerus* Bernhauer, 1911 (fig. 61),

Erichsonius, and some species of *Hesperus* Fauvel, 1874. Metasternum with anterior projection more narrowly rounded in some species of *Cafius* and *Hesperus*, rarely partially obsolete in some species of *Cafius* and *Neobisnius* Ganglbauer, 1895.

The subtribe Craspedomerina, which was established by Bernhauer (1911: 88, as Craspedomeri) for the genus *Craspedomerus*, was based on the supposed presence of an additional oblique line connecting the superior and inferior lines of the pronotal hypomeron. However, this line is in fact the ventrally deflected superior line, and the pronotal lateral margin is narrowly, somewhat irregularly swollen, imitating a xanthopygine-like superior line (fig. 88). The empodial setae are missing in *Craspedomerus* (fig. 71), and the genus agrees with all characters listed above, confirming the assignment of this genus to Philonthina, as suggested recently by Hayashi (1997: 491).

Subtribe Quediina

All members of this subtribe have the pronotal hypomeron strongly inflexed below the anterior angles of the pronotum, meeting the prosternum at a sharp angle (up to 90°), and separated from it by the notosternal suture (fig. 76); the anterior angles of the pronotum are produced beyond the anterior margin of the pronotum (fig. 76) (the inflection is less apparent in some taxa, e.g., *Quedionuchus*). The infraorbital ridge is usually complete ventrolaterally on the head (fig. 77); this ridge is never complete in any other subtribe of Staphylinini. The nuchal ridge is usually very strong and becomes confluent with the infraorbital ridge, but the infraorbital ridge often can be seen to join the postgenal ridge laterally as a fine line. The dorsal basal ridge is absent from the neck, a character shared only with Tachyporinae, *Erichsonius*, and *Gabronthus* of Philonthina. The members of Quediina also share the character states delineated below.

Ligula minutely emarginate medioapically (as in members of Anisolinina; it is distinctly emarginate or bilobed in most Staphylinina; figs. 35–37), rarely entire (fig. 89). Palpifer with one strong apical seta, accompanied by one shorter seta (most *Quedius*, as well as *Velleius* Leach, 1819, and *Velleiopsis* Fairmaire, 1882) or by several shorter setae (*Hemiquedius* Casey, 1915), by one minute seta (*Bolitogyrus* Chevrolat, 1842, *Heinzia* Korge, 1972, *Heterothops*, *Quedius* [*Quedionuchus*]), or apparently without additional setae (*Acylophorus*, *Anaquedius* Casey, 1915, *Anchocerus*, *Beeria* Hatch, 1957, *Quedius* [*Raphirus* Stephens, 1829], *Valdiviodes* Smetana, 1981). Mentum with two anterolateral setae on each side (most *Quedius* [fig. 90], sometimes separated as in *Hemiquedius*, *Quedius* [*Paraquedius* Casey, 1915, *Raphirus*]) or with several setae (*Velleius*), or one seta (*Anaquedius*, *Beeria*, *Bolitogyrus*, *Heterothops*); there are no setae on the mentum in *Acylophorus*. Maxillary palpus usually without setae. Gula with transverse basal impression very narrow, distinct only along basal marginal carina, apparently absent in *Heterothops* and *Smilax*. Mandible with dorsolateral ridge ranging from poorly defined, to absent (*Acylophorus*, *Anaquedius*, *Bolitogyrus*, *Hemiquedius*, *Heterothops*, *Indoquedius* Cameron, 1932, *Valdiviodes*), and always very close to lateral margin when present (fig. 91). Postmandibular ridge absent; ventral basal and postgenal ridges present. Neck with middle portion of disc impunctate.

Pronotal hypomeron with superior marginal line situated entirely on lateral margin, not deflexed under anterior angle of pronotum before continuing onto anterior margin of pronotum (fig. 75); inferior marginal line of pronotal hypomeron becoming obsolete along anterolateral margin of coxal cavity in typical members of Quediina (fig. 76). Anterior marginal line of pronotum gradually becoming separated from the margin mediad in many genera, also often becoming obsolete. Proepimeron highly developed and well sclerotized in almost all typical Quediina (including *Beeria*, and as in most Tachyporini). Prosternum with basisternum usually moderately prominent, evenly convex anteriad, relatively flat behind two long setae, and usually without carina (as in Philonthina). Sternacostal ridge usually straight, distinctly oblique. Furcasternum usually relatively declivous, often moderately carinate. Mesosternum with long setae situated (often not in regular pattern) on and/or behind broadly raised discal area, which follows contours of

margin of projection, so that margins appear depressed, well defined, never with transverse carina. Metasternum projects very little between middle coxae (as in most Philonthina), or not at all (e.g., *Acylophorus*). Empodial setae present between claws of all tarsi.

NOTES: Maxillary palpus with setae in some more unusual Quediina (*Anchocerus*, *Astrapaeus* Gravenhorst, 1802, *Euryporus* Erichson, 1839, *Indoquedius*, *Strouhalium* Scheerpeltz, 1962). Infraorbital ridge strongly reduced or missing entirely in *Astrapaeus*, *Beeria*, *Heinzia*, *Quedius* (*Quedionuchus*, some *Microsaurus* Dejean, 1833), and *Valdiviodes* Smetana, 1981. Nuchal ridge present only dorsally in *Beeria*, rudimentary in *Valdiviodes*, and not distinctly converging with infraorbital ridge in *Anchocerus*, *Heterothops*, *Quedius* (*Megaquedius* Casey, 1915, *Microsaurus*).

Pronotal epimeron apparently fused with peritreme in *Acylophorus* and *Anchocerus*; hypomeron deflexed against margin of peritreme and proepimeron apparently absent in *Heterothops*. Sternacostal ridge moderately produced anteriad along keel in *Anaquedius*, *Beeria*, and *Quedius* (*Megaquedius*, *Paraquedius*, *Quedionuchus*, some *Microsaurus*). Empodial setae sometimes unevenly developed (*Acylophorus* lineage).

In the above diagnosis, several genera have been omitted because they have very few characters in common with the Quediina; on the other hand, many are typical of Philonthina or Xanthopygina (e.g., *Glyphesthus* Kraatz, 1858 and *Moeocerus* Fauvel, 1899, which are actually members of Philonthina, and *Haematodes* and *Scariphaeus* Erichson, 1839, which will be dealt with at a later date [in prep.]).

SUBTRIBE ANISOLININA

In all north temperate members of this subtribe, the superior and inferior marginal lines of the pronotal hypomeron are not joined, and the inferior line becomes obsolete along the lateral margin of the prosternum (fig. 92) (as in *Agelosus* or *Ocypus* [*Matidus*] of Staphylinina), but the hypomeron clearly does not extend anteriad along the anterior margin of the pronotum. In the Anisolinina, this conformation may occur because the superior line is not distinctly deflexed under the anterior angles of the pronotum, and the pronotum is highly convex; as a result, only a very narrow portion of the dorsal surface of the pronotum is visible in ventral view at the anterior angle. The members of this subtribe also share the character states delineated below.

Ligula minutely emarginate medioapically (fig. 93). Palpifer with only one strong lateroapical seta (*Anisolinus*) (fig. 17), or with one additional shorter, finer medioapical seta (*Amichrotus* Sharp, 1889) (fig. 95). Both labial and maxillary palpi with apical segment asetose, elongate, distinctly fusiform; second segment of maxillary palpus with medial margin obtusely rounded apically, with insertion of third segment entirely in lateral half of apex (fig. 84). Mentum with two anterolateral setae on each side. Mandibles long, sickle-shaped (fig. 94), each with one broad tooth at middle (fig. 96), with dorsolateral ridge well developed, close to lateral margin; mandibular prostheca long, lanceolate, with single series of long, individual plumose ciliae clearly discernible, shortening near apex. Gula with transverse basal impression well delimited anteriad, either by narrowly rounded ridge or by abrupt impression of gula in front. Postmandibular ridge rudimentary to short; ventral basal ridge following base of gular sutures closely up to postgena; base of infraorbital ridge extending little beyond lateral bend of postgenal ridge, arching toward nuchal ridge dorsad on neck, but (together with basal ridge) obscured mesad by punctures on disc (especially in *Amichrotus*); nuchal ridge present dorsally, becoming obsolete near apex of arms of dorsal basal ridge (as in Philonthina). Neck with moderately dense, moderate punctures on disc (as in *Ocypus* s. str., *Platydracus*, and others of Staphylinina).

Pronotum with hypomeron visible in lateral view for most of its length except below anterior angle of pronotum, where it is slightly inflexed, therefore meeting prosternum at flat angle; both sclerites fused, notosternal suture therefore absent (as in Philonthina, Staphylinina, and Xanthopygina). Proepimeron absent. Prosternum with entire basisternum depressed or flattened, with very little convexity anteromedially, so that intercoxal

depression well delimited anteriad, and/or well-defined transverse ridge present at variable distance behind anterior margin (fig. 97). Metasternum with anterior projection very long, apex narrowly (*Anisolinus*) to moderately rounded (*Amichrotus*) (fig. 98). Empodial setae present between claws of all tarsi, but usually very small (fig. 67).

NOTES: Many members of this subtribe resemble in general habitus, and even in the shape of the mandibles and in the development of the mouthparts, those of the subtribe Philonthina, particularly some species of *Philonthus* from the Cyanipennis group (Schillhammer, 1998a: 102). The two anterolateral setae on each side of the mentum, the densely punctate surface of the neck, the long metasternal intercoxal process, and presence of the empodial setae differentiate them immediately.

SUBTRIBE STAPHYLININA

With the exception of some species of *Dinothenarus* s. str. (fig. 38), all members of this subtribe have the ligula emarginate or bilobed, although the emargination is occasionally more or less minute (figs. 35–37). The superior marginal line of the pronotal hypomeron is deflected under the anterior angles of the pronotum, so that the deflected portion of the disc is visible in ventral view (figs. 42–44); the superior and inferior marginal lines are almost always joined along or behind the posterolateral margin of the prosternum (figs. 42–44). Members of Staphylinina also share the character states delineated below.

Palpifer with one strong lateral and one finer medial seta apically, medial seta at least half as long as lateral seta (figs. 121, 156); or with one strong subapical and several shorter setae (*Creophilus*, *Emus*, *Hadrotes*, *Miobdelus*, *Ocypus* [most members of *Ocypus* and *Matidus*; fig. 149], *Physetops*, *Protogoerius*, *Thinopinus*). Mentum usually with one long anterolateral seta and one shorter seta laterad to it (fig. 99). Mandible usually with well-developed dorsolateral ridge, well removed from lateral margin and bordered by deep depression (as in Xanthopygina). Postmandibular ridge almost always of xanthopygine type when present, directed toward subocular puncture. This ridge is longest in *Ontholestes*, distinct and almost reaching infraorbital puncture in *Abemus*, *Thoracostrongylus*, and *Platydracus*, and variably short to rudimentary in *Dinothenarus*, *Ocypus* (*Pseudocypus*), and *Staphylinus*. Neck always with dorsal basal ridge (as in Philonthina and Xanthopygina), although usually with anterior extensions confused by dense punctation on disc. Gula with transverse impression at base usually distinct, usually not well delimited anteriad. Base of infraorbital ridge extends at most slightly in front of postgenal ridge laterally, or is entirely rudimentary where postgenal ridge extends laterad (as in *Platydracus*), apparently only more significantly extended anteriad in *Agelosus*. Nuchal ridge almost always complete, reaching or coming close to base of infraorbital ridge laterally. Neck with disc densely punctate, with fine to umbilicate punctures (figs. 40, 41) generally separated by at most one diameter of puncture.

Pronotum with hypomeron no more than moderately inflexed at anterior angles of pronotum, meeting prosternum at a very flat angle, with both sclerites fused, and notosternal suture therefore absent (fig. 56) (as in Philonthina, Anisolinina, and Xanthopygina). Proepimeron, when present, always membranous and varying from well to poorly developed (figs. 51, 56). Acetabulum of middle coxae often with deep depression behind intercoxal process of mesosternum (unique within Staphylinini), as in *Miobdelus*, *Ocypus*, *Thinopinus*, *Protogoerius*, and some *Dinothenarus* (*Parabemus*), also with variably shaped carinae behind projection in *Agelosus*, *Ascialinus*, *Hadrotes*, *Tasgius* (fig. 154), and some *Ocypus* (especially *Pseudocypus*). Metasternum usually distinctly projecting between middle coxae. Empodial setae present between claws of all tarsi (fig. 68).

NOTES: Mentum with cluster of variable anterolateral setae in *Emus* and *Naddia*. Mandible with dorsolateral ridge weaker and closer to margin in *Tasgius* (*Rayacheila*), in which mandible is unusually narrow. Mandibular prostheca highly variable in Staphylinina, but unusual developments (e.g., distinctly bilobed supporting structure as in *Abemus* [fig. 12] or *Dinothenarus*, or sup-

porting structure long, lanceolate or parallel-sided with setae only near the apex [figs. 13–15]) have not been seen in the other subtribes of Staphylinini. Postmandibular ridge deflected behind maxilla in *Eucibdelus*. Gula with transverse basal impression indistinct in *Eucibdelus*, weak in *Protogoerius* and *Tasgius* (*Tasgius*), in which gula tumid to near base; delimited anteriad by narrowly rounded arcuate ridge in *Ontholestes* and *Thoracostrongylus*; limited by broader, more posteriad depression in gula in *Abemus*, *Emus*, and *Naddia*. Nuchal ridge obsolete laterally in *Miobdelus*, some *Ontholestes*, and *Protogoerius*, and obsolete mesially in *Creophilus*, *Hadrotes*, and *Thinopinus*. Neck with punctures entirely obsolete on disc in *Creophilus*, *Hadrotes*, and *Thinopinus*. Pronotal epimeron absent in *Eucibdelus*, *Ocypus*, *Physetops*, *Protogoerius*, and *Staphylinus* (fig. 57), *Wasmannellus*, and in some *Dinothenarus* and *Tasgius*.

Superior line of pronotal hypomeron becoming variably indistinct or obsolete near anterior angle in *Creophilus*, *Hadrotes*, *Thinopinus*, and *Wasmannellus* (fig. 49); inferior line very close and parallel to superior line along prosternal margin in *Ocypus* (*Ocypus* and *Matidus*) (fig. 48); superior line poorly deflected and two lines widely separated in *Agelosus* (fig. 46), but *Agelosus* shares many characters with *Ocypus* (*Ocypus*). Metasternum with anterior projection very broadly rounded in *Ascialinus*, *Physetops*, and *Protogoerius*.

Subtribe Xanthopygina

Most members of this subtribe have a complete postmandibular ridge on the head (fig. 81), although frequently irregular, always distinct anteriorly, and usually reaching past subocular puncture, with at least curved ridges extending to near postocular puncture. The dorsal basal ridge is always present on the neck (fig. 80). The superior and inferior marginal lines of the pronotal hypomeron are not joined and are well separated. The inferior line always continues uninterrupted and separately along the prosternal margin and almost always continues around the anterior angles of the pronotum to the anterior margin of the pronotum (fig. 79), where it usually joins the superior line. In cases where the inferior line becomes obsolete at the anterolateral angle of the prosternum (as in *Algon* Sharp, 1874, *Allostenopsis* Bernhauer, 1921, *Eugastus*, and *Tympanophorus* Nordmann, 1837), the two lines are widely separated and the superior line is never deflected below the anterior angles of the pronotum, nor is the disc of the pronotum visible in any part in ventral view. These and the other members of Xanthopygina also share the character states delineated below.

Ligula entire or no more than slightly sinuate medioapically (*Plociopterus*, fig. 19). Palpifer with one strong lateral, slightly subapical seta, and usually one finer medioapical seta only up to half length of long seta. Mentum with two anterolateral setae: one long medial seta, one fine lateral seta. Mandible with basolateral ridge usually highly developed, distinctly removed from lateral margin, and bordered by deep depression. Gula with transverse impression at base almost always well developed, delimited anteriorly by either a narrowly rounded, anteriorly arcuate ridge (*Eugastus*, *Nordus* Blackwelder, 1952, *Philothalpus* Kraatz, 1857, *Elmas*, *Plociopterus*, *Styngetus* Sharp, 1884, *Tympanophorus*), or more typically by a distinct transverse carina that limits base of depressed gula. Infraorbital ridge extending significantly anteriad of lateral bend of postgenal ridge (as in some Quediina, but unlike Philonthina and Staphylinina). Neck with disc only finely punctate (though never only micropunctulate as in Philonthina), with moderate punctures only laterally (fig. 80).

Hypomeron of pronotum no more than moderately inflexed below anterior angles of pronotum, meeting prosternum at a flat angle (often angled slightly anteriad), with both sclerites fused, and notosternal suture therefore absent (fig. 53). Proepimeron present in relatively few genera, always membranous and never more than moderately developed (unlike in most Quediina). Prosternum with basisternum rarely carinate, and then only weakly so in front of sternacostal ridge, otherwise sternacostal ridge usually strong and projecting medially. Mesosternum never with distinct, arcuate ridge before series of long setae (unlike Philonthina), with highly variable placement. Acetabulum of middle coxae

never more than moderately depressed behind mesosternal intercoxal process. Metasternum with anterior projection always well developed, margins always complete and never converging more than rectangularly along coxal margins, although apex sometimes broadly rounded. Empodial setae always present between tarsal claws.

NOTES: Postmandibular ridge short and deflected slightly ventrad behind maxilla in *Elmas*, *Glenus*, and *Tympanophorus*; *Triacrus* Nordmann, 1837 has short sections near postocular puncture. Pronotal hypomeron with superior line becoming obsolete near anterior angles in *Dysanellus transverserugosus* Bernhauer, 1921, some *Gastrisus*, most *Plociopterus*, and most *Xanthopygus* (this is clearly a secondary fading of the line). Palpifer with one long and two shorter setae apically in *Trigonopselaphus* Gemminger and Harold, 1868, with several shorter setae in *Triacrus* and only one long seta in *Elmas* and *Plociopterus*. Mentum with anterolateral setae shifted mediad in *Tympanophorus*. Gula with weak basal impression in *Glenus*.

Pronotal epimeron present in *Algon*, some *Dysanellus* Bernhauer, 1911, *Gastrisus*, and *Trigonopselaphus*, and reduced in *Nausicotus* Sharp, 1884, *Paraxenopygus* Bernhauer, 1911, *Polyphematiana* Strand, 1914, *Xanthopygus*, and *Xenopygus* Bernhauer, 1906 (fig. 53). Prosternum weakly carinate in front of sternacostal ridge in some *Philothalpus*, some *Plociopterus*, some *Styngetus*, and some *Tympanophorus*. Mesosternum with medial carina in *Algon*, *Allostenopsis*, *Eugastus*, some *Gastrisus*, and *Plociopterus*.

KEY TO NORTH TEMPERATE GENERIC-LEVEL TAXA ASSOCIATED WITH *STAPHYLINUS* SENSU LATO

The following key includes only taxa that are relevant for the understanding and proper assessment of the *Staphylinus* complex of genera, and thus the Palearctic taxa of Staphylinina of *Eucibdelus* lineage (with dilated front tibiae), *Liusus* Sharp, 1889, and *Hadropinus* Sharp, 1889, and the Nearctic taxa *Hadrotes* and *Thinopinus* are not included. These genera are easily distinguishable from any genus of the *Staphylinus* complex, and they also differ in their ecology. Members of the *Eucibdelus* lineage are arboricol–floricol (there are a few exceptions, e.g., *Trichocosmetes* Kraatz, 1859), and members of the remaining genera are restricted to saline sea beaches, with both of these habitats being strictly avoided by members of the *Staphylinus* complex.

1. Disc of pronotum and most of disc of neck virtually impunctate and asetose . . . . . ***Creophilus*** Leach, 1819
– Disc of pronotum and disc of neck variably punctate and setose 2
2. Intercoxal process of mesosternum wide, transverse apically (fig. 101), middle coxae therefore widely separated. First five antennal segments lacking dense appressed pubescence, last six segments forming slightly differentiated, loose club. Hind trochanters sexually dimorphic; in male, very long and apically extended into long, curved apophyse. Entire head, most of pronotum, and apical portion of abdomen with conspicuous, long, dense golden-yellowish pubescence . . . . . ***Emus*** Leach, 1819
– Intercoxal process of mesosternum narrow, acute to broadly rounded apically (figs. 59, 60, 63), middle coxae therefore contiguous or narrowly separated; rarely, if middle coxae widely separated (subgen. *Chaetodracus* of *Platydracus*), then other characters of the couplet agree. At most first four antennal segments lacking dense appressed pubescence, last six segments not forming club. Hind trochanters simple, not sexually dimorphic. Pubescence of body different 3
3. Puncture bearing postocular seta on head situated distinctly closer to posterior margin of head than to posterior margin of eye (fig. 102). Head more or less dilated posteriad (very slightly so in *P. brevicornis*). Submentum with anterior margin beaded throughout. Paramere of aedeagus somewhat dorsoventrally flexible, lacking sensory peg setae . . . . . ***Platydracus*** Thomson, 1858
   a. Middle coxal cavities margined posteriorly . . . . . Subgen. *Platydracus* Thomson, 1858
   – Middle coxal cavities not margined posteriorly . . . . . Subgen. *Chaetodracus* J. Müller, 1926
– Puncture bearing postocular seta on head situated distinctly, or at least appreciably, closer to posterior margin of eye than to

posterior margin of head (figs. 103, 104). Head not appreciably dilated posteriad (slightly so in some *Ontholestes*), with posterior corners variably, obtusely rounded, or if dilated posteriad, then posterolateral portions of head each extended posteriad as rounded lobe (fig. 105). Submentum with anterior margin usually not beaded throughout. Paramere of aedeagus to great extent immovably attached to median lobe, with or without sensory peg setae, or if somewhat dorsoventrally flexible and without sensory peg setae, then posterolateral portions of head each extended posteriad as rounded lobe (fig. 105) 4

4. Posterolateral portions of head each extended posteriad as rounded lobe (fig. 105). Eyes almost perfectly round to scarcely oval. Mandibles each markedly short with very wide basal portion, no more than twice as long as width at base and usually less so (figs. 9, 105). Width of mentum less than three times its maximum length. Pronotum with lateral margins abruptly explanate starting a short distance behind anterior angles, giving appearance of an indentation (fig. 106). Paramere of aedeagus somewhat dorsoventrally flexible, without sensory peg setae . . . . . ***Naddia*** Fauvel, 1867

– Posterolateral portions of head not extended posteriad (figs. 103, 104), slightly so in some *Ontholestes*, in which eyes are longer than tempora (fig. 107). Eyes oval or ovate. Mandibles each variably long with moderately wide basal portion, distinctly (more than twice) to considerably longer than width at base (figs. 8, 10, 108). Width of mentum at least three times its maximum length. Pronotum in dorsal view with lateral margins not appearing indented behind anterior angles (figs. 109, 110, 159). Paramere of aedeagus to great extent immovably attached to median lobe, with or without sensory peg setae 5

5. Superior line of pronotal hypomeron markedly and rather abruptly deflected ventrad, before or at most at middle of pronotum, anterior portion of superior line therefore situated markedly below basal portion in lateral view (figs. 111, 112). Puncture bearing first lateral macroseta on pronotum distant from superior line, separated from it by at least four diameters of puncture (figs. 111, 112) . . 6

– Superior line of pronotal hypomeron moderately and rather gradually deflected ventrad at variable distance between middle of pronotum and anterior angles of pronotum, anterior portion of superior line therefore situated only slightly to moderately below basal portion in lateral view (figs. 113, 114). Puncture bearing first lateral macroseta on pronotum close to superior line, separated from it by no more than two diameters of puncture (figs. 113, 114) 13

6. Dorsal portion of neck continuous with dorsal surface of head due to absence of dorsal portion of nuchal ridge (fig. 115). Medial edge of each mandible with only one simple tooth. Body conspicuously elongate, appearing cylindrical . . . . . ***Physetops*** Mannerheim, 1830

– Dorsal portion of neck separated from dorsal surface of head by nuchal ridge (figs. 40, 116). Medial edge of at least one mandible with more than one tooth. Body not conspicuously elongate and cylindrical 7

7. Mesosternum with fine, short, medial longitudinal carina at base, or with fully developed, long medial carina (figs. 117, 118) 8

– Mesosternum without medial longitudinal carina (figs. 59, 60) 9

8. Anterior angles of pronotum extended angulately (fig. 44). Mesosternum with fully developed, long medial carina (fig. 117) . . . . . ***Ontholestes*** Ganglbauer, 1895

– Anterior angles of pronotum obtuse, not extended angulately. Mesosternum with fine, short, medial carina at base (fig. 118) . . . . . ***Thoracostrongylus*** Bernhauer, 1915

9. Medial edge of mandibular prostheca copiously ciliate along entire length, with extensive basal group of long ciliae and sparser distal group originating on separate, elongate supporting arm, appearing therefore as more or less bilobed, or even multilobed (fig. 12) 10

– Medial edge of mandibular prostheca variably, usually much less copiously, ciliate, without extensive basal group of ciliae originating on separate supporting arm, distinctly not appearing bilobed, sometimes narrow and elongate with ciliae present only near or at apex (figs. 13–16) 11

10. Long serial setae on mesosternum (in more or less transverse or arcuate pattern) each originating in enlarged, more or less pitlike puncture (fig. 59). Deflected portion of pronotum extensively ex-

posed in ventral view, from at least near posterior margin of pronotal epimeron (fig. 54). Mentum with anterolateral, setae-bearing portions each at same level as disc of mentum and not separated from it by obtuse carina (fig. 120). Mandibles each without deep subrectangular indentation, with or without small subbasal tooth (fig. 121). Pronotal epimeron broadly rounded or absent . . . . . ***Dinothenarus*** Thomson, 1858

a. Ligula entire, not bilobed, rarely incised apically (fig. 38). Mandibles each with small subbasal tooth. Body extensively covered with lush, variegate tomentose pubescence . . . . . Subgen. *Dinothenarus* Thomson, 1858

– Ligula emarginate or more or less bilobed (fig. 119). Mandibles each without small subbasal tooth. Body without lush, variegate tomentose pubescence, although some variegate pubescence may be rarely present . . . . . Subgen. *Parabemus* Reitter, 1909

– Long serial setae on mesosternum (in more or less V-shaped pattern), each originating behind a small elevation, not in an enlarged puncture (fig. 122). Deflected portion of pronotum moderately exposed near anterior angles in ventral view, from about anterior edge of pronotal epimeron (fig. 56). Mentum with anterolateral, setae-bearing portions each obliquely deflected at an angle and therefore not at same level as disc of mentum, separated from it by obtuse carina (fig. 123). Mandibles each with small subbasal tooth in deep subrectangular emargination (fig. 124). Pronotal epimeron well developed, projecting triangularly . . . . . ***Abemus*** Mulsant and Rey, 1876

11. Middle coxal cavities not margined posteromedially (fig. 64). Body with isolated patches of yellow tomentose pubescence on head and usually also on pronotum . . . . . ***Staphylinus*** Linné, 1758

– Middle coxal cavities margined posteromedially (figs. 62, 63). Body without isolated patches of yellow tomentose pubescence on head and pronotum 12

12. Head with small, round, shallow, smooth, pitlike depressions among usual punctation (fig. 125). Posterior basal line on first three visible abdominal tergites gently bisinuate (fig. 126) . . . . . ***Miobdelus*** Sharp, 1889

– Head with usual punctation, without shallow, smooth pitlike depressions (fig. 103). Posterior basal line on first three visible abdominal tergites simple, straight . . . . . ***Ascialinus*** Bernhauer, 1933

13. Vertex of head with slight, obtusely elevated carina, branching anteriorly in form of a T. Pronotum distinctly narrowed anteriad, disc with smooth, slightly elevated (gradually more so posteriorly) medial line, separating two indefinite, shallow impressions in front of posterior margin of pronotum . . . . . ***Apostenolinus*** Bernhauer, 1934

– Vertex of head and pronotum without structures described above, although pronotum often with impunctate median strip 14

14. Superior and inferior lines of pronotal hypomeron distinctly, widely separated at anterior angle, with inferior line disappearing along prosternal margin (fig. 46) . . . . . ***Agelosus*** Sharp, 1889

– Superior and inferior lines of pronotal hypomeron not widely separated near anterior angle, usually connected before or at anterior angle of pronotum, although sometimes running close to each other anteriorly and not distinctly merging (figs. 48, 50, 52) 15

15. Mandibles each with only one simple tooth on medial margin, or falciform, without tooth on medial margin (figs. 4, 5). Last segment of maxillary palpus setose (fig. 29) . . . . . ***Tasgius*** Stephens, 1829

a. Mandibles each with one simple tooth on medial margin (fig. 5) . . . . . Subgen. *Tasgius* Stephens, 1829

– Mandibles each simple, falciform, without tooth on medial margin (fig. 4) . . Subgen. *Rayacheila* Motschulsky, 1845

– Mandibles each, or at least left mandible, with two or more teeth on medial margin (figs. 127, 128); if each mandible with only one simple tooth, then last segment of maxillary palpus asetose (fig. 129) 16

16. Mandibles each with only one simple tooth on medial margin 17

– Mandibles each, or at least left mandible, with two or more teeth on medial margin (figs. 127, 128) 18

17. Posterior basal line on first three visible abdominal tergites (best visible on tergite II) obtusely extended posteriad on each lateral portion, base of tergite between extensions depressed, depression delimited laterally by short oblique carina situated at middle of each lateral extension of basal line. Last segment of labial palpus short, truncate apically, either more or less parallel-sided or var-

iably dilated apicad. Dorsal portion of aedeagus variably sclerotized . . . ***Ocypus*** Leach, 1819, pars (*Aulacocypus* J. Müller, 1925)

– Posterior basal line on first three visible abdominal tergites simple, not extended posteriad on each lateral portion, bases of tergites without short oblique carina. Last segment of labial palpus distinctly fusiform. Dorsal portion of aedeagus almost entirely membranose . . . . . ***Protogoerius*** Coiffait, 1956

18. Bases of first four visible abdominal tergites not appreciably transversely impressed. Hind tibia with spines on dorsolateral face (fig. 130). Last segment of labial palpus of variable shape, in general fusiform, or more or less parallel-sided and truncate apically (figs. 131, 132) . . . . . ***Ocypus*** Leach, 1819

a. Posterior basal line on first three visible abdominal tergites (best visible on tergite 2) obtusely extended posteriad on each lateral portion, base of tergite between extensions depressed, with depression delimited laterally by short oblique carina situated at middle of each lateral extension of basal line . . . . . Subgen. *Aulacocypus* J. Müller, 1925

– Posterior basal line on first three visible abdominal tergites simple, not extended posteriad on each lateral portion . . . . . b

b. Last segment of maxillary palpus setose (fig. 25) . . . . . Subgen. *Matidus* Motschulsky, 1860

– Last segment of maxillary palpus asetose (fig. 133) c

c. Last segment of both maxillary and labial palpus elongate, longer than wide, in general fusiform, narrowly subtruncate apically (figs. 23, 131). Palpifer usually with two apical setae (fig. 128) . . . . . Subgen. *Pseudocypus* Mulsant and Rey, 1876

– Last segment of at least labial palpus short, no more than moderately longer than wide, broadly truncate apically (figs. 132, 133). Palpifer usually with three apical setae (as in fig. 149) . . . . . Subgen. *Ocypus* Leach, 1819

– Bases of first four visible abdominal tergites markedly transversely impressed and with punctation different from that on rest of tergites. Hind tibia without spines on dorsolateral face. Last segment of labial palpus short, distinctly dilated anteriad, widely truncate, securiform . . . . . ***Wasmannellus*** Bernhauer, 1920

THE GENERA

The following treatment of each taxon lists the type species and, if required, discusses taxonomic and other information important for justification and understanding of the new concepts presented. No full formal descriptions and detailed information about the type species are given, since they do not fit in the intended scope of this paper.

Creophilus Leach, 1819

TYPE SPECIES: *Staphylinus maxillosus* Linné, 1758.

COMMENTS: Members of this genus may be easily recognised by the following shared character states: (1) palpifer with one long subapical seta and three to four shorter apical setae; (2) disc of pronotum and most of dorsal face of pronotum virtually impunctate and asetose; (3) middle coxae widely separated by broadly rounded apical margin of mesosternum; (4) pronotal hypomeron with superior line becoming obsolete near anterior angles of pronotum and not joining the inferior line (fig. 49); (5) presence, on both dorsal and ventral faces of body, of long, more-or-less variegate pubescence varying in color from black to grayish-silver, grayish-golden, yellowish-red, or brownish-red (such pubescence not present in a few species occurring elsewhere); (6) anterior projection of metasternum very broad, with margins obsolete; and (7) dorsal apicolateral lobe of hind coxa without distinct spines, or spines very fine.

Further character states include: mandibles each with microsculpture on mediobasal portion; mandibular prostheca copiously ciliate along entire length, with long, dense basal ciliae gradually shortening apicad; postmandibular ridge absent; deflected portion of pronotal disc visible in ventral view from about anterior edge of pronotal epimeron, which is well developed and membranous; metasternum oblique, highly convex between coxae, then horizontal.

This genus is assigned by some authors (e.g., Coiffait, 1974: 557; Moore and Legner, 1979: 32) to the subtribe Xanthopygina

based on the configuration of the superior and inferior lines of the pronotal hypomeron (see above). Although *Creophilus* (with *Hadrotes* and *Thinopinus*) seems to be intermediate between the two subtribes, characters 1, 6, and 7 above are shared exclusively with members of the Staphylinina; together with the absence of the postmandibular ridge, these confirm their closer affinity with the Staphylinina.

Emus Leach, 1819

TYPE SPECIES: *Staphylinus hirtus* Linné, 1758.

COMMENTS: Species of this genus are quite distinctive by the long, matted, black, golden-yellow, and whitish-gray pubescence of the body, and by the characters used in the key to genera.

Further character states include: mandible with small rectangular tooth basad of large middle tooth; mandibular prostheca long, parallel-sided, with ciliae only near apex; postmandibular ridge rudimentary; palpifer with several apical and many discal, coarse setae; mentum with arcuate carina between basal angles, separating ellipsoidal membranous basal portion from small anterolateral sclerotized portions, which are deflected anterolaterad and bear a cluster of setae; superior and inferior lines of pronotal hypomeron connected just behind posterolateral angle of prosternum; deflected portion of pronotal disc visible in ventral view from near posterior margin of proepimeron, which is well developed and membranous; sternacostal ridge bisinuate, transverse, roughly parallel to anterior prosternal margin; anterior projection of metasternum very broad, margins obsolete.

Naddia Fauvel, 1867

TYPE SPECIES: *Caranistes westermanni* Erichson, 1840.

COMMENTS: Members of this genus share the following character states: (1) posterolateral portions of head extended posteriad as rounded lobes (fig. 105); (2) eyes distinctly shorter than tempora, almost perfectly round to scarcely oval; (3) mandibles short and wide basally (fig. 9) (see key for details); (4) width of mentum less than three times its maximum length; (5) lateral margins of pronotum abruptly explanate a short distance behind anterior angles, giving appearance of an indentation (fig. 106); and (6) paramere of aedeagus somewhat dorsoventrally flexible, without sensory peg setae.

Further character states include: outer antennal segments slightly asymmetrical to subserrate; mentum with cluster of variable anterolateral setae; maxillary palpus with apical segment stoutly flattened, with last two broadening to apex; last segment of labial palpus short, fusiform, setose; mandibular prostheca lanceolate, with short ciliae along medial margin; postmandibular ridge rudimentary; postgenal ridge present only laterally; superior line of pronotal hypomeron moderately deflexed ventrad between middle of pronotum and anterior angles of pronotum, with anterior portion of superior line therefore situated only moderately below basal portion in lateral view; deflected portion of pronotal disc visible in ventral view only from edge of coxal insertion; hypomeron very broad at middle; proepimeron well developed, membranous; series of long setae on mesosternum situated on small tubercles in a very broadly U-shaped pattern (shared with members of *Platydracus*); mesosternal intercoxal process with margins slightly concave, narrowly rounded apically; metasternum oblique, highly convex between coxae, horizontal posteriorly; dorsal apicolateral lobe of metacoxa with one short, fine spine.

Ontholestes Ganglbauer, 1895

TYPE SPECIES: *Staphylinus murinus* Linné, 1758.

COMMENTS: The species of this genus share four distinctive synapomorphies: (1) anterior angles of pronotum angulately extended anteriad (fig. 44); (2) marginal line of pronotal hypomeron narrowly rounded at prosternal margin (fig. 44); (3) mesosternum with complete, medial longitudinal carina (fig. 117); and (4) mentum with long anterolateral seta near lateral margin, lateral seta minute to absent.

Further character states include: outer segments of antenna variably asymmetrical; maxillary and labial palpus both with last segment asetose, fusiform; mandibles each

with dorsolateral ridge distinct, removed from margin, bordered by deep, broad depression basally; mandibular prostheca copiously ciliate along entire length, with long, irregular, dense basal ciliae gradually shortening apicad; apical segments of both maxillary and labial palpus distinctly elongate fusiform, without setae; postmandibular ridge present; postgenal ridge arched to base of gula; superior line of pronotal hypomeron rather abruptly deflexed ventrad around middle of pronotum, with anterior portion of superior line therefore situated markedly below basal portion in lateral view; pronotal epimeron long, subtriangular; prosternum highly prominent, sloping abruptly to anterior margin, with strong, convex carina starting between macrosetae; series of long setae on mesosternum arranged in subtransverse row on each side of median carina; mesosternal intercoxal process angulate to broadly truncate apically; metasternum oblique, highly convex between coxae, anterior projection with acutely converging margins (fig. 117); dorsal apicolateral lobe of metacoxa without apparent spines.

Thoracostrongylus Bernhauer, 1915

TYPE SPECIES: *Ontholestes javanus* Bernhauer, 1915.

Parontholestes Coiffait, 1982 (**syn. nov.**) (type species: *Parontholestes nepalicus* Coiffait, 1982).

COMMENTS: Species of this genus share the synapomorphy of a short, medial carina at base of mesosternum (fig. 118). They also share a submentum with apical margin beaded.

Further character states include: eyes large, prominent, tempora short, evenly rounded toward narrow neck, which is little over one-third total width of head; maxillary and labial palpus both with last segment asetose, fusiform; mandibular prostheca short, copiously ciliate along entire length, with long, dense basal ciliae gradually shortening apicad; mentum with two lateral setae; postmandibular ridge present; postgenal ridge bent toward gula from lateral bend; superior line of pronotal hypomeron rather abruptly deflexed ventrad around middle of pronotum, with anterior portion of superior line therefore situated markedly below basal portion in lateral view; deflected portion of pronotal disc visible from distinctly behind epimeron in ventral aspect; proepimeron poorly developed, very membranous; prosternum very long (length about three-fourths width), with distinct, straight carina from behind macrosetae, continuing on furcasternum; serial long setae on mesosternum arranged in broadly U-shaped pattern behind an elevated arcuate ridge behind median carina; mesosternal intercoxal process very narrowly rounded apically; metasternum as in *Ontholestes*; dorsal apicolateral lobe of metacoxa with one short, fine spine located distinctly subapically; scutellum very long, almost extending halfway to apex of elytra.

We were able to study the holotype of *Parontholestes nepalicus*, deposited in the collection of the Forschungsinstitut Senckenberg (SMF C 15051), Frankfurt a. M., Germany. It has all the characters of the genus *Thoracostrongylus*, including the presence of a fine short carina at the base of mesosternum, despite the statement ''Mésosternum non caréné'' in the original description (Coiffait, 1982: 72). The name *Parontholestes* therefore becomes a junior synonym of *Thoracostrongylus*.

We also studied the holotype of *Thoracostrongylus martensi* Coiffait, 1982, deposited in the same institution (SMF C 15143). The holotype cannot be distinguished from specimens of *Abemus olivaceus* Cameron, 1928. The name *T. martensi* must therefore be transferred to *Abemus*, where it becomes a junior synonym of *A. olivaceus*.

Abemus Mulsant and Rey, 1876

TYPE SPECIES: *Staphylinus chloropterus* Panzer, 1796.

COMMENTS: Members of this genus share the following character states: (1) mandibles with similarly developed teeth, each with large tridentate middle tooth (individual dents not at same plane) and a small tooth basad of it in a deep, subrectangular indentation (fig. 124); (2) mandibular prostheca appearing bilobed or even multilobed, with extensive basal group, and long distal group of ciliae originating on separate supporting arm (fig. 12); (3) mentum with anterolateral

portions (bearing two anterolateral setae) each obliquely deflected at an angle and therefore not at same level as disc of mentum, separated from it by obtuse carina (fig. 123); and (4) postmandibular ridge almost reaching infraorbital puncture, running close to eye basally, infraorbital puncture situated three to four diameters from margin of eye.

Further character states include: maxillary and labial palpi both with last segment asetose, fusiform; mandibles each with dorsolateral ridge as in *Ontholestes* or *Thoracostrongylus*; submentum with anterior margin not beaded; lateral end of nuchal ridge distinctly, but moderately, removed from nuchal constriction, directed toward level of transverse postgenal ridge; epimeron of prothorax well developed, projecting triangularly (fig. 111); prosternum moderately prominent with broadly rounded slope anteriad, with prominent, arcuate carina continuing evenly onto furcasternum; mesosternum with long serial setae originating behind small elevations in more-or-less V-shaped pattern (fig. 122), mesosternal intercoxal process rather acute apically, mesocoxal acetabulum moderately impressed behind; metasternum more or less horizontal, with little difference in convexity between projections and disc.

Platydracus Thomson, 1858

TYPE SPECIES: *Staphylinus stercorarius* Olivier, 1795.

COMMENTS: Members of this genus share the following character states: (1) puncture bearing postocular seta on head situated distinctly closer to posterior margin of head than to posterior margin of eye (fig. 102); and (2) paramere of aedeagus devoid of any sensory peg setae and attached to median lobe in such a way that it is somewhat dorsoventrally flexible.

Further character states include: mandibular teeth (on both mandibles) appearing in two planes, dorsal and ventral, in most species (fig. 7); mandibular prostheca with dense patches of ciliae, ciliae long at base, gradually shortening apicad, with prostheca therefore appearing as more or less bilobed (fig. 11); maxillary and labial palpi with apical segments moderately elongate, fusiform, without setae (figs. 134, 135); submentum with apical margin beaded throughout; posteroventral margin of eye distinctly oblique, postmandibular ridge rapidly diverging from it and bordered by even series of setae basally, reaching about halfway or more to subocular puncture, which is separated from margin of eye by at least four, and usually more than eight diameters of puncture; nuchal ridge complete, directed toward transverse postgenal ridge laterally, and only moderately removed from nuchal constriction; pronotal hypomeron markedly broader at middle, with superior line distinctly rounded anteriorly, joining inferior line well behind posterolateral angle of prosternum, deflected portion of pronotal disc visible from at, or behind, posterior edge of coxal insertion (fig. 136); pronotal epimeron well developed, triangular (fig. 52); prosternum sloping moderately, never abruptly in front of macrosetae, sternacostal ridge almost straight, slightly arched posteriad; mesosternum without ridges on intercoxal projection, with series of macrosetae on small elevations in broadly U-shaped pattern; mesocoxal acetabulum weakly to moderately impressed behind, never with medial carinae extending from projection; anterior metasternal projection with margins complete (except in *Chaetodracus*), converging less than rectangularly; metasternum more or less horizontal, with little difference in convexity between anterior projection and disc; dorsal apicolateral lobe of metacoxae with two to seven coarse spines.

Subgenus *Platydracus* Thomson, 1858.

Neotasgius J. Müller, 1925 (**syn. nov.**) (type species: *Ocypus brevicornis* Weise, 1877; nec Motschulsky, 1862 = *P. brachycerus*, **nom. nov.**).

COMMENTS: Members of this subgenus share the characters of posteromedially margined middle coxal cavities (fig. 137) and of the narrow intercoxal mesosternal process, no more than moderately widely separating the middle coxae.

Neotasgius was established by J. Müller (1925: 41) as a subgenus of *Staphylinus*. However, the type species of *Neotasgius* in fact shows all typical character states of *Platydracus*, although its narrow body shape, with the narrow head not much dilated posteriad, renders it an unusual habitus.

Subgenus *Chaetodracus* J. Müller, 1926 (type species: *Staphylinus patricius* Bernhauer, 1915).

COMMENTS: The type species of this subgenus is distinctive not only by the posteromedially margined middle coxal cavities (a character shared with the members of *Staphylinus*, see fig. 64), but also by the wide intercoxal process of the mesosternum that very widely separates the middle coxae, similar to that in *Emus*. Additional species belonging to this subgenus may ultimately be found among the east Palearctic species of *Platydracus*.

REMARKS ON SOME SPECIES OF *PLATYDRACUS*

1. *Platydracus brachypterus* (Kraatz, 1859: 76), described in *Staphylinus*, is preoccupied by *Staphylinus brachypterus* Geoffroy, 1785: 167, now a synonym of *Aleochara curtula* (Goeze, 1777: 730); by *Staphylinus brachypterus* Marsham, 1802: 510, now a synonym of *Aploderus caelatus* (Gravenhorst, 1802); and by *Staphylinus brachypterus* Brullé, 1839: 59, now in *Protogoerius*. A replacement name, *Platydracus brevipennis*, **nom. nov.**, is hereby proposed for *Platydracus brachypterus* (Kraatz).

2. *Platydracus oculatus* (Bernhauer, 1929: 110), described in *Staphylinus*, is preoccupied by *Staphylinus oculatus* Fabricius, 1775: 265, now a valid name in *Creophilus*; and by *Staphylinus oculatus* O. F. Müller, 1776: 99. A replacement name, *Platydracus oculosus*, **nom. nov.**, is hereby proposed for *Platydracus oculatus* (Bernhauer).

3. *Platydracus violaceus* (Gravenhorst, 1802: 162), described in *Staphylinus*, is preoccupied by *Staphylinus violaceus* Olivier, 1795: 8 (now in *Plochionocerus*). The name *Platydracus cupripennis* (Melsheimer, 1844: 35) becomes the valid name for this species (**stat. nov.**).

4. *Platydracus vulpinus* (Nordmann, 1837: 53) has an older synonym, *Platydracus immaculatus* (Mannerheim, 1830: 22). Both species were described in *Staphylinus*. Erichson (1839: 379) treated *Staphylinus immaculatus* tentatively as identical with *S. vulpinus*, but all subsequent authors simply listed Mannerheim's name as a synonym, despite its seniority. The status of these two species can only be established after the study of Mannerheim's original material. We therefore continue to use the longstanding Nordmann name and consider *Staphylinus immaculatus* a doubtful name.

5. *Platydracus yunnanensis* (Bernhauer, 1943: 76), described in *Staphylinus*, is preoccupied by *Platydracus yunnanensis* (Bernhauer, 1933: 48), also described in *Staphylinus*. A replacement name, *Platydracus yunnanicus*, **nom. nov.**, is proposed for *Platydracus yunnanensis* (Bernhauer, 1943).

Staphylinus Linné, 1758 (**stat. nov.**)

TYPE SPECIES: *Staphylinus erythropterus* Linné, 1758.

COMMENTS: All members of this genus share the synapomorphy of the middle coxal cavities not margined posteromedially (fig. 64). In addition, they share (1) superior line of pronotal hypomeron markedly and relatively abruptly deflexed ventrad, before or at most at middle of pronotum, with its anterior portion situated markedly below basal portion in lateral view (fig. 112); (2) bicolored black body with red elytra and legs red excluding coxae; and (3) presence of yellow tomentose pubescence on head and usually also on pronotum, and paired yellow tomentose patches on abdominal tergites.

Further character states include: right mandible with one stout, apically truncate, subemarginate or slightly emarginate tooth, left mandible with two dorsal teeth, and with one somewhat smaller tooth in more ventral plane (fig. 138); mandibular prostheca narrow, elongate, with ciliae present only at apex (fig. 15); last segment of maxillary palpus fusiform, narrower and markedly shorter than segment three, asetose (fig. 24); ligula emarginate; last segment of labial palpus fusiform, narrower and markedly longer than segment two, asetose (fig. 139); anterior margin of submentum inwardly arcuate, without bead; postmandibular ridge rudimentary to very short; base of infraorbital ridge on the neck distinctly recurved toward nuchal ridge dorsally, sometimes reaching it; superior and inferior lines of pronotal hypomeron connected well before anterior angles of pronotum (fig. 57); epimeron of prothorax absent (fig. 50); prosternum with middle portion of basisternite broadly rounded or gradually

sloping anteriad; serial long setae on mesosternum originating in moderately impressed punctures in subtransverse to broadly arcuate arrangement; spines on dorsal apicolateral lobe of hind coxae small, almost indistinguishable in size from other setae.

This is a new concept of this genus, restricted to the species around *S. erythropterus* and *S. caesareus*. Six Palearctic and one Nearctic species are at present included in the genus.

Dinothenarus Thomson, 1858 (**stat. nov.**)

TYPE SPECIES: *Staphylinus pubescens* DeGeer, 1774.

COMMENTS: Members of this genus share the following character states: (1) mandibular prostheca bilobed, with basal group of long ciliae and sparser distal group originating on separate supporting arm; and (2) long serial setae on mesosternum situated on anterior edges of enlarged, more-or-less pitlike punctures, in subtransverse to broadly U-shaped pattern (fig. 59).

Further character states include: right mandible with one broad tooth at middle, left mandible with two teeth or with one stout, apically emarginate tooth at middle, with all teeth in same (dorsal) plane; maxillary palpus with apical segment moderately elongate, distinctly fusiform, narrower and subequal in length to segment three, asetose (figs. 23, 28); apical segment of labial palpus distinctly fusiform, narrower and markedly longer than segment three, usually with a few, sometimes with many, fine setae (fig. 38); mentum usually with semicircular fine basal carina extending variably between basolateral angles (figs. 119, 120); postmandibular ridge rudimentary to extended less than halfway to infraorbital puncture, infraorbital puncture from 4 to 10 diameters distant from margin of eye; postgenal ridge usually broadly obsolete and often deflected obliquely anteriad toward gula, especially in members of *Parabemus*; superior line of pronotal hypomeron markedly and relatively abruptly deflected ventrad, before or at most at middle of pronotum, with its anterior portion situated markedly below basal portion in lateral view (fig. 111), deflected portion of pronotal disc visible in ventral view from behind posterior margin of epimeron (especially in members of *Parabemus*) to near the posterior pronotal angles (especially in *Dinothenarus* [*Dinothenarus*]); pronotal epimeron ranging from moderately developed to virtually absent; dorsal apicolateral lobe of hind coxa often with more than three (up to six) distinctly spinelike coarser setae.

Subgenus *Dinothenarus* Thomson, 1858.

Protabemus Scheerpeltz, 1966 (type species: *Staphylinus xanthocephalus* Kraatz, 1859).

COMMENTS: Members of this subgenus share the following character states: body extensively covered with lush, variegated pubescence of tomentose character (figs. 140, 141); at least mandibles and adjacent areas, and usually large portions of ventral surface of head bicolored, with distinct testaceous to rufotestaceous areas; ligula virtually entire (fig. 38), rarely incised apically (e.g., in *D. xanthocephalus*); anteromedial portion of prosternum highly prominent, forming a rounded knob which slopes abruptly anteriad and markedly delimits the transverse marginal depression; sternacostal ridge distinctly arched posteriad toward keel, usually coming close to posterior margin of furcasternum (fig. 54); mesosternal intercoxal process with margins more or less straight, converging subrectangularly until just before rectangular apex, margins without bead apically, slightly explanate; mesocoxal acetabulum only slightly depressed behind projection; margins of anterior metasternal projection never converge at less than right angle, although apex varies from moderately to broadly rounded; disc of metasternum always horizontal, on same plane as body.

The subgenus contains six Palearctic and one Nearctic species at present.

Subgenus *Parabemus* Reitter, 1909 (**stat. nov.**) (type species: *Staphylinus fossor* Scopoli, 1772).

Parocypus Bernhauer, 1915 (**syn. nov.**) (type species: *Staphylinus dehradunensis* Bernhauer, 1915).

Hypabemus Scheerpeltz, 1966 (**syn. nov.**) (type species: *Staphylinus chrysocomus* Mannerheim, 1830).

COMMENTS: Members of this subgenus share the following character states: body

with patches of variegated pubescence; ventral surface of head piceous to dark rufous, without distinctly bicolored areas; ligula emarginate or bilobed (fig. 119), anteromedial portion of prosternum usually only moderately prominent, with distinct, but broadly rounded, slope anteriad; sternacostal ridge slightly oblique, relatively straight to moderately arched posteriad toward keel; mesosternal intercoxal process with margins concave, converging distinctly less than rectangularly, with apex acute to narrowly rounded, margins distinctly beaded, at least near apex (fig. 142); mesocoxal acetabulum slightly depressed to deeply depressed behind projection, with concavity below apex; some species with metasternum short and at an oblique angle to plane of body.

The type species of both *Parocypus* and *Hypabemus* share the character states of *Parabemus*, as they were presented above, and therefore there is no justification for keeping them as separate subgenera.

This is a new, expanded concept of this subgenus that includes 12 east Palearctic/Oriental species previously assigned to *Parocypus*, as well as 5 Nearctic species that were previously listed as members of the genus ''Staphylinus.'' One of the Nearctic species (*D. pleuralis*) was assigned by Smetana (1965a: 10) to *Abemus* (as a subgenus of *Staphylinus* at that time), but Frank (1979: 236) assigned it correctly to *Parabemus*, based on larval characters. Additional Palearctic and Oriental species will likely be added to this subgenus in the future.

Remarks on Some Species of *Dinothenarus*

1. *Dinothenarus fokiensis* (Bernhauer, 1933: 32) (*Staphylinus*). Bernhauer (loc. cit.) described the species as a member of the subgenus *Parocypus* of *Staphylinus* and compared it to ''*Staph. dehradunensis*.'' Since *Parocypus* becomes a junior synonym of *Parabemus* (see above), Bernhauer's assignment of this species was quite correct. We were able to study the holotype from ''Foo-chow'' in the Bernhauer collection in Chicago and another male specimen, compared with the holotype, from the Scheerpeltz collection, Wien, labelled as follows: ''China Prov. Fo-Kien G. Siemssen.'' We confirm that *Staphylinus fokiensis* is a member of the subgenus *Parabemus* of *Dinothenarus*. The above two specimens were compared to the lectotype of *Dinothenarus insignis* (J. Müller, 1926) (see below) and were found to be conspecific. The name *D. fokiensis* therefore becomes a junior synonym of *D. insignis* (**syn. nov.**).

2. *Dinothenarus fossor* (Scopoli, 1772: 109) (*Staphylinus*). Fabricius (1792: 523) described *Staphylinus fossor* based on specimen(s) of unknown provenience. Erichson (1839a: 377) cited *S. fossor* Fabricius as a subsequent reference of *Staphylinus fossor* Scopoli, 1772. However, Fabricius (loc. cit.) redescribed the species, using the same name *S. fossor* as had Scopoli (loc. cit.) before him. The name *S. fossor* Fabricius, 1792 therefore becomes a junior synonym of *Staphylinus fossor* Scopoli, 1772 (**syn. nov.**).

3. *Dinothenarus ganglbauerianus* (Bernhauer, 1938: 101) (*Staphylinus*). Bernhauer (loc. cit.) described this species as a member of the subgenus *Xanthocypus* of *Staphylinus*. Recently, Hayashi (1995: 45) studied the holotype of this species from Kamikochi, Japan (see Hayashi, loc. cit., for the detailed label data), and redescribed it. He considered the species to be a member of the genus *Ocypus*, very closely related to ''*Ocypus similis*,'' but at the same time he pointed out some unique characteristics of the species. We were able to study the holotype and concluded, based mainly on thoracic structures, on the shape of the mandibular prostheca, and on the configuration of the aedeagus, that it belongs to the subgenus *Parabemus* of the genus *Dinothenarus* and is related to *D. insignis*. *Dinothenarus insignis* occurs in southern China (Fujian) and supposedly also in Japan (see below). However, *D. insignis*, which is a large and conspicuous species, was apparently never rediscovered in Japan (see Shibata, 1984: 88), which may indicate that one of Müller's original specimens may have been mislabelled, and that the species does not really occur in Japan. The same actually applies also to *D. ganglbauerianus* (see Shibata, 1984: 94); we therefore also believe that the holotype of *D. ganglbauerianus* is likely mislabelled and that this species in fact does not belong to the Japanese fauna. This

would confirm the difficulties Hayashi (1995: 45) expressed, based on different grounds, about the reliability of the type locality of *D. ganglbauerianus*. The aedeagi of *D. insignis* and *D. ganglbauerianus* resemble in general configuration those of some members of the genus *Ocypus*, which contributed to Hayashi's (1995: 56) conclusion that *D. ganglbauerianus* was closely related to ''*Ocypus similis*'' (see above). However, we believe that this similarity in the configuration of the aedeagus is convergent.

4. *Dinothenarus insignis* (J. Müller, 1926b: 41) (*Staphylinus*). Müller (loc. cit.) described this species as a member of the subgenus *Parocypus* of the genus *Staphylinus*, based on two specimens: one from ''China merid.'' and one from ''Japonia.'' The specimen from China is apparently deposited in the Zoologisches Museum der Humboldt-Universität, Berlin (not seen), the other one in the Natural History Museum, London. We were able to study the latter specimen (female), which is labelled as follows: ''Ocypus n. sp./Type [round label with red margin]/Typus/Japan. G. Lewis. 1910-320/St. (Parocypus) insignis n. sp. Det. J. Müller.'' The specimen is in fair shape (the right hind tibia and tarsus are missing, and most of the pubescence of the dorsal side of the body is gone, but the remnants permit reconstruction of its original pattern). The specimen is hereby designated as the lectotype of *D. insignis*; the label ''LECTOTYPE Staphylinus insignis J. Müller A. Smetana des. 1999'' was attached to it.

Miobdelus Sharp, 1889

TYPE SPECIES: *Miobdelus brevipennis* Sharp, 1889.

COMMENTS: Members of this genus share the following character states: (1) head with macrosetae and some of other setae originating in punctures expanded into round, shallow, smooth depressions (fig. 125); (2) mandibular prostheca lanceolate, with moderately long setae along entire medial margin (fig. 143); and (3) posterior basal line on first three visible abdominal tergites gently bisinuate (fig. 126).

Further character states include: palpifer with one long subapical and two shorter apical setae; apical segments of maxillary and labial palpi moderately elongate, distinctly fusiform, with only that of labial palpus setose (figs. 144, 145); postmandibular ridge absent; nuchal ridge present only dorsally, becoming obsolete well before base of infraorbital ridge laterally; dorsal disc of neck with umbilicate punctures without visible interspaces; pronotal epimeron small; long serial setae on mesosternum originating on edge of feeble, irregular, very broadly U-shaped ridge; mesosternal intercoxal process acute apically, margin finely beaded throughout (fig. 60); acetabulum of middle coxae deeply depressed, nearly vertical behind projection; anterior metasternal projection with margins converging quite obtusely, apex very broadly rounded.

The genus at present contains only one species, *M. brevipennis* from Japan. However, the genus in fact includes many undescribed species in Taiwan and in mainland China, all of which live mostly at higher mountain elevations. A review of these species is under preparation by the senior author.

Physetops Mannerheim, 1830

TYPE SPECIES: *Staphylinus tataricus* Pallas, 1773.

COMMENTS: Members of this genus share the following character states: (1) dorsal portion of neck continuous with dorsal surface of head, due to absence of dorsal portion of nuchal ridge (fig. 115); (2) disc of head and pronotum micropunctulate between larger punctures (fig. 115); and (3) middle abdominal tergites notably swollen, especially in apical half, as convex as sternites, together with convexity of pronotum and length of elytra and body, giving body an overall cylindrical appearance.

Further character states include: mandibles long, each with one blunt tooth on medial edge, dorsolateral ridge weak and relatively close to margin; prostheca long, thin, lanceolate, with short ciliae along medial margin, becoming progressively longer to moderate near apex; palpifer with one long subapical and two shorter apical setae; apical segment of both labial and maxillary palpus setose; apex of last segment of labial palpus obliquely widened; submentum broadly inwardly ar-

cuate, without bead; postmandibular ridge rudimentary; gular sutures most approximate distinctly anteriad of middle, gradually widely diverging posteriad; postgenal ridge distinct only laterally; lateral portion of nuchal ridge directed anteriad toward transverse postgenal ridge; superior line of pronotal hypomeron markedly and relatively abruptly deflected ventrad near middle of pronotum, deflected portion of pronotal disc visible from well behind broadest portion of hypomeron in ventral view; superior and inferior lines of pronotal hypomeron almost coalesce at margin of coxal cavity, then run very closely parallel along entire lateral margin of prosternum; pronotal epimeron absent; prosternal basisternite sloping very gradually from anterior margin almost to sternacostal ridge medially, furcasternum abruptly declivous, forming a sharp toothlike process medially at sternacostal ridge; intercoxal depression relatively long, shallow; long serial setae on mesosternum originating in large, rounded depressions forming an irregular U-shaped ridge; apex of mesosternal intercoxal process acute, forming a blunt toothlike process, with a rounded carina extending into the moderately depressed mesocoxal acetabulum behind; anterior metasternal projection with margins converging highly obtusely, very broadly rounded apically; dorsal apicolateral lobe of metacoxa usually with one distinctly subapical, coarse spine, and several finer ones in an uneven series basad to it.

Ascialinus Bernhauer, 1933

TYPE SPECIES: *Ascialinus beckeri* Bernhauer, 1933.

COMMENTS: The only species of this genus is characterized by the following character states: mandibles each similarly shaped, with deep subbasal indentation and two similar short, angular teeth at middle; base of gula highly swollen, transverse impression very fine, along margin; pronotal hypomeron finely setose (but see below); mesosternal intercoxal process with margins obsolete, disc entirely, irregularly tumid, with angulate finlike process at apex, extended behind as a long straight carina into deeply depressed acetabulum.

Further character states include: prostheca long, lanceolate, with short ciliae along entire medial edge, gradually longer to moderate at apex; apical segment of maxillary palpus asetose, with apex slightly wider than width at middle, apical segment of labial palpus with many fine setae, apex expanded to about two times width at base, slightly oblique; postmandibular ridge absent; postgenal ridge highly oblique, reaching gular suture, very broadly rounded laterally; superior and inferior lines of pronotal hypomeron run closely anteriad for some distance, merge along prosternal margin; prothoracic epimeron moderately developed; prosternum long, more than half as long as maximum width; sternacostal ridge medially extended anteriad into short, acute, slightly elevated process; elytra short, broadly depressed along base; anterior metasternal projection with margins converging obtusely, very broadly rounded apically; metasternum very short, at distinctly oblique angle to plane of body, not visibly canaliculate medially; dorsal apicolateral lobe of hind coxa with very fine spinelike setae, almost indistinguishable from other setae; empodial setae very long.

The species seems to be close to some members of the subgenus *Matidus* of *Ocypus*. *Ascialinus* may actually contain more species in the east Palearctic area, particularly in mainland China; the finely setose pronotal hypomeron may be an autapomorphy of *A. beckeri*.

Apostenolinus Bernhauer, 1934

TYPE SPECIES: *Apostenolinus cariniceps* Bernhauer, 1934.

COMMENTS: In addition to its large size (23 mm), the single species of this genus may be easily recognized by the following character states: (1) head, pronotum, and elytra dark bluish; (2) outer four segments of antenna whitish-yellow; and (3) pronotum markedly narrowed anteriad toward narrow head, which is distinctly attenuated posteriad.

Further character states include: mandibles rather long and slender, with acute apices, medial margin of each with only one tooth, tooth on left mandible short, broadly truncate, tooth on right mandible broadly triangular, rather acute; eyes slightly shorter (not longer, as stated in the original description)

than tempora (ratio 0.86); puncture bearing postgenal macroseta situated much closer to posterior margin of eye than to posterior margin of head; superior line of pronotal hypomeron moderately and rather gradually deflexed ventrad at about apical fourth of length of pronotum, joining inferior line of pronotal hypomeron well before anterior angles, anterior portion of superior line situated only moderately below basal portion in lateral view; pronotal epimeron absent; surface of pronotum with microsculpture of fine, short, mostly oblique striae; mesosternum without transverse carina; punctation of elytra very dense, corneous; surface with dense, fine, rugose microsculpture, appearing dull; abdominal tergites with posterior basal line very gently bisinuate.

The status of this taxon cannot be established with certainty at present. The only known male specimen of *A. cariniceps* is somewhat damaged (see below), and it has lost all mouthparts (including mandibular prostheca) due to dermestid damage. Bernhauer (1934: 9) established it as a subgenus of *Staphylinus*. The general habitus of the species is certainly conspicuous, as noted already by Bernhauer (loc. cit.), mainly due to the combination of the narrow head and the pronotum markedly narrowed anteriad. Bernhauer (loc. cit.) described the pronotum as ''vor dem Schildchen mit zwei grossen, langen Längseindrücken.'' The impressions are in fact somewhat irregular, and since the pronotum is definitely cracked anteriorly, there is a distinct possibility that the pronotum may have been exposed to excessive pressure that caused not only the cracking but also the two irregular impressions; in other words, the impressions may be artificial and not characteristic of the species.

Due to the configuration of the pronotum, particularly the development of the superior and inferior lines, *Apostenolinus* is not a member of the ''*Dinothenarus–Staphylinus*'' lineage. The impressions on the head and pronotum (if really present on the latter) are likely an autapomorphy. *Apostenolinus* is considered here as a separate genus only tentatively, pending the availability of more specimens for study.

Protogoerius Coiffait, 1956

TYPE SPECIES: *Staphylinus brachypterus* Brullé, 1839 (nec Geoffroy, 1785) (= *Protogoerius brullei*, **nom. nov.**).

COMMENTS: The single species of this genus has the habitus of an *Ocypus*; it has two main identifying character states: (1) gula tumid almost to fine basal carina, transverse impression very faint (fig. 146); (2) dorsal portion of median lobe of aedeagus almost entirely membranous.

Further character states include: mandibles each with one strong, broadly triangular tooth on medial edge in front of a deep, angular indentation, with dorsolateral ridge not distinctly removed from lateral margin (fig. 147); palpifer with one subapical and three shorter apical setae; apical segment of maxillary and labial palpi moderately elongate, distinctly fusiform, only that of labial palpus setose (fig. 148); prostheca parallel-sided, elongate with long ciliae only at apex; nuchal ridge present only dorsally, becoming obsolete well before base of infraorbital ridge laterally; dorsal basal ridge very short, ending at very base of infraorbital ridge; superior and inferior lines of hypomeron run very closely parallel for some distance anteriorly, gradually merging along prosternal margin; prothoracic epimeron absent; prosternum with short transverse ridge on keel behind two macrosetae; mesocoxal acetabulum deeply depressed, with straight carina sloping obliquely behind intercoxal process; margins of anterior metasternal projection converging at a highly obtuse angle, projection very short; metasternum very short, at an oblique angle to plane of body, with no visible medial line; dorsal apicolateral lobe of hind coxa with only one or two very fine spines; empodial setae very long.

Brullé's (1839: 59) name *Staphylinus brachypterus* is preoccupied by *Staphylinus brachypterus* Geoffroy, 1785: 176, now a synonym of *Aleochara curtula* (Goeze, 1777), and by *Staphylinus brachypterus* Marsham, 1802: 510, now a synonym of *Aploderus caelatus* Gravenhorst, 1802. The replacement name *Protogoerius brullei*, **nom. nov.**, is hereby proposed for it.

Ocypus Leach, 1819 (**stat. nov.**)

TYPE SPECIES: *Staphylinus cyaneus* Paykull, 1789 (= *Staphylinus ophthalmicus* Scopoli, 1763).

COMMENTS: All members of this genus share the following character states: mandibular dorsolateral ridge not distinctly removed from lateral margin, especially in dorsal view; prostheca long, lanceolate, with short setae along medial margin, becoming progressively longer to moderate near apex; postmandibular ridge very short to absent; last segment of labial palpus in general variably fusiform, or more or less parallel-sided and truncate apically (figs. 131, 132); superior and inferior lines of hypomeron run very closely parallel for some distance anteriorly, either never distinctly merging or gradually merging along prosternal margin, superior line moderately and rather gradually deflected ventrad, with its anterior portion situated only slightly to moderately below basal portion in lateral view (figs. 113, 114); prothoracic epimeron absent (fig. 113); deflected portion of pronotal disc visible in ventral view from along coxal insertion (a little farther posteriad in *Pseudocypus*); anterior medial portion of prosternum sloping very gradually anteriad; mesocoxal acetabulum deeply impressed, vertical to convexly carinate behind intercoxal process.

Subgenus *Ocypus* Leach, 1819.
Goerius Westwood, 1827 (**syn. nov.**) (type species: *Staphylinus olens* O. Müller, 1764).
Xanthocypus J. Müller, 1925 (**syn. nov.**) (type species: *Ocypus weisei* Harold, 1877).

COMMENTS: Members of this subgenus share the following character states: mandibular prostheca with long ciliae (fig. 13); palpifer with one long subapical and two shorter apical setae (as in fig. 149); apical segment of labial palpus with many setae (fig. 132), at least as large as that of maxillary palpus, which is asetose, fusiform; mentum without arcuate ridge basally; submentum not distinctly beaded; eye rarely more than half length of tempus, genal seta removed from margin of eye by at least four diameters of its puncture, usually more; lateral end of nuchal ridge distinctly removed from nuchal constriction, directed distinctly posteriad of transverse postgenal ridge.

The type species of *Goerius* and *Xanthocypus* fit well within the subgenus *Ocypus*, as it is characterized herein, particularly as far as the characters on the mouthparts are concerned. Some species, such as *O. weisei*, *O. quadrimaculatus*, *O. auroguttatus*, and *O. wasmanni*, may appear conspicuous due to the presence of striking patches of bright tomentose pubescence, but in all other respects they are typical members of the subgenus *Ocypus*.

Subgenus *Matidus* Motschulsky, 1860 (**stat. nov.**) (type species: *Matidus forficularius* Motschulsky, 1860).

COMMENTS: Members of this subgenus share the following character states: mandibular prostheca with ciliae very short; palpifer with one long subapical and one or two shorter apical setae (fig. 149); apical segment of both maxillary and labial palpus with many setae (figs. 150, 151), apical segment of maxillary palpus not distinctly fusiform, with apex broadened, almost as wide as width at middle of segment, that of labial palpus distinctly fusiform; mentum without arcuate ridge basally; submentum not distinctly beaded; eye rarely more than half length of tempus; genal seta removed from margin of eye by at least four times diameter of its puncture; lateral end of nuchal ridge distinctly removed from nuchal constriction, directed distinctly posteriad of transverse postgenal ridge.

Subgenus *Pseudocypus* Mulsant and Rey, 1876 (**stat. nov.**) (type species: *Staphylinus mus* Brullé, 1832).
Protocypus J. Müller, 1923 (**syn. nov.**) (type species: *Ocypus fulvotomentosus* Eppelsheim, 1889).
Atlantogoerius Coiffait, 1956 (type species: *Ocypus sylvaticus* Wollaston, 1865).
Fortunocypus Coiffait, 1964 (type species: *Ocypus fortunatarum* Wollaston, 1871).
Nudabemus Coiffait, 1982 (**syn. nov.**) (type species: *Nudabemus caerulescens* Coiffait, 1982).

COMMENTS: Members of this subgenus share the following character states: mandibular prostheca with long ciliae (fig. 13); palpifer with one long subapical and one shorter

apical seta (fig. 128); apical segment of labial palpus with many setae (fig. 131), that of maxillary palpus asetose, both distinctly fusiform; mentum almost always with fine, broadly arcuate ridge extending for variable distance from posterior margin between basolateral angles; submentum with anterior margin beaded (usually finely) throughout; eye usually longer than tempus, less frequently variably shorter; genal seta removed from margin of eye by no more than three times diameter of its puncture; lateral end of nuchal ridge only moderately removed from nuchal constriction, directed to level of transverse postgenal ridge; superior and inferior lines of hypomeron merging along prosternal margin.

The type species of *Nudabemus* conforms, with a few exceptions, to the subgenus *Pseudocypus*, particularly in the configuration of the mandibular teeth, palpifer (one short apical seta), submentum (weakly beaded), and prosternum; the mesocoxal acetabulum is deeply impressed and convexly carinate behind the intercoxal projection, and the metasternum is short and oblique. The species is somewhat unusual for *Pseudocypus* (but similar to *O. aethiops*, or to the east Palearctic species previously assigned to *Protocypus*); the apical segment of the labial palpus is relatively broad and slightly obliquely truncate apically (but as in *O. fulvipennis* or *O. mus*); the superior line of the pronotal hypomeron is rather abruptly deflected ventrad, at a point relatively close to the anterior pronotal angle, yet it merges with the inferior line before the prosternal margin (as in *O. mus*); the hind tibia has only one spine on its dorsolateral face; the punctation on the head and pronotum is coarse and the elytra are short (as in the east Palearctic species previously assigned to *Protocypus*).

Ocypus quadrimaculatus, assigned by Coiffait (1982: 31) to *Nudabemus*, is quite different from the type species of *Nudabemus* and belongs to the subgenus *Ocypus* s. str. (see above).

Nudabemus may represent a separate lineage of east Palearctic species, occurring in the Himalayas and particularly in the mountains of mainland China and it may deserve a subgeneric status; however, until the taxonomy of this fauna is better known, we prefer to unite *Nudabemus* with *Pseudocypus*, as characterized herein.

The type species of *Protocypus* is a typical representative of mainly east Palearctic groups of species of *Pseudocypus* that in general resemble members of the subgenus *Matidus* (or even *Ocypus*). However, in all other character states, particularly those of the mouthparts, they fit well within the subgenus *Pseudocypus*, as characterized herein.

Subgenus *Aulacocypus* J. Müller, 1925 (type species: *Ocypus gloriosus* Sharp, 1874).

COMMENTS: Members of this subgenus share the following character states: (1) mandibles each with one simple tooth on medial margin; (2) each lateral portion of posterior basal line on first three visible abdominal tergites obtusely extended posteriad, with base of tergite between extensions depressed, depression delimited laterally by short oblique carina situated at middle of each lateral extension of posterior basal line.

Further character states include: maxillary palpus with apical segment short, as broad at apex as at base; apical segment of labial palpus short, truncate apically, either more or less parallel-sided, or variably dilated apicad, with apex up to almost three times its width at base.

J. Müller (1925: 40) erected *Aulacocypus* as a subgenus of *Staphylinus* to accommodate two species (see the checklist) that share the distinctive character state of the posterior basal line of the first three visible abdominal tergites (see the key and above). This character state, combined with the simple tooth on medial margin of each mandible, justifies the retention of a separate subgenus within *Ocypus* for these two species, and tentatively for another species from China (see comment under *O. kansuensis* below).

REMARKS ON SOME SPECIES OF *OCYPUS*

1. *Ocypus almorensis* (Cameron, 1932). Cameron (1932: 204) described the species (in *Staphylinus*) from specimens from ''West Almora: Kali Valley, alt. 9000 feet'' and ''Punjab: Triun, alt. 9300 feet.'' We were able to study one of the male syntypes in the Natural History Museum, London, England, labelled as follows: ''Triun, 9,300 ft Dharm-

sala. Punjab. H. G. C./M. Cameron. Bequest. B.M. 1955-147./Staphylinus (Ocypus) almorensis.'' The specimen is in very good shape. It was dissected, and the aedeagus and the genital segment were glued to the plate with the beetle. It is hereby designated as the lectotype of *Staphylinus almorensis*; the label ''LECTOTYPE Staphylinus almorensis Cameron A. Smetana des. 1999'' was attached to it. The specimen cannot be distinguished from those of *Ocypus helleni* J. Müller that occur in northern Pakistan and in Kashmir. The name *O. almorensis* becomes a junior synonym of *O. helleni* (**syn. nov.**). The corresponding determination label was attached to the specimen.

2. *Ocypus auricomus* (Lindberg, 1953: 4), described in *Staphylinus*, is preoccupied by *Staphylinus auricomus* Brullé, 1842: pl. 5, fig. 6, now a synonym of *Glenus chrysis* (Gravenhorst, 1806), and by *Staphylinus auricomus* Cameron, 1929: 65. The name *Ocypus mateui* (Coiffait, 1954: 170), listed at present as a junior synonym of *O. auricomus*, becomes the valid name of this species (**stat. nov.**).

3. *Ocypus bimaculatus* (Cameron, 1932: 207), described in *Staphylinus*, is preoccupied by several names in *Staphylinus*, the oldest one being *Staphylinus bimaculatus* Schrank, 1798: 644, now a synonym of *Lordithon trinotatus* (Erichson, 1839b: 409). The replacement name *Ocypus cameroni*, **nom. nov.**, is hereby proposed for *Ocypus bimaculatus* (Cameron, 1932).

4. *Ocypus fulvotomentosus* Eppelsheim, 1889: 172. The collection at the Naturhistorisches Museum in Wien, Austria, contains one male specimen under this name. It is labelled as follows: ''Kan-ssa 1885 G. Patanin/ c. Eppelsh. Steind. d./fulvotomentosus det. Bernhauer/fulvotomentosus det. J. Müller/ TYPUS.'' The specimen is in good condition; however, the entire left middle leg, outer three segments on left hind tarsus, and the entire right middle tarsus are missing. It was dissected and the aedeagus was glued to a plate attached to the pin, with the beetle. The specimen is hereby designated as the lectotype of *O. fulvotomentosus*; the label ''LECTOTYPE Ocypus fulvotomentosus Eppelsheim A. Smetana des. 1997'' was attached to it.

5. *Ocypus hauseri* (Bernhauer, 1933: 32). The collection at the Field Museum of Natural History, Chicago, Illinois, contains one male specimen (holotype) under this name. It is labelled as follows: ''Kalgan Jnn-shan 980–2100 m/285/Hauseri Brh. Typus unic./ Hauseri Bernh.Typus unic./Chicago NHMus M. Bernhauer Collection.'' The specimen is in very good condition. It was dissected, compared to the lectotype of *O. fulvotomentosus* (see above), and was found to be conspecific with it. The name *O. hauseri* becomes a junior synonym of *O. fulvotomentosus* (**syn. nov.**); the holotype was labelled accordingly.

6. *Ocypus himalayicus* (Cameron, 1935: 288) (*Staphylinus*). Cameron (loc. cit.) described the species from a single female from Karakorum range. The holotype, deposited at the Natural History Museum, London, England, is labelled as follows: ''Type [round disc with red margin]/Sind valley 2000–2800 m 2–5.V.1929/Nederlandsche Karakorum-Expeditie J. A. Sillem leg./M. Cameron. Bequest. B.M. 1955-147./Staphylinus himalayicus Cam. TYPE.'' The specimen is in fair shape (last segment of left front tarsus and claws of middle right tarsus are missing, and most of the pubescence of the head and pronotum is missing as well). The specimen cannot be distinguished from those of *Ocypus* (*Pseudocypus*) *helleni* J. Müller that occurs in northern Pakistan and in Kashmir. The name *O. himalayicus* becomes a junior synonym of *O. helleni* (**syn. nov.**). The corresponding determination label was attached to the specimen.

7. *Ocypus italicus* (Aragona, 1830: 10). By coincidence, Erichson (1840: 406) later redescribed this species as new, using the same name as Aragona. Subsequent authors considered Erichson's description as a subsequent citation of Aragona's species. However, based on Erichson's treatment of his *Ocypus italicus*, including his comments under ''Obs.,'' there is little doubt that Erichson considered it a new species. Therefore, the name *Ocypus italicus* Erichson, 1840 becomes a junior synonym of *Ocypus italicus* (Aragona, 1830) (**syn. nov.**).

8. *Ocypus kansuensis* (Bernhauer, 1933: 33) (*Staphylinus*). Bernhauer (loc. cit.) described the species as a member of the sub-

genus *Xanthocypus* of *Staphylinus*. We were able to study the male holotype deposited in the Bernhauer collection at the Field Museum of Natural History, Chicago, Illinois. It is labelled as follows: ''Kansou mer. Hoei-Siee./286./Mittel-China don. Dr. G. Hauser/ kansuensis Brnh. typ. unic./Chicago NHMus M. Bernhauer Collection/kansuensis Brnh. typus un. Xanthocypus.'' The specimen is in fair condition. Only three basal segments of the left antenna are present, the pronotum is longitudinally cracked on the left side, and the mesosternum and metasternum are damaged, again on the left side. The specimen was obviously exposed to dorsoventral pressure. It was dissected, and the aedeagus and genital segment were glued to the plate with the beetle. By the form of the mandibles, the shape and setation of the last segment of the labial palpus, the thoracic structures, the characteristic configuration of the posterior basal line of the first three visible abdominal tergites, as well as by the form of the aedeagus, the species fits the subgenus *Aulacocypus* of *Ocypus*.

9. *Ocypus kobensis* Cameron, 1930: 207. The collection at the Natural History Museum, London, England, contains one male specimen (holotype) under this name. It is labelled as follows: ''Type [round label with red margin]/X/JAPAN Kobe Harada 7.XI '19 [last line illegible]/538/Ocypus kobensis TYPE Cam./M. Cameron. Bequest. B.M. 1955-147.'' The specimen was dissected (apex of the abdomen was damaged before the dissection), and the aedeagus and the genital segment (damaged) were glued to the plate with the beetle. The specimen was compared to the lectotype of *Ocypus lewisius* (see below) and was found to be conspecific. The name *Ocypus kobensis* is therefore a junior synonym of *Ocypus lewisius* (**syn. nov.**); the holotype was labelled accordingly.

10. *Ocypus lewisius* Sharp, 1874: 33. The collection at the Natural History Museum, London, England, contains four conspecific specimens of the original series under this name, as follows: spec. 1 (male): ''Type [round label with red margin]/Beach Kobe Oct. 69 [on underside of plate with beetle]/ Sharp Coll. 1905-313./Ocypus lewisius. type D.S.'' Spec. 2 (male, dissected, genital segment and aedeagus on plate with beetle): ''Ocypus lewisius Yokohama. Japan. Lewis [on plate with beetle]/Japan G. Lewis./Sharp Coll. 1905-313.'' Spec. 3 (female): ''Ocypus lewisius Yokohama. 27.3.880. Lewis [on plate with beetle]/Japan. G. Lewis./Sharp Coll. 1905-313.'' Spec. 4 (male): ''Japan. G. Lewis. 1910-320./Iokii Tanaka/lewisius Shp det. J. Müller.'' The second male specimen (dissected) is hereby designated as the lectotype of *Ocypus lewisius*; the label ''Lectotype Ocypus lewisius Sharp A. Smetana des. 1999'' was attached to it.

11. *Ocypus nero* (Faldermann, 1835: 118) was recently used by Pilon (1991: 105) as a valid name to replace the misidentified *Staphylinus similis* Fabricius, 1792: 521. Fabricius (loc. cit.) did not describe *Staphylinus similis* as a new species; he attributed it to Paykull. The species Paykull (1789: 10) described as *Staphylinus similis* is today in *Tasgius* (*Rayacheila*), so another name was needed for the species known for a long time as *Staphylinus similis* Fabricius. Pilon (loc. cit.) chose *Staphylinus nero* as a name, without giving any reasons. However, the name *Staphylinus nitens* Schrank, 1781: 231, used for the species already by Fauvel (1874: 411), is older, and therefore *Ocypus nitens* (Schrank) becomes the valid name for this species (**stat. nov.**).

12. *Ocypus orientalis* (Bernhauer and Schubert, 1914: 389), established as a replacement name for *Staphylinus tomentosus* Baudi, 1869: 384 (nec Gravenhorst, 1802: 161), is preoccupied by *Staphylinus orientalis* Motschulsky, 1858: 67, now a synonym of *Creophilus maxillosus*. The replacement name *Ocypus orientis*, **nom. nov.**, is hereby proposed for *Ocypus orientalis* (Bernhauer and Schubert, 1914).

13. *Ocypus pullus* Hochhuth, 1849: 121 and *Ocypus simulator* Eppelsheim, 1878: 420. These two species were declared as being possibly identical by Eppelsheim (1887: 432) and by J. Müller (1926d: 14); however, Müller (loc. cit.) suggested this co-identification only tentatively, and he pointed out some differences between them. Both species belong to a difficult group, and their status can only be determined by the study of Hochhuth's original material, particularly of the characters on the aedeagus. They very likely are not identical and are therefore both

listed in the checklist as separate species. The aedeagus of the holotype of *O. simulator* (''Turcia Merkl'') was illustrated by Smetana (1965b: 40); the second specimen of the original series of *O. simulator* comes from ''Acarnanien.'' *Ocypus pullus* was described from specimens ''Aus verschiedenen Gegenden Kaukasiens.''

14. *Ocypus rossii* (Jarrige, 1954: 164) (*Staphylinus cupreus* Rossi, 1790: 248; nec *Staphylinus cupreus* Fourcroy, 1785: 173). Coiffait (1974: 495, 513) recognized three subspecies of this species (under the name of *P. cupreus*): *P. cupreus cupreus* from western and southwestern Europe, *P. cupreus sericeicollis* from the east Mediterranean region, and *P. cupreus fulvicupreus* from the island of Cyprus. The three subspecies were based on differences in the shape of the apical portion of the paramere of the aedeagus. In fact, the apical portion of the paramere, as well as that of the median lobe, shows distinct variability that is not geographically delimited. The differences given in the key by Coiffait (1974: 495) cannot be confirmed (based on substantial material from the entire geographical range of the species). Therefore, the two subspecies are placed in synonymy with the nominal species. Jarrige (loc. cit.) proposed the name *O. rossii* as a replacement name (see above). However, three older synonyms are available: *Goerius confinis* Stephens, 1832: 211, *Ocypus angustatus* Stephens, 1832: 212, and *Staphylinus sericeicollis* Ménétriés, 1832: 143. Based on the concept discussed above, the latter name by Ménétriés was chosen. The name *Ocypus sericeicollis* (Ménétriés) is therefore the valid name of this species (**stat. nov.**).

Agelosus Sharp, 1889

TYPE SPECIES: *Goerius carinatus* Sharp, 1874.

Apecholinus Bernhauer, 1933 (**syn. nov.**) (type species: *Apecholinus kaiseri* Bernhauer, 1933).

COMMENTS: Members of this genus share the following two character states: (1) infraorbital ridge extended significantly anteriad of postgenal ridge (fig. 152); and (2) superior and inferior lines of pronotal hypomeron distinctly, widely separated at anterior angles of pronotum, with inferior line becoming obsolete along prosternal margin, deflected portion of pronotal disc only narrowly visible near anterior angles in ventral view (fig. 46).

Further character states include: most other characters shared with species of *Ocypus* (*Ocypus*), with following exceptions: labial palpus more broadly expanded apically, up to 1.5 times width at base (fig. 153); lateral margins of mentum relatively long, straight, as in *O.* (*Matidus*) *brenskei* (Reitter, 1884); mesosternum with sharp, convex carina behind intercoxal process, as in *O.* (*Ocypus*) *affinis* Wollaston, 1864.

The type species of *Apecholinus* agrees in all character states with the members of the genus *Agelosus*, except for the dual punctation (fine and coarse) on the dorsal side of the head and on the pronotum. The character state of the dual punctation is not considered to be sufficient for retaining a separate taxon for the species.

Wasmannellus Bernhauer, 1920

TYPE SPECIES: *Wasmannellus tristis* Bernhauer, 1920.

COMMENTS: Members of this genus share the following character states: (1) superior line of pronotal hypomeron moderately separate from inferior line anteriorly, becoming obsolete near anterior angle of pronotum; (2) bases of first four visible abdominal tergites markedly transversely impressed, with punctation different from that on rest of tergites; (3) hind tibia without spines on dorsolateral face.

Further character states include: apical segment of maxillary palpus asetose, almost as wide apically as at middle; apical segment of labial palpus setose, apex expanded to about 1.5 times width of base, slightly obliquely securiform; lateral end of nuchal ridge distinctly removed from nuchal constriction, directed distinctly posteriad of transverse postgenal ridge; pronotal hypomeron very broad at middle, deflected portion of pronotal disc visible only from anterior edge of coxal insertion in ventral view; prothoracic epimeron absent; medial margin of sternacostal ridge extended anteriad into sharp, finlike carina; serial setae on mesosternum inserted along edge of elevated, irregular ridge parallel to margins; mesosternal

intercoxal process with margins converging acutely, acute at apex, distinctly margined throughout; margins of anterior metasternal projection converge rectangularly, very broadly rounded at apex.

The genus at present contains only two species, but there is at least one additional undescribed species in the eastern part of the Palearctic region (mainland China).

Tasgius Stephens, 1829 (**stat. nov.**)

TYPE SPECIES: *Astrapaeus rufipes* Latreille, 1806 (= *Staphylinus pedator* Gravenhorst, 1802).

COMMENTS: Members of this genus share the following character states: (1) mandibles without teeth, or each with only one poorly differentiated tooth (figs. 4, 5); (2) apical segment of all palpi with many setae; (3) mesosternal intercoxal process highly acute apically, extended posteriad into very deeply depressed acetabulum as sharp, straight to highly convex, or even angulate carina (fig. 154).

Further character states include: palpifer with one long lateral subapical seta and one shorter medioapical seta; base of infraorbital ridge distinctly recurved toward nuchal ridge dorsally; prothoracic epimeron ranging from absent to moderately developed, broadly rounded in all subgenera; prosternum long, at least half as long as maximum width (fig. 155); series of long setae on mesosternum inserted along edge of a feeble, irregular, broadly U-shaped ridge, close to margins of projection; dorsal apicolateral lobe of hind coxa with two to three very short, relatively fine spines.

Subgenus *Tasgius* Stephens, 1829.

Pseudotasgius Seidlitz, 1891 (**syn. nov.**) (type species: *Staphylinus pedator* Gravenhorst, 1802).

Paratasgius Jarrige, 1952 (**syn. nov.**) (type species: *Staphylinus ater* Gravenhorst, 1802).

COMMENTS: Members of this subgenus share the following character states: (1) mandibles each with only one poorly differentiated tooth, moderately narrow basally (fig. 5); (2) prostheca long, lanceolate, with short ciliae along medial margin, becoming gradually longer to moderate at apex (fig. 14); (3) maxillary palpus with apical segment variable, from as broad at apex as at base to 1.5 times as broad; apical segment of labial palpus with apex broadened from about 1.5–2 times its width at base.

Further character states include: mandibular dorsolateral ridge rarely represented by more than a fine line, always very close to lateral margin; mentum frequently with more than two setae near anterolateral angles along anterior margin; submentum with anterior margin straight; postmandibular ridge absent, rarely weak but reaching almost halfway to infraorbital puncture; gula tumid to near base, with basal transverse impression very fine and along margin; postgenal ridge directed obliquely anteriad; inferior line of pronotal hypomeron runs close to superior line for some distance anteriad, never distinctly merging with it and becoming obsolete along prosternal margin (*T. pedator*), or merging just behind prosternal margin (*T. ater*) (fig. 155); sternacostal ridge not distinctly arched posteriad, but straight and slightly oblique toward keel; anterior metasternal projection with margins converging highly obtusely.

Pseudotasgius is based on the same type species. *Paratasgius* was based on a single character: the presence of the prothoracic epimeron. Since the development of the prothoracic epimeron varies within *Tasgius* (see above), there is no justification for recognizing *Paratasgius* as a separate taxon, as was done, for example, by Coiffait (1974: 517).

Subgenus *Rayacheila* Motschulsky, 1845 (**stat. nov.**) (type species: *Rayacheila inderiensis* Motschulsky, 1845).

Anodus Nordmann, 1837 (nec Spix, 1829) (**syn. nov.**) (type species: *Staphylinus morio* Gravenhorst, 1802).

Alapsodus Tottenham, 1939 (**syn. nov.**) (type species: *Staphylinus morio* Gravenhorst, 1802).

Allocypus Coiffait, 1964 (**syn. nov.**) (type species: *Staphylinus winkleri* Bernhauer, 1906).

Metocypus Coiffait, 1964 (**syn. nov.**) (type species: *Staphylinus globulifer* Geoffroy, 1785).

Paralapsodus Coiffait, 1974 (**syn. nov.**) (type species: *Staphylinus solskyi* Fauvel, 1875).

COMMENTS: Members of this subgenus share the following character states: (1) mandibles each without teeth, falciform, flat, very narrow to near base (fig. 4); and (2) mandibular prostheca elongate, narrow, par-

allel-sided, with ciliae only near apex (fig. 16).

Further character states include: maxillary palpus with apical segment variable, from as broad at apex as at base to 1.5 times as broad; apical segment of labial palpus with apex broadened from about 1.5 to more than 4 times its width at base (variable within species, with base sometimes very narrow); mentum short, with an even, broadly rounded transverse discal swelling between basolateral angles so that basal portion depressed and anterior portion slightly deflected at an angle to submentum (fig. 156); submentum with anterior margin broadly, arcuately rounded (fig. 156); postmandibular ridge absent; postgenal ridge directed obliquely anteriad, broadly obsolete or confused near gula; lateral end of nuchal ridge directed toward, or anteriad of, transverse postgenal ridge; inferior line of pronotal hypomeron runs close to superior line for some distance anteriad, merging with it along prosternal margin; prosternum with long, broadly arcuate fine carina behind macrosetae medially (fig. 157); sternacostal ridge distinctly arched posteriad, or distinctly oblique toward keel; anterior metasternal projection with margins converging highly obtusely, apex broadly rounded (fig. 158).

Until recently, this subgenus was known under the name *Alapsodus*, a name provided by Tottenham (1939: 225) to replace the preoccupied Nordmann name *Anodus*. However, Boháč (1988: 553) revised the type specimen of the type species of *Rayacheila* (*R. inderiensis*, incorrectly cited by Boháč [loc. cit.] as described in *Ocypus*) and recognized it as a species of *Metocypus*. Since *Metocypus*, along with *Allocypus* and *Paralapsodus*, is a superfluous taxon based solely on aedoeagal characters, which was already placed in synonymy with *Alapsodus* by Dvořák (1984: 66), *Rayacheila* becomes the valid name of the taxon.

Remarks on Some Species of *Tasgius*

1. *Tasgius amoenus* (Reitter, 1909: 122), described in *Staphylinus*, is preoccupied by *Staphylinus amoenus* Olivier, 1795. The replacement name *Tasgius amoenanus*, **nom. nov.**, is proposed for it.

2. *Tasgius bicolor* (Cameron, 1944: 11). The collection at the Natural History Museum, London, England, contains one male specimen (holotype) under this name. It is labelled as follows: ''Type [round label with red margin]/Govt. Entomologist, Punjab CI/ Under leaves in sweet potato field Ayallpur 23.6.1939 M. A. Ghani/Pres. by Imp. Inst. Ent. B.M. 1940/S. (Ocypus) bicolor TYPE Cam.'' The mouthparts (including both palpi) and mandibles confirm the assignment of this species to *Tasgius* (*Tasgius*). A label ''belongs to Tasgius (Tasgius) Det. A. Smetana 1999'' was attached to the specimen.

3. *Tasgius eppelsheimianus* (Jakobson, 1909: 510). This is a replacement name for *Ocypus rufipes* Eppelsheim, 1884: 15 (nec *Astrapaeus rufipes* Latreille, 1806: 285), commonly used for the species. At the time of the replacement, both names were listed in *Staphylinus*. Although both are now in different genera, a junior secondary homonym replaced before 1961 is permanently invalid (Art. 59[b] of the Code). Bernhauer (1900: 55) described *Ocypus rufipes* var. *obscuripes*, which predates Jakobson's replacement name and may be in fact the valid name of this species. However, the status of this ''variety'' is not clear at present, and therefore we consider it as a doubtful name pending a revision of Bernhauer's original material.

CHECKLIST OF NORTH TEMPERATE TAXA

This checklist cites, at the generic level, only valid taxa, new synonyms, and from previously recognized synonyms only those that are for some reason important; similarly, at the specific level, only currently recognized, valid specific and subspecific (or ranked as subspecific at least once in the past) names are given, with the exception of a few synonyms of importance, and the new synonyms. Valid names are in italics; synonyms in roman type. A complete listing of all names, at both generic and specific levels, including complete references, will be available in the upcoming world catalog of Staphylinidae by Herman.

As specified in the title of this paper, the species listed occur only in the northern temperate zone, that is in the Palearctic and Ne-

arctic Regions, with some overlap into the northern areas of the Oriental Region and into the Neotropical Region. The limits of the Palearctic Region are identical, mainly for practical reasons, with those specified for the contributors to the *Catalogue of the Coleoptera of the Palearctic Region*, which is in preparation. The southern limits of the Palearctic Region are, from west to east, as follows: Atlantic Islands (including Azores), Africa north of Sahara (Morocco, Algeria, Tunisia, Egypt), the entire Arabian Peninsula (including Socotra), all of Pakistan, areas along the base of the Himalayas (Kashmir, Himachal Pradesh, Uttar Pradesh, Nepal, Sikkim and Darjeeling, Bhutan, Arunachal Pradesh), all of mainland China (including Hainan), Taiwan, Japan (including Ryukyus and Bonin Isles), and the Kuril Islands.

The taxa at the subspecific level are listed as they are recognized at present; however, many of them, in addition to those presented in this paper, will be placed in synonymy once the complexes are properly studied (see also the Introduction). This is particularly true for those erected for *Ocypus* (*Ocypus*) *ophthalmicus*, even quite recently (Drugmand, 1998), and, to a lesser extent, for *Ocypus picipennis* (see the new synonymies under this species). The new synonymies at the subspecific level presented in the following checklist are those that were established based on the study of much material (not necessarily type material), including the variability of the apical portion of the median lobe and the paramere of the aedeagus. When additional details (e.g., data on the original material studied) were deemed necessary (this information is given for all new synonymies at specific level, but see *Platydracus* below), these were given in ''Remarks on Some Species'' under the proper genus/subgenus. The synonymies presented in the genus *Platydracus* are based on the results of the study of the original material by Newton (in litteris), and he should be credited with them. The species described by Li (1992) and by Li and Chen (1993) from China were left in the genera to which the authors assigned them; these assignments may not be correct.

The following abbreviations are used in the checklist: Pa (= Palearctic); Ne (= Nearctic); Nt (= Neotropical); Or (= Oriental).

CREOPHILUS LEACH, 1819

C. maxillosus (Linné, 1758) – Pa, Or, Ne
- *C. maxillosus maxillosus* (Linné, 1758) – Pa
- *C. maxillosus villosus* (Gravenhorst, 1802) – Ne

C. sikkimensis Wendeler, 1927 – Pa
C. villipennis Kraatz, 1859 – Pa, Or

EMUS LEACH, 1819

E. griseosericans Fairmaire, 1894 – Pa
E. hirtus (Linné, 1758) – Pa

NADDIA FAUVEL, 1867

N. assamensis Cameron, 1932 – Pa, Or
N. atripes Bernhauer, 1939 – Pa
N. chinensis Bernhauer, 1929 – Pa
N. decipiens Cameron, 1932 – Pa, Or
N. ishiharai Shibata, 1994 – Pa
N. malaisei Scheerpeltz, 1965 – Or, Pa
N. miniata Fauvel, 1895 – Pa, Or
N. monticola Shibata, 1994 – Pa
N. rufipennis Bernhauer, 1915 – Or, Pa
N. taiwanensis Shibata, 1979 – Pa
N. wittmeri Coiffait, 1982 – Pa, Or

ONTHOLESTES GANGLBAUER, 1895

O. aurosparsus (Fauvel, 1895) – Pa, Or
O. callistus (Hochhuth, 1849) – Pa
O. chalcopygus (Hochhuth, 1849) – Pa
O. cingulatus (Gravenhorst, 1802) – Ne
O. dieckmanni Smetana, 1958 – Pa
O. gracilis (Sharp, 1874) – Pa
O. hairaerensis Li and Chen, 1993 – Pa
O. haroldi (Eppelsheim, 1884) – Pa
O. hayashii Li, 1992 – Pa
O. inauratus (Mannerheim, 1830) – Pa
O. marginalis (Gené, 1836) – Pa
O. murinus (Linné, 1758) – Pa, Ne
O. oculatus (Sharp, 1874) – Pa
O. orientalis Bernhauer, 1906 – Pa
O. paramurinus Li and Chen, 1993 – Pa
O. proximus Kirschenblat, 1936 – Pa
O. simulator Kirschenblat, 1936 – Pa
O. tenuicornis (Kraatz, 1859) – Pa
O. tessellatus (Geoffroy, 1785) – Pa

THORACOSTRONGYLUS BERNHAUER, 1915
(Parontholestes Coiffait, 1982)

T. birmanus (Fauvel, 1895) – Pa, Or
T. costatus (Fauvel, 1895) – Or, Pa
T. formosanus Shibata, 1982 – Pa
T. malaisei Scheerpeltz, 1965 – Or, Pa
T. miyakei Bernhauer, 1943 – Pa
T. nepalicus (Coiffait, 1982) – Pa – (**comb. nov.**) (from *Parontholestes*)
T. velutinus Scheerpeltz, 1965 – Or, Pa

ABEMUS MULSANT AND REY, 1876

A. chloropterus (Panzer, 1796) – Pa
A. hebraeus (Smetana, 1978) – Pa – (**comb. nov.**) (from *Staphylinus*)
A. olivaceus (Cameron, 1928) – Pa – (**comb. nov.**) (from *Staphylinus*)
A. martensi (Coiffait, 1982) (**comb. nov., syn. nov.**) (from *Thoracostrongylus*)

PLATYDRACUS THOMSON, 1858
Subgenus *Platydracus* Thomson, 1858
(Neotasgius J. Müller, 1925)

P. aeneoniger (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. amamiensis Ito, 1982 – Pa
P. asemus (Kraatz, 1859) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. aeneicollis (Bernhauer, 1911) (**comb. nov.**) (from *Staphylinus*)
P. aureofasciatus (Motschulsky, 1862) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. teter (Bondroit, 1913) (**comb. nov.**) (from *Staphylinus*)
P. aurosericans (Fairmaire, 1891) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. becquarti (Bernhauer, 1938) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. brachycerus (**nom. nov.**) – Pa
P. brevicornis (Weise, 1877) (nec Motschulsky, 1862) (**comb. nov.**) (from *Ocypus*)
P. brevicornis (Motschulsky, 1862) – Pa
P. paganus Sharp, 1874
P. brevipennis (**nom. nov.**) – Pa
P. brachypterus (Kraatz, 1859) (nec Geoffroy, 1785; nec Marsham, 1802; nec Brullé, 1839) (**comb. nov.**) (from *Staphylinus*)
P. caliginosus (Erichson, 1839) – Ne, Nt
P. ejulans (Tottenham, 1939)
P. campestris Coiffait, 1977 – Pa
P. catalonicus Coiffait, 1967 – Pa
P. centralis (Sharp, 1884) – Ne, Nt – (**comb. nov.**) (from *Staphylinus*)
P. modestus (Sharp, 1884) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. fusiformis (Casey, 1915) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. chalcescens (Sharp, 1889) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. chalcocephalus (Fabricius, 1801) – Pa
P. chapmani (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. chinensis (Bernhauer, 1914) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. cinnamopterus (Gravenhorst, 1802) – Ne
P. coeruleipennis Coiffait, 1983 – Pa
P. collaris Coiffait, 1977 – Pa
P. comes (LeConte, 1863) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. consularis (Bernhauer, 1915) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. cupripennis (Melsheimer, 1845) – Ne – (**comb. nov., stat. nov.**) (from *Staphylinus*)
P. violaceus (Gravenhorst, 1802) (nec Olivier, 1795) (**syn. nov.**)
P. fenyesi (Bernhauer, 1917) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. dauricus (Mannerheim, 1830) – Pa
P. demissus (J. Müller, 1925) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. dudgeoni (Cameron, 1932) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. exulans (Erichson, 1839) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. femoratus (Fabricius, 1801) – Ne, Nt – (**comb. nov.**) (from *Staphylinus*)
P. varipes (Sachse, 1852) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. flavopunctatus (Latreille, 1804) – Pa
P. formosae (Bernhauer, 1933) – Pa
P. fossator (Gravenhorst, 1802) – Ne
P. fulvipes (Scopoli, 1763) – Pa
P. fuscolineatus (Bernhauer, 1934) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. goryi (Laporte, 1835) – Pa, Or – (**comb. nov.**) (from *Staphylinus*)
P. auripennis (Kraatz, 1859) (**comb. nov.**) (from *Staphylinus*)
P. hauserianus (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. hypocrita (J. Müller, 1925) – Pa
P. immaculatus (Mannerheim, 1830) (see com-

ment under *P. vulpinus* under *Platydracus* above)
P. imperatorius (Bernhauer, 1916) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. impotens (Eppelsheim, 1889) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. indicus (Kraatz, 1859) – Pa, Or – (**comb. nov.**) (from *Staphylinus*)
P. lineatus (Walker, 1859) (**comb. nov.**) (from *Staphylinus*)
P. inornatus (Sharp, 1874) – Pa
P. kasyi (Scheerpeltz, 1962) – Pa
P. kiulungensis (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. kiushiuensis (Bernhauer, 1939) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. latebricola (Gravenhorst, 1806) – Pa
P. lomii (Cerruti, 1951) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. maculipennis (Kraatz, 1859) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. meridionalis (Rosenhauer, 1847) – Pa
P. montanus Coiffait, 1977 – Pa
P. mortuorum (Bernhauer, 1912) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. muellerianus (Scheerpeltz, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. banghaasi (J. Müller, 1932) (nec *Staphylinus banghaasi* Bernhauer, 1915) (**comb. nov.**) (from *Staphylinus*)
P. mysticus (Erichson, 1840) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. fluviaticus (Casey, 1915) (**comb. nov., syn. nov.**)
P. nepalensis (Scheerpeltz, 1976) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. oculosus (**nom. nov.**) – Pa
P. oculatus (Bernhauer, 1929) (nec Fabricius, 1775; nec O. F. Müller, 1776) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. opaciceps (Scheerpeltz, 1976) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. parvulus (**nom. nov.**) – Pa, Or
P. parvus (Cameron, 1932) (nec Solier, 1849) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. perniger (Scheerpeltz, 1976) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. perreaui Coiffait, 1984 – Pa
P. phoenicurus (Nordmann, 1837) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. macgregori (Cooper, 1933) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. pinorum (Casey, 1915) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. plebejus (Bernhauer, 1915) – Pa
P. praelongus (Mannerheim, 1830) – Ne
P. pratti (Scheerpeltz, 1962) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. pseudopaganus (Bernhauer, 1914) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. pseudopaganus pseudopaganus (Bernhauer, 1914)
P. pseudopaganus pseudopatricius (J. Müller, 1926) (**comb. nov.**) (from *Staphylinus*)
P. reitterianus (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. riojanus Hozman, 1977 – Pa
P. rutilicauda (Horn, 1879) – Ne – (**comb. nov.**) (from *Ocypus*)
P. sachalinensis (Matsumura, 1911) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. semipurpureus (Kraatz, 1859) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. sepulchralis (Erichson, 1839) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. modestus (Fall, 1907) (nec Sharp, 1884) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. neomexicanus (Bernhauer and Schubert, 1914) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. sharpi (Fauvel, 1901) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. sparsus (Cameron, 1932) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. speculifrons (Bernhauer, 1939) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. stercorarius (Olivier, 1795) – Pa
P. stercorarius stercorarius (Olivier, 1795)
P. stercorarius fuscofemoratus (J. Müller, 1923)
P. subaeneipennis (Scheerpeltz, 1976) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. subaeneus (Roth, 1851) – Pa
P. subauronotatus Coiffait, 1977 – Pa
P. submarmorellus (Schubert, 1908) – Pa
P. subviridis (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. sumakowi (Bernhauer, 1911) – Pa
P. tarsalis (Mannerheim, 1843) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. submetallicus (LeConte, 1861) (**comb. nov.**) (from *Staphylinus*)
P. lucanus (Horn, 1894) (**comb. nov., syn. nov.**) (from *Staphylinus*)

P. curticollis (Bernhauer, 1917) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. temporalis (Casey, 1915) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. tomentosus (Gravenhorst, 1802) – Ne
P. cubae (Jacquelin du Val, 1857) (**comb. nov., syn. nov.**) (from *Ocypus*)
P. ussuriensis (Solsky, 1871) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. vicarius (Sharp, 1889) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. viduatus (Fabricius, 1801) – Ne
P. maculosus (Gravenhorst, 1802)
P. viridanus (Horn, 1879) – Ne – (**comb. nov.**) (from *Staphylinus*)
P. triplicans (Casey, 1924) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. vulpinus (Nordmann, 1837) – Ne
P. wittmeri Coiffait, 1977 – Pa
P. yolensis (Cerruti, 1951) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. yunnanensis (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
P. yunnanicus (**nom. nov.**) – Pa
P. yunnanensis (Bernhauer, 1943) (nec Bernhauer, 1933) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. zonatus (Gravenhorst, 1802) – Ne
P. badius (Mannerheim, 1830) (**syn. nov.**)
P. quadraticeps (Casey, 1924) (**comb. nov., syn. nov.**) (from *Staphylinus*)
P. caseyi (Scheerpeltz, 1933) (**comb. nov., syn. nov.**) (from *Staphylinus*)

Subgenus *Chaetodracus* J. Müller, 1926

P. patricius (Bernhauer, 1915) – Pa

STAPHYLINUS LINNÉ, 1758 (**stat. nov.**)

S. caesareus Cederhjelm, 1798 – Pa
S. caesareus caesareus Cederhjelm, 1798
S. caesareus corporaali Sainte Claire Deville, 1927
S. daimio Sharp, 1889 – Pa
S. dimidiaticornis Gemminger, 1851 – Pa
S. erythropterus Linné, 1758 – Pa
S. erythropterus erythropterus Linné, 1758
S. erythropterus springeri J. Müller, 1923
S. medioximus Fairmaire, 1852 – Pa
S. ornaticauda (LeConte, 1863) – Ne
S. rubricornis (Adám, 1987) – Pa
S. ruficornis Bernhauer, 1913 (nec Gravenhorst, 1802; nec Latreille, 1804; nec O. Costa, 1839)

DINOTHENARUS THOMSON, 1858 (**stat. nov.**)

Subgenus *Dinothenarus* Thomson, 1858
(Protabemus Scheerpeltz, 1966)

D. capitatus (Bland, 1864) – Ne
D. choui Smetana, 1992 – Pa
D. flavocephalus (Goeze, 1777) – Pa
D. flavocephalus flavocephalus (Goeze, 1777)
D. flavocephalus adonis (Coiffait, 1956)
D. pubescens (DeGeer, 1774) – Pa
D. ruficeps (Cameron, 1932) – Pa
D. sagaris Smetana, 1992 – Pa
D. xanthocephalus (Kraatz, 1859) – Pa

Subgenus *Parabemus* Reitter, 1909 (**stat. nov.**)
(Parocypus Bernhauer, 1915)
(Hypabemus Scheerpeltz, 1966)

D. arrosus (Eppelsheim, 1890) – Pa – (**comb. nov.**) (from *Parabemus*)
D. badipes (LeConte, 1863) – Ne – (**comb. nov.**) (from *Staphylinus*)
D. chrysocomus (Mannerheim, 1830) – Pa – (**comb. nov.**) (from *Parabemus*)
D. coiffaiti Bordoni, 1977 – Pa – (**comb. nov.**) (from *Parabemus*)
D. dehradunensis (Bernhauer, 1915) – Pa – (**comb. nov.**) (from *Ocypus*)
D. fossor (Scopoli, 1772) – Pa – (**comb. nov.**) (from *Parabemus*)
D. fossor (Fabricius, 1792) (**comb. nov., syn. nov.**)
D. baderlei (Scheerpeltz, 1966) (**comb. nov.**)
D. ganglbauerianus (Bernhauer, 1939) – Pa – (**comb. nov.**) (from *Ocypus*)
D. insignis (J. Müller, 1926) – Pa – (**comb. nov.**) (from *Staphylinus*)
D. fokiensis (Bernhauer, 1933) – Pa – (**comb. nov., syn. nov.**) (from *Staphylinus*)
D. kiautschauensis (Bernhauer, 1916) – Pa – (**comb. nov.**) (from *Staphylinus*)
D. luteipes (LeConte, 1861) – Ne – (**comb. nov.**) (from *Staphylinus*)
D. nigrellus (Horn, 1879) – Ne – (**comb. nov.**) (from *Ocypus*)
D. pleuralis (LeConte, 1861) – Ne – (**comb. nov.**) (from *Staphylinus*)
D. prainae (Eppelsheim, 1895) – Pa – (**comb. nov.**) (from *Staphylinus*)

D. saphyrinus (LeConte, 1861) – Ne – (**comb. nov.**) (from *Ocypus*)
D. sibiricus (Gebler, 1830) – Pa – (**comb. nov.**) (from *Parabemus*)
D. szechuanensis (Bernhauer, 1935) – Pa – (**comb. nov.**) (from *Staphylinus*)

MIOBDELUS SHARP, 1889

M. brevipennis Sharp, 1889 – Pa

PHYSETOPS MANNERHEIM, 1830

P. ahrendti Wendeler, 1921 – Pa
P. giganteus Semenov, 1906 – Pa
P. herculeanus Semenov, 1906 – Pa
P. spilleri Bernhauer, 1923 – Pa
P. tataricus (Pallas, 1773) – Pa

ASCIALINUS BERNHAUER, 1933

A. beckeri Bernhauer, 1933 – Pa

APOSTENOLINUS BERNHAUER, 1934

A. cariniceps (Bernhauer, 1934) – Pa

PROTOGOERIUS COIFFAIT, 1956

P. brullei (**nom. nov.**) – Pa
P. brachypterus (Brullé, 1839) (nec Geoffroy, 1785; nec Marsham, 1802)

OCYPUS LEACH, 1819 (**stat. nov.**)
Subgenus *Ocypus* Leach, 1819
(Goerius Westwood, 1827)
(Xanthocypus J. Müller, 1925)

O. affinis Wollaston, 1864 – Pa
O. alfierii (Bernhauer, 1925) – Pa
O. auroguttatus (Cameron, 1932) – Pa, Or – (**comb. nov.**) (from *Nudabemus*)
O. baronii (Coiffait, 1982) – Pa – (**comb. nov.**) (from *Nudabemus*)
O. caerulescens (Coiffait, 1982) – Pa – (**comb. nov.**) (from *Nudabemus*)
O. cameroni (**nom. nov.**)
O. bimaculatus (Cameron, 1932) (nec Schrank, 1798; nec Gravenhorst, 1802; nec Marsham, 1802) (**comb. nov.**) (from *Staphylinus*)
O. curtipennis Motschulsky, 1849 – Pa
O. integer Abeille, 1900
O. gridellii (J. Müller, 1924)
O. libanoticus (J. Müller, 1950) (as subsp. of *O. gridellii*) (**syn. nov.**)
O. kyproticus Coiffait, 1964 (as subsp. of *O. gridellii*)
O. pseudolens Coiffait, 1964 (as subsp. of *O. gridellii*)
O. cyaneopubens (Reitter, 1913) – Pa
O. festae (J. Müller, 1926) – Pa
O. miwai (Bernhauer, 1943) – Pa
O. olens (O. Müller, 1764) – Pa, Ne
O. olens olens (O. Müller, 1764)
O. olens azoricus (Méquignon, 1942)
O. ophthalmicus (Scopoli, 1763) – Pa
O. ophthalmicus ophthalmicus (Scopoli, 1763)
O. cyanochloris Hochhuth, 1849
O. baicalensis (Eppelsheim, 1887) (as variety of *O. ophthalmicus*)
O. ophthalmicus atrocyaneus (Fairmaire, 1860)
O. ibericus Coiffait, 1964 (as subsp. of *O. ophthalmicus*)
O. pernigrus Coiffait, 1964 (as subsp. of *O. ophthalmicus*) (**syn. nov.**)
O. ophthalmicus hypsibatus (Bernhauer, 1899)
O. ophthalmicus balcanicus (J. Müller, 1923)
O. ophthalmicus balearicus (J. Müller, 1926)
O. ophthalmicus rodopensis Coiffait, 1971
O. ophthalmicus benoiti Drugmand, 1998
O. ophthalmicus brigitteae Drugmand, 1998
O. quadrimaculatus (Cameron, 1932) – Pa, Or – (**comb. nov.**) (from *Nudabemus*)
O. rhaeticus Eppelsheim, 1873 – Pa
O. wasmanni (Bernhauer, 1920) – Pa – (**comb. nov.**) (from *Nudabemus*)
O. weisei Harold, 1877 – Pa – (**comb. nov.**) (from *Agelosus*)

Subgenus *Matidus* Motschulsky, 1860 (**stat. nov.**)

O. albanicus (J. Müller, 1943) – Pa
O. alpestris (Erichson, 1840) – Pa
O. bernhaueri (J. Müller, 1925) – Pa
O. biharicus (J. Müller, 1926) – Pa
O. brenskei (Reitter, 1884) – Pa
O. bisetosus (J. Müller, 1943) (as form of *O. brenskei*) (**syn. nov.**)
O. holosetosus (J. Müller, 1943) (as subsp. of *O. brenskei*) (**syn. nov.**)
O. brevipennis (Heer, 1839) – Pa
O. brevipennis brevipennis (Heer, 1839)
O. brevipennis pseudoalpestris (J. Müller, 1926)

O. brunnipes (Fabricius, 1781) – Pa
O. brunnipes brunnipes (Fabricius, 1781)
O. brunnipes intermedius (J. Müller, 1911)
O. caroli (Jarrige, 1943) – Pa
O. cerceticus Coiffait, 1964 – Pa
O. chevrolatii (Baudi, 1848) – Pa
O. alsaticus Coiffait, 1964 (as subsp. of *O. chevrolatii*) (**syn. nov.**)
O. pseudobrevipennis Coiffait, 1964 (as subsp. of *O. chevrolatii*) (**syn. nov.**)
O. vesubiensis Coiffait, 1964 (as subsp. of *O. chevrolatii*) (**syn. nov.**)
O. zimmermanni Korge, 1965 (as subsp. of *O. chevrolatii*) (**syn. nov.**)
O. coreanus (J. Müller, 1925) – Pa
O. deuvei Coiffait, 1978 – Pa
O. forficularius (Motschulsky, 1860) – Pa
O. korgei Smetana, 1965
O. frater Smetana, 1965 – Pa
O. heinzi Smetana, 1965 – Pa
O. hissaricus Dvořák, 1984 – Pa
O. hochhuthi Eppelsheim, 1878 – Pa
O. italicus (Aragona, 1830) – Pa
O. italicus (Erichson, 1840) (**syn. nov.**)
O. garganicus Fiori, 1894 (**syn. nov.**)
O. silensis Fiori, 1894 (as variety of *O. italicus*) (**syn. nov.**)
O. mirtensis J. Müller, 1943 (as subsp. of *O. italicus*) (**syn. nov.**)
O. khnzoriani Coiffait, 1967 – Pa
O. kuntzeni (J. Müller, 1926) – Pa
O. longimanus Smetana, 1965 – Pa
O. macrocephalus (Gravenhorst, 1802) – Pa
O. manceps Smetana, 1965 – Pa
O. matilei Jarrige, 1971 – Pa
O. iranicus (Smetana, 1971)
O. megalocephalus (Nordmann, 1837) – Pa
O. milleri Quedenfeldt, 1882 – Pa
O. milleri milleri Quedenfeldt, 1882
O. milleri robustus Coiffait, 1964
O. nitens (Schrank, 1781) (**stat. nov.**)
O. similis (Fabricius, 1792) (misidentification, nec Paykull, 1789)
O. nero (Faldermann, 1835) (**syn. nov.**)
O. nitens nitens (Schrank, 1781)
O. nitens semialatus (J. Müller, 1904)
O. nitens grigiensis (Reitter, 1918)
O. nitens ochropus (J. Müller, 1950)
O. nubigena Smetana, 1965 – Pa
O. ormayi (Reitter, 1887) – Pa
O. ottomanus Fauvel, 1900 – Pa
O. pedemontanus (J. Müller, 1924) – Pa
O. pedemontanus pedemontanus (J. Müller, 1924)
O. pedemontanus pyrenaeus (J. Müller, 1924)
O. pedemontanus cantabricus (J. Müller, 1926)
O. ponticus Smetana, 1968 – Pa
O. pullus Hochhuth, 1849 – Pa
O. quadraticeps (Ménétriés, 1832) – Pa
O. reimoseri (Bernhauer, 1906) – Pa
O. simulator Eppelsheim, 1878 – Pa
O. solarii (J. Müller, 1923) – Pa
O. syriacus Baudi, 1848 – Pa
O. syriacus syriacus Baudi, 1848
O. syriacus primigenius (J. Müller, 1923)
O. tenebricosus (Gravenhorst, 1846) – Pa
O. depolii (J. Müller, 1924)
O. torvus Smetana, 1965 – Pa
O. trapezensis Coiffait, 1964 – Pa
O. turcicus (Bernhauer, 1923) – Pa

Subgenus *Pseudocypus* Mulsant and Rey, 1876 (**stat. nov.**)
(Protocypus J. Müller, 1923)
(Atlantogoerius Coiffait, 1956)
(Fortunocypus Coiffait, 1964)
(Nudabemus Coiffait, 1982)

O. addendus (Lindberg, 1953) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. aeneocephalus (DeGeer, 1774) – Pa, Ne – (**comb. nov.**) (from *Pseudocypus*)
O. aereus Cameron, 1928 – Pa
O. aethiops (Waltl, 1835) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. luigionii (J. Müller, 1926) (as subsp. of *O. aethiops*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. almensis Coiffait, 1967 – Pa
O. angustulus Eppelsheim, 1888 – Pa
O. anophthalmicus (Hernandéz and Aguiar, 1988) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. apterus (Scheerpeltz, 1976) – Pa – (**comb. nov.**) (from *Staphylinus*)
O. canariensis Gemminger and Harold, 1868 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. densissimus (Bernhauer, 1933) – Pa – (**comb. nov.**) (from *Staphylinus*)
O. dorsalis Sharp, 1889 – Pa
O. eppelsheimi Reitter, 1887 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. excisus (J. Müller, 1950) – Pa – (**comb. nov.**) (from *Pseudocypus*)

O. libanicus Coiffait, 1956 (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. fortunatarum Wollaston, 1871 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. fujiensis Naomi, 1992 – Pa
O. fulvipennis Erichson, 1840 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. fulvotomentosus Eppelsheim, 1889 – Pa
O. hauseri (Bernhauer, 1933) (**comb. nov., syn. nov.**) (from *Staphylinus*)
O. fuscatoides (Coiffait, 1964) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. fuscatus (Gravenhorst, 1802) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. abbreviatus (Motschulsky, 1858) (**comb. nov.**) (from *Pseudocypus*)
O. fuscoaeneus Solsky, 1871 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. graeseri Eppelsheim, 1887 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. graeseri graeseri Eppelsheim, 1887
O. graeseri brunneopubens (J. Müller, 1926) (**comb. nov.**) (from *Pseudocypus*)
O. hagai Naomi, 1992 – Pa
O. hakusanus Naomi, 1992 – Pa
O. helleni (J. Müller, 1926) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. almorensis (Cameron, 1932) – Pa – (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. himalayicus (Cameron, 1935) – Pa – (**comb. nov., syn. nov.**) (from *Staphylinus*)
O. hidanus Watanabe, 1987 – Pa
O. himalaycus (Coiffait, 1982) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. impennis (Fauvel, 1882) – Pa – (**comb. nov.**) (from *Staphylinus*)
O. inexspectatus Eppelsheim, 1887 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. iyonus Naomi, 1992 – Pa
O. izayoi Naomi, 1992 – Pa
O. jeannei Coiffait, 1980 – Pa
O. kendappa Naomi, 1992 – Pa
O. kiimontanus Naomi, 1992 – Pa
O. kisonus Naomi, 1992 – Pa
O. lewisius Sharp, 1874 – Pa
O. kobensis Cameron, 1930 (**syn. nov.**)
O. mateui (Coiffait, 1954) – Pa – (**comb. nov., stat. nov.**) (from *Pseudocypus*)
O. auricomus (Lindberg, 1953) (nec Brullé, 1842; nec Cameron, 1929) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. montanus (Cameron, 1942) – Pa – (**comb. nov.**) (from *Staphylinus*)
O. mus (Brullé, 1832) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. transadriaticus (J. Müller, 1926) (as subsp. of *O. mus*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. tauricus (J. Müller, 1932) (as subsp. of *O. mus*) (**comb. nov.**)
O. nemotoi Naomi, 1992 – Pa
O. nepalicus (Coiffait, 1981) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. nigroaeneus Sharp, 1889 – Pa
O. rambouseki (J. Müller, 1925)
O. obscuroaeneus Fairmaire, 1852 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. obscuroaeneus obscuroaeneus Fairmaire, 1852
O. algiricus (J. Müller, 1932) (as subsp. of *O. obscuroaeneus*) (**comb. nov.**) (from *Pseudocypus*)
O. atlasicus (Coiffait, 1974) (as subsp. of *O. obscuroaeneus*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. horsti (Coiffait, 1974) (as subsp. of *O. obscuroaeneus*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. obscuroaeneus schatzmayri (J. Müller, 1923) (**comb. nov.**) (from *Pseudocypus*)
O. ohtsukaorum Naomi, 1992 – Pa
O. orientis (**nom. nov.**) – Pa
O. orientalis (Bernhauer and Schubert, 1914) (nec Motschulsky, 1858) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. picipennis (Fabricius, 1792) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. picipennis picipennis (Fabricius, 1792)
O. abbruzzensis (J. Müller, 1926) (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. aprutianus (J. Müller, 1926) (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. herzegovinensis (J. Müller, 1932) (as subsp. of *O. picipennis*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. picipennis graecus (Scheerpeltz, 1958) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. anatolicus (Coiffait, 1964) (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. andorranus (Coiffait, 1964) (as subsp.

of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. pindensis (Coiffait, 1964) (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. bulgaricus (Coiffait, 1970) (as subsp. of *O. picipennis*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. rodopensis (Coiffait, 1971) (as subsp. of *O. picipennis*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. ponticus (Coiffait, 1978) (as subsp. of *O. picipennis*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. picipennis altaiensis (J. Müller, 1926) (**comb. nov.**) (from *Pseudocypus*)
O. picipennis barbarus (J. Müller, 1926) (**comb. nov.**) (from *Pseudocypus*)
O. marocanus (Coiffait, 1964) (as subsp. of *O. picipennis*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. picipennis caucasicus (J. Müller, 1926) (**comb. nov.**) (from *Pseudocypus*)
O. picipennis fallaciosus (J. Müller, 1926) (**comb. nov.**) (from *Pseudocypus*)
O. maritimus Coiffait, 1956 (as subsp. of *O. picipennis*) (**comb. nov.**)
O. picipennis nevadensis (J. Müller, 1926) (**comb. nov.**) (from *Pseudocypus*)
O. asturicus Coiffait, 1956 (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. cerdanicus Coiffait, 1956 (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. gallicus Coiffait, 1956 (as subsp. of *O. picipennis*) (**comb. nov.**) (from *Pseudocypus*)
O. teruelensis (Coiffait, 1976) (as subsp. of *O. picipennis*) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. plagiicollis (Fairmaire, 1891) – Pa – (**comb. nov.**) (from *Staphylinus*)
O. sabi Naomi, 1992 – Pa
O. scutiger Sharp, 1889 – Pa
O. semenowi Reitter, 1887 – Pa
O. septentrionalis Watanabe, 1984 – Pa
O. sericeicollis (Ménétriés, 1832) – Pa – (**comb. nov., stat. nov.**) (from *Pseudocypus*)
O. cupreus (Rossi, 1790) (nec Fourcroy, 1785) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. angustatus Stephens, 1832 (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. confinis Stephens, 1932 (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. rossii (Jarrige, 1954) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. fulvicupreus (Coiffait, 1956) (**comb. nov., syn. nov.**) (from *Pseudocypus*)
O. sericeomicans (Bernhauer, 1931) – Pa – (**comb. nov.**) (from *Staphylinus*)
O. serotinus (Adám, 1992) – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. smetanai Naomi, 1992 – Pa
O. subaenescens Wollaston, 1864 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. svozili Dvořák, 1984 – Pa
O. sylvaticus Wollaston, 1865 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. umbricola Wollaston, 1864 – Pa – (**comb. nov.**) (from *Pseudocypus*)
O. yamato Naomi, 1992 – Pa
O. yoroi Naomi, 1992 – Pa
O. yuinus Naomi, 1992 – Pa

Subgenus *Aulacocypus* J. Müller, 1925

O. gloriosus Sharp, 1874 – Pa
O. kansuensis (Bernhauer, 1933) (**comb. nov.**) (from *Staphylinus*) (see comment under *Ocypus* above)
O. parvulus Sharp, 1874 – Pa
O. subtilis Tikhomirova, 1973 – Pa

AGELOSUS SHARP, 1889
(Apecholinus Bernhauer, 1933)

A. carinatus (Sharp, 1874) – Pa
A. chinensis Li, 1992 – Pa
A. fraternus (Fairmaire, 1891) – Pa
A. kaiseri (Bernhauer, 1933) – Pa
A. ohkurai Hayashi, 1978 – Pa
A. unicolor Naomi, 1983 – Pa
A. unicolor unicolor Naomi, 1983
A. unicolor masaoi Hayashi, 1991

WASMANNELLUS BERNHAUER, 1920

W. stevensi (Cameron, 1932) – Pa – (**comb. nov.**) (from *Staphylinus*)
W. tristis Bernhauer, 1920 – Pa

TASGIUS STEPHENS, 1829 (**stat. nov.**)
Subgenus *Tasgius* Stephens, 1829
(Pseudotasgius Seidlitz, 1891)
(Paratasgius Jarrige, 1952)

T. amiculus (J. Müller, 1925) – Pa

T. ater (Gravenhorst, 1802) – Pa, Ne
T. atronitidus (Reitter, 1909) – Pa
T. bicolor (Cameron, 1944) – Pa – (**comb. nov.**) (from *Staphylinus*)
T. deuvei Coiffait, 1984 – Pa
T. pedator (Gravenhorst, 1802) – Pa
T. peyerimhoffi (J. Müller, 1926) – Pa
T. planipennis (Aubé, 1842) – Pa
T. praetorius (Bernhauer, 1915) – Pa – (**comb. nov.**) (from *Ocypus*)
T. sikkimensis (Bernhauer, 1920) – Pa
T. transversiceps (Luze, 1904) – Pa

Subgenus *Rayacheila* Motschulsky, 1845 (**stat. nov.**)
(Anodus Nordmann, 1837; nec Spix, 1829)
(Alapsodus Tottenham, 1939)
(Allocypus Coiffait, 1964)
(Metocypus Coiffait, 1964)
(Paralapsodus Coiffait, 1974)

T. algericus (Coiffait, 1964) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. amoenanus (**nom. nov.**) – Pa
T. amoenus (Reitter, 1909) (nec Olivier, 1795) (**comb. nov., syn. nov.**) (from *Alapsodus*)
T. arrowi (J. Müller, 1932) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. bellicosus (Fairmaire, 1855) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. bucharicus (Bernhauer, 1912) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. bulgaricus (Coiffait, 1971) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. caspius (Bernhauer, 1906) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. depressus (Hochhuth, 1849) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. doriae (J. Müller, 1932) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. eppelsheimianus (Jakobson, 1909) – Pa – (**comb. nov.**) (from *Alapsodus*) (see comment under *Tasgius* above for var. *obscuripes* Bernhauer, 1900)
T. falcifer (Nordmann, 1837) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. falcifer falcifer (Nordmann, 1837)
T. falcifer aliquoi (Bordoni, 1976) (**comb. nov.**)
T. globulifer (Geoffroy, 1785) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. gracilicornis (Hochhuth, 1849) – Pa – (**comb. nov.**) (from *Ocypus*)
T. ensifer (J. Müller, 1932) (**comb. nov.**) (from *Alapsodus*)
T. herculeanus (Coiffait, 1964) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. inderiensis (Motschulsky, 1845) – Pa
T. limbifrons (Hochhuth, 1849) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. lusitanicus (J. Müller, 1943) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. maderae (Jarrige, 1943) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. melanarius (Heer, 1839) – Pa, Ne – (**comb. nov.**) (from *Alapsodus*)
T. melanarius melanarius (Heer, 1839)
T. melanarius sahlbergi (J. Müller, 1926) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. messor (Nordmann, 1837) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. minax (Mulsant and Rey, 1861) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. morsitans (Rossi, 1790) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. compressus (Marsham, 1802) (**comb. nov.**) (from *Alapsodus*)
T. fulvipes (Motschulsky, 1858) (**comb. nov.**) (from *Alapsodus*)
T. myops (J. Müller, 1925) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. nigrinus (Lucas, 1849) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. olympicus (Baudi, 1857) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. pendjabensis (Bernhauer, 1915) – Pa – (**comb. nov.**) (from *Staphylinus*)
T. pliginskii (Bernhauer, 1915) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. rubripennis (Reiche and Saulcy, 1856) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. solskyi (Fauvel, 1875) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. solskyi solskyi (Fauvel, 1875)
T. solskyi bosphoranus (J. Müller, 1926) (**comb. nov.**) (from *Alapsodus*)
T. tricinctus (Aragona, 1830) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. tricolor (Coiffait, 1974) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. walkeri (Fauvel, 1898) – Pa – (**comb. nov.**) (from *Alapsodus*)
T. winkleri (Bernhauer, 1906) – Pa, Ne – (**comb. nov.**) (from *Alapsodus*)

The following Palearctic species of *Staphylinus*

sensu lato, unknown to us at present, cannot be placed with certainty in the new concepts of genera and/or subgenera. They are listed alphabetically (by species) in the original combination:

Ocypus (*Goerius*) *aenescens* Eppelsheim, 1889
Ocypus altissimus Coiffait, 1977
Ocypus ambiguus Coiffait, 1964
Ocypus bhutanicus Coiffait, 1977
Ocypus bureschi Coiffait, 1971
Staphylinus (*Goerius*) *caeruleoides* Scheerpeltz, 1976
Staphylinus (*Goerius*) *coeruleus* Cameron, 1932
Ocypus cyclopus Peyron, 1858
Staphylinus (*Goerius*) *duplicatus* J. Müller, 1943
Staphylinus griseipennis Fairmaire, 1889
Ocypus (*Neotasgius*) *harbinensis* Li and Chen, 1993
Ocypus (*Ocypus*) *japonicus* Sawada, 1965
Parocypus krejcii Coiffait, 1984
Ocypus (*Neotasgius*) *liaoningensis* Li and Chen, 1993
Staphylinus (*Abemus*) *marginatus* Cameron, 1944
Ocypus murgulensis Coiffait, 1978
Ocypus nudicollis Coiffait, 1977
Ocypus opacus Roth, 1851
Staphylinus (*Goerius*) *pecoudi* Jarrige, 1954
Ocypus? *queinneci* Coiffait, 1984
Ocypus sikkimensis Coiffait, 1985
Staphylinus (*Ocypus*) *suturalis* Matsumura, 1911
Ocypus testaceipes Fairmaire, 1887

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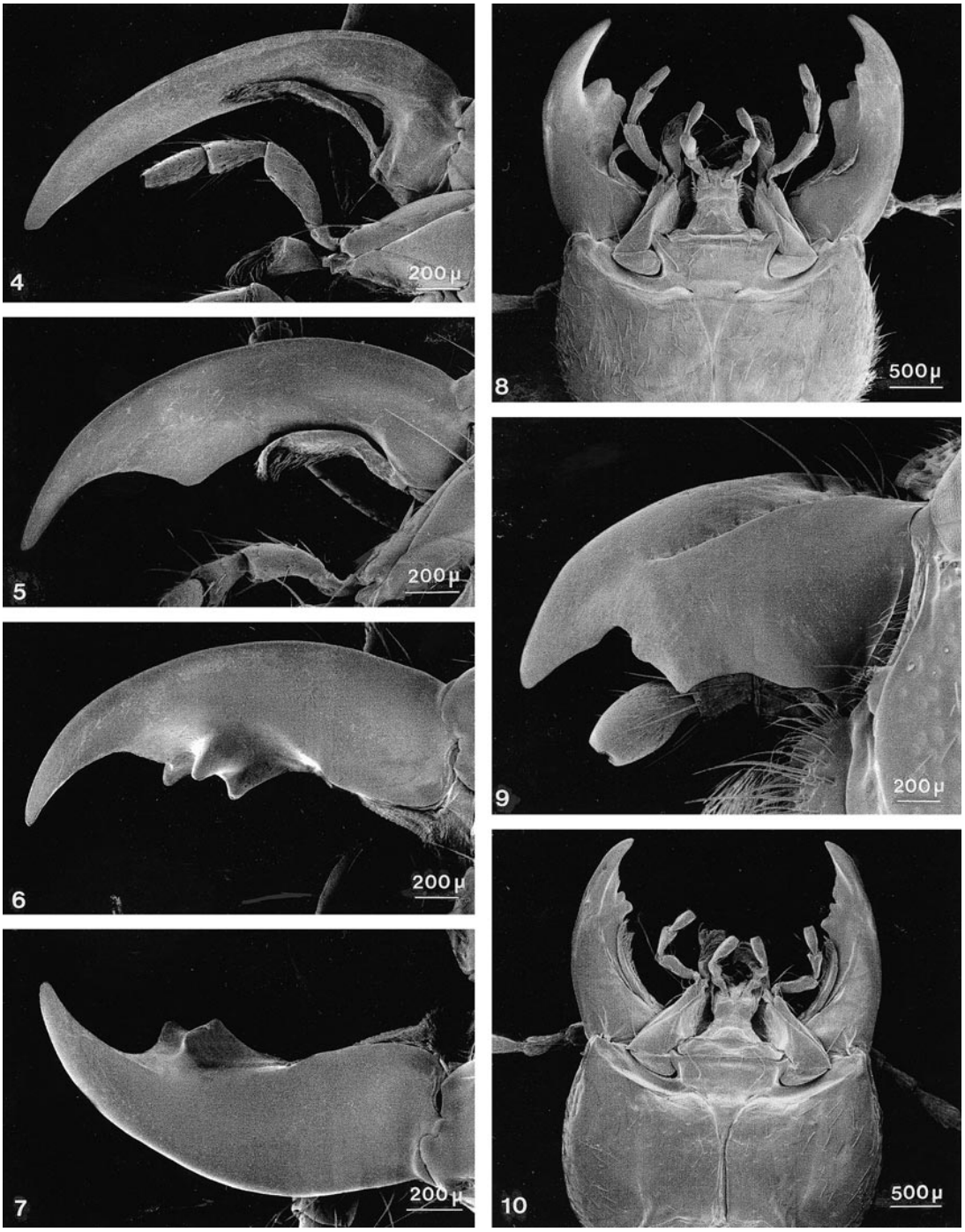
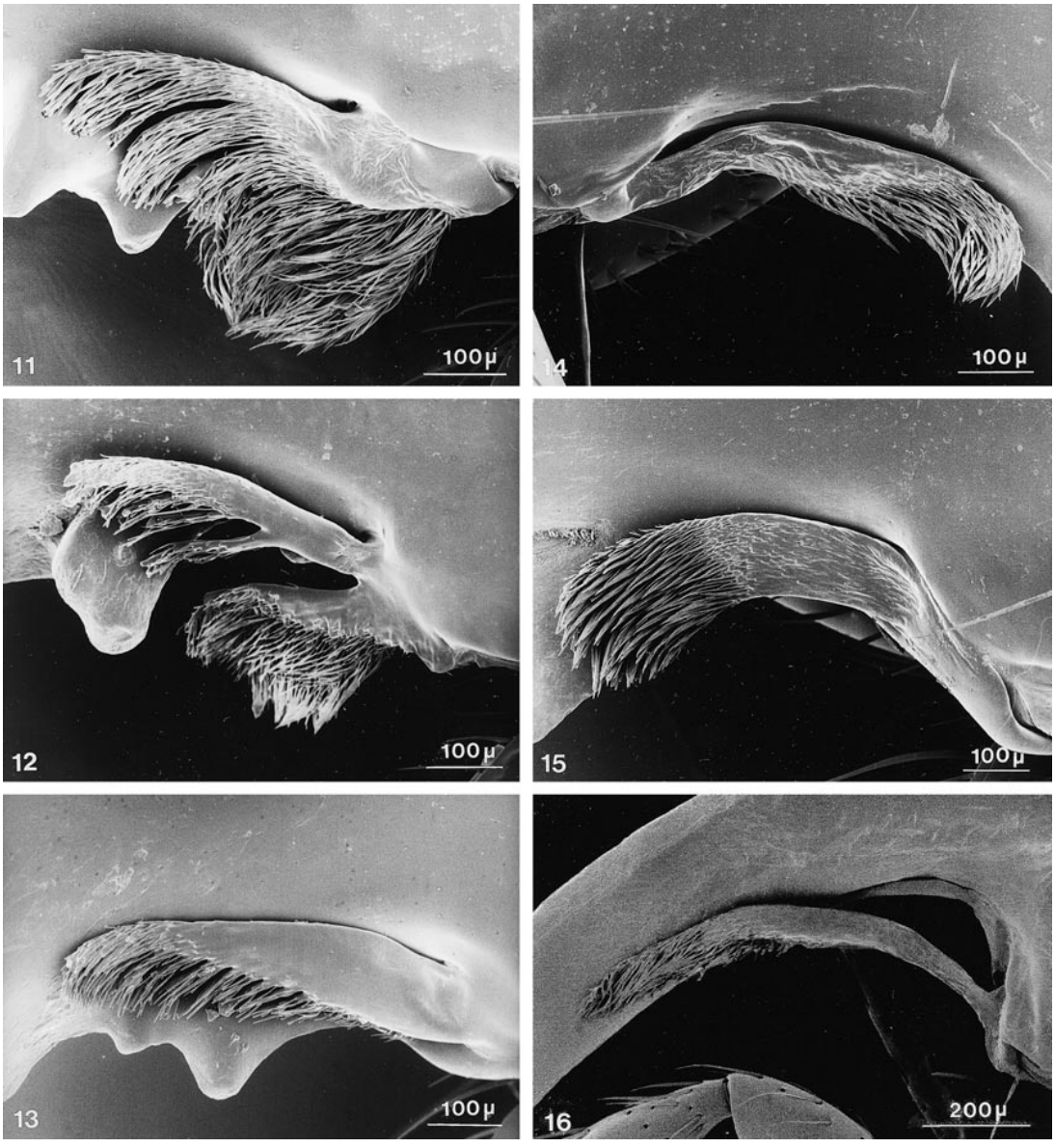
INDEX OF SPECIES AND GENERIC SYNONYMS

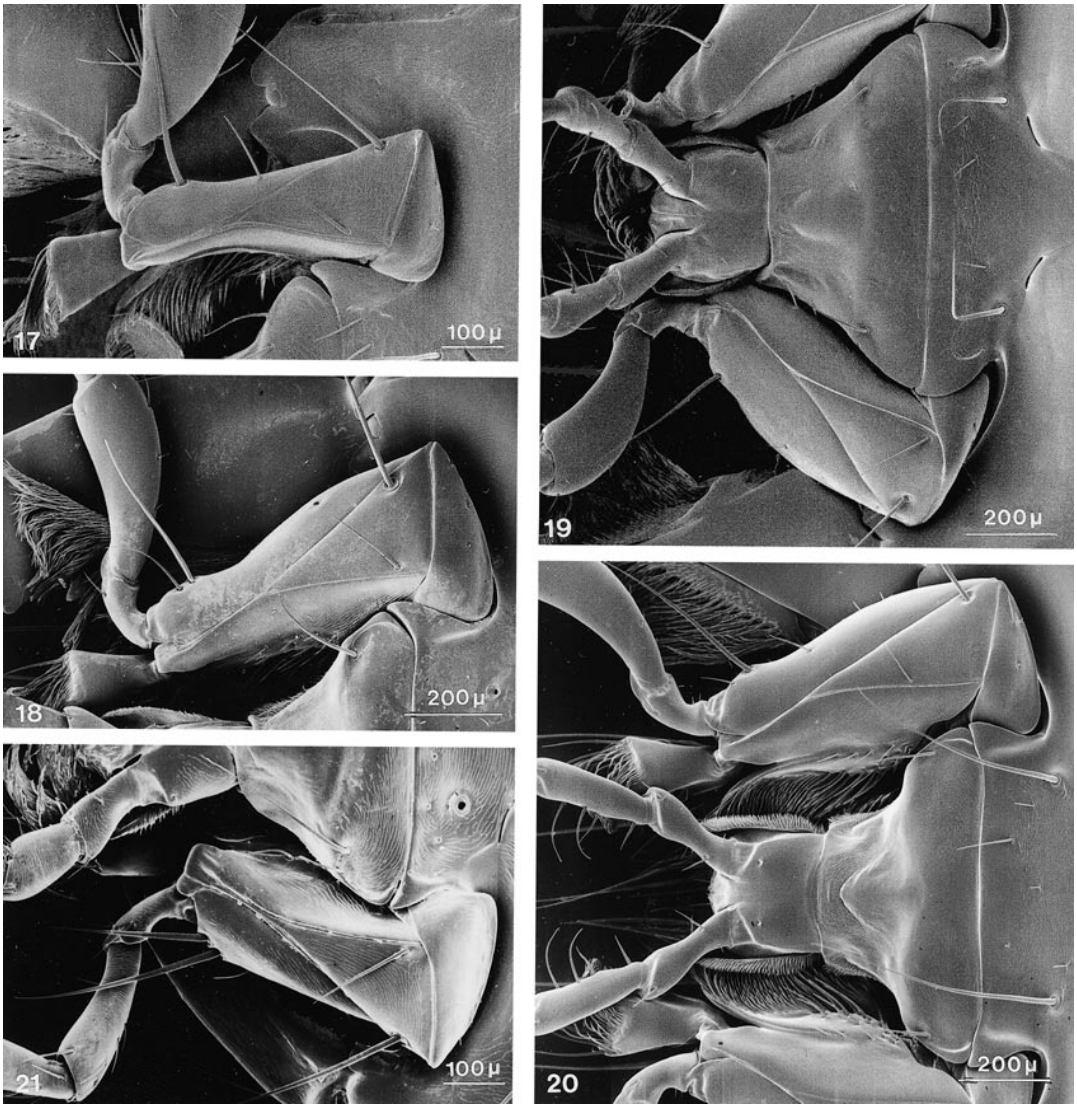
Original combinations, when included, are in parentheses. Current combinations are in brackets. Valid genera and subgenera of Staphylinina studied in detail in this paper are in boldface type. Valid species and generic names are in italic type and synonyms are in roman type.



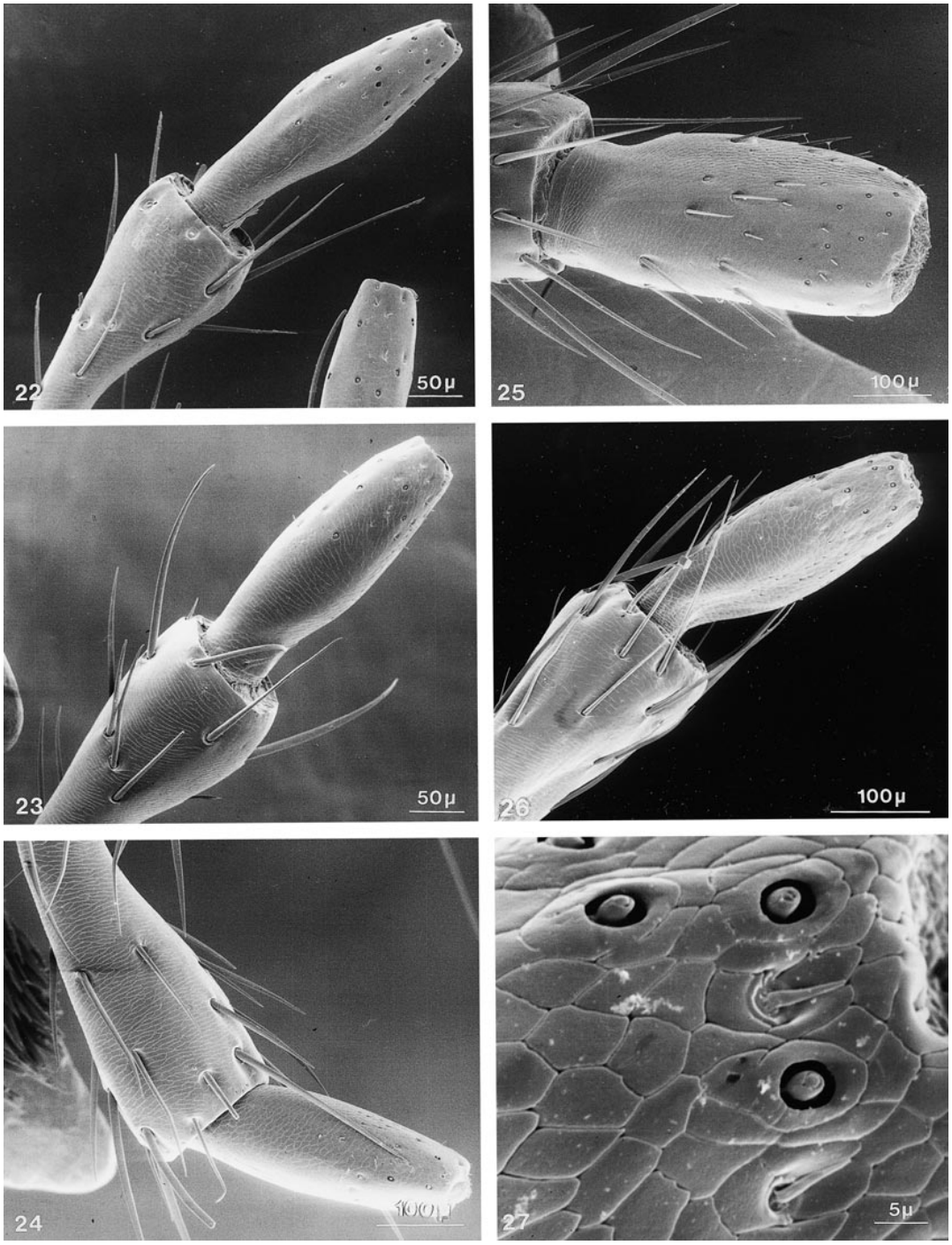
Figs. 4–10. **4**. *Tasgius melanarius*, left mandible, ventral view. **5**. *Tasgius ater*, left mandible, ventral view. **6**, **7**. *Platydracus stercorarius*: left and right mandibles (both in ventral view). **8**. *Staphylinus erythropterus*, both mandibles, ventral view. **9**. *Naddia* sp., right mandible, dorsal view. **10**. *Ocypus ophthalmicus*, both mandibles, ventral view.



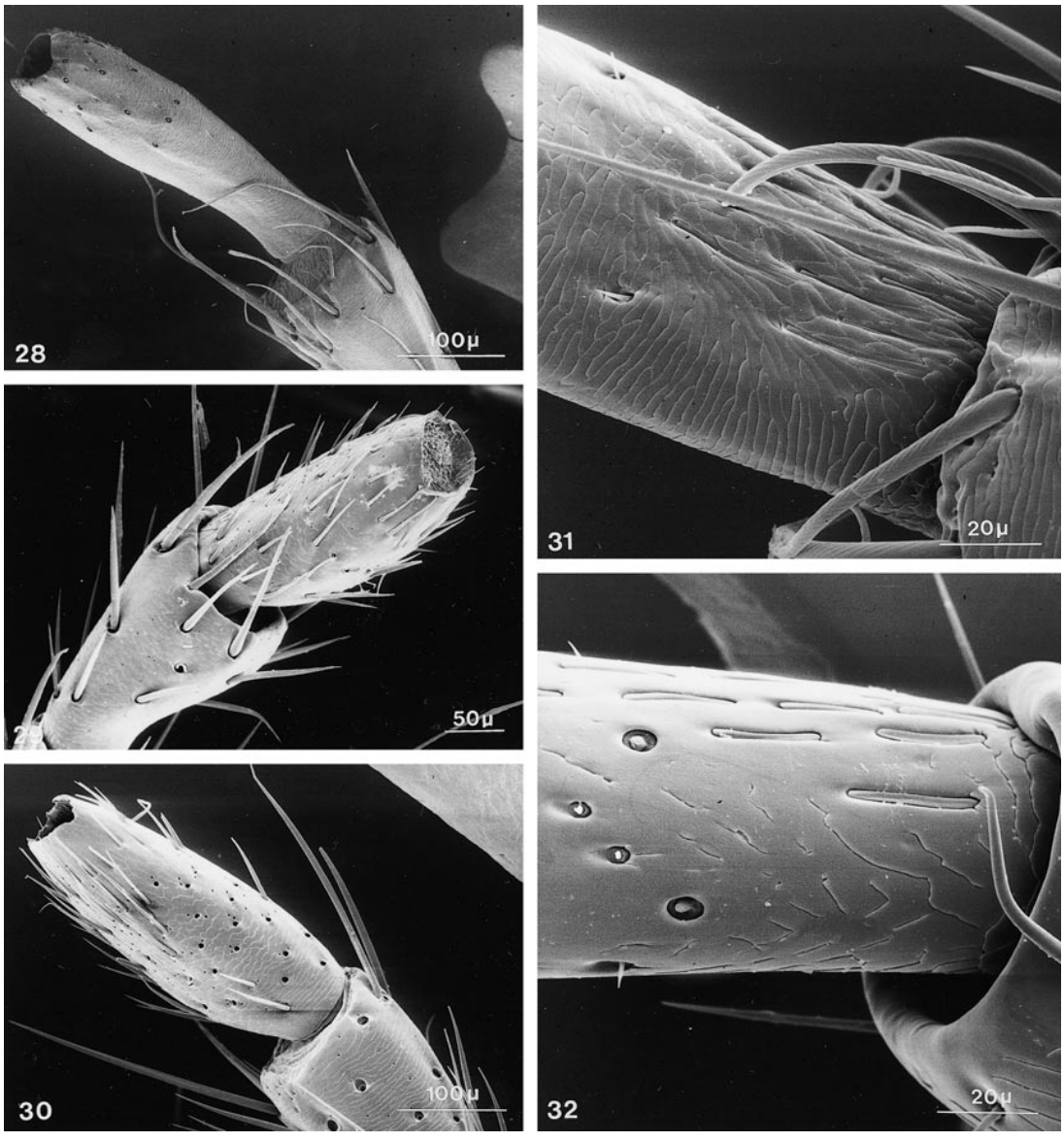
Figs. 11–16. **11**. *Platydracus stercorarius*, right mandibular prostheca, ventral view. **12**. *Abemus chloropterus*, left mandibular prostheca, ventral view. **13**. *Ocypus picipennis*, left mandibular prostheca, ventral view. **14**. *Tasgius ater*, left mandibular prostheca, ventral view. **15**. *Staphylinus dimidiaticornis*, left mandibular prostheca, ventral view. **16**. *Tasgius melanarius*, left mandibular prostheca, ventral view.



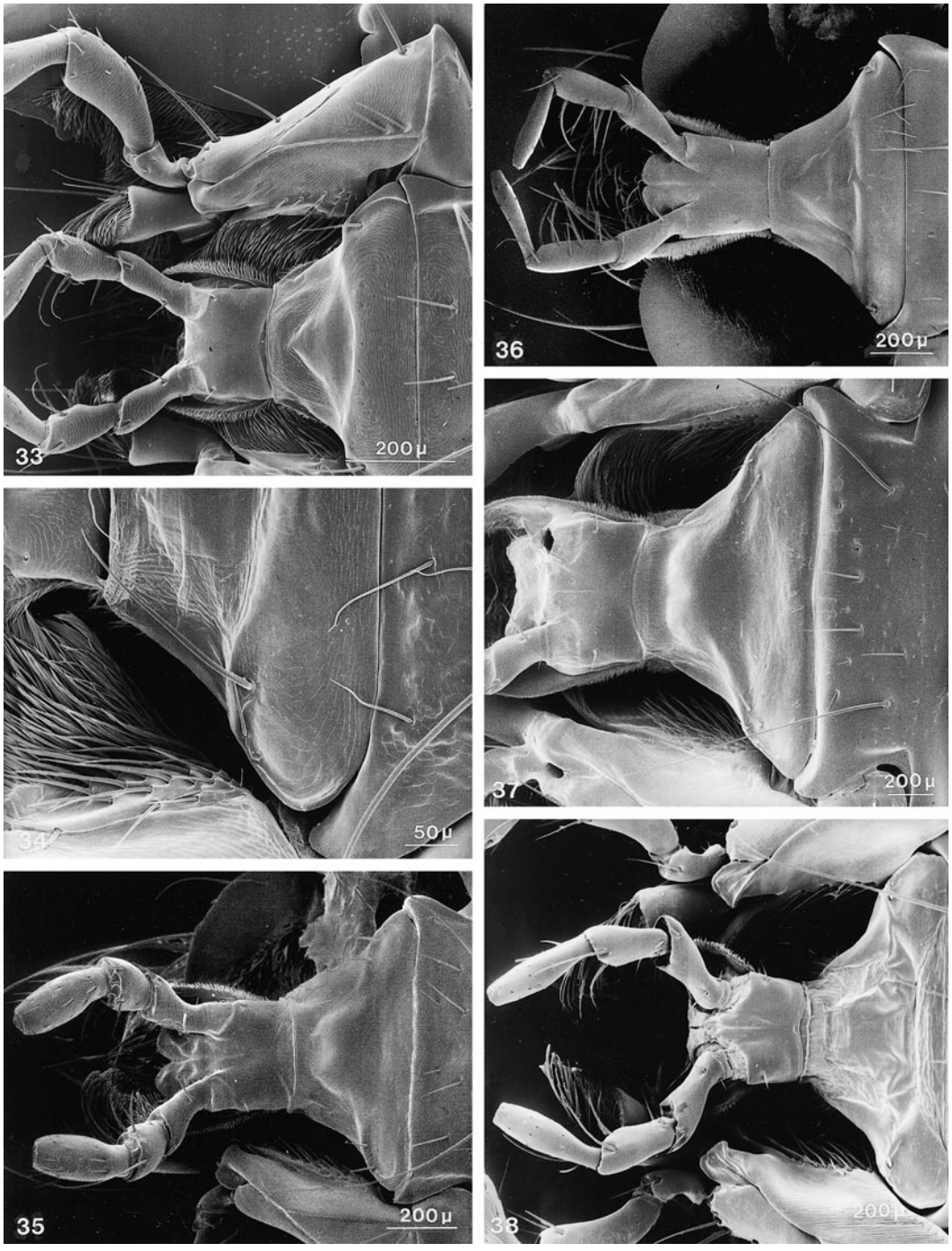
Figs. 17–21. **17**. *Anisolinus elegans*, left maxilla, ventral view. **18**. *Craspedomerus* sp., left maxilla, ventral view. **19**. *Plociopterus comptus*, right maxilla and mentum, ventral view. **20**. *Philonthus caeruleipennis*, labium, mentum, and left maxilla, ventral view. **21**. *Quedius laticollis*, right maxilla, ventral view.



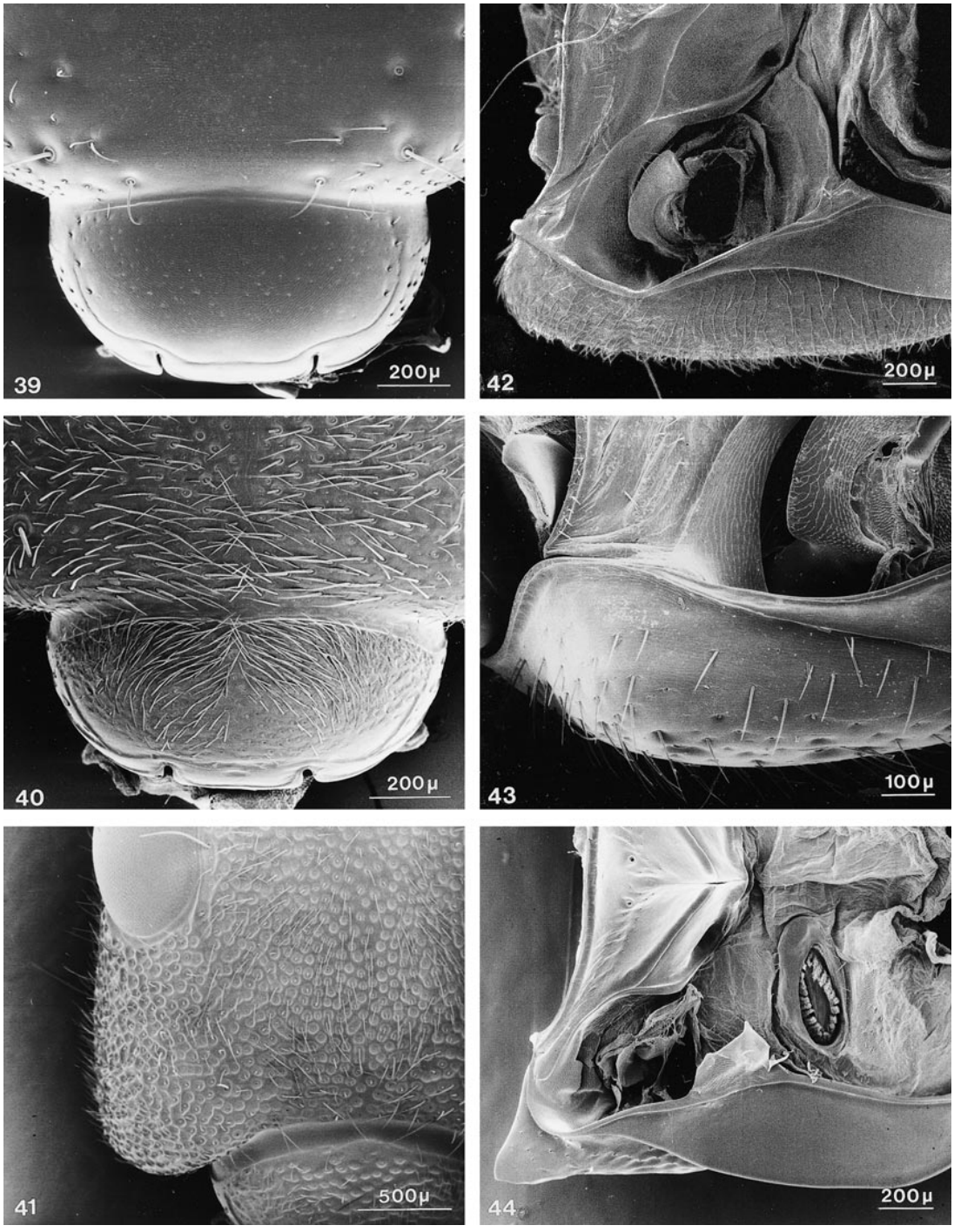
Figs. 22–27. **22**. *Dinothenarus pubescens*, last segment of maxillary palpus. **23**. *Ocypus sylvaticus*, last segment of maxillary palpus. **24**. *Staphylinus dimidiaticornis*, last segment of maxillary palpus. **25**. *Ocypus tenebricosus*, last segment of maxillary palpus. **26**. *Staphylinus erythropterus*, last segment of maxillary palpus. **27**. *Staphylinus erythropterus*, peglike setae in glandular openings on last segment of maxillary palpus.



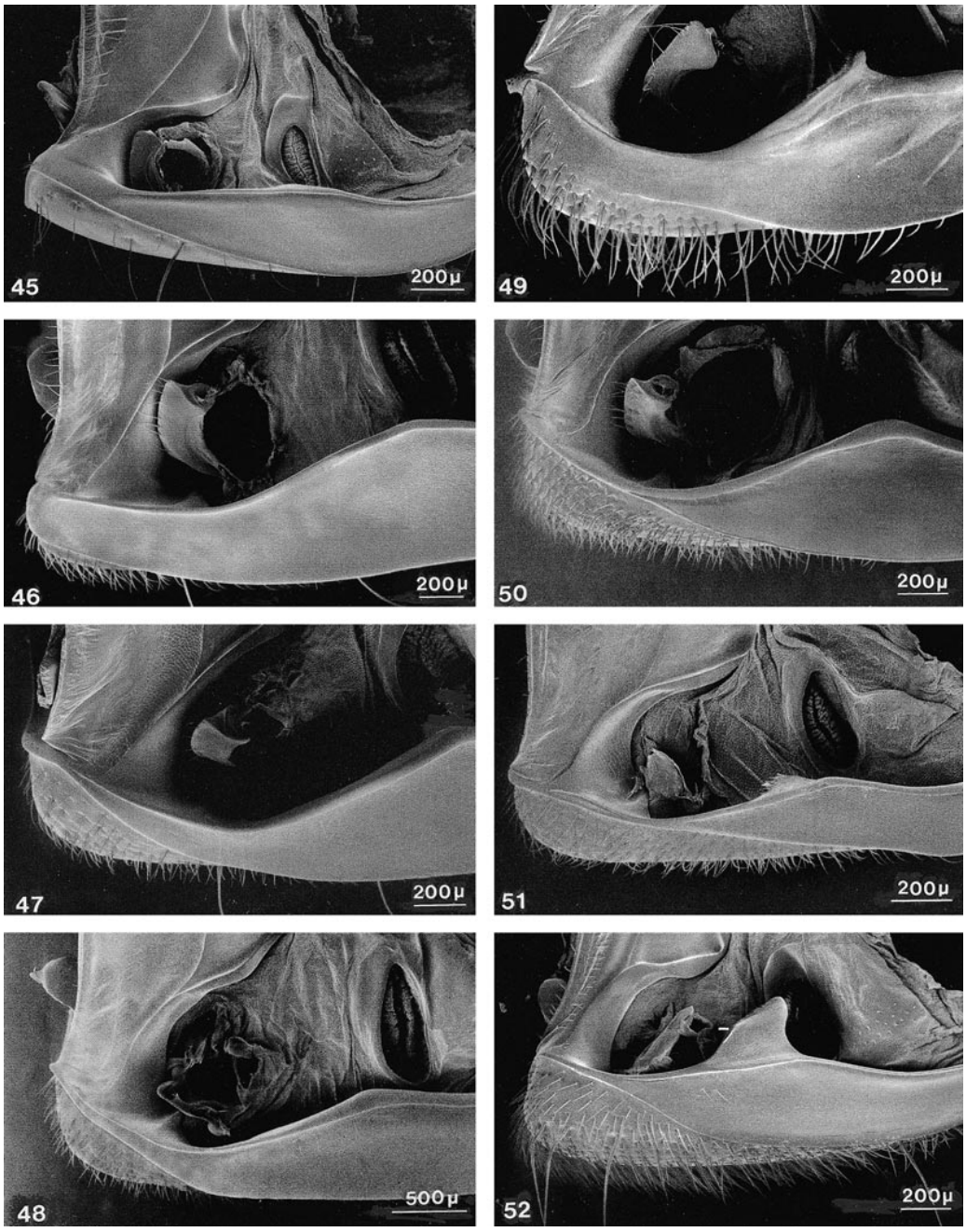
Figs. 28–32. **28**. *Dinothenarus fossor*, last segment of maxillary palpus. **29**. *Tasgius ater*, last segment of maxillary palpus. **30**. *Tasgius melanarius*, last segment of maxillary palpus. **31**. *Ontholestes murinus*, longitudinal furrows at base of last segment of maxillary palpus. **32**. *Philonthus politus*, longitudinal furrows at base of last segment of maxillary palpus.



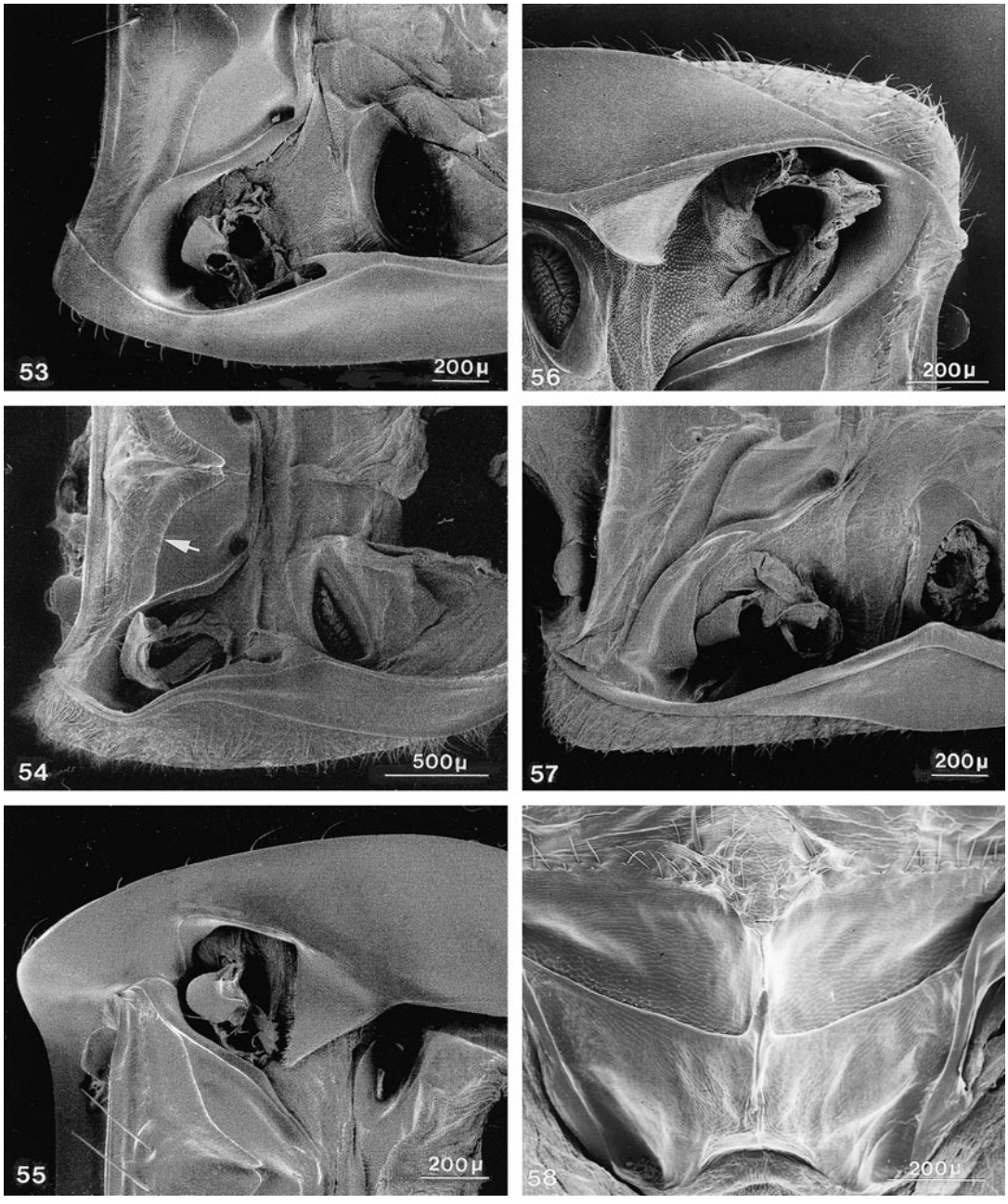
Figs. 33–38. **33**. *Philonthus politus*, labium, mentum, submentum, and left maxilla, ventral view. **34**. *Amichrotus* sp., anterolateral setae on mentum. **35**. *Ocypus picipennis*, labium, mentum, and submentum. **36**. *Ontholestes cingulatus*, labium, mentum, and submentum. **37**. *Ocypus tenebricosus*, labium, mentum, and submentum. **38**. *Dinothenarus pubescens*, labium, labial palpus, and mentum.



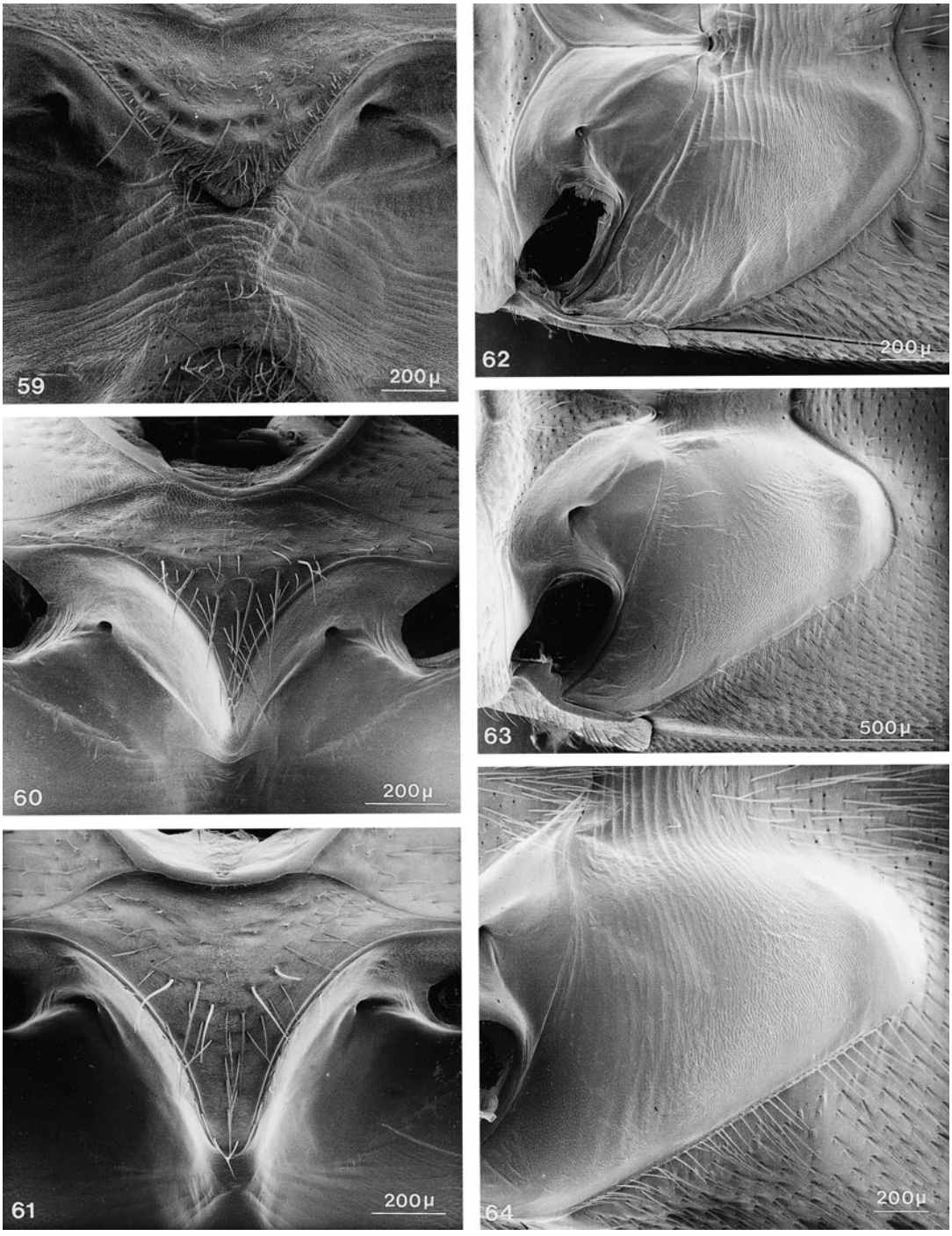
Figs. 39–44. **39**. *Philonthus politus*, dorsal face of neck. **40**. *Abemus chloropterus*, dorsal face of neck. **41**. *Naddia* sp., left posterior corner of head, and part of dorsal face of neck. **42**. *Dinothenarus fossor*, joining of superior and inferior marginal lines of pronotal hypomeron, ventral view. **43**. *Tasgius ater*, joining of superior and inferior marginal lines of pronotal hypomeron, ventral view. **44**. *Ontholestes murinus*, joined marginal lines of pronotal hypomeron, narrowly rounded at anterolateral margin of prosternum, and angulately extended anterior angles of pronotum, ventral view.



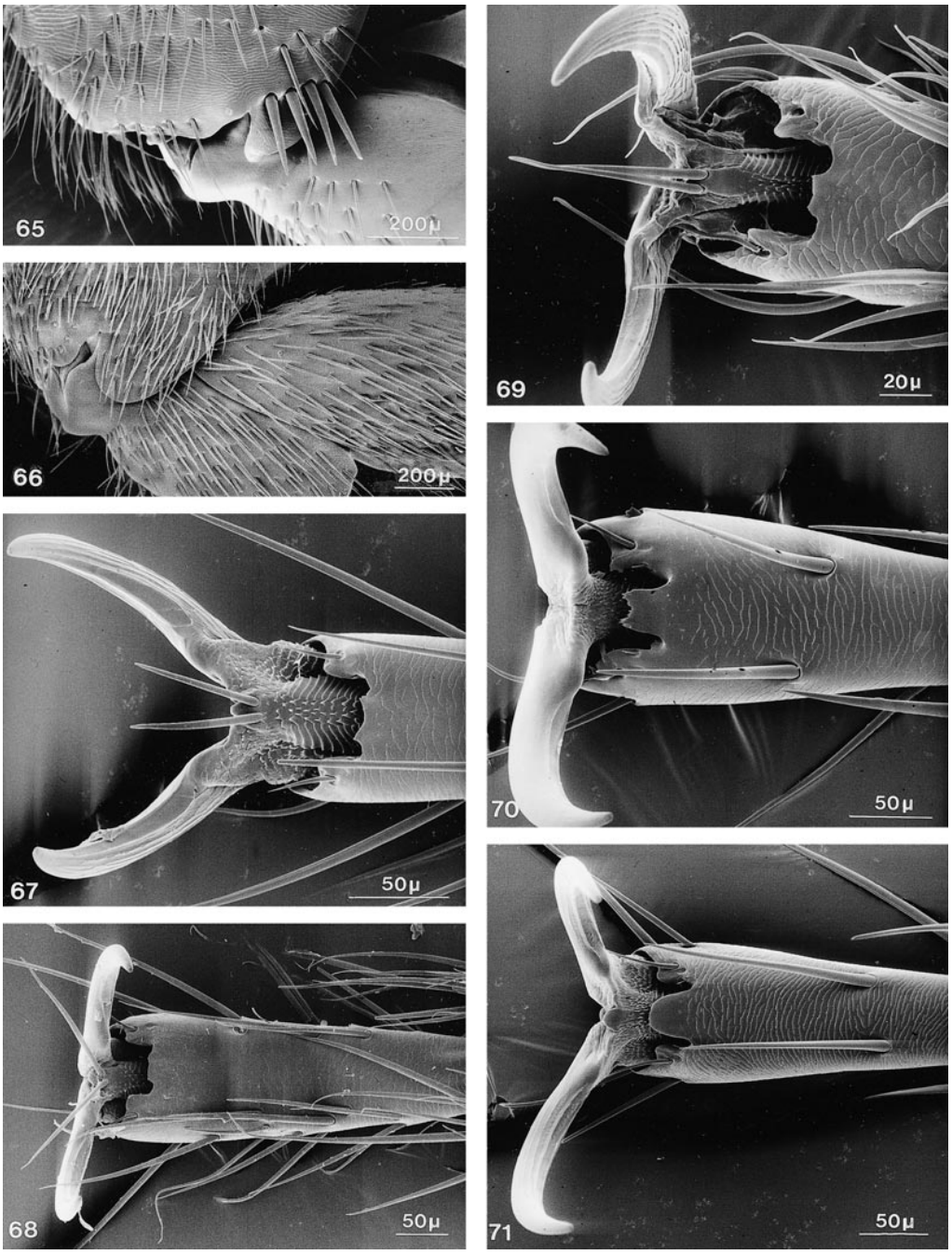
Figs. 45–52. **45**. *Philonthus caeruleipennis*, superior and inferior marginal lines of pronotal hypomeron not joined, ventral view. **46**. *Agelosus carinatus*, superior and inferior marginal lines of pronotal hypomeron distinctly not joined, ventral view. **47**. *Ocypus weisei*, superior and inferior marginal lines of pronotal hypomeron not quite joined, ventral view. **48**. *Ocypus tenebricosus*, superior and inferior marginal lines of pronotal hypomeron not quite joined, ventral view. **49**. *Creophilus maxillosus*, superior marginal line of pronotal hypomeron becoming obsolete near anterior angles, ventral view. **50**. *Staphylinus dimidiaticornis*, joining of superior and inferior marginal lines of pronotal hypomeron, ventral view. **51**. *Miobdelus* sp., joining of superior and inferior marginal lines of pronotal hypomeron, ventral view. **52**. *Platydracus stercorarius*, superior and inferior marginal lines of pronotal hypomeron not quite joined, appearing as a grooved carina anteriorly, ventral view.



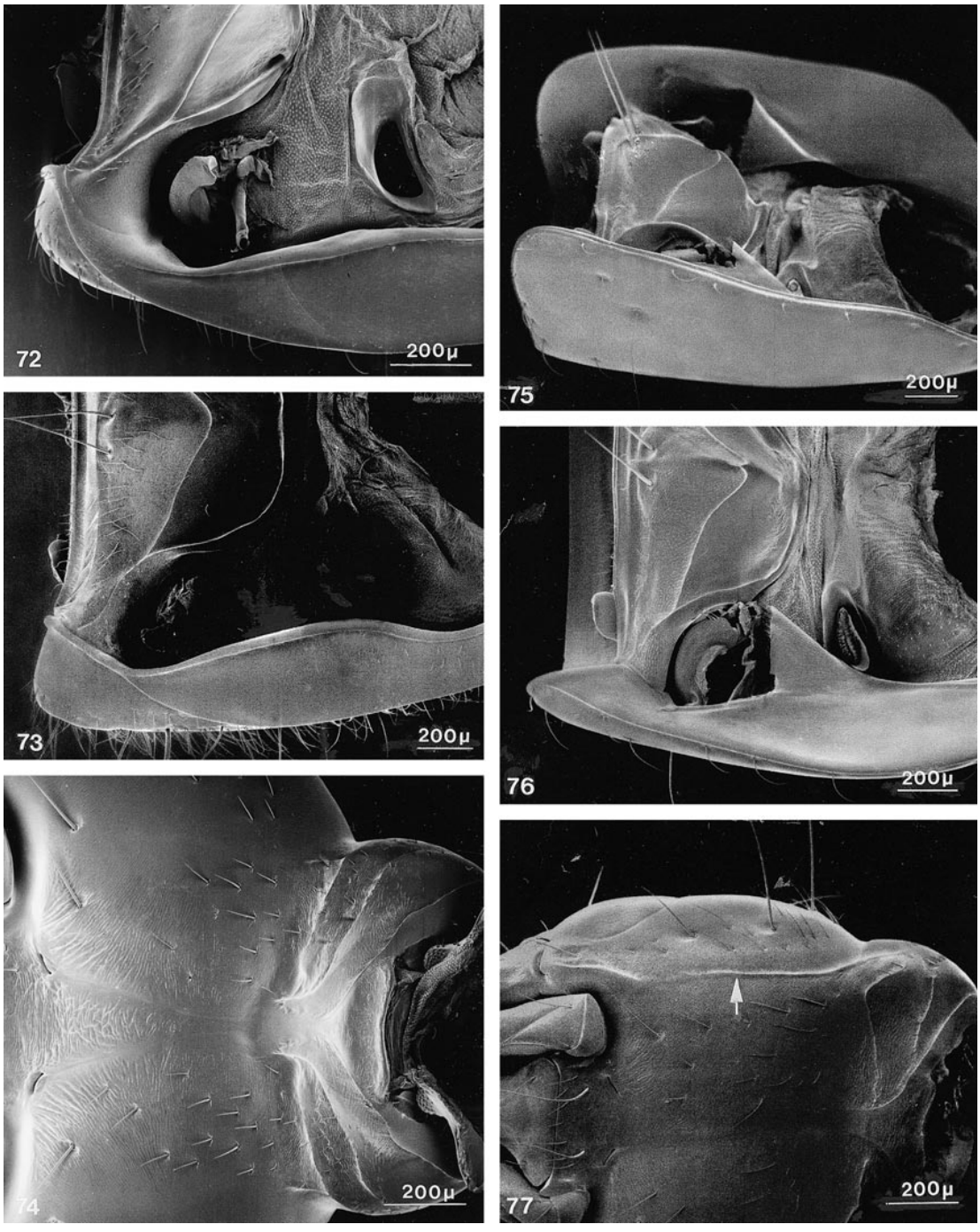
Figs. 53–58. **53**. *Xanthopygus analis*, disc of pronotum virtually invisible in ventral view. **54**. *Dinothenarus pubescens*, joining of superior and inferior marginal lines of pronotal hypomeron and prosternum with strongly arched sternacostal ridge (arrow), ventral view. **55**. *Quedius laticollis*, proepimeron, ventral view. **56**. *Abemus chloropterus*, proepimeron, ventral view. **57**. *Staphylinus erythropterus*, proepimeron absent. **58**. *Ocypus ophthalmicus*, medial margin of sternacostal ridge forming a prominent finlike carina.



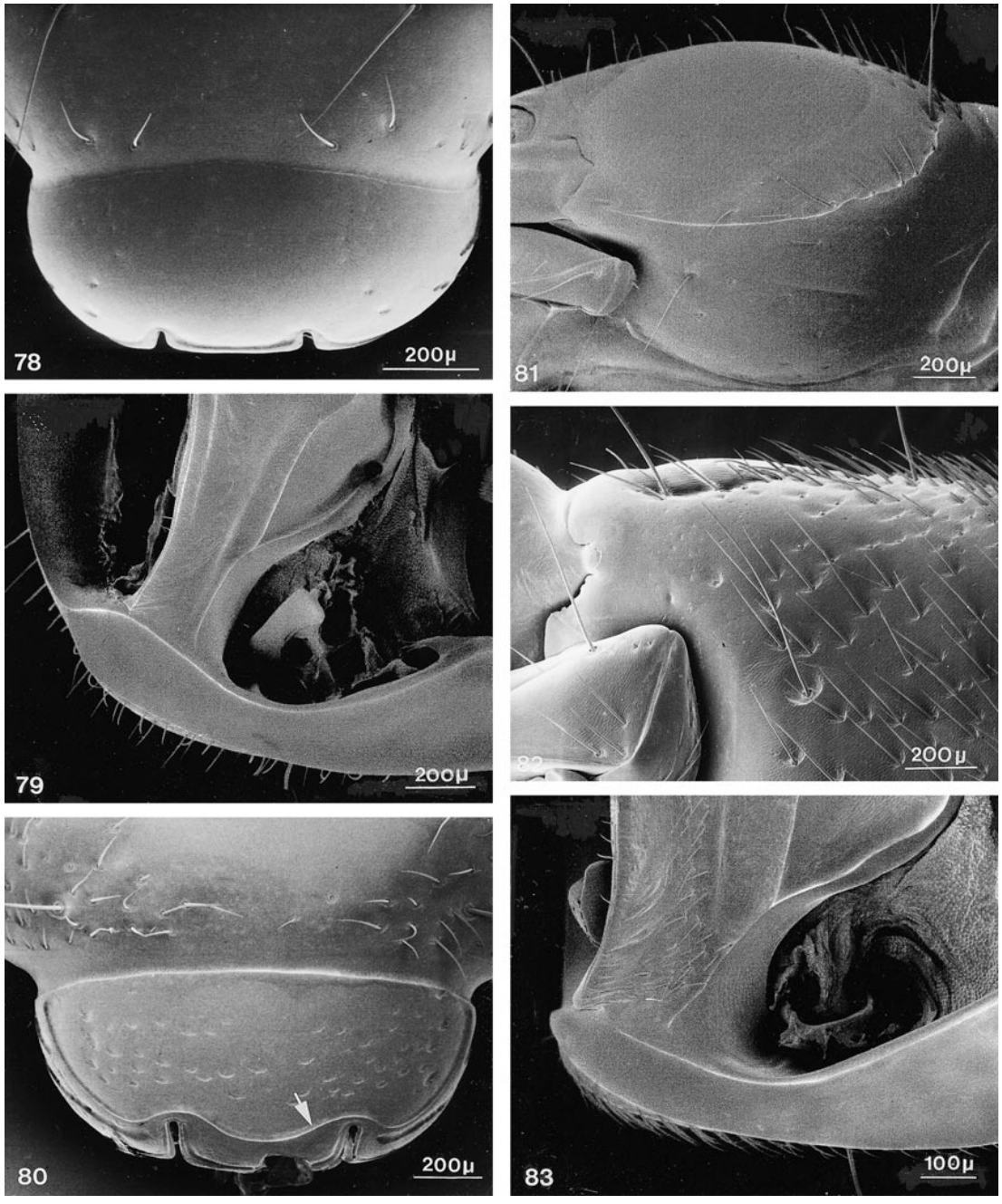
Figs. 59–64. **59**. *Dinothenarus pubescens*, series of long setae (some represented only by their sockets) on mesosternum. **60**. *Miobdelus* sp., series of long setae on mesosternum. **61**. *Craspedomerus* sp., series of long setae on mesosternum without transverse ridge. **62**. *Tasgius melanarius*, mesocoxal acetabulum. **63**. *Ocypus weisei*, mesocoxal acetabulum. **64**. *Staphylinus dimidiaticornis*, mesocoxal cavities, not margined posteromedially.



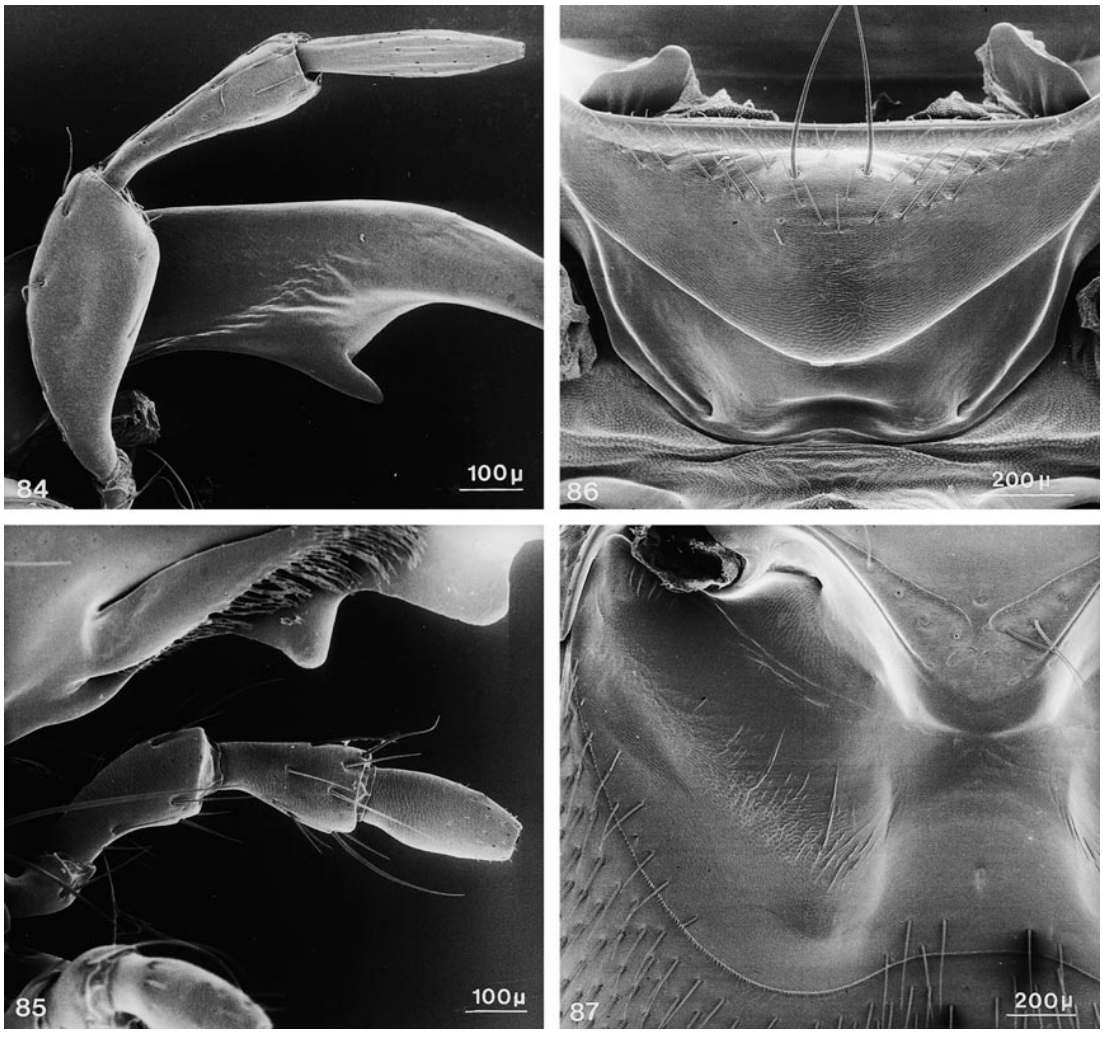
Figs. 65–71. **65**. *Dinothenarus pubescens*, dorsal apicolateral lobe of hind coxa, with a series of spinelike setae. **66**. *Ontholestes cingulatus*, dorsal apicolateral lobe of hind coxa with serial setae almost indistinguishable from other setae. **67**. *Anisolinus elegans*, empodial setae of middle tarsus, ventral view. **68**. *Miobdelus* sp., empodial setae of middle tarsus, ventral view. **69**. *Quedius laevicollis*, empodial setae of middle tarsus, ventral view. **70**. *Philonthus splendens*, apical portion of last segment of middle tarsus, empodial setae absent, ventral view. **71**. *Craspedomerus* sp., apical portion of last segment of middle tarsus, empodial setae absent, ventral view.



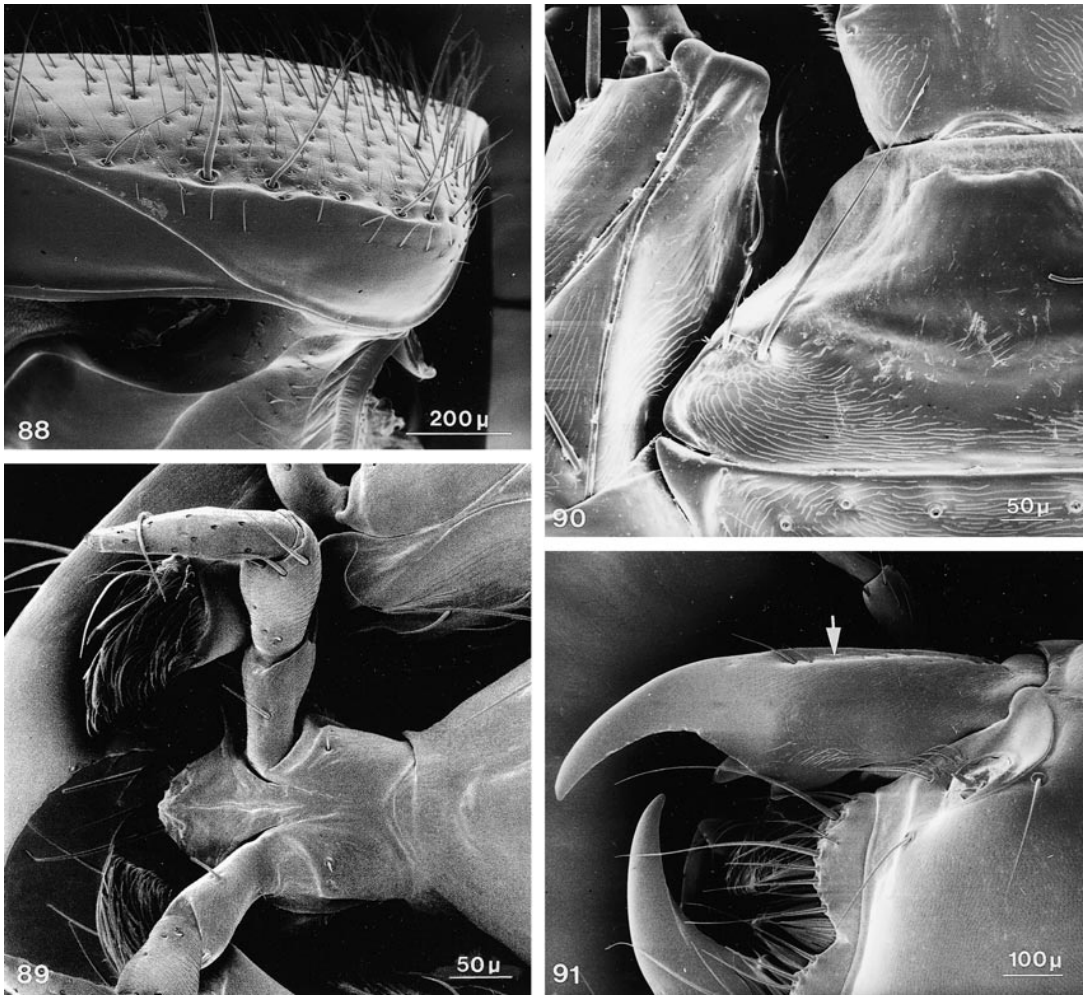
Figs. 72–77. **72**. *Philonthus politus*, anterior portions of superior and inferior marginal lines of pronotal hypomeron, ventral view. **73**. *Craspedomerus* sp., anterior portions of superior and inferior marginal lines of pronotal hypomeron, ventral view. **74**. *Philonthus politus*, ventral view of head, no infraorbital ridge. **75**. *Quedius laticollis*, superior marginal line of pronotal hypomeron not deflected under anterior angle of pronotum, ventrolateral view. **76**. *Quedius laticollis*, pronotal hypomeron and prosternum, notosternal suture present. **77**. *Quedius rainieri*, head with infraorbital ridge (arrow), oblique ventral view.



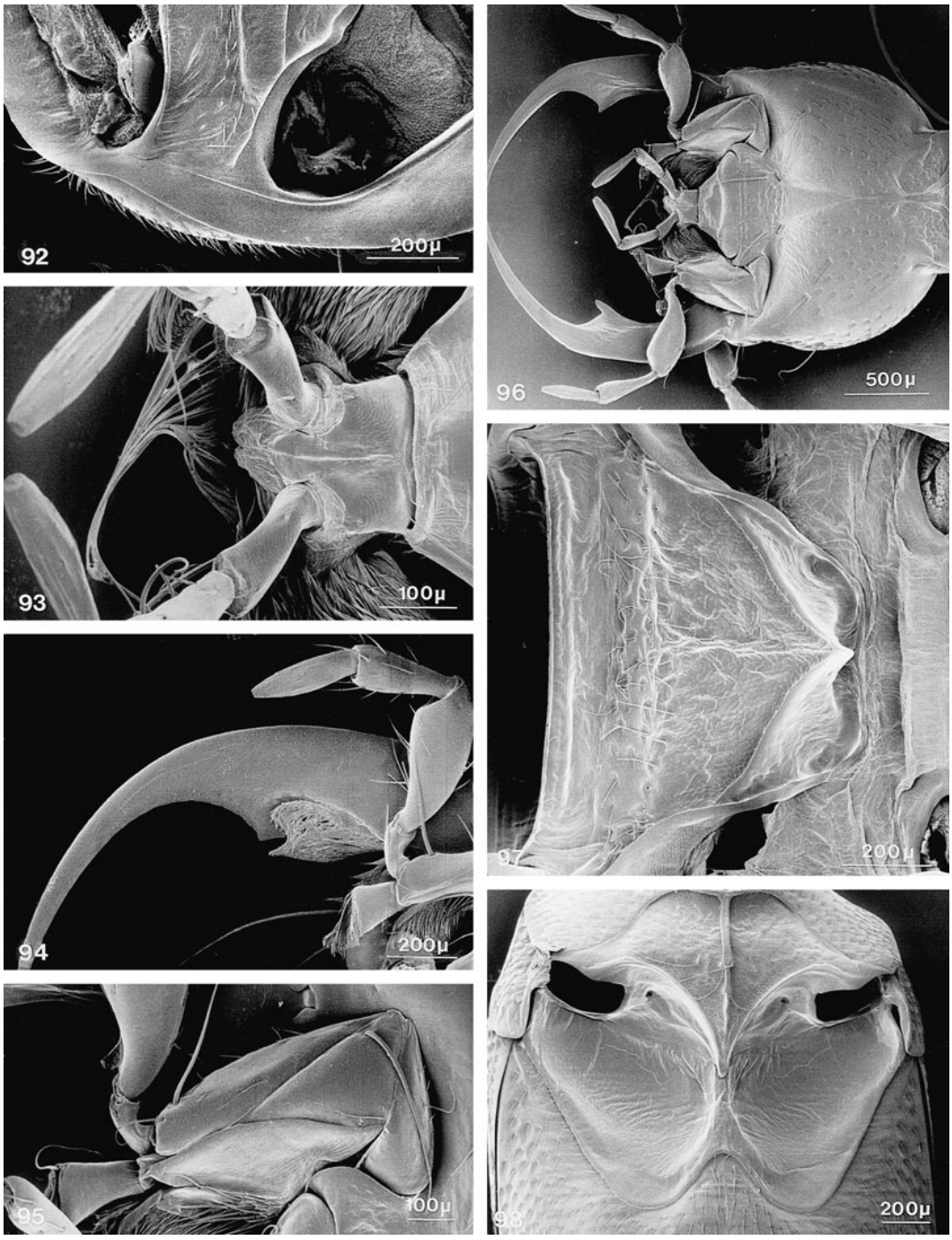
Figs. 78–83. **78**. *Quedius rainieri*, dorsal face of neck, dorsal basal ridge absent. **79**. *Xenopygus analis*, superior marginal line of pronotal hypomeron not deflected under anterior angle of pronotum, ventral view. **80**. *Xenopygus analis*, dorsal face of neck, dorsal basal ridge present (arrow). **81**. *Xenopygus analis*, head with postmandibular ridge, ventrolateral view. **82**. *Ocypus weisei*, head with rudimentary postmandibular ridge, ventral view. **83**. *Anisolinus elegans*, superior marginal line of pronotal hypomeron not distinctly deflected under anterior angle of pronotum, ventral view.



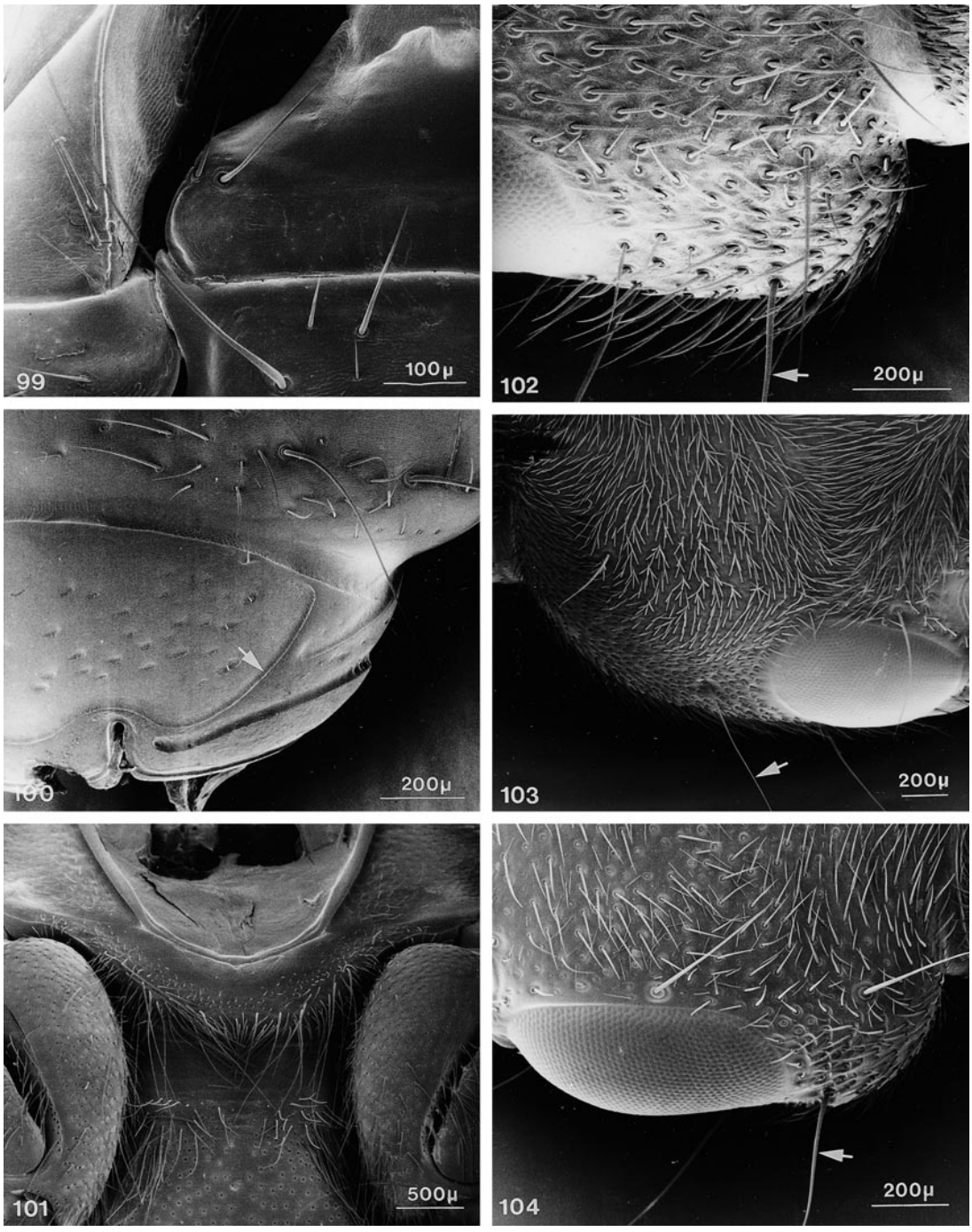
Figs. 84–87. **84**. *Amichrotus* sp., maxillary palpus. **85**. *Ocypus picipennis*, maxillary palpus. **86**. *Philonthus caeruleipennis*, prosternum. **87**. *Philonthus caeruleipennis*, mesosternum, showing transverse ridge, and anterior metasternal projection.



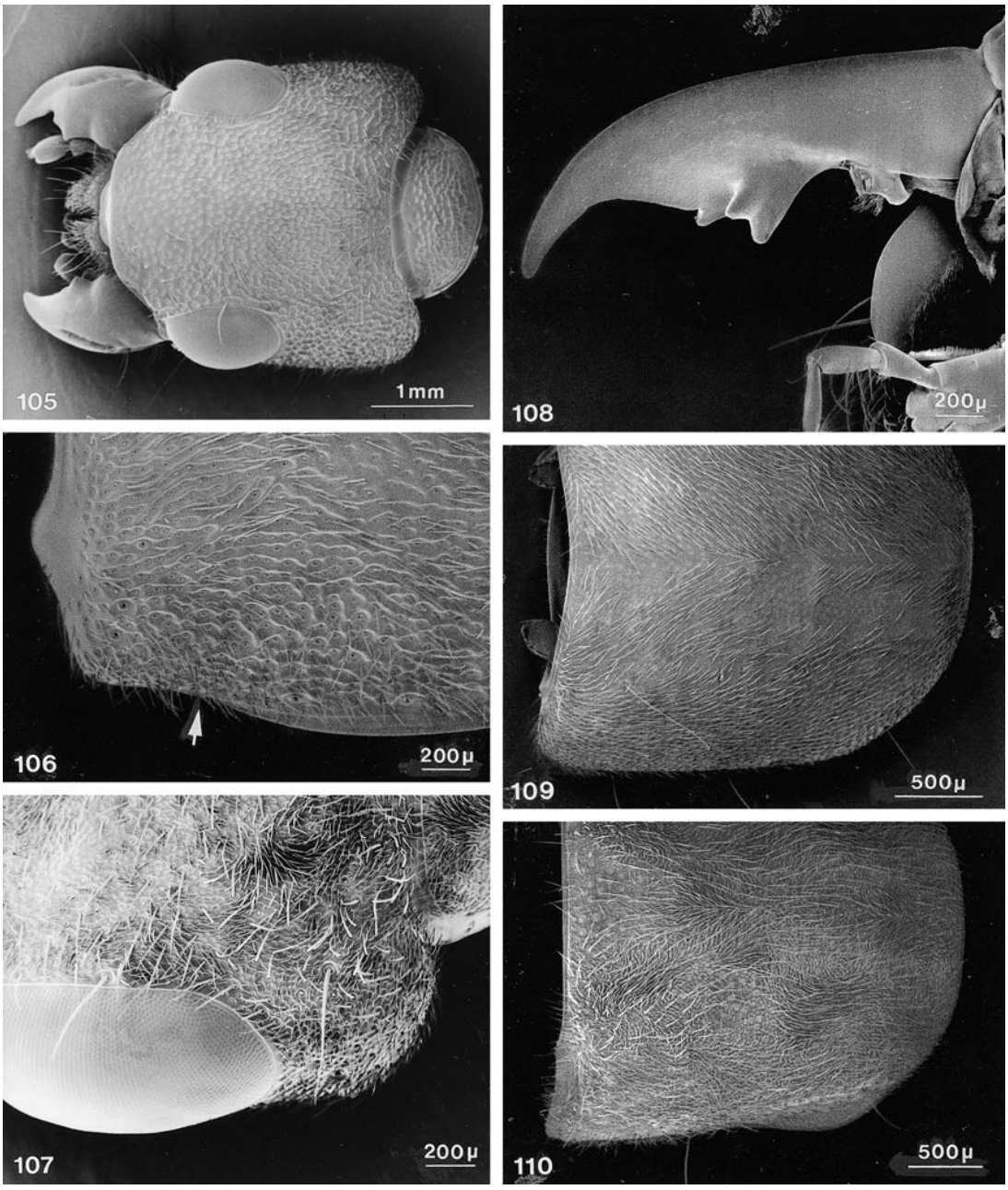
Figs. 88–91. **88**. *Craspedomerus* sp., narrowly, somewhat irregularly swollen lateral margin of pronotum, imitating the superior marginal line of pronotum, lateral view. **89**. *Quedius rainieri*, ligula not emarginate. **90**. *Quedius laticollis*, mentum with two anterolateral setae. **91**. *Quedius rainieri*, right mandible with dorsolateral ridge (arrow), dorsal view.



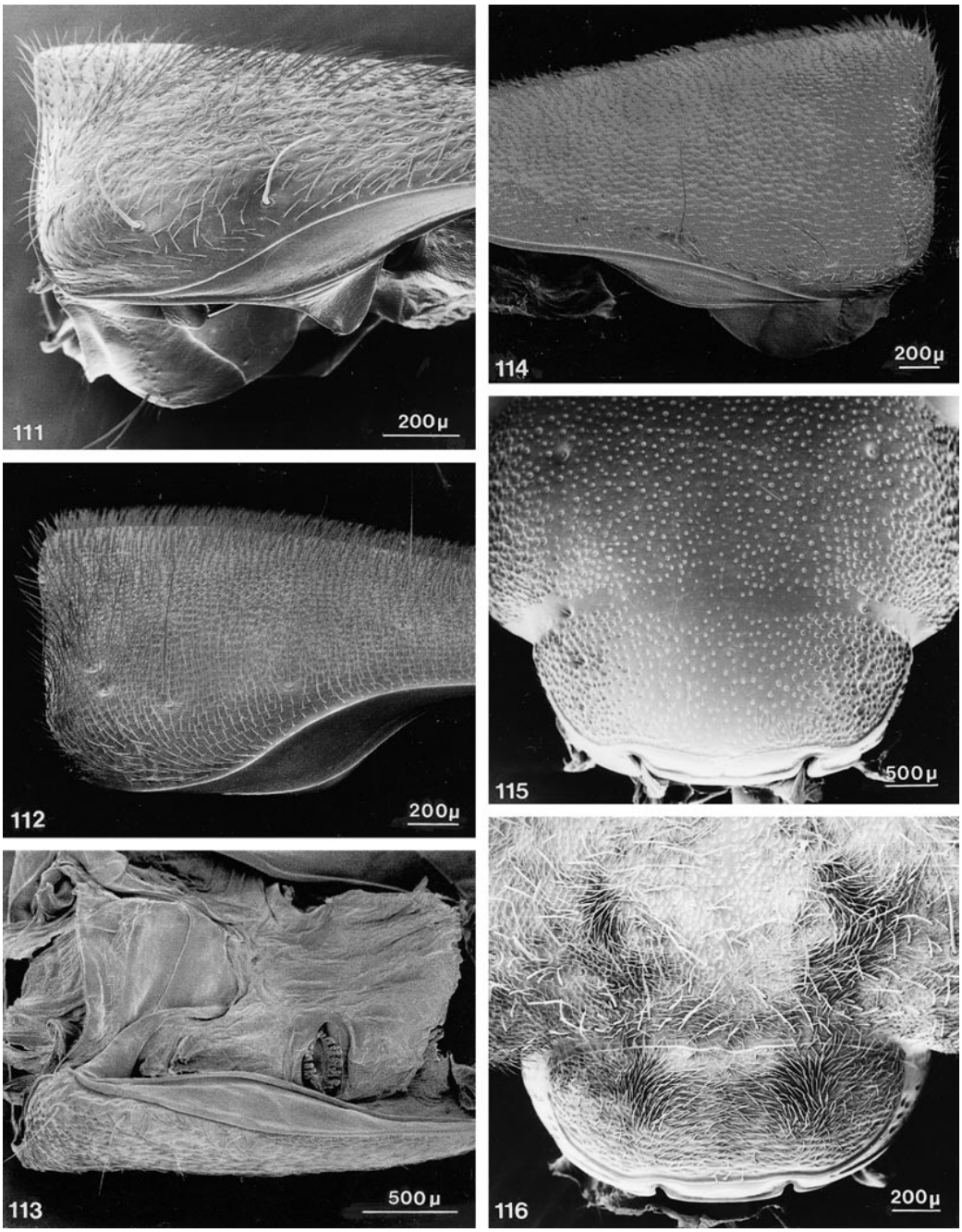
Figs. 92–98. **92**. *Amichrotus* sp., superior and inferior marginal lines of pronotal hypomeron not joined, ventral view. **93**. *Amichrotus* sp., ligula minutely emarginate. **94**. *Anisolinus elegans*, left mandible, ventral view. **95**. *Amichrotus* sp., palpifer with two apical setae. **96**. *Amichrotus* sp., mandibles, ventral view. **97**. *Amichrotus* sp., prosternum. **98**. *Amichrotus* sp., mesosternum with longitudinal carina, and anterior metasternal projection.



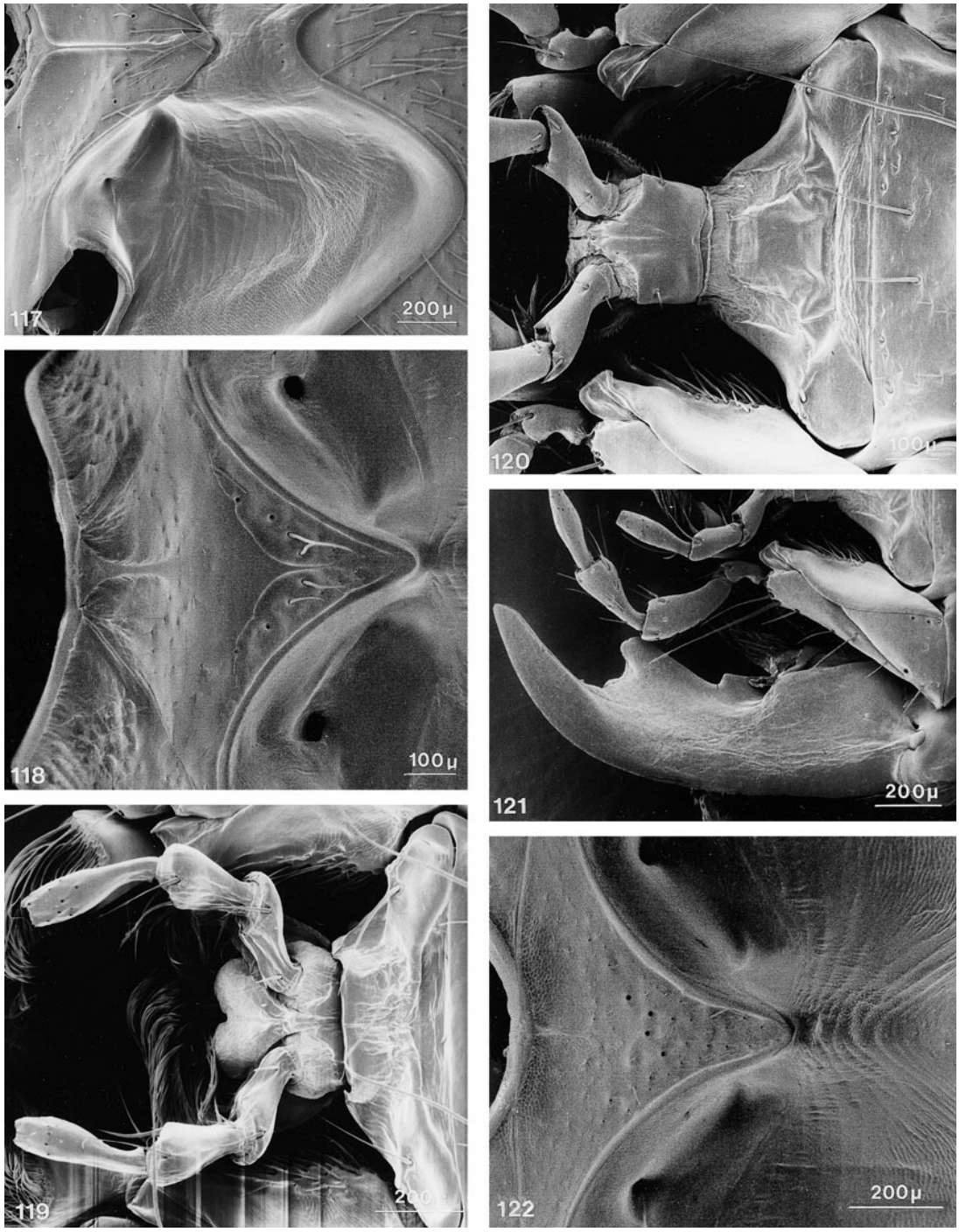
Figs. 99–104. **99**. *Dinothenarus badipes*, mentum with two setae. **100**. *Xenopygus analis*, right dorsal face of neck, with dorsal basal ridge (arrow). **101**. *Emus hirtus*, intercoxal process of mesosternum widely separating middle coxae. **102**. *Platydracus fossator*, left posterolateral area of head, showing postocular seta (arrow), dorsal view. **103**. *Staphylinus erythropterus*, right posterolateral area of head, showing postocular seta (arrow), dorsal view. **104**. *Abemus chloropterus*, left posterolateral area of head, showing postocular seta (arrow), dorsal view.



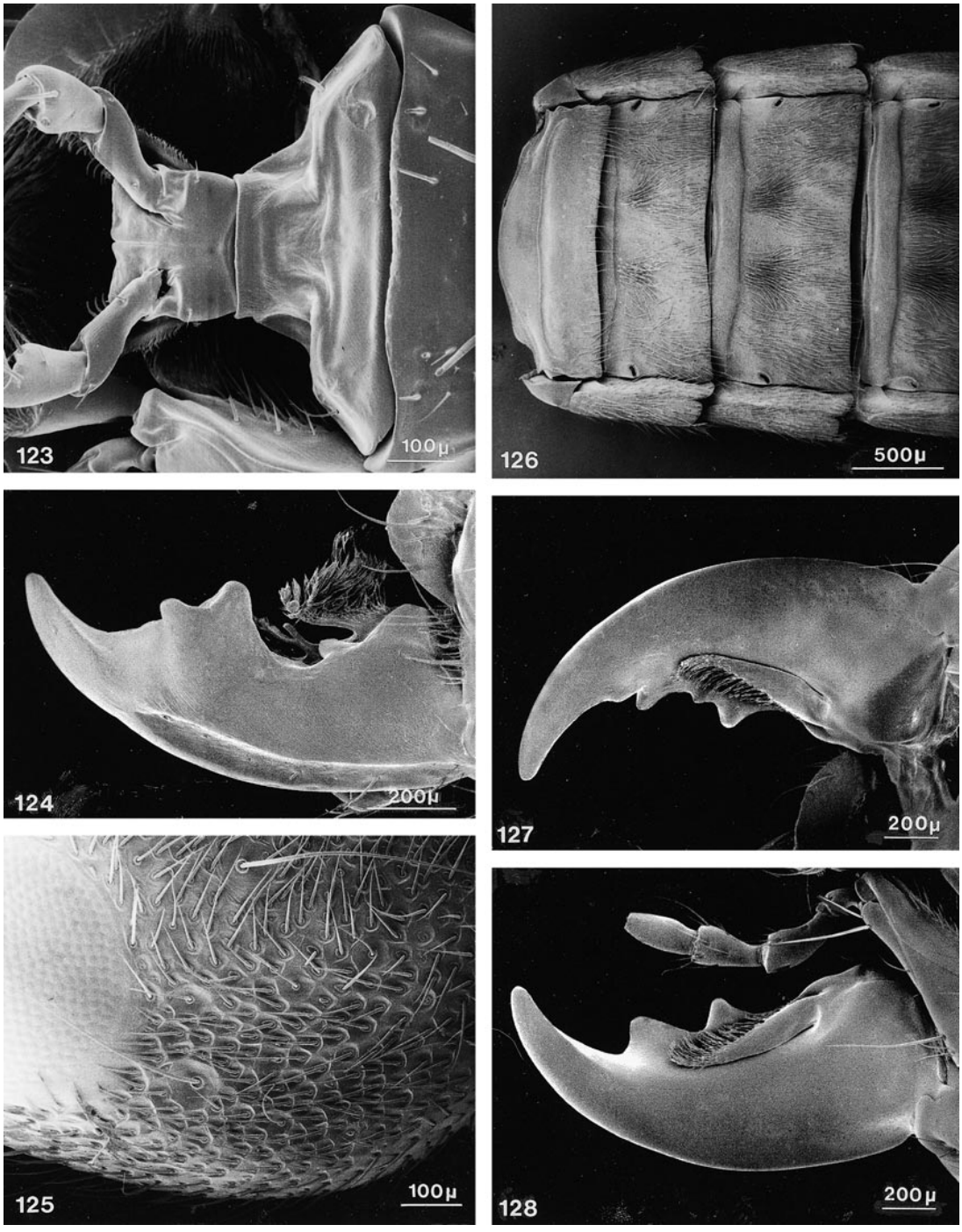
Figs. 105–110. **105**. *Naddia* sp., head, dorsal view. **106**. *Naddia* sp., left anterior portion of pronotum. **107**. *Ontholestes cingulatus*, left posterior area of head, showing eye and tempus, dorsal view. **108**. *Ontholestes cingulatus*, left mandible, ventral view. **109**. *Ocypus nitens semialatus*, pronotum, dorsal view. **110**. *Ontholestes cingulatus*, pronotum, dorsal view.



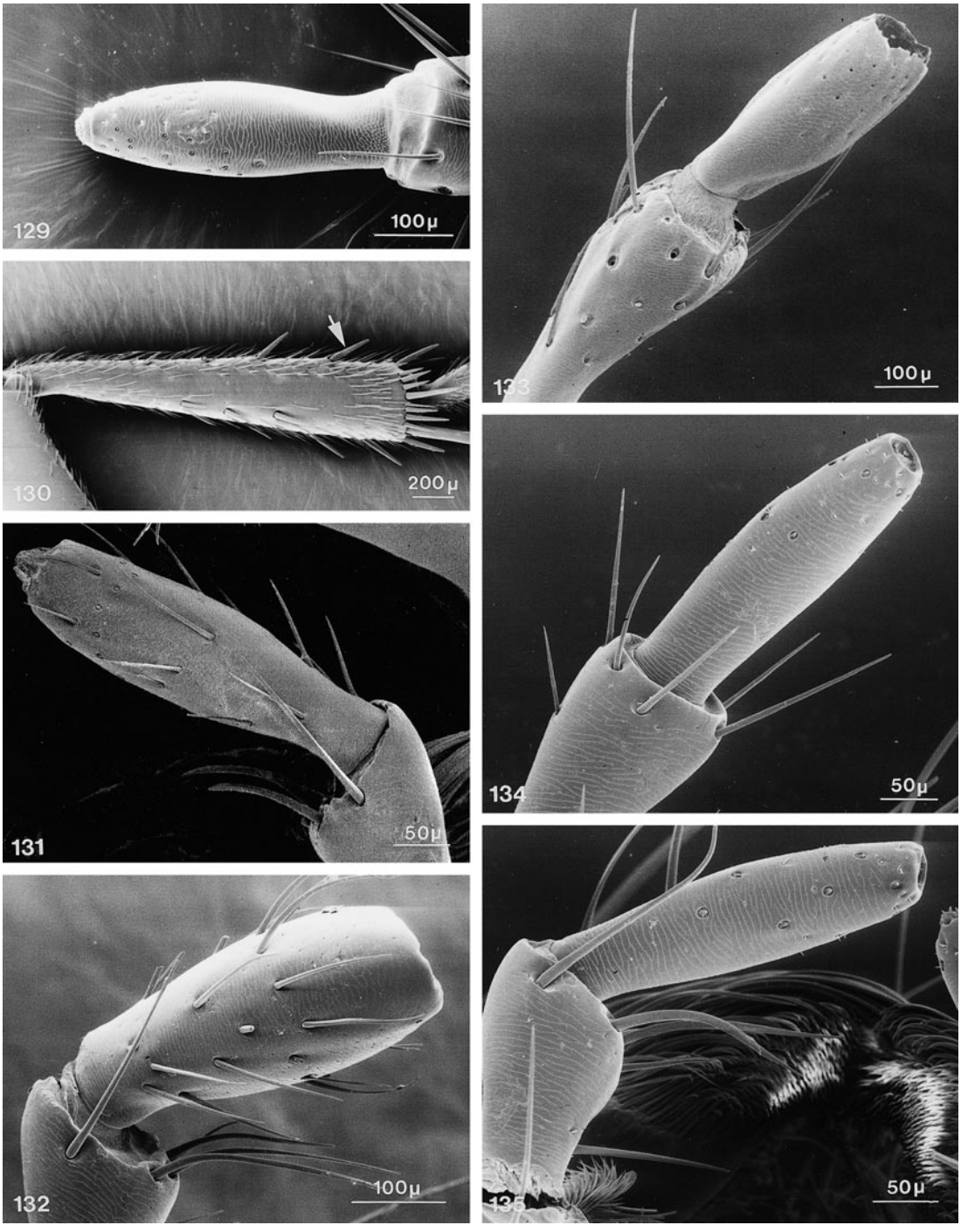
Figs. 111–116. **111**. *Dinothenarus pubescens*, pronotum showing both marginal lines of pronotal hypomeron, and two lateral macrosetae, lateral view. **112**. *Staphylinus erythropterus*, pronotum showing both marginal lines of pronotal hypomeron, and two lateral macrosetae, lateral view. **113**. *Ocypus ophthalmicus ophthalmicus*, pronotum showing both marginal lines of pronotal hypomeron, and two lateral macrosetae, ventrolateral view. **114**. *Ocypus nitens semialatus*, pronotum showing both marginal lines of pronotal hypomeron, and two lateral macrosetae, lateral view. **115**. *Physetops* sp., dorsal face of neck, with dorsal portion of nuchal ridge missing. **116**. *Ontholestes cingulatus*, dorsal face of neck, with nuchal ridge.



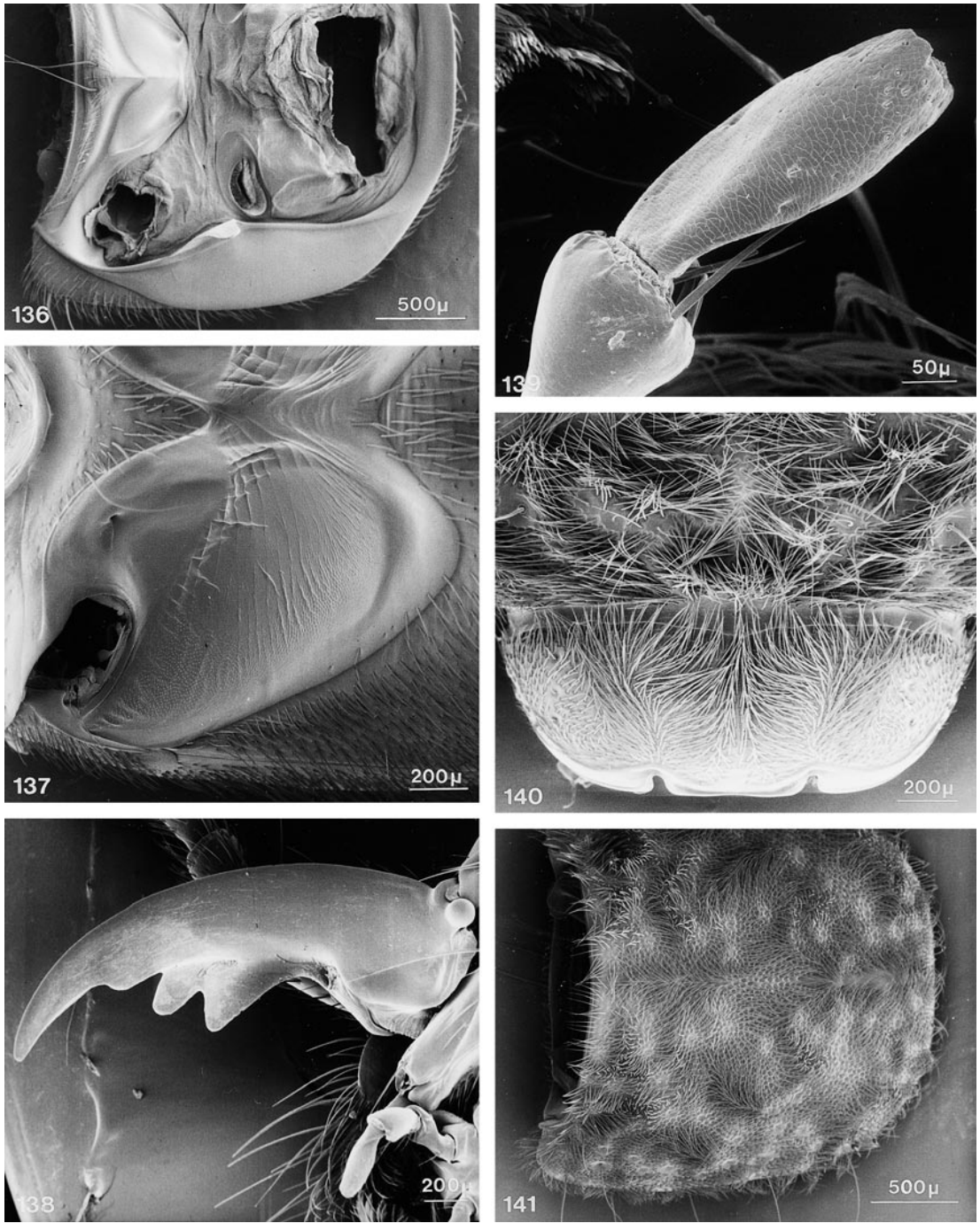
Figs. 117–122. **117**. *Ontholestes murinus*, mesosternum with fully developed medial carina. **118**. *Thoracostrongylus* sp., mesosternum with short medial carina at base. **119**. *Dinothenarus fossor*, labium with emarginate ligula, ventral view. **120**. *Dinothenarus pubescens*, labium and mentum. **121**. *Dinothenarus pubescens*, right mandible and right maxilla, ventral view. **122**. *Abemus chloropterus*, mesosternum, showing sockets of serial setae originating behind small elevations.



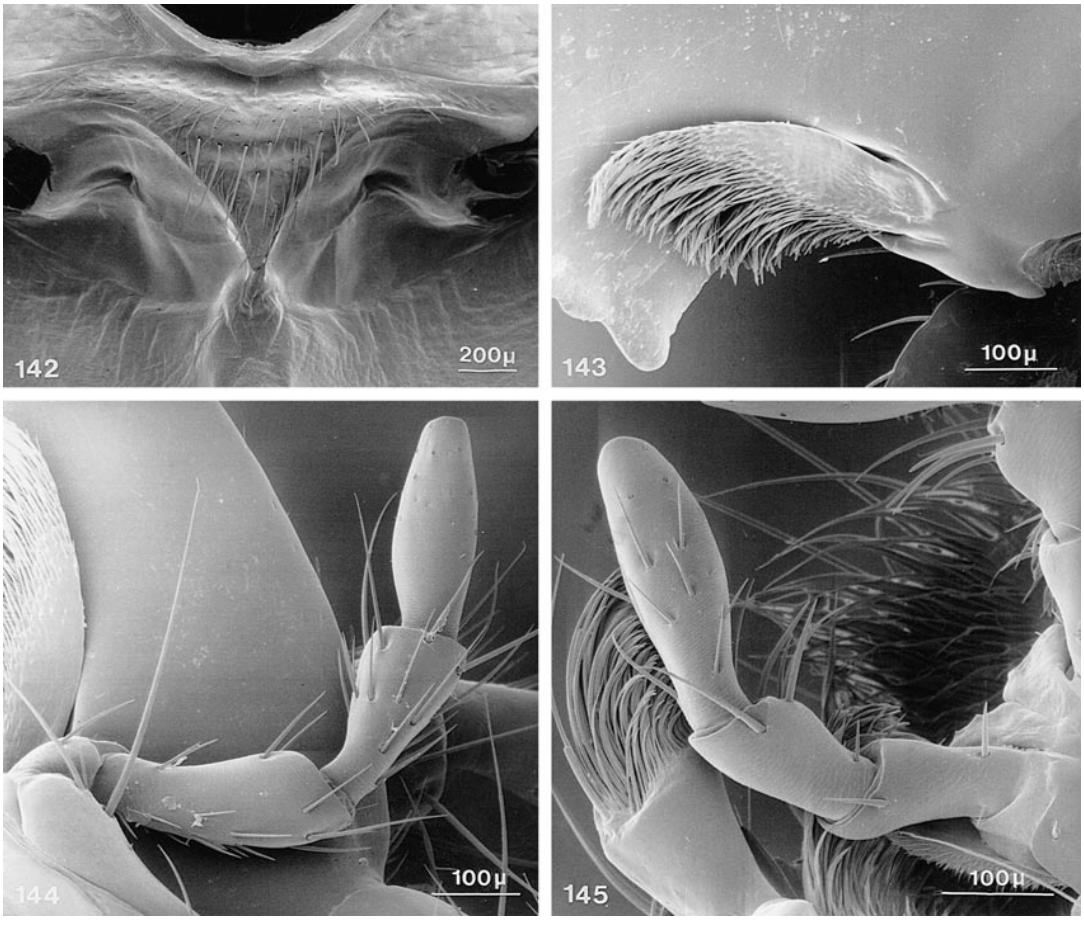
Figs. 123–128. **123**. *Abemus chloropterus*, labium and mentum. **124**. *Abemus chloropterus*, left mandible, dorsal view. **125**. *Miobdelus* sp., posterolateral portion of head, showing pitlike depressions. **126**. *Miobdelus* sp., first three visible abdominal tergites, showing bisinuate posterior basal line. **127**. *Ocypus picipennis picipennis*, left mandible, ventral view. **128**. *Ocypus picipennis picipennis*, right mandible, ventral view.



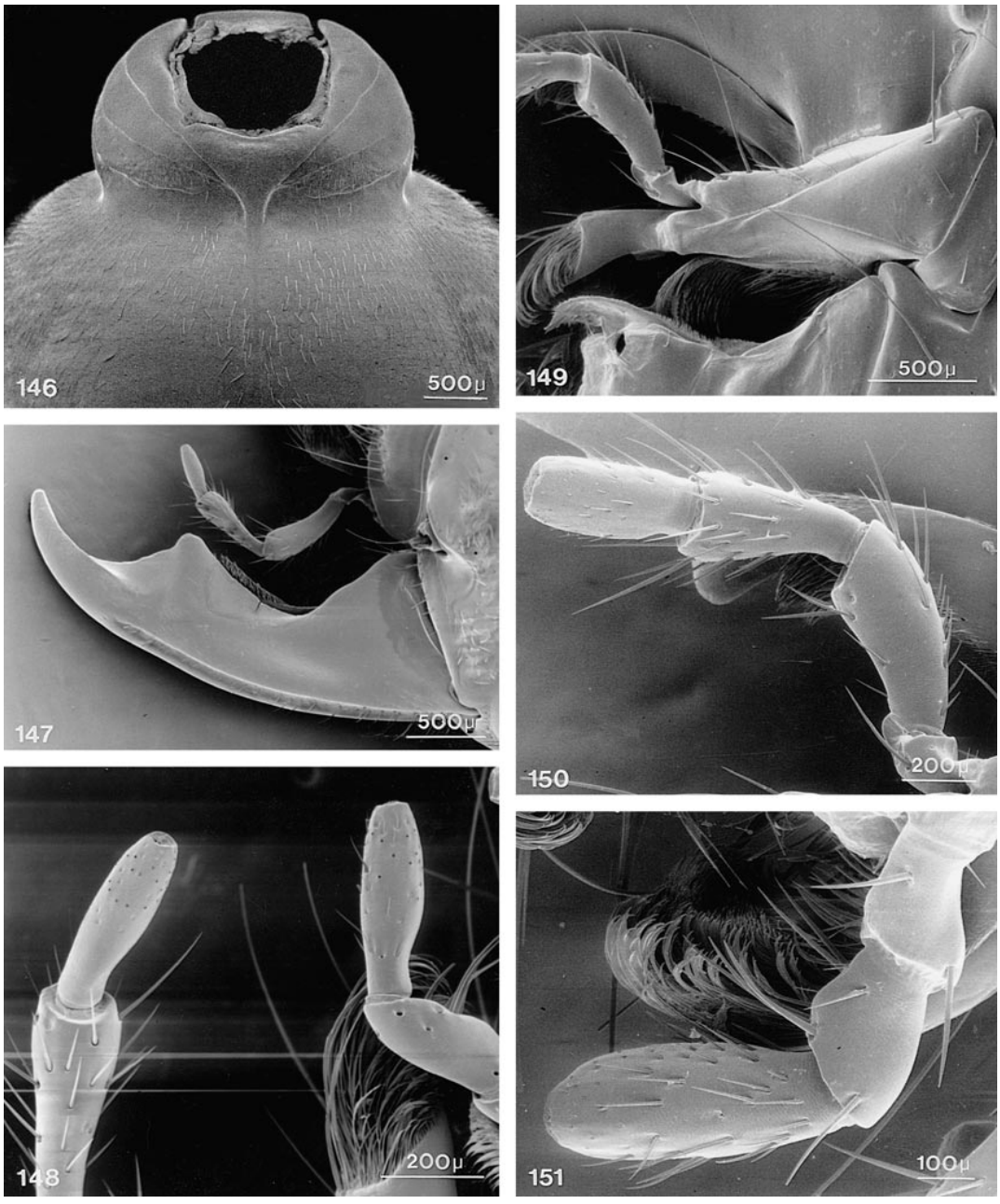
Figs. 129–135. **129**. *Protogoerius brullei*, last segment of maxillary palpus. **130**. *Ocypus picipennis picipennis*, hind tibia with spines (arrow) on dorsolateral face. **131**. *Ocypus mus*, last segment of labial palpus. **132**. *Ocypus weisei*, last segment of labial palpus. **133**. *Ocypus olens*, last segment of labial palpus. **134**. *Platydracus stercorarius*, last segment of maxillary palpus. **135**. *Platydracus stercorarius*, last segment of labial palpus.



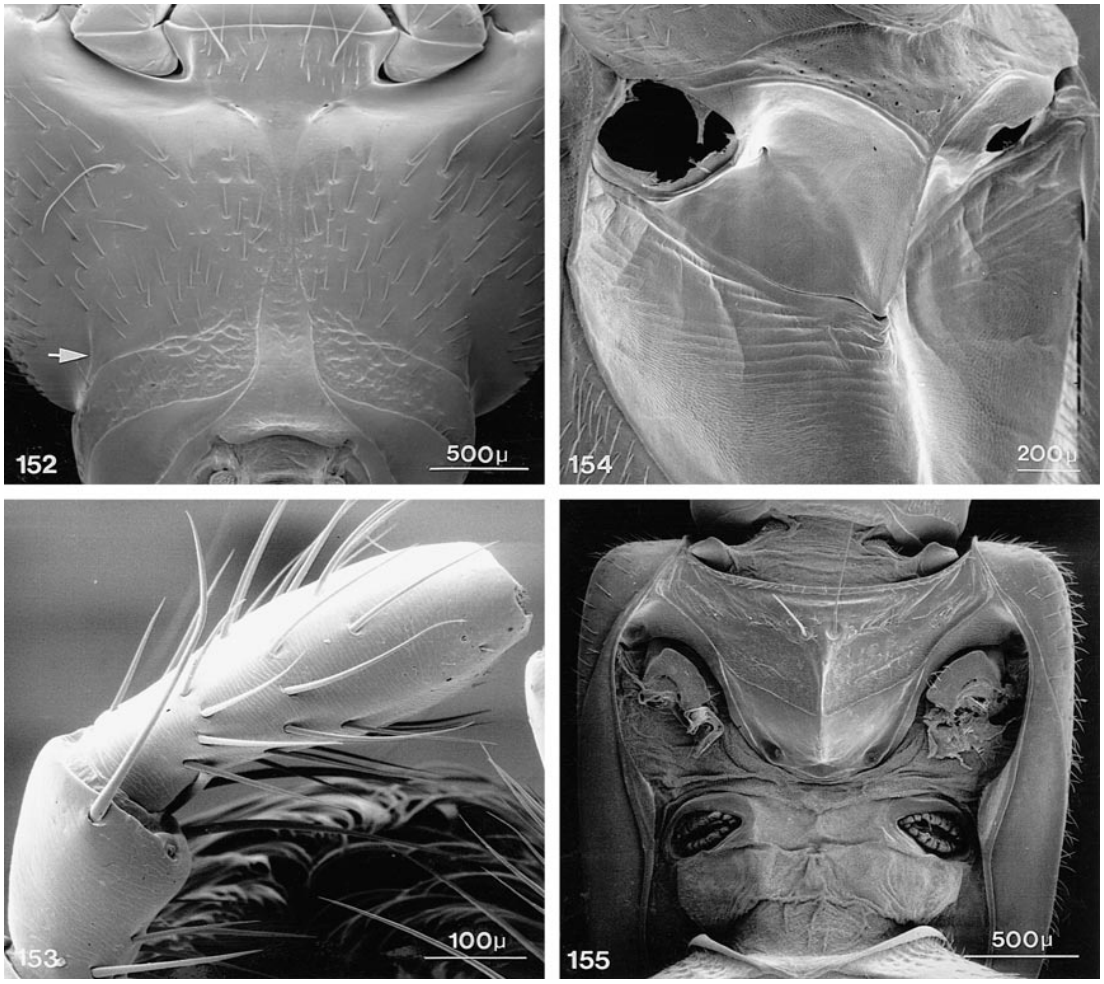
Figs. 136–141. **136**. *Platydracus stercorarius*, pronotal hypomeron, ventral view. **137**. *Platydracus stercorarius*, right coxal cavity, ventral view. **138**. *Staphylinus dimidiaticornis*, left mandible, ventral view. **139**. *Staphylinus erythropterus*, last segment of labial palpus. **140**. *Dinothenarus pubescens*, posteromedial portion of head and neck with pubescence, dorsal view. **141**. *Dinothenarus pubescens*, pronotum with pubescence.



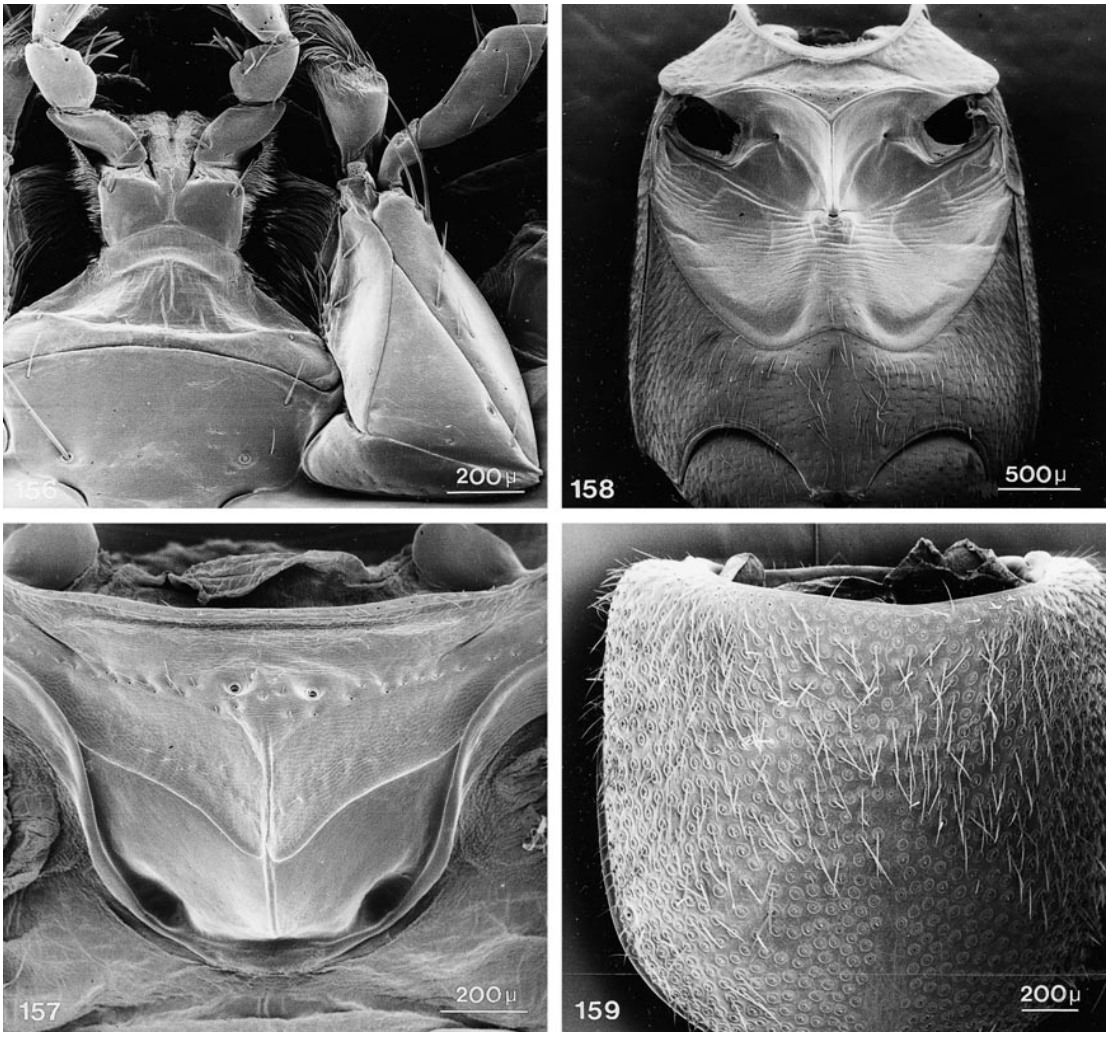
Figs. 142–145. **142**. *Dinothenarus fossor*, mesosternum. **143**. *Miobdelus* sp., left mandibular prostheca, ventral view. **144**. *Miobdelus* sp., maxillary palpus. **145**. *Miobdelus* sp., labial palpus.



Figs. 146–151. **146**. *Protogoerius brullei*, underside of head, showing gula. **147**. *Protogoerius brullei*, left mandible, dorsal view. **148**. *Protogoerius brullei*, maxillary (left) and labial palpus (right). **149**. *Ocypus tenebricosus*, maxilla, showing setae on palpifer. **150**. *Ocypus tenebricosus*, maxillary palpus. **151**. *Ocypus tenebricosus*, labial palpus.



Figs. 152–155. **152**. *Agelosus carinatus*, underside of head, showing abbreviated infraorbital ridge (arrow). **153**. *Agelosus carinatus*, last segment of labial palpus. **154**. *Tasgius melanarius*, mesosternal intercoxal process. **155**. *Tasgius ater*, pronotal hypomeron and prosternum.



Figs. 156–159. **156**. *Tasgius melanarius*, mentum and submentum. **157**. *Tasgius melanarius*, prosternum. **158**. *Tasgius melanarius*, metasternum, showing anterior metasternal projection. **159**. *Platydracus stercorarius*, pronotum.