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Systematics and phylogenetic relationships of the genera in the Carpelimus group (Coleoptera: Staphylinidae: Oxytelinae)*

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Abstract – The systematics of the staphylinid subfamily Oxytelinae FLEMING, 1821 are investigated. Phylogenetic relationships among the *Carpelimus* group of genera (*Blediotrogus*, *Pareiobledius*, *Mimopaederus*, *Teropalpus*, *Ochthephilus*, *Carpelimus*, *Xerophygus*, *Trogactus*, *Thinodromus*) are analyzed using 70 characters (most previously unstudied) and 45 exemplar taxa from the subfamily. Based on the results of this analysis, a hypothesis of the relationships among the genera and tribes of Oxytelinae is presented. The following new synonymies are proposed: *Thinodromus* KRAATZ, 1857 = *Apocellagria* CAMERON, 1920, syn. n.; *Aploderus* STEPHENS, 1833 = *Bledioschema* SMETANA, 1967, syn. n. The tribe Planeustomini JACQUELIN DU VAL, 1857 is to include the genera *Manda* BLACKWELDER, 1952 and *Planeustomus* JACQUELIN DU VAL, 1857. The limits of the tribe Oxytelini are expanded to contain the former Thinobiini J. SAHLBERG, 1876 less Blediini ÁDÁM, 2001, with the latter being recognized as a valid taxon. The problems with generic limits in the tribe Oxytelini are addressed. Based on the character variability found throughout the whole tribe, new definitions for *Oxytelus* GRAVENHORST, 1802 and *Anotylus* THOMSON, 1859 are proposed, resulting in the following synonymies: *Oxytelus* GRAVENHORST, 1802 = *Hoplitodes* FAUVEL, 1904, syn. n., = *Anisopsis* FAUVEL, 1904, syn. n., = *Paroxytelopsis* CAMERON, 1933, syn. n., = *Anisopsidius* FAGEL, 1960, syn. n.; *Anotylus* THOMSON, 1859 = *Oxytelopsis* FAUVEL, 1895, syn. n., = *Rimba* BLACKWELDER, 1952, syn. n. The state of knowledge on the larvae of the subfamily (with attention to tribal classification) is summerized. A new key for genera of Oxytelinae is presented. In order to use them in the phylogenetic analysis, 5 new species are described: *Xerophygus hreblayi* sp. n., *Carpelimus bifidus* sp. n., *Thinodromus juanfernandezianus* sp. n., *Thinodromus schillhammeri* sp. n., *Trogactus ocellatus* sp. n. With 129 figures and one table.

Key words – Coleoptera, Staphylinidae, Oxytelinae, history of study, new characters, phylogeny, generic revision, synonymy, key, new species.

INTRODUCTION

Relative to the other staphylinid subfamilies, the state of knowledge regarding Oxytelinae is not bad. The subfamily is now well defined and delimited and

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there is a relatively recent phylogenetic analysis (HERMAN 1970) done with modern methods. Therefore, the reasons for the present study, the reexamination of the phylogenetic relationships within this subfamily and the *Carpelimus* group of genera requires explanation. HERMAN's (1970) previous study omitted characters in genitalia almost entirely; this study will demonstrate that these characters provide substantial phylogenetic information for analysis of relationships among species-groups and in some instances, genera. Also, a wealth of new taxa has been discovered and partially described in the past 35 years and these require reconsideration of phylogenetic hypotheses. The hypothesized lineage informally known as the *Carpelimus* group (*Blediotrogus*, *Pareiobledius*, *Teropalpus*, *Ochthephilus*, *Carpelimus*, *Xerophygus*, *Trogactus*, *Thinodromus*) is seriously affected by the above factors, and its detailed analysis is rewarding both in terms of taxonomic information (more reliable characters for identification) and reconstruction of the relationships among the genera in Oxytelinae.

Genus groups – as an informal suprageneric rank – are preferred to be used because of the unresolved relationships. It is anticipated that this study will be followed by others, incorporating larval characters or molecular data, probably necessitating further taxonomic changes. In accordance with this, the primary goals of this study are to discuss the classification of the entire subfamily, to analyze the phylogeny of the genera of the *Carpelimus* group that is most affected by the omission of the genital characters, and to present a new key for the valid genera using the newly introduced characters.

GENERAL CHARACTERISTICS OF THE OXYTELINAE

Diagnosis of the subfamily

Characters commonly used for delimiting the subfamily Oxytelinae are: (1) presence of secretory openings on tergum IX which is divided by tergum X, and (2) presence of a fully developed sternite II (in more derived taxa). This latter character is indicated by the appearance of seven complete, articulated segments on the ventral side of the abdomen, exclusive of the smaller genital segments (segments IX and X), which are usually visible at the apex. Oxytelines are small to medium sized beetles, typically ranging from 1.0 to 8.0 mm, but a few exceptions are found; some of the smallest known beetles belong in this subfamily, with body length of a mere 0.5 mm and maximum width of less than 0.1 mm. The colouration is normally inconspicuous, with only a few taxa having metallic or bright colours; most are piceous to testaceous. Some taxa are notable for pronotal or cephalic horns, these are in most cases secondary sexual characteristics for males and either less developed or absent in females (in a few very rare examples the horns are more developed in females).

Number of species, distribution

The subfamily includes exactly 2,000 named, extant species at the time of the last catalog (HERMAN 2001). Most species belong to three major lineages: (1) *Bledius* contains approximately 400 described species; (2) *Carpelimus* and *Thinodromus* combined have 600 (with approximately 400 and 200 described species in each of these genera, respectively); (3) *Oxytelus* and *Anotylus* have approximately 550 (150 and 400, respectively). The remaining ca. 400 species are shared among the smaller or more basal genera. The subfamily is distributed worldwide, although not all genera have a worldwide distribution. About half of the genera are known almost exclusively from temperate regions: *Platydeleaster*, *Deleaster*, *Syntomium*, *Mitosynum*, *Coprophilus*, *Manda*, *Eppelsheimius*, *Ochthephilus* from the Northern Hemisphere and *Oxypius*, *Homalotrichus*, *Coprostygnus*, *Blediotrogus*, *Pareiobledius*, *Teropalpus* from the Southern Hemisphere.

Ecology and feeding habits

There are two characteristic types of habitats for this subfamily: (1) moss, sand and gravel on banks of water bodies and (2) dung or decaying plant material. Among the genera of the *Carpelimus* group, referred to in HERMAN (1983*b*) as the "*Carpelimus* lineage", the *Carpelimus* species are found in muddy riparian habitats along river and stream banks, at ponds, and they are ubiquitous in such habitats. *Thinodromus* and *Ochthephilus* typically prefer riparian habitats associated with fast, running waters, where they live in moss (Fig. 6), debris on banks (Fig. 7) or gravelly spots (Fig. 4); members of these genera prefer higher elevations and clean water, therefore their occurrence is more limited. The tropical taxa (e.g. *Trogactus*) can be found primarily but not exclusively at higher elevations, in a variety of habitats, but mostly in leaf-packs at the banks of fast streams (Fig. 8). They also occur at lower elevations, especially where there are no mountain ranges (e.g. Amazonia). The genera of the *Thinobius* group, referred to in HERMAN (1983*b*) as the "*Thinobius* lineage", *Thinobius*, *Neoxus* and *Sciotrogus*, live in more sand-dominated streambanks (Fig. 5). The genera of Blediini burrow in sandy riverbanks or seashores, usually well away from the water but in habitats that are still wet. Some of the taxa in the Oxytelini are often found in dung and some of the species are known to be associated with ants. Very recently, a couple of species of

Oxytelinae were also discovered to be specialized to endogeous or rather semi-endogeous (i.e. depth-living) habitats (LÖBL & RYCHLÍK 1994, SAWADA 1971, PACE 1993, GUSAROV & MAKRANCZY 2004). The so far known species belong to *Carpelimus* and *Thinobius*, but it is possible that such specialization exists in other lineages as well. Most species are good fliers, therefore they are captured frequently in flight intercept traps (FIT's) or light traps (UV, blacklight). The numbers of individuals collected by these methods (mostly *Carpelimus*, but also *Thinodromus*, *Anotylus*, *Bledius*, *Deleaster* and occasionally other genera) can be high, so they are prominent in pest monitoring trap samples.

Although there is very little convincing evidence about their feeding habits, the most widely accepted hypothesis is that they eat particles of decaying plant material and algae. There is one report of an oxyteline feeding on living vascular plant tissue (CHITTENDEN 1915). There are a few reports of possible carnivorous habits, for example HERMAN (1970) mentioned *Deleaster trimaculatus* having been "observed eating the soft parts of freshly killed insects." There have been abundant suggestions that *Bledius* eat other insects, but investigation of the gut content of larvae revealed only algae, diatoms and abundant sand (PAULIAN 1941, reporting this for larval *Bledius spectabilis*).

Importance in ecosystems

Although oxytelines in terms of number of described species represent less than 5% of the family Staphylinidae, some species are so abundant that the sheer number makes them an important factor in biological systems. In periaquatic situations and decaying plant matters (especially dung), the Oxytelinae makes up for approximately 50% of the individuals of Staphylinidae. Species of *Anotylus* swarming near swampy areas at dusk can be a nuisance to people (especially bikers). It must also be noted that certain oxyteline genera (e.g. *Thinobius*), once abundant, occur exclusively on lower parts of rivers still with lots of sand and gravel deposits, and this is the kind of habitat that is most endangered worldwide, because of buildings, construction and water reservoirs, all destroying the conditions that are necessary for these tiny beetles (MAKRANCZY 2004). Some of the higher parts of the water systems are protected in mountain ranges, but once the rivers reach the plains, they are no longer clean and do not have the bends where they deposit debris of various sizes (ranging from fine sand to coarse gravel).

MAJOR EVENTS IN THE HISTORY OF THE OXYTELINE CLASSIFICATION

The beginnings: description of the common European taxa (1758–1840)

Immediately following the works of LINNAEUS and FABRICIUS, not many species of Staphylinidae were described. Emphasis was given to the more alluring (and accessible) families of Coleoptera. In the early 1800s, however, this was to change rapidly. GRAVENHORST was the first to monograph Staphylinidae. In fact, we can consider him the first staphylinid specialist. It is remarkable that before 1802 only 310 species and 6 genera of Staphylinidae were named. GRAVENHORST alone in his two milestone works (GRAVENHORST 1802, 1806) added 330 species and 14 genera. As early as 1806, he also speculated about the relatedness of the then known taxa and his opinion on the relationships (at least as far as Oxytelinae is concerned) has been mostly confirmed by later investigators. Most of the "genera" on his chart are now subfamilies. It should be also noted that in the first half of the 1800s, there were competing names in use for the family Staphylinidae: "brachelytra" and "microptera" are just two of those that were eventually abandoned in favor of "staphylinids".

Broadening the scope (1840–1969)

The next 130 years brought two very important advancements. After ERICHSON's works on the classification of the world fauna (ERICHSON 1837, 1839*a*, *b*, 1840), a system prevailed for more than a hundred years, the mass description of species-group taxa started rapidly with a worldwide scope. The second is the refinement of the generic classification; the naming of the vast majority of genera and subgenera occured during this period. Six important figures shaped the classification of Oxytelinae: FAUVEL, SHARP, BERNHAUER, CAMERON, SCHEERPELTZ and FAGEL. The volume and status of the subfamily was often debated; for example JEANNEL & JARRIGE (1949) considered Oxytelidae as a separate family, while TIKHOMIROVA (1973) maintained the Oxytelinae in a broad sense, including the currently recognized subfamily Omaliinae and others in it. Both of these views had followers, so such arrangements are still found in modern literature.

The revolution (1970–1995)

The currently accepted phylogeny-based classification is the product of three very influential workers: LEE HERMAN, PETER HAMMOND and ALFRED NEWTON.

LEE HERMAN redefined the subfamily Oxytelinae (HERMAN 1970). The two major changes within the subfamily he introduced were the elevation of *Anotylus* to generic rank (resulting in new combinations of some 400 species-group names) and the break-up of *Trogophloeus* (now a junior synonym to *Carpelimus*) and placement of species of *Trogophloeus* into *Carpelimus* and *Thinodromus* (and some small genera), again resulting in changes of names for hundreds of taxa. The limitations of his work resulted from the facts that in the 1960s it was still difficult to obtain museum specimens via mail; dissections of type specimens, especially extraction of genitalia were often not permitted or were discouraged. Dr. HERMAN went to great lengths to visit as many collections as possible at the time. He studied at least the tarsal segmentation, usually by removing one leg from the types and studying that under high magnification to verify generic placement. The new generic system he created has stood the test of time. It is mostly his arrangement that is the basis of current classifications. A relatively few erroneous placements and omissions were corrected later either by him or other workers. His second big project dealt with the *Bledius* group, carried out over a span of 16 years, it resulted in four major revisions (HERMAN 1972, 1976, 1983*a*, 1986), which still provide the standard of excellence for anyone interested in the subfamily.

PETER HAMMOND invested much time to the study of the genus *Anotylus* (HAMMOND 1976*a*, *b*, HAMMOND *et al.* 1979), but his works usually contain references to classification of the whole subfamily. He redefined *Anotylus* and treated many species of the *Platystethus*, *Anotylus* and *Oxytelus* lineages in comprehensive works (HAMMOND 1971, 1975). His works were unusual for being based on the study of a vast number of museum specimens, many of which were also collected and observed by himself throughout the world. The species-group concept did not gain much popularity until about twenty years ago, and HAMMOND was amongst the first to apply it to Oxytelinae. Further milestone works in use of species-groups to organize species in very large genera were LEE HERMAN's aforementioned revisions of species groups in *Bledius*, culminating in the 1986 book, which subdivided the whole 400-plus taxon into species groups on a worldwide basis.

ALFRED NEWTON discovered a strange beetle, which he later named *Oxypius* (NEWTON 1982) which he first thought to be a piestine. He immediately recognized that the taxon was closely related to *Euphanias*, another controversial taxon then placed in the subfamily Piestinae. Later he realized that they both in fact belong to Oxytelinae, but the characterization of the subfamily and the interpretation of some characters had to be changed in order to accomodate these taxa. These results sparked his interest in the phylogeny of the basal lineages of Oxytelinae. Based on his reanalysis of evidence regarding presence of a complete second sternum and an analogous situation in another subfamily (Osoriinae, Eleusini), he changed the polarity of this character to consider the free second sternite to be a derived character (NEWTON 1982). The resulting change in the placement of taxa marked the birth of the presently recognized tribal classification of basal Oxytelinae. Although NEWTON realized the problems with the tribal classification at the time of the *Oxypius* article (NEWTON 1982), only in 1992 did he present a formal tribal classification (NEWTON & THAYER 1992*a*).

The Tree of Life phylogeny

Until now the phylogeny displayed on the Tree of Life webpage (address: http://tolweb.org/tree?group=Oxytelinae) has been the most accepted hypothesis of relationships among genera of oxytelines (NEWTON 1995). This tree is primarily a reworking of HERMAN (1970); the data are inferred from the tree and character list published (HERMAN 1970, NEWTON 1982) but with additions and modifications plus more basal taxa. The presented phylogenetic relationships are not documented by published characters or analyses. This phylogeny is not very well supported; in fact, analysis of character sets in the literature using more modern computer programs would result in collapse of many branches. The changes implied by this tree affect the tribal classification primarily, which was already outlined in NEWTON & THAYER (1992*a*). Three out of the oxyteline tribes are monophyletic in this tree, but the basal lineage of Thinobiini (*Manda*, *Eppelsheimius*, etc.) is paraphyletic – a problem left unresolved.

Gildenkov's phylogeny

In the last part of his series of books, GILDENKOV (2001) presented a new hypothesis on the relationships of the genera of Oxytelinae. He used 70 characters and weighted the ones he thought most important. He did not use the word outgroup and all his taxa are in the ingroup. The characters were polarized a priori, possibly on the basis of unstated outgroups. He did not, however, explain why he polarized transformation series in one way and not the other. The species he used in his data matrix are not mentioned, nor whether he observed these characters himself or used published data. Further, he did not mention how he produced his tree, though it appears to have been produced manually without formally defining the procedure. Only one tree was presented, without explanation of why it was thought to be better than any other possible tree. Parsimony was not mentioned. Essentially, the data could not be checked; this analysis was arbitrary. He specifically said that features of the mandibles, legs and the metendosternite are adaptive

Fig. 1. Phylogenetic hypothesis of Oxytelinae from the Tree of Life webpage (NEWTON 1995)

characters and do not help in reconstructing the phylogeny, but rather they illustrate adaptations of lineages. He a priori excluded the characters of the metendosternite from the analysis, but did use some features of mandibles and legs. Finally, he mapped the "adaptive" characters on his tree. He linked the adaptive characters with different life styles ("zhiznennaya forma") and assigned all genera of Oxytelinae to five life-style categories. Although the work was largely based on HERMAN's (1970) and NEWTON's (1982) publications, some other papers by these authors are strangely ignored (or at least their results are not accepted, without explanation). For example, the sister-group relationship of *Bledius* and *Eppelsheimius*, established by HERMAN (1983*b*) is not accepted (without explanation). In contrast to the four tribes recognized by earlier authors, GILDENKOV (2003) proposed a five tribe classification. The genera included in Gildenkov's tribes are rather different from the system outlined in HERMAN's or NEWTON's publications, the Tree of Life webpage and the one proposed in the present work. In his system, the name of the fifth tribe (Mandini GILDENKOV, 2003) is a replacement of Acrognathini REITTER, 1909, but for which there is an older name, Planeustomini JACQUELIN DU VAL, 1857 (see new classification on p. 98).

New generic descriptions

After the reassignment of *Euphanias* to Oxytelinae (NEWTON 1982) and the discovery of *Oxypius* (NEWTON 1982) three additional new genera were described: *Mitosynum* CAMPBELL, 1982, *Platydeleaster* SCHÜLKE, 2003 and *Jerozenia* HERMAN, 2003. These genera are monotypic, so while they contribute to the understanding of evolutionary tendencies, they leave the basic classification scheme of Oxytelinae unchanged. SCHÜLKE's (2003) description of *Platydeleaster* contains a discussion of its proposed placement and changes in the understanding of relationships among basal Oxytelinae. This discussion, however, was not supported by any formal analysis or character matrix. The newest described genus, *Jerozenia* HERMAN, 2003 is apparently a basal member of the tribe Oxytelini (as the author suggested indirectly). Two specimens were collected from a raiding column of an unspecified species of ant, one in flight, so it is probable that, as with *Ecitoclimax* (to which *Jerozenia* is supposed to be most closely related), this taxon is associated with ants. KASTCHEEV (2003) proposed another generic name, *Coprostyzus*, based on a species newly described and represented by two female specimens from Kazakhstan. Neither of the two types were examined by me, and based on the description alone it is not clear that the new species indeed deserves generic status (for this decision, male specimens would be essential). The character KASTCHEEV based the new genus on also (partially) occurs in *Coprophilus longicollis*. Very recently, additional undescribed species were found by the present author in previously monobasic genera (*Crassodemus*, *Ecitoclimax*), and both of these new discoveries necessitated some changes in the definitions of the genera.

Fig. 2. The strict consensus tree (Acctran optimization). Numbers above hatchmarks refer to characters. Numbers below hatchmarks indicate state transformation (to the state indicated). Homoplasious characters indicated with open marks. (Tree length = 266, Consistency Index = 0.36, Retention Index = 0.64)

Paleontology

The oldest known staphylinid was discovered in the United States, on the Virginia – North Carolina border (VMNH 734), dated Late Triassic, but not named (Fig. 1 in FRASER *et al.* 1996). As with most compression fossils, it is impossible to examine the critical characters in order to place the taxon among subfamilies or tribes. The earliest described (named) staphylinid taxon is *Anicula inferna*† RYVKIN, 1985; an excellent photograph of this species is on p. 177 (Fig. 229) of PONOMARENKO (2002). This species was placed in Olisthaerinae (now believed to be close to or included in the Tachyporinae). The age of this fossil is Early to Middle Jurassic; it was found in Novospasskoye (Siberia, eastern Transbaikalia). The oldest fossils of Oxytelinae were described from the Jurassic of Karatau. Karatau (a group of localities, the most famous being Aulie [=Mihailovka]) is in Kazakhstan, dated Late Jurassic, approx. 155 Mya. *Mesoxytelus parvus*† TIKHOMIROVA, 1968 and *M. mandibularis*† TIKHOMIROVA, 1968 possess features characteristic of either Thinobiini (general shape of forebody, but especially the strongly rounded elytral apex, reminiscent of *Thinobius* and *Bledius*) and three longitudinal ridges on the pronotum, characteristic of most, but not all, *Oxytelus* and *Anotylus*. This makes it probable that these species are closely related to the most recent common ancestor of these two lineages. These lineages themselves are obviously quite ancient compared to the known age of other staphylinid groups. Well-preserved fossils that actually allow placement into tribes (or even genera) only exist for *Lesteva* (Omaliinae, in tribe Anthophagini) and *Tachinus* (Tachyporinae, in tribe Tachyporini). Two other interesting oxyteline fossils were described by RYVKIN (1990) from Russia; they are *Turgaphloeus pubescens*† RYVKIN from Turg (or Turga, K11), Lower Cretaceous, Lower Neocomian (Turginskaya Formation) (approx. 145 Mya) and *Morda mora*† RYVKIN from Daia (or Daya, J33), Upper Jurassic (Glushkovskaya Formation) (approx. 150 Mya). These taxa are similar to species presently known in the genera *Carpelimus* and *Thinodromus*. Two species of *Megalymma*† TIKHOMIROVA, 1980 from the Manlay Formation (Lower Cretaceous, approx. 120 Mya), are listed as belonging in the subfamily by HERMAN (2001). These were assigned to Oxytelinae in the original author's sense, where the subfamily also included the Omaliini. The description suggests that these species are more related to omaliines, therefore they should be removed from Oxytelinae. Apart from the fossil record, another good argument for the age of the major lineages in Oxytelinae is that members of the more recently derived lineages are found in New Zealand, although with restricted specific and generic diversity compared to oxytelines on the continents. According to the current hypothesis (LAIRD & BRADSHAW 2004), New Zealand separated from Gondwana in the mid-Cretaceous (approx. 100 Mya), and was not reconnected to any major landmass

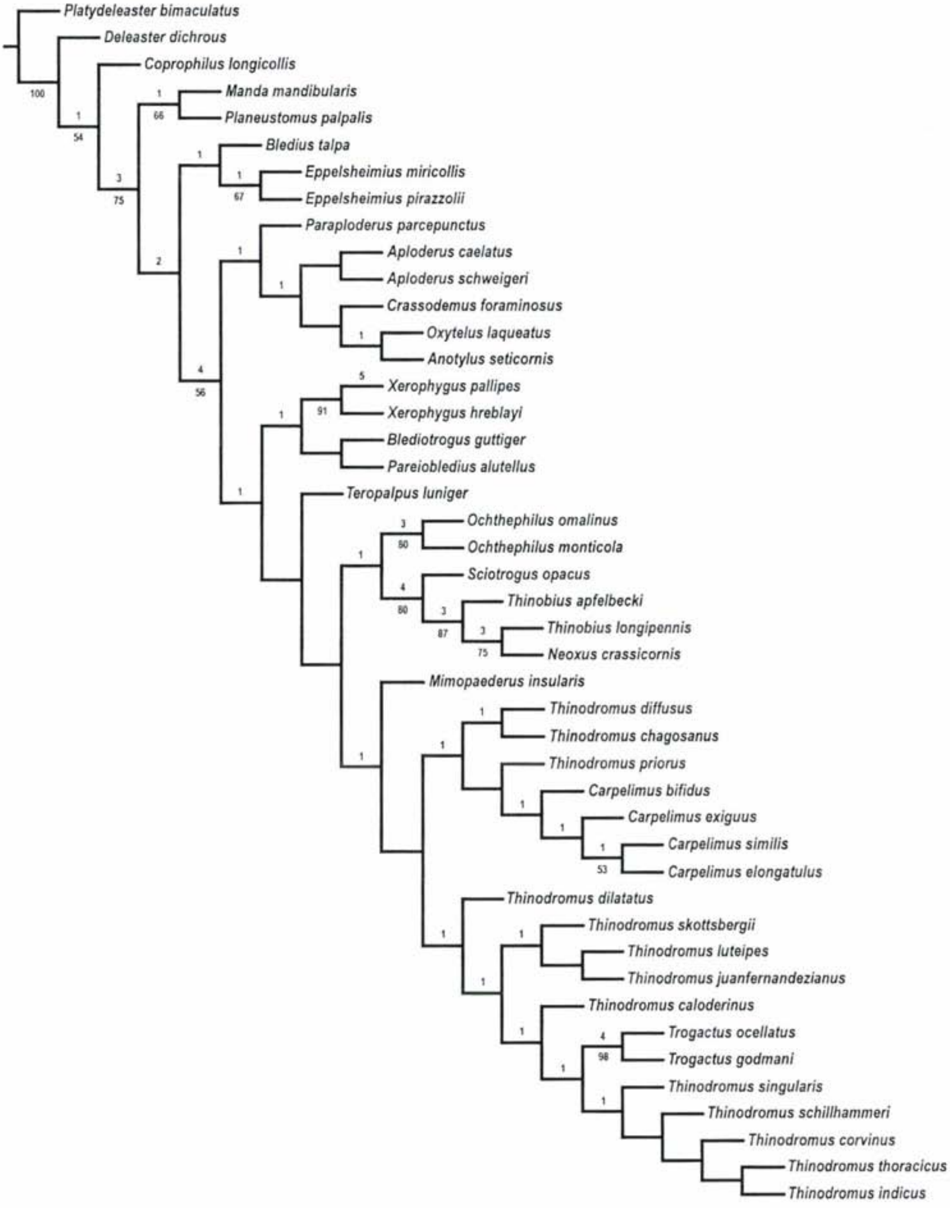


Fig. 3. One of the 32 most parsimonious trees. Bremer support values are shown above nodes. Bootstrap values are shown under nodes. Only nodes with bootstrap values above 50 are shown. (Tree length = 258, Consistency Index = 0.37, Retention Index = 0.65)

later. Consequently, the lineages found there must have originated earlier than the separation; if true, then some of the genera now recognized were already differentiated prior to 100 Mya. One can argue that the arrival of some groups might have happened later than the separation of New Zealand from Gondwana; the chance for this depends on a lot of poorly studied factors, like oceanic currents and the dispersal ability of oxyteline species. However, such long-distance, overwater dispersal does not appear to be common, for example the whole subfamily Steninae, members of which occupy rather similar habitats to those of Oxytelinae, is absent from New Zealand (KLIMASZEWSKI *et al.* 1996).

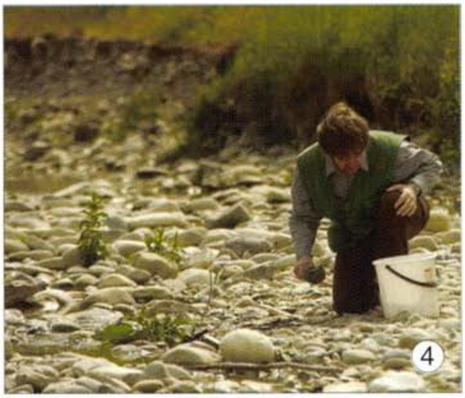
MATERIALS AND METHODS

Material studied

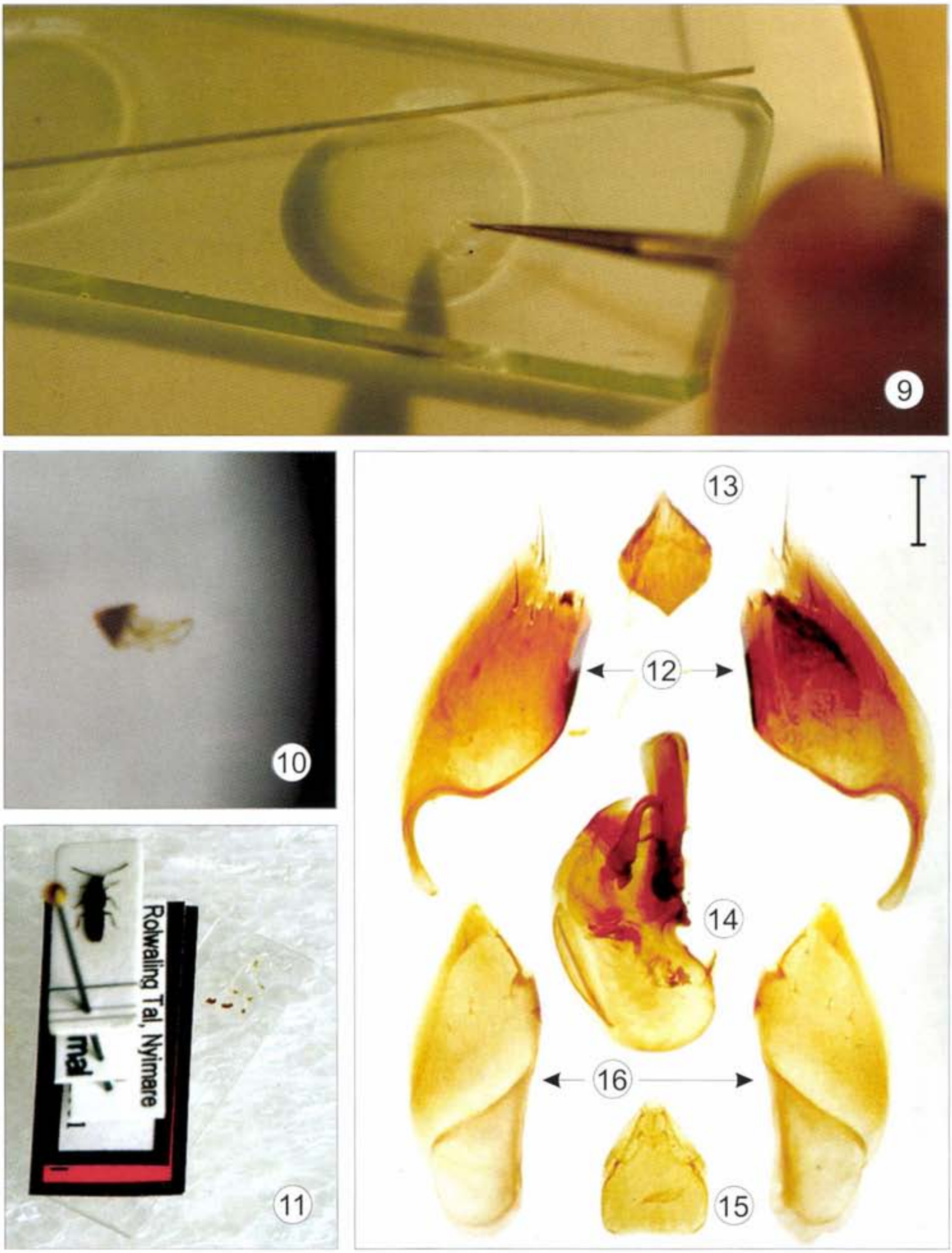
Out of the ten genera of the ingroup, the study of *Ochthephilus*, *Xerophygus* and *Trogactus* was done with a revisionary approach. The rest of the genera were investigated also on a worldwide basis, but the selection of taxa for detailed study was focused on faithfully representing their known diversity in the analysis. The creation of species groups based on real phylogenetic affinities was a goal, but for the larger genera (*Carpelimus*, *Thinodromus*) such systems are still preliminary and incomplete and subject to many changes as more taxa are described or studied. For this project, nearly ten thousand specimens were studied, either as part of the revisions or material necessary to assess the variability of characters in other genera. Although specimens for this project was borrowed from a much greater number of institutions, the following list is confined to the depositories of the material actually studied for the analysis:

AMNH = American Museum of Natural History, New York City, New York, USA; BMNH = The Natural History Museum, London, England; CASC = California Academy of Sciences, San Francisco, California, USA; FMNH = Field Museum of Natural History, Chicago, Illinois, USA; HNHM = Hungarian Natural History Museum, Budapest, Hungary; ISNB = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MHNG = Muséum d'Histoire Naturelle, Geneve, Switzerland; MNNC = Museo Nacional de Historia Natural, Santiago, Chile; MRAC = Musée royal de l'Afrique centrale, Tervuren, Belgium; MZLU = Museum of Zoology, Lund University, Lund, Sweden; NHMB = Naturhistorisches Museum, Basel, Switzerland; NHMW = Naturhistorisches Museum Wien, Vienna, Austria; NHRS = Naturhistoriska Riksmuseet, Stockholm, Sweden; NMPC = National Museum (Natural History), Prague, Czech Republic; NZAC = New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand; SEMC = Natural History Museum, University of Kansas, Lawrence, Kansas, USA; SMNS = Staatliches Museum für Naturkunde in Stuttgart, Stuttgart, Germany; USNM = National Museum of Natural History, [formerly: United States National Museum], Washington D.C., USA; ZMHB = Museum für Naturkunde der Humboldt Universität, Berlin, Germany; cSch = private collection of MICHAEL SCHÜLKE, Berlin, Germany; cGdR = private collection of GUILLAUME DE ROUGEMONT, Mont de Marsan, France; cKle = private collection of ANDREAS KLEEBERG, Berlin, Germany.

Types – The interpretation of nearly all names mentioned in this work is based on the study of the relevant type specimens. More than 200 primary types were examined for the ingroups (including



Figs 4–8. 4 = The author uses the flotation method for *Ochthephilus flexuosus* MULSANT & REY, 1856 in Chancy, k. Geneva, Switzerland (photo: H. SCHILLHAMMER, May 2004). 5 = Wide streambank of fine gravel with sandy patches in the Cerna valley at Ţaţu, jud. Mehedinţi, Romania, habitat of *Thinobius* sp. (photo: GY. MAKRANCZY, April 2002). 6 = Large rocks covered with thick moss layer frequently under flowing water, Kôprova Dolina, Vyšná Závrat, western High Tatry, Slovakia, habitat of *Ochthephilus* sp. (photo: GY. MAKRANCZY, July 1999). 7 = Old flood debris stuck between roots of fallen trees and shrubs in a creek valley near Zhongdian, Yunnan, China, habitat of *Thinodromus* and *Ochthephilus* sp. (photo: M. SCHÜLKE, August 2003). 8 = Leaf packs at the streambank are habitat of *Trogactus* sp. in a tropical cloud forest in La Paz waterfall garden, near Poas Volcano, Costa Rica. (photo: D. J. L'HOSTE, October 2002).



Figs 9–16. 9 = Cavity slide covered with a regular microscope slide; tiny structures handled with forceps and a piece of tissue paper. 10 = Abdominal segments VIII–X immersed in solution. 11 = Plastic microslide attached to the pin of specimen. 12–13 = *Anotylus seticornis* (FAUVEL, 1895): 12 = tergites IX and 13 = in Euparal embedded preparation (scale 0.2 mm). 14–16 = *Anotylus* sp. 14 = aedeagus, 15 = tergite X and 16 = tergites IX with enlarged platelike ventral strut (in Euparal embedded preparation) (scale 0.2 mm).

types of synonymized names), and for a significant portion for the genera used as outgroups. Considering the many authors who contributed to the knowledge of Oxytelinae this was a major task.

Methods of preparation

Preparation techniques for the genitalia. The whole study is based largely on a new preparation technique for the genitalia (and genital segments) and the features investigated due to their accessibility attained by these preparations. There are many techniques described in the literature; they belong to two major groups:

1. Slide mounting techniques: these are based on regular microscope (glass) slides and different covering (cover slips, spacing, or none of these). These methods also require a mounting medium in which the structures are embedded and which fills the space between the glass surfaces. The two regularly used mounting media in entomology are Canada Balsam and Euparal. Preferences towards these vary depending on the investigator, the group studied and the goals of the study.

2. Preparations made for identification structures still attached to pinned specimen: there is a great array of techniques used, which range from dried structures glued to mounting card, structure placed in microvial in glycerine and pinned under the specimen to embedded structures either on microslides or on a mounting card itself. The usefulness and value of these techniques vary according to the goals of the investigation and the taxon studied. Some general principles are as follows:

a. groups with strongly sclerotized and reasonably large aedeagi (most Staphylininae and Paederinae) can be studied successfully with dry mounts (as in technique 2 above), with only occasional exceptions, when the aedeagus has to be made transparent or is specially structured (e.g. Othiini, Xantholinini);

b. the embedding system (described in technique 1 above) has distinct advantage in groups with lightly sclerotized aedeagi, and where sclerotized internal structures are critically important (Oxytelinae, Omaliinae, Steninae, Tachyporinae);

c. groups with strongly sclerotized aedeagi, but with a delicate internal sac, that can only be studied when everted (Oxyporinae, many Aleocharinae) or require other manipulation, may best be studied using the microvial system (also under technique 2 above).

Below, I discuss only the embedding system, since this is the only major method offering success with Oxytelinae. In the literature and identification practices seen, the most widespread methods are embedding of structures in a drop of mounting medium (often glue) on the card or using a separate plastic slide (which can be pinned under the specimen) with some kind of either water-soluble, or other solvent-based mounting medium. Both methods impose difficulties and dangers: (1) the glue may not be readily removable from the preparation, therefore damaging it; or (2) the mounting medium after drying over long periods, may lose transparency or split from the object or the plastic slide. The chance of such disasters happening depends mainly on the chemical nature and cleanliness of the plastic card on which the structures are mounted, the cleanliness and condition of the medium, and the way it is applied. I experimented with the embedding system for years. For development and perfection of my technique, credit should be given to Dr. MIKAEL SÖRENSSON (Lund, Sweden) and Dr. JAN KLIMASZEWSKI (Quebec, Canada), who gave considerable advice and supplied mounting materials. The goal was to produce a microslide preparation that can be pinned under the specimen (Fig. 11) and still allow convenient examination of very delicate structures like female genitalia. For the above mentioned reasons a microscopic slide preparation was always out of the question, but the transparency, optical clarity and methods of study had to be near that of regular microscope slides. An appropriately clean and medium-thin (approx. 0.5 mm thickness) plastic microslide with a drop of Euparal mounting medium proved the best approximation. Having removed it from the pin of a specimen, placed on top of a microscope slide, such preparation could be studied under a compound microscope up to 400 times magnification, occasionally higher, and provided clear, sharp images. This is mainly due to the superior optical properties of the Euparal. The method described below gives a good compromise between satisfying the needs of individual, detailed investigation and serial identification work.

Genital preparation method for plastic microslides attached to the pins of the specimens. The key object of this preparation method is a cavity slide covered with a normal microscopic slide (Fig. 9). This provides easy-to-access area with little airspace; this latter feature is important, because little solvent tends to evaporate very fast, lots of solvent makes it difficult to find/manipulate the object. The appropriate cavity slide (deep cavity, double, 3mm thickness) avoids the very inconvenient situation of the alcohol running in between the glasses of the cavity slide and the one covering it. This is never a problem with the potassium hydroxide solution or the distilled water, but it is with the absolute (100%) ethyl alcohol because of its different surface tension.

1. Dissect in distilled water (on the card, a separate wet cardboard or tissue paper or as you like). For some kinds of staphylinid beetles, especially the very small ones, it is advantageous to detach the tip of abdomen (eighth segments and thereafter) and keep this unit together (Fig. 10) until it is placed into the Euparal drop and only further dissect it within the drop.

2. Place the object into a drop of cold, concentrated potassium hydroxide solution in the cavity of the slide. It should be left there for about 5 hours at room temperature, depending on the sclerotization and pigmentation. Heating and even boiling is suggested by other authors (e.g. HANLEY & ASHE 2003), but this may destroy delicate structures and was not used by me.

3. Remove the object and place it into a drop of distilled water; neutralization of the potassium hydroxide can be facilitated by adding a very little acetic acid to the distilled water (it should not be more concentrated than 2–4% acid, otherwise it causes shrinking and distortion of the structures). This drop should be in another cavity slide; a difficulty is that the object may dry out while moved from one drop of solution to another. This can be avoided by moving it either with a sharpened wooden stick or with a tiny piece of paper tissue held by a forceps (Fig. 9). Both absorb enough fluid to keep the object wet while being moved, yet not enough to corrupt the fluid in the next step. The washing can last from a few minutes to days but care must be taken to avoid accidental drying with longer washing times.

4. Next step is an alcohol dehydration series: first 20% then 80%, finally 100% ethyl alcohol. The concentrations are approximate, with the exception of the last. When the object is moved through all these solutions, staying for about 20 minutes in each, it is ready to be moved from the 100% ethyl alcohol into a droplet of Euparal on the plastic slide (see 5 below). The alcohol evaporates very rapidly, leaving air bubbles in the structures, so the last step has to be done with the greatest care and speed. For very delicate objects, an intermediate step, immersion in Euparal Essence before the transfer to Euparal, may be advisable to avoid shrinking or distortion.

5. Finally, prepare a suitable plastic slide (suggested dimensions: 6 × 19 mm) with a little drop of Euparal on it. The droplet should be just large enough to fully cover the object when it is placed into it. Then the object is moved into the Euparal drop. When the object settles (1 minute), dissection must be done within the drop and the parts arranged in the order and orientation preferred for study. The first little drop will dry within a few minutes, because its dilution by the alcohol contained in the structures themselves. The reason of transferring the objects to such a small amount of medium is to quickly fix the objects on the slide, so that the dissected parts will not float around and become fixed in undesirable positions. After about 10 to 20 minutes, another small drop should be added on top. Some experimentation is needed with the necessary time and the amount of Euparal, since it may differ with size, and certain other characteristics specific to the taxon studied. The preparation must not left to dry completely in the first small drop stage (dangers: air bubbles, distortion). Gradually in-

creasing the time intervals to eventually days, more Euparal should be added, until it covers every object on the slide fully. In some cases, most importantly, when the aedeagus of a unique specimen should be examined or drawn from several aspects, it is preferable to embed the aedeagus in Euparal on a separate plastic slide after dissection. For the reasons of clarity and occasional shifting, it is not good to make drawings from freshly made preparations. Turning the object to provide another orientation after several days will require dissolving the Euparal preparation by adding another drop of medium or solvent. It is inconvenient and potentially damaging to do with all the other objects in the same preparation, because the previously desirable orientations will be destroyed. Objects other than the aedeagus of the male do not require turning once they are correctly positioned in the preparation. By placing the aedeagus on a separate plastic slide, only the aedeagal preparation needs to be softened for re-orientation.

Handling of already made preparations. Dissolving an embedded preparation is easy; a drop of absolute ethyl alcohol added on top of the medium will dissolve the Euparal within a few minutes. It may be necessary to add several other drops of alcohol with intervals of a minute or so until the embedded objects are floating freely.

Tips on repairing bad preparations. The most common problem with such preparations is that (1) the objects are badly positioned or (2) they have internal air bubbles (which make their interior blurry or invisible). In both cases the embedded preparation (or parts of it) must be dissolved. To remove air bubbles, the object should be placed in Euparal Essence, which usually helps getting rid of the bubbles in the course of a few hours to several days depending on the nature of the object and the size of the bubbles.

Slide preparations. For some characters used in the phylogenetic analysis, it was necessary or advantageous to make permanent, full-body preparations on glass microscope slides. The methods and arrangement on the slide were based on the work by HANLEY & ASHE (2003), only slightly modified to fit the characteristics of this taxon (boiling of parts in potassium hydroxide avoided, hydrogen peroxide only occasionally used to bleach the exoskeleton of very strongly sclerotized, dark specimens).

Photography and drawing

Habitus photographs, scanning electron microscopy (SEM). The photographic material used in this paper came from a variety of sources. Many of the habitus photographs were prepared by the author from multi-layered shots taken with either Nikon D70 or a Canon EOS-1D digital camera using Microptics' Digital Lab system. Some were donated by other specialists or taken at various museums. An attempt was made to use the best available specimens. The different layers, when available, were montaged by hand using Adobe Photoshop 7.0. Dry specimens for SEM photographs were sputter coated for about 5 minutes with gold+palladium (60:40) which produces a layer approximately 35 nm thick, and then studied using a LEO 1550 Field Scanning Electron Emission Microscope. Habitus photographs were prepared using a Microptics ML1000 Digital Imaging System.

Illustrations of structural details. The illustrations one can find in literature of the most important diagnostic details are predominantly line drawings. In a few cases, one can also find SEM images and regular print photography. While the advantage of the SEM photography primarily lies in the great depth of field and clarity for very small objects, providing a great 3-D sense, the pictures often tend to deviate from what is observed on an actual specimen examined with a dissecting microscope. Advantages of illustrations using regular photography are the fidelity of the image to how a worker finds these objects when identifying specimens or making a dissection, but the drawbacks are the shallow depth of field and resulting low clarity. I think that this method should be reserved for documentation purposes (e.g. for particularly important type specimens), rather than for illustration of diagnostic features. While the amount of time required to take a photograph is much less than preparing a good quality line drawing, the latter is usually superior in terms of emphasis on the relevant details and comparability. The relevant details (diagnostic features) differ greatly often even between closely related taxa. For this reason, the illustration styles developed for the different groups emphasize different structures and achieve that by a variety of techniques.

Line drawings. Illustrations of mouthparts are a standard for modern taxonomic works on staphylinids. Great difficulty was encountered here, because for this subfamily there was no developed style for detailed mouthpart illustrations, so it had to be created in the course of this study. The works used for reference are GUSAROV (2003) and HANLEY (2003) on Aleocharinae, where the mouthpart structures are so critical that the illustrations and naming of structures are far more developed than for any other staphylinid group. One of the greatest novelties of this work is the extensive use of a female genital structure here called the ring structure, most likely homologous to the accessory sclerite of female omaliines (and some other subfamilies) (ZANETTI, pers. comm.) and possibly derived from sternum X. The name ring structure refers to the usually ring-like shape of this structure in many species, although in some cases it is more complicated, barely resembling a ring. The significance of this structure is that in many groups, where the females could not be reliably identified, this structure gives a reasonable (although quite laborous) means of identifying them. It is also useful in associating unique female-only type series with the correct species, therefore fixing the identity of a species. This feature is now extensively used in those groups (*Carpelimus*, *Thinodromus*) where the ring structure is more complicated and therefore provides good characters for distinguishing closely related species. Because of its relative simplicity, for many genera treated herein, the spermatheca is of limited use in differentiating species. The situation is different for the *Thinobius* group of genera, where the spermathecal duct has a longer sclerotized part and is often good for identification of species. For most of the taxa treated in this work, a novel illustration approach for the aedeagi was used. (1) The taxa that have complicated, multi-layered inner structures are shown in 3 drawings: side view, outer shell of aedeagus from frontal view and inner structures of aedeagus from frontal view. (2) The taxa in which certain parameral structures have importance, and also those in which the internal structures and the base of the parameres tend to be at the same spot from frontal view, are shown with about 15° tilt. This helps to avoid the overlap and gives the viewer an impression of the three dimensionality of the structures. The words dorsal, ventral and lateral are abandoned in favor of frontal view (which means seen from the side of basal pore) and side view. Some issues regarding the use of these terms are discussed by GUSAROV (2002), but more importantly, many oxyteline groups tend to have their genitalia rotated in the abdomen and the degree of this often differs between specimens. For specimens already dissected, the original position of the genitalia could not be determined. Mostly these disadvantages required change to new terminology. An effort has been made to name and homologize the sclerites of the internal sac of the median lobe. This was a novel approach, although similar work has been done in the Aleocharinae by BRUNDIN (1944) and YOSII & SAWADA (1976), who were notable for investigating an enormous depth of structural detail (but especially the latter author's work focuses on the setation in mouthparts rather than the morphology and homologies of the aedeagi). Some terminology was also borrowed from the works of KLIMASZEWSKI (1984) and GUSAROV (2003). The dissections themselves were made using a Wild M8 dissecting microscope, but investigations of surface sculptures, mandibular structures and other tiny details were carried out with Olympus microscopes (SZ60, SZH). Most drawings were made using an Olympus BH-2 compound microscope with drawing tube (camera lucida). This microscope was extensively used for examination of very small details, it offers the feature of Nomarski differential interference. Although this feature cannot be fully used with non regular microscope slides, the quality and detail of the picture is still excellent.

CHARACTERS AND CLASSIFICATION

New characters studied

The morphology of the Staphylinidae was extensively studied by BLACKWELDER (1936) and NAOMI (1987*a*, *b*, 1988*a*, *b*, *c*, *d*, 1989*a*, *b*, *c*, *d*, 1990), however, these works barely go beyond mentioning of some features specific to Oxytelinae, and do not discuss the variability within the subfamily. The generic revision by HERMAN (1970) introduced a few new characters, primarily the ones used in his analysis. GILDENKOV (2001) examined the variability of some traditional characters (aedeagus, spermatheca, tarsal and tibial features, mandibles and the metendosternite) but concluded that most of these are of little use in classification. The origin of this project was the discovery of the usefulness of the last visible, full abdominal segments and terminalia in the identification of taxa in the *Carpelimus* group. Previously the only taxa where the abdominal segments received proper attention and illustration in the literature belonged in the tribe Oxytelini: the genera *Apocellus*, *Anotylus*, *Oxytelus* and *Platystethus* all possess peculiar structures on the genital segments of the abdomen. Sometimes these are secondary sexual characteristics, so that only males have them – which are extensively used in the identification to species (CAMERON 1930 and countless others since). These structures in taxa outside the above mentioned genera rarely were mentioned, certainly not enough to facilitate identification. One good example is in *Ochthephilus*, where authors generally had agreed that the male genitalia were useless for identification to the species level (SMETANA 1967, LOHSE 1964). It turns out that not only were these authors wrong about this, but the characters in the genital abdominal segments alone permit identification of all the 15 central European species (MAKRANCZY 2001). The situation is similar with most other genera of the *Carpelimus* group and even in the *Thinobius* group. Species whose females could not be identified earlier can now be diagnosed safely even without association of male specimens (MAKRANCZY 2002, 2004 and SCHÜLKE & MAKRANCZY 2003). Based on experience with other groups, the characters in the terminalia and the genitalia itself carry much phylogenetic information. Although I am aware of TORRE-BUENO's different interpretation of the terms terminalia (which in his sense also includes the genitalia) and genitalia, throughout this work they will be used for separate suites of characters.

The genera studied

The history of the genera and their hypothesized relationships were explained roughly in the previous chapters. The break-up of the tribe Coprophilini into Deleasterini, Coprophilini and Thinobiini by NEWTON & THAYER (1992*a*) and the establishment of the sister-group relationship between *Bledius* and *Eppelsheimius* were the last major landmarks in the classification of the subfamily. Within the tribe Thinobiini, the *Thinobius* group (*Thinobius*, *Neoxus* and *Sciotrogus*) stood separate from the *Carpelimus* group since HERMAN's (1970) generic revision. The *Carpelimus* group in the present sense consists of the genera *Blediotrogus*, *Pareiobledius*, *Teropalpus*, *Ochthephilus*, *Thinodromus*, *Trogactus*, *Xerophygus* and *Carpelimus*. The phylogenetic reletionships among these genera were originally thought to be quite important for the phylogeny of the whole subfamily (giving resolution to most of the poorly defined clades). Later I realized that the inclusion of representative taxa of all the major clades within the former tribe Thinobiini (genera like *Manda*, *Planeustomus*, *Crassodemus*, *Aploderus* and representatives of the tribe Blediini) is necessary to properly reconstruct relationships. Therefore the range of taxa in the outgroup was expanded to include all the above listed taxa in the hope that they will provide information determining the relatedness and paraphyly of the former Thinobiini to Oxytelini. The range of the ingroup taxa was not changed even after the analysis revealed that they in fact do not form a monophyletic group. In the references section, only those publications are listed that introduced names hereby changing their status (and their currently valid names). For the rest of the synonyms, please refer to HERMAN (2001), who adequately details their taxonomic history. In the descriptions of genera, the character states are followed by their character number used in the analysis. This helps finding them in the character matrix (Table 1) and comparing their distribution among the treated taxa. The figures illustrating the previously unused characters are referenced in the character list.

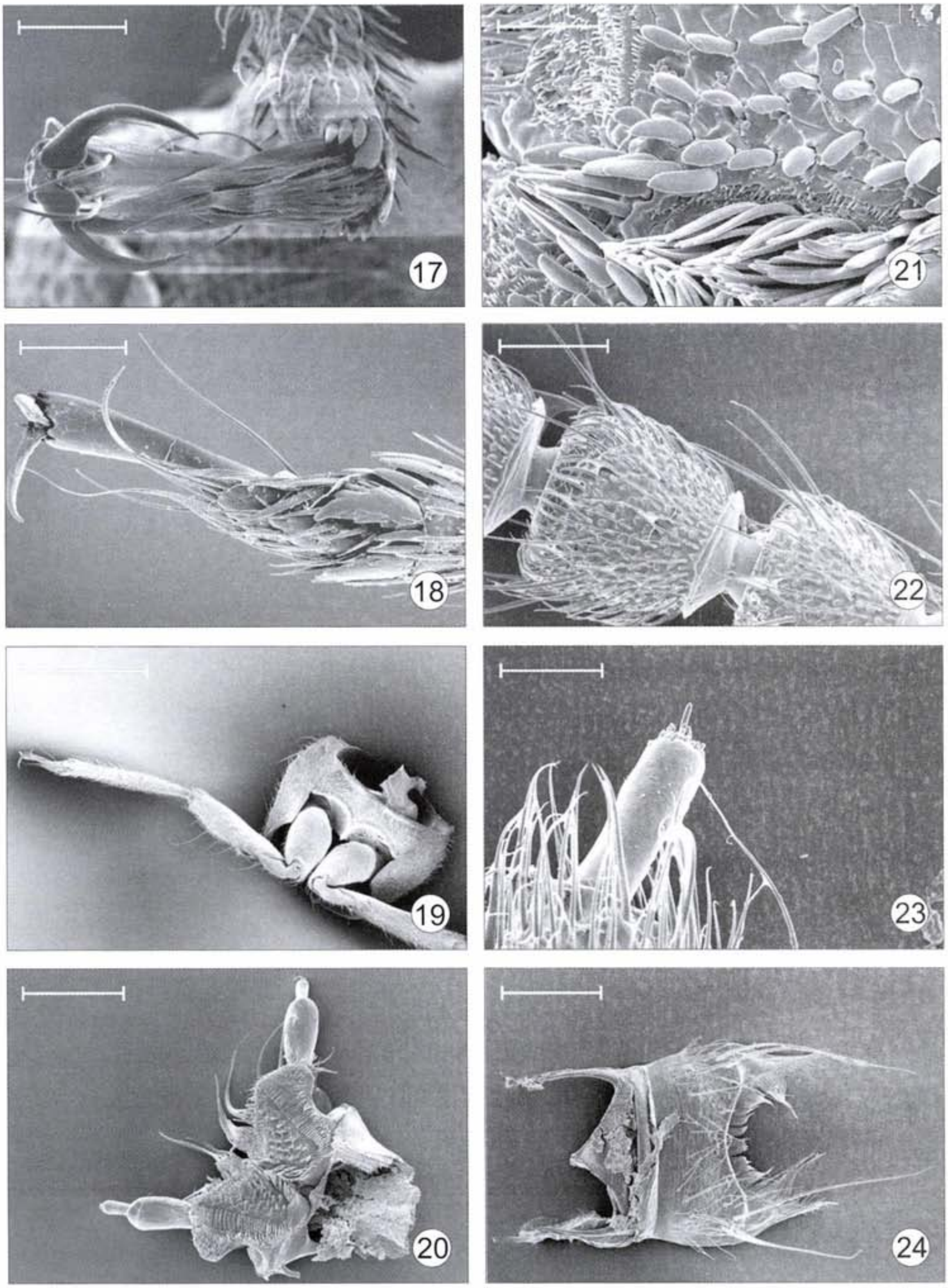
Blediotrogus SHARP, 1900

Blediotrogus SHARP, 1900 (type species: *Blediotrogus guttiger* SHARP, 1900)

Description – Medium-sized (3.0–4.5 mm), usually dark brown, but some species reddish or yellowish brown. Head and pronotum usually more weakly pubescent than the elytra and especially the abdomen. Elytra parallel-sided, a large spot at the postero-apical corners either lighter or darker than the rest of the elytra; the size and distinctness of this spot varies greatly. Temples distinct, abdomen broadest at (or around) the 6th segment. Tibia with spines. The difference between sexes in the formation of sternum VIII is often very small, sexes are hard to recognize (males usually have broader tip of terminalia). – Head. Clypeus [**1**] well developed, epistomal suture [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent, but not on anterior portion. Head [**5**] without dorsal midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] divided, transverse [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal setae [**10**] on epipharynx absent. Hypopharynx [**11**] undivided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] present. Front of hypopharynx [**14**] not entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate with central stick continuing till end. Last palpomere of maxillary palp [**17**] fully formed, strongly bulbous basally, digitiform sensillae [**18**] present on last palpomere, arranged [**19**] in parallel fashion. Labial palp [**20**] not hairy. Antennae [**21**] straight and [**22**] moderately elongated. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] not exposing protrochantins. – Legs. Tibia [**26**] with mid-tibial spur(s) and [**27**] spines or rows of stiff setae. Tarsal segmentation [**28**] 3–3–3 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] absent, carina [**41**] not present on any sternites. Fimbriate edge [**42**] on tergite VII unmodified. Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its

Table 1. Data matrix of character states for the *Carpelimus* group and outgroup taxa. Inapplicable states are shown as "–"

	0	1	2	3	4	5	6	7
	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0
Platydeleaster bimaculatus	000000000	0000000000	0000000000	0000000000	0000000000	0000000000	000000-0--	0
Deleaster dichrous	000100000	0000000000	0000000000	0001000000	0000000000	0000100000	000020-0--	0
Coprophilus longicollis	010000000	0000100001	0000000000	0000001000	0000100100	0000240000	000010-0--	0
Manda mandibularis	101001001	0000000000	0000011000	0001001011	0000000000	0000140000	0000211000	1
Planeustomus palpalis	101002001	0000000001	0000011011	0000001111	0000000000	0000040000	0000210000	0
Crassodemus foraminosus	000100102	1101110001	1000011010	0101001111	0000201000	0000200000	0001011000	1
Aploderus caelatus	000100102	1001000002	0000001020	0101001111	0000201000	0000200000	0104010100	0
Aploderus schweigeri	000100102	1001000002	0000011020	0101001111	0020201000	0000200000	0104010100	0
Paraploderus parcepunctus	000100102	1101000002	0000011020	0101001111	1000200000	0010231100	0304211100	0
Oxytelus laqueatus	010100002	1001000302	0000011020	0101001111	1000201000	11-0210100	0004010100	0
Anotylus seticornis	000100002	1101000302	0000010020	0101001111	2000211000	01-0200000	0102011101	0
Bledius talpa	000100102	0010110002	0100010010	0001101111	0000200000	0000210000	1201211000	0
Eppelsheimius miricollis	000100003	0010010001	0100000000	0001101111	0000201000	0000040000	0000210000	0
Eppelsheimius pirazzolii	000100003	0010010002	0100000000	0001101111	0000201000	0000040000	0000210000	0
Sciotrogus opacus	000100012	111000133-	0000001130	-101011111	1000200000	0010211000	0000111000	0
Thinobius apfelbecki	000100012	1010001202	0000101130	-101111111	1000200000	0000200000	0002111001	0
Thinobius longipennis	000100012	1010001202	0001101130	-101111111	1000200000	0000240000	0013210001	0
Neoxus crassicornis	000100012	1010001202	0000111130	-101101111	1000200000	0000240000	0013211001	0
Blediotrogus guttiger	000200102	1011001102	0000011000	1101001111	0000200000	0000210000	0001211100	1
Pareiobledius alutellus	000100102	1011000102	0000011010	1101001111	0000201000	0000210000	0001211000	1
Teropalpus luniger	000000102	1011001102	0000011100	0101001111	0010200000	0000230000	0000211100	0
Ochthephilus omalinus	000100002	1000002102	0000001100	1101001110	0000200000	0000100000	000010-0--	0
Ochthephilus monticola	000100002	1000001102	0000001100	1101001110	0010200000	0000000001	100010-0--	0
Carpelimus similis	000100102	1010002202	0000011120	1101001111	0000200000	01-0210000	1104111100	0
Carpelimus exiguus	000100102	1010002202	0000010120	1101001111	0000201000	01-0210000	0104111100	1
Carpelimus elongatulus	000100102	1010002202	0000011120	1101001111	0000200000	01-0210000	1104111100	0
Carpelimus bifidus	000100102	1010101202	0000011120	1101001111	0000200000	01-0210001	0104211000	0
Xerophygus pallipes	000100102	111111233-	0000011000	1101001111	0010211000	0000200000	0111211101	0
Xerophygus hreblayi	000110102	101111233-	0000011000	1101001111	0000211000	0000210000	0011211101	0
Mimopaederus insularis	000100102	1010101102	2000011100	1101001111	0100200000	0000230000	0000111100	0
Thinodromus priorus	000100102	1010102202	0000011100	1101001111	0000200000	0011210000	0204211100	1
Thinodromus dilatatus	000100102	1111101202	0000011100	1101001111	0000200000	0010222010	1004111100	0
Thinodromus corvinus	000100102	1010001322	2000011100	1101001111	0000200000	0010202011	1004011000	0
Thinodromus caloderinus	000100102	1110101322	2000011100	1101001111	0001200000	0001220000	1004111010	0
Thinodromus skottsbergii	000100102	1110101202	0000010100	0101001111	0000200000	0011220000	1004211101	0
Thinodromus juanfernandezianus	000100102	1110101202	2000011100	0101001111	0020201000	0001220000	1104211101	0
Thinodromus luteipes	000100102	1110001202	2000011100	1101001111	0000200000	0001220000	1104211101	0
Thinodromus diffusus	000100102	1111002312	0000011100	1101001111	0000200010	0001200000	0104011110	0
Thinodromus chagosanus	000100102	1110102202	0000011100	1101001111	0000200000	0000210000	0104111110	1
Thinodromus thoracicus	000100102	101010233-	2000011100	1101001111	0000200001	0000211010	1204111100	0
Thinodromus indicus	000100102	1010102322	2000011100	1101001111	0000200000	0000220011	1004211100	0
Thinodromus schillhammeri	000100102	1010102322	2000011100	1101001111	0000200000	0000210001	1104211000	0
Thinodromus singularis	000100102	1010102322	2000011100	1101001111	0000200000	0000210000	1004111000	0
Trogactus ocellatus	000100102	111010133-	2010011100	1111001111	0100200000	0000210000	1004210000	0
Trogactus godmani	000100102	1110101312	2010011100	1111001111	0100200000	0000210000	1004210000	0



Figs 17–24. *Ochthephilus praepositus* MULSANT et REY, 1878: 17 = tarsal lobes from ventral view (scale 50 µm). *Xerophygus pallipes* MOTSCHULSKY, 1857: 18 = tarsal lobes (scale 40 µm); 19 = pronotum from ventral view (scale 400 µm); 20–21 = hypopharynx (scales 100 and 20 µm); 22 = midantennal segments (scale 50 µm); 23 = last segment of maxillary palp (scale 20 µm); 24 = labrum (scale 120 µm).

basolateral parts [**45**] not fused to tergum IX. – Secondary sexual characters. Macrocephaly [**46**] absent, macrothoracy [**47**] absent. Sternum VII without spines [**48**] or row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX [**51**] present, with setae [**52**] on apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] simplified, truncated. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, without extra lobe [**59**] or membranous region [**60**], without setae [**61**]. Without visible pump and flagellum [**62**]. – Female terminalia. Female genital appendages [**63**] are divided into coxites, valvifers but no styli. Sclerites (possible remnant of sternum X) [**64**] appear as small ring. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided, not associated with invisible [**67**] spermathecal gland, tubular portion [**68**] not penetrating distal bulb, umbilicus [**69**] absent. Sclerotized "tube" [**70**] can be found.

Diversity and distribution – *Blediotrogus* contains about 5 known species. Occurs in Australia, New Zealand and Chatham Islands. Frequently found on seashores, under moist high-tide beach wrack.

Pareiobledius BERNHAUER, 1934

Pareiobledius BERNHAUER, 1934 (type species: *Bledius alutellus* BERNHAUER, 1934)

Description – Medium-sized (2.0–3.0 mm), usually dark brown, but some species reddish. Body weakly pubescent. Elytra parallel-sided, temples distinct, abdomen broadest at (or around) the 6th segment. Tibia with spines. The difference between sexes in the formation of sternum VIII is often very small, sexes are hard to recognize (males usually have broader tip of terminalia). Male macrocephaly present, but weakly expressed. – Head. Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent at least anteriorly. Head [**5**] without dorsal midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] divided, transverse [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] undivided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] present. Front of hypopharynx [**14**] not entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] composed of central stick with intermediate plate-like enlargement. Last palpomere of maxillary palp [**17**] fully formed, strongly bulbous basally, digitiform sensillae [**18**] present on last palpomere, arranged [**19**] in parallel fashion. Labial palp [**20**] not hairy. Antennae [**21**] straight. Antennae [**22**] moderately elongated. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] not exposing protrochantins. – Legs. Tibia [**26**] with mid-tibial spur(s) and [**27**] spines or rows of stiff setae. Tarsal segmentation [**28**] 4–4–4 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] absent, carina [**41**] not present on any sternites. Fimbriate edge [**42**] on tergite VII unmodified. Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its basolateral parts [**45**] not fused to tergum IX. – Secondary sexual characters. Macrocephaly [**46**] present, macrothoracy [**47**] absent. Sternum VII without spines

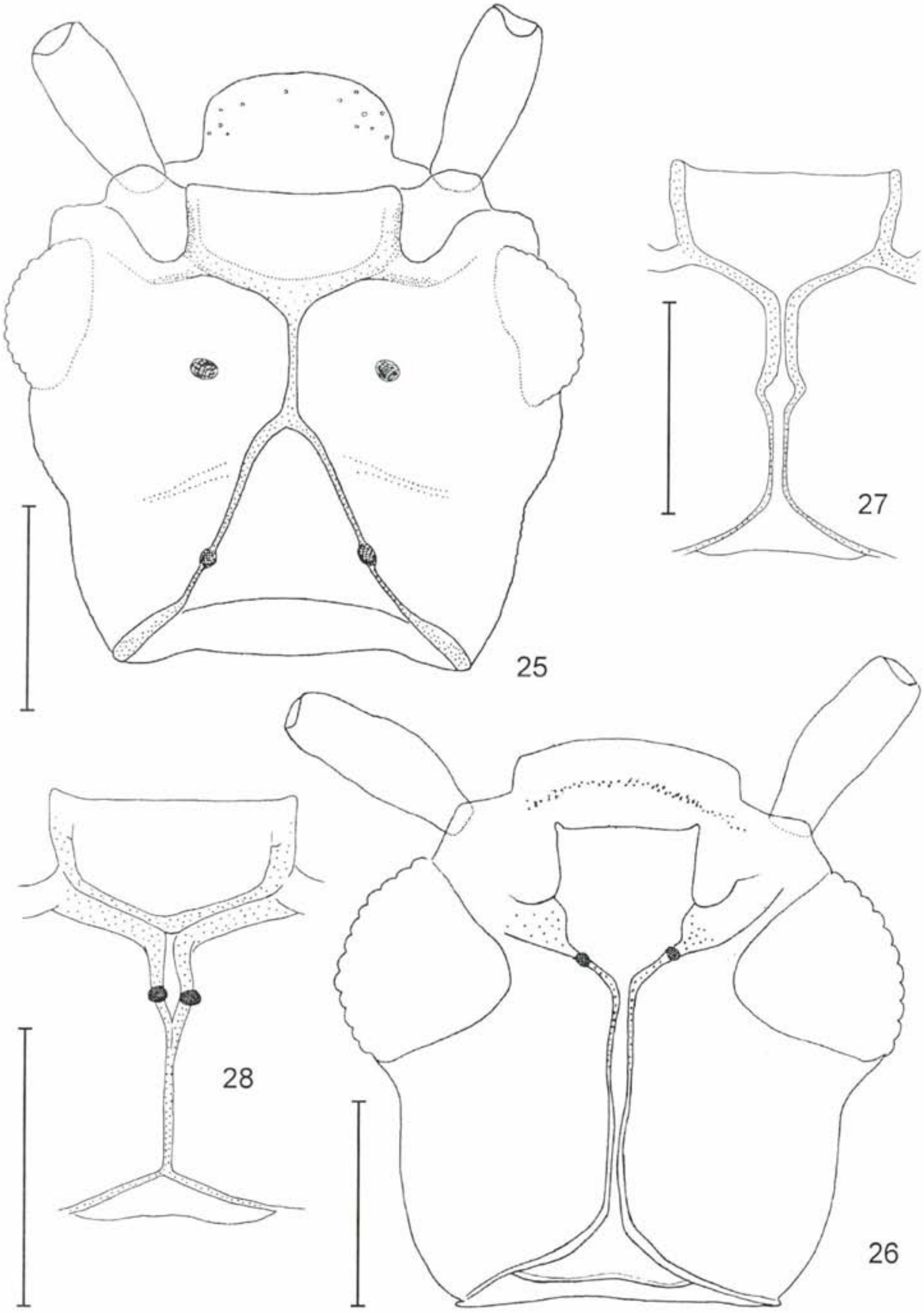
[48] or row of modified setae **[49]**. The apical edge of sternite VIII **[50]** shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX **[51]** present, with setae **[52]** on apex. – Male genitalia. Aedeagus median lobe **[53]** bulb-like, internal sclerites **[54]** present, symmetrical/paired. Apical opening **[55]** simplified, truncated. Median face membranous **[56]**, without apicomedial hook **[57]**. Parameres **[58]** not wrapping, without extra lobe **[59]** or membranous region **[60]**, without setae **[61]**. Without visible pump and flagellum **[62]**. – Female terminalia. Female genital appendages **[63]** are divided into coxites, valvifers but no styli. Sclerites (possible remnant of sternum X) **[64]** appear as small ring. – Female genitalia. Spermatheca **[65]** sclerotized. Receptacle **[66]** divided, not associated with visible **[67]** spermathecal gland, tubular portion **[68]** not penetrating distal bulb, umbilicus **[69]** absent. Sclerotized "tube" **[70]** can be found.

Diversity and distribution – Pareiobledius is an Afrotropical genus (Southern Africa and Madagascar), with 3 described species, other new species possible but of unconfirmed status. Its characteristic habitat is on seashores, under kelp.

Teropalpus SOLIER, 1849

Teropalpus SOLIER, 1849 (type species: *Teropalpus suturalis* SOLIER, 1849)

Description – Medium-sized (2.5–4.0 mm), usually dark brown, but some species reddish to pale yellowish brown. Body very densely pubescent. Elytra parallel sided, temples developed, abdomen broadest at (or around) the 6th segment. The difference between sexes in the formation of sternum VIII is often very small, sexes are hard to recognize (males usually have broader tip of terminalia). – Head. Clypeus **[1]** well developed, epistomal sulcus **[2]** present. Eyes **[3]** not extending to the ventral portion of the head. Gular sulci **[4]** narrowly separated anteriorly, more widely separated posteriorly. Head **[5]** without dorsal midline keel. The mola **[6]** on the mandibles separated, well developed. Labrum **[7]** divided, transverse **[8]**. Setation behind front of labrum **[9]** in middle much smaller, irregular or missing. Dorsal seta **[10]** on epipharynx absent. Hypopharynx **[11]** undivided, without coriaceous field **[12]** on ventral side. Lateral row of bulbous setae **[13]** present. Front of hypopharynx **[14]** not entirely covered with setae, no setae **[15]** on mid-line. Median sclerotized plate of hologlossa **[16]** anteriorly enlarged into a plate with central stick continuing till end. Last palpomere of maxillary palp **[17]** fully formed, strongly bulbous basally, digitiform sensillae **[18]** present on last palpomere, arranged **[19]** in parallel fashion. Labial palp **[20]** not hairy. Antennae **[21]** straight and **[22]** moderately elongated. – Thorax. Prosternal process **[23]** pointed, scutellum **[24]** without pubescence, hypomera **[25]** not exposing protrochantins. – Legs. Tibia **[26]** with mid-tibial spur(s), but **[27]** without spines or rows of stiff setae. Tarsal segmentation **[28]** 3–3–3 with no pseudosegment **[29]** and basal articles **[30]** uncompressed. Ventral setae **[31]** modified to form tarsal lobes, last tarsomere **[32]** only with sparse setae. – Elytra. Elytra **[33]** without puncture-rows, elytral suture **[34]** parallel, epipleural ridge **[35]** present. – Abdomen. Abdomen **[36]** with two pairs of laterosclerites. Intersegmental membrane **[37]** without brickwall pattern. Second sternite **[38]** fully developed, first sternite **[39]** completely absent. Tergal basolateral ridges **[40]** absent, carina **[41]** not present on any sternites. The fimbriate edge **[42]** on tergite VII modified into comb. Tergum X **[43]** not divided, its dorsal struts **[44]** not developed, its basolateral parts **[45]** not fused to tergum IX. – Secondary sexual characters. Macrocephaly **[46]** absent, macrothoracy **[47]** absent. Sternum VII without spines **[48]** or row of modified setae **[49]**. The apical edge of sternite VIII **[50]** shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX **[51]** present, with setae **[52]** on



Figs 25–28. 25 = Head of *Ochthephilus flexuosus* MULSANT et REY, 1856; 26 = same of *Manda mandibularis* (GYLLENHAL, 1827) (scales on both 0.3 mm). 27 = Gular sutures of *Teropalpus luniger* (FAUVEL, 1867); 28 = same of *Blediotrogus guttiger* SHARP, 1900 (scales on both 0.2 mm).

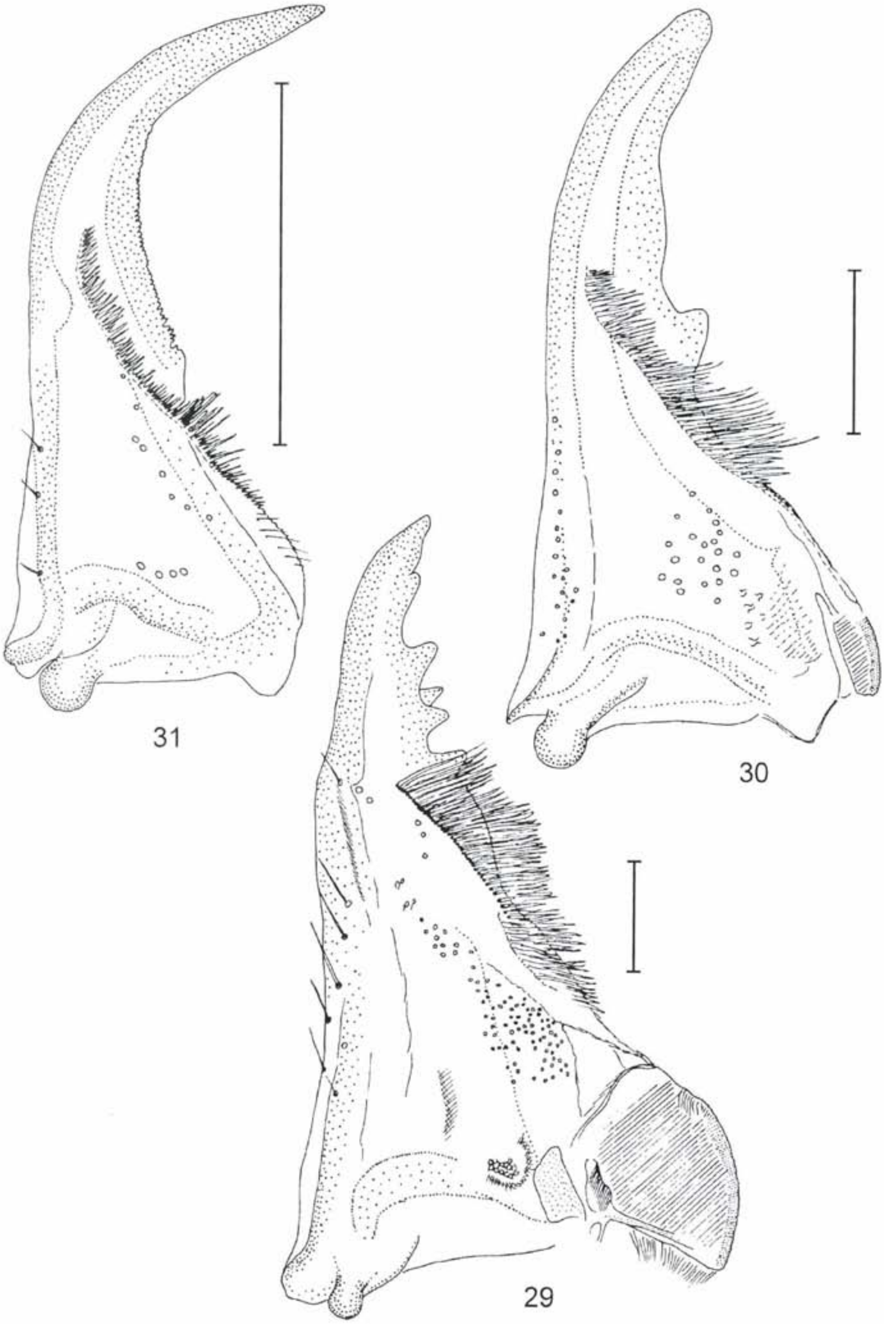
apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] well developed, modified into clasping structure. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, without extra lobe [**59**] or membranous region [**60**], without setae [**61**]. Without visible pump and flagellum [**62**]. – Female terminalia. Female genital appendages [**63**] are divided into coxites, valvifers and styli. Sclerites (possible remnant of sternum X) [**64**] appear as small ring. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided, not associated with invisible [**67**] spermathecal gland, tubular portion [**68**] not penetrating distal bulb, umbilicus [**69**] absent. Sclerotized "tube" [**70**] cannot be found.

Diversity and distribution – *Teropalpus* contains about 10 species. The origins of this invasive genus are in the temperate Southern Hemisphere, but from there it spread to virtually everywhere in the world where major marine ports can be found. It was reported from many temperate localities in the Northern Hemisphere (e.g. England, California). Not much is known about its bionomics, but specimens are found on seashores, under driftwood and algae.

Mimopaederus CAMERON, 1936

Mimopaederus CAMERON, 1936 (type species: *Mimopaederus insularis* CAMERON, 1936)

Description – Medium-sized (3.5–4.8 mm), usually reddish dark brown to black. Body very weakly pubescent, almost bare. Temples distinct. The pronotum is conspicuously elongated and cylindrical, so that the lateral margins cannot be observed from dorsal view. Elytra significantly reduced, the species flightless. Tergum VIII with characteristic formation, often very useful in distinguishing species. – Head. Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [3] not extending to the ventral portion of the head. Gular sulci [4] confluent at least anteriorly. Head [**5**] without dorsal midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] divided, transverse [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] undivided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] absent. Front of hypopharynx [**14**] not entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate with central stick continuing till end. Last palpomere of maxillary palp [**17**] fully formed, strongly bulbous basally, digitiform sensillae [**18**] present on last palpomere, arranged [**19**] in parallel fashion. Apex of penultimate segment of labial palp [**20**] hairy. Antennae [**21**] straight. Antennae [**22**] moderately elongated. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] exposing protrochantins. – Legs. Tibia [**26**] with mid-tibial spur(s), but [**27**] without spines or rows of stiff setae. Tarsal segmentation [**28**] 3–3–3 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] absent, carina [**41**] present at the base of second sternites. Fimbriate edge [**42**] on tergite VII unmodified. Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its basolateral parts [**45**] not fused to tergum IX. – Secondary sexual



Figs 29–31. Right mandibles: 29 = *Crassodemus* sp. (scale 0.1 mm); 30 = *Manda mandibularis* (GYLLENHAL, 1827) (scale 0.1 mm); 31 = *Planeustomus palpalis* (ERICHSON, 1839) (scale 0.05 mm).

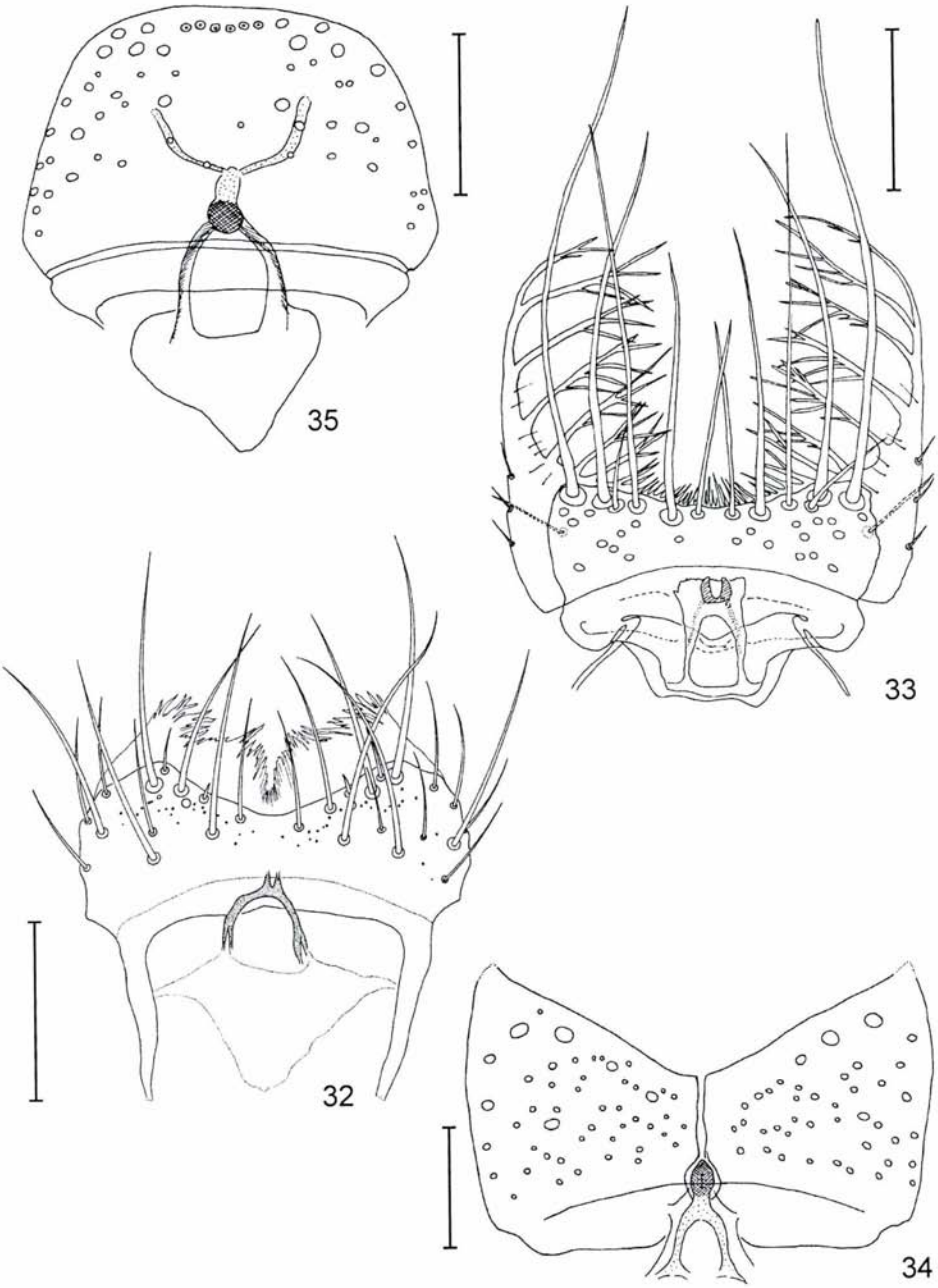
characters. Macrocephaly [**46**] absent, macrothoracy [**47**] absent. Sternum VII without spines [**48**] or row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX [**51**] present, with setae [**52**] on apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] well developed, modified into clasping structure. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, without extra lobe [**59**] or membranous region [**60**], without setae [**61**]. Without visible pump and flagellum [**62**]. – Female terminalia. Female genital appendages [**63**] are divided into coxites, valvifers and styli. Sclerites (possible remnant of Sternum X) [64] appear as small ring. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided, not associated with invisible [**67**] spermathecal gland, tubular portion [**68**] not penetrating distal bulb, umbilicus [**69**] absent. Sclerotized "tube" [**70**] cannot be found.

Diversity and distribution – *Mimopaederus* is an enigmatic taxon appearing to be exclusively South Pacific; in fact only known from 2 species occurring on Rapa Island -also called Rapa Iti to distinguish it from Rapa Nui (Easter Island). Rapa is the remnant of a collapsed volcano, its submerged crater forming the island's harbour. The age of the island is estimated 4.13–5.02 Myo (MUNSCHY *et al.* 1998). Its area is 40 km^2, latitude 27°36', no coral reefs surrounding. The highest peak on the island is Mt. Perahu (650m). Specimens of *Mimopaederus* were most often collected associated with leaves; either beaten from bushes or extracted from leaf litter. One of the species occurs in lower altitudes, the other is found exclusively around the peak of Mt. Perahu at an altitude of 550–630 m. This genus is supposed to be closely related to *Thinodromus*, it may actually be derived from an ancestor of that genus. Apart from the fully developed female genital appendages and characteristic body form, it is very similar to *Thinodromus*. The age of the island is rather young. How this taxon got there and what it's ancestor was is therefore open to speculation.

Ochthephilus MULSANT et REY, 1856

Ochthephilus MULSANT et REY, 1856 (type species: *Ochthephilus flexuosus* MULSANT et REY, 1856)
Ancyrophorus KRAATZ, 1857 (type species: *Trogophloeus omalinus* ERICHSON, 1840)
Misancyrus DES GOZIS, 1886 (type species: *Ancyrophorus emarginatus* FAUVEL, 1871)
Psilotrichus LUZE, 1904 (type species: *Psilotrichus elegans* LUZE, 1904)
Ochthephilinus EICHELBAUM, 1915 (type species: *Ochthephilus flexuosus* MULSANT et REY, 1856)
Stictancyrus SCHEERPELTZ, 1950 (type species: *Ochthephilus flexuosus* MULSANT et REY, 1856)

Description – Small to medium-sized (2.0–5.0 mm), usually dark brown, but some species reddish coloured, with the smallest ones pale yellowish brown. Elytra parallel-sided, temples developed, abdomen broadest at (or around) the 6th segment. Tergum VIII with characteristic formation, often very useful in distinguishing species. The difference between sexes in the formation of sternum VIII is often very small, sexes are hard to recognize (males usually have broader tip of terminalia). – Head.

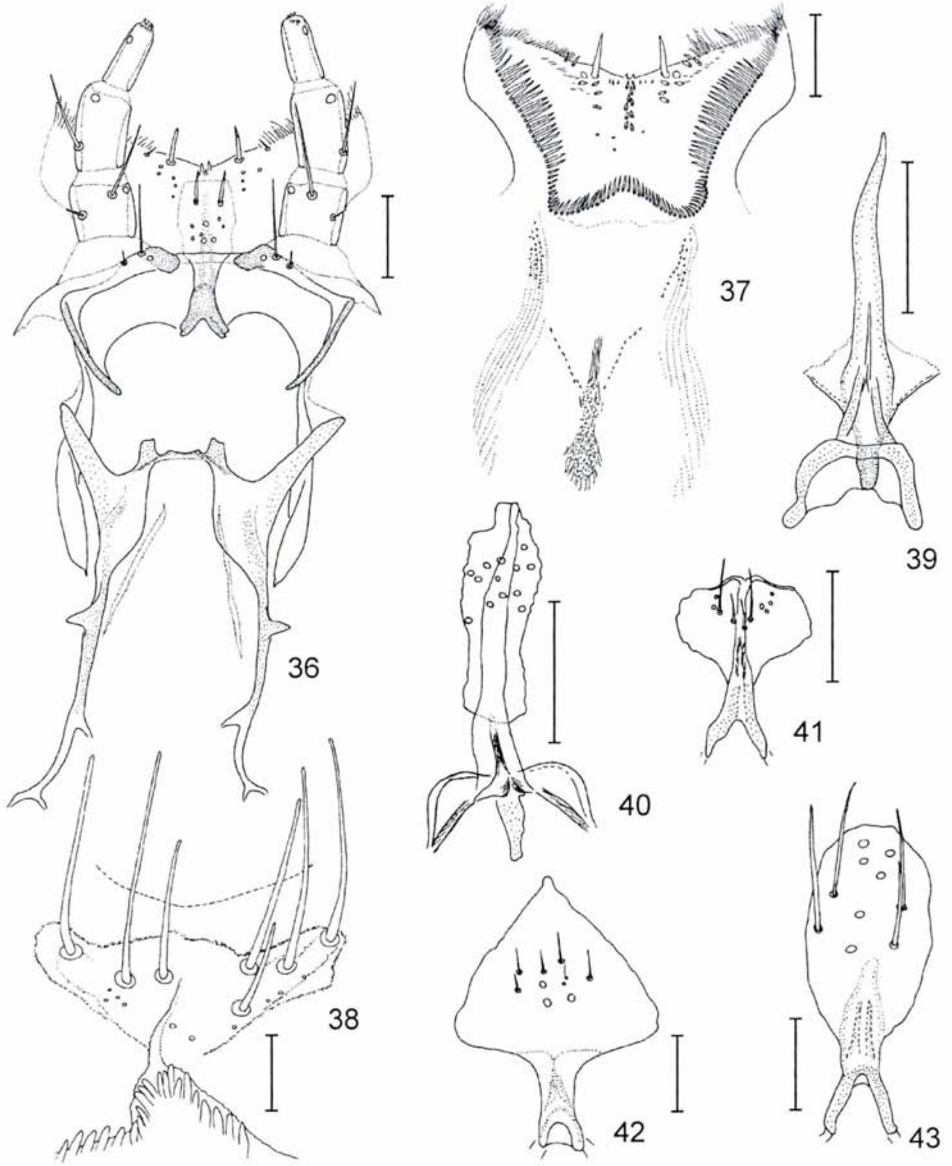


Figs 32–35. Labrum of: 32 = *Ochthephilus flexuosus* MULSANT et REY (scale 0.1 mm); 33 = *Planeustomus palpalis* (ERICHSON, 1839); 34 = *Thinodromus juanfernandezianus* sp. n.; 35 = *Sciotrogus opacus* (setation and epipharyngeal lobes not shown on 34-35) (scales on all three 0.05 mm).

Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent at least anteriorly. Head [**5**] without dorsal midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] undivided, transverse [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] undivided, with coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] absent. Front of hypopharynx [**14**] not entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate with central stick either or not continuing till end. Last palpomere of maxillary palp [**17**] fully formed, strongly bulbous basally, digitiform sensillae [**18**] present on last palpomere, arranged [**19**] in parallel fashion. Labial palp [**20**] not hairy. Antennae [**21**] straight and [**22**] moderately elongated. The 7th antennomere is usually asymmetrical, in a few species this is very well expressed. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] exposing protrochantins. – Legs. Tibia [**26**] with mid-tibial spur(s) but [**27**] without spines or rows of stiff setae. Tarsal segmentation [**28**] 5–5–5 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brick-wall pattern. Second sternite [**38**] fully developed, first sternite [**39**] present as 2 small sclerites embedded in the membrane of the second. Tergal basolateral ridges [**40**] absent, carina [**41**] not present on any sternites. Fimbriate edge [**42**] on tergite VII sometimes modified into comb. Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its basolateral parts [**45**] not fused to tergum IX. – Secondary sexual characters. Macrocephaly [**46**] absent, macrothoracy [**47**] absent. Sternum VII without spines [**48**] or row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but bears no tubercles. – Male terminalia. Male (Figs 59–60, 62–64) sternum IX [**51**] present, with setae [**52**] on apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present or absent, if present, asymmetrical/unpaired. Apical opening [**55**] well developed, not modified into clasping structure. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, sometimes with extra lobe [**59**], sometimes with membranous region [**60**], without setae [**61**]. Without visible pump and flagellum [**62**]. – Female terminalia. Female (Figs 59, 61, 65–67) genital appendages [**63**] are divided into coxites, valvifers and styli. Sclerites (possible remnant of sternum X) [**64**] appear as small ring. – Female genitalia. Spermatheca [**65**] unsclerotized (characters **66**, **68**, **69** therefore not applicable).

Spermathecal gland [**67**] visible. Sclerotized "tube" [**70**] cannot be found.

Diversity and distribution – *Ochthephilus* have approximately 70 species occurring throughout the Nearctic and Palearctic regions, including the western range of the Himalayas, the Chinese states Sichuan and Yunnan and montanous Taiwan. Occurrence of the genus in Northern Burma is likely, but yet unconfirmed. The species exclusively live in sand and gravel on streambanks, mosses on rocks near streams or in similarly wet habitats in caves. Most species are confined to higher elevations, with very few specimens/species found in lowlands (usually special, azonal areas).



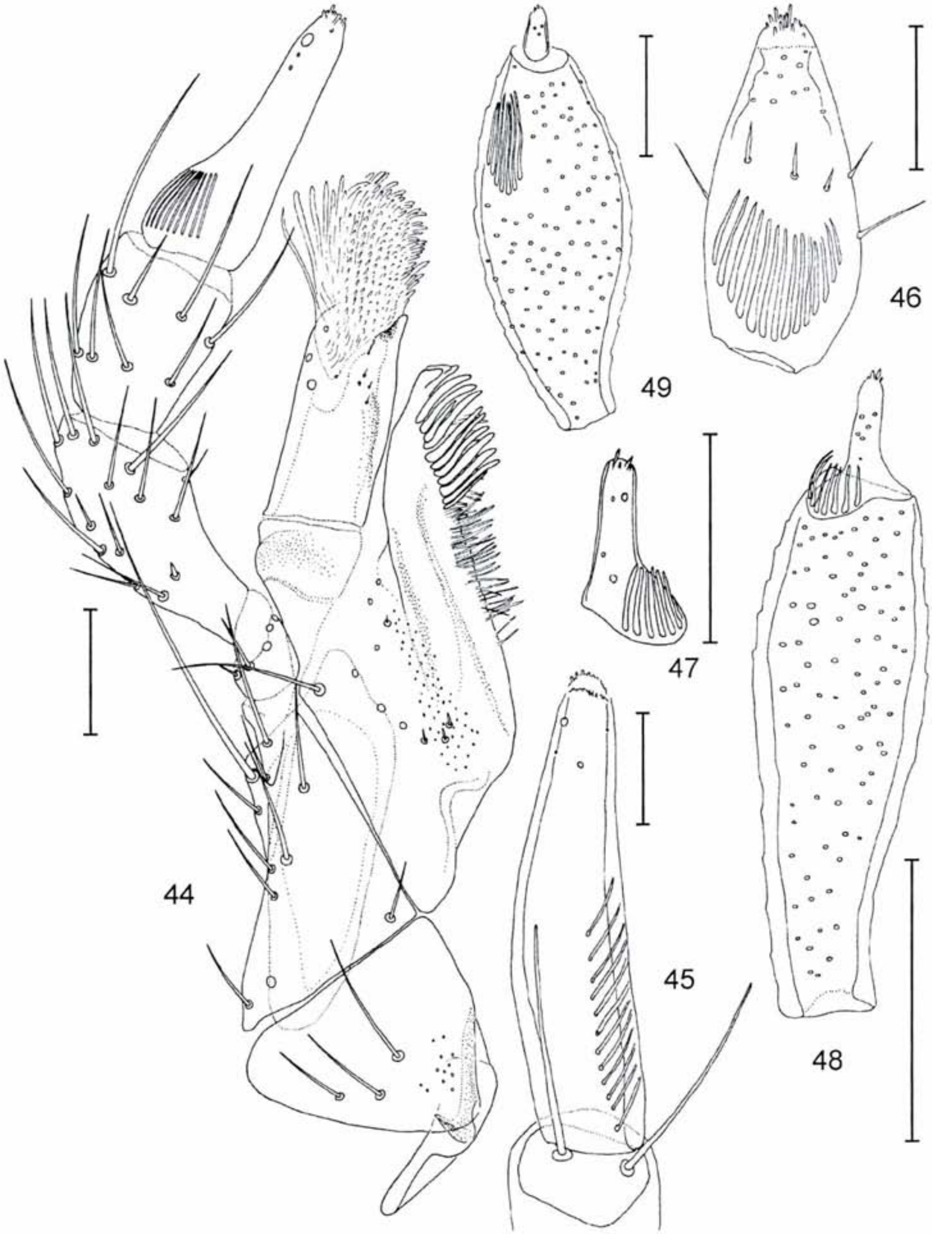
Figs 36–43. 36 = Labium of *Ochthephilus flexuosus* MULSANT et REY, 1856. 37 = Hypopharynx of *Ochthephilus flexuosus* MULSANT et REY, 1856. 38 = Ventral coriaceous field on hypopharynx of *Platydeleaster bimaculatus* SCHÜLKE, 2003 (scales on all three 0.05 mm). 39 = Platelike armature in hypopharynx of *P. bimaculatus* SCHÜLKE, 2003 (scale 0.05 mm); 40 = same of *Coprophilus longicollis* CAMERON, 1941 (scale 0.05 mm); 41 = same of *Carpelimus bifidus* sp. n. (scale 0.03 mm); 42 = same of *Thinodromus chagosanus* (BERNHAUER, 1922) (scale 0.025 mm); 43 = same of *T. schillhammeri* sp. n. (scale 0.025 mm).

Xerophygus KRAATZ, 1859

Xerophygus KRAATZ, 1859 (type species: *Trogophloeus pallipes* MOTSCHULSKY, 1857)

Description – Medium to large-sized (3.0–5.8 mm), usually dark brown, but some species may be slightly reddish. Body either weakly or densely pubescent, in the latter case the size of the hairs not uniform. Elytra parallel-sided, temples developed, abdomen broadest at (or around) the 6th segment. Mandibles often very well developed. Tibia with spines or dense rows of stiff setae. Males can be regognized by their macrocephaly (sometimes weakly expressed); often the apical edge of sternite VIII truncated whereas that of the female sternite VIII slightly rounded. – Head. Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent at least anteriorly. Head [**5**] with or without dorsal midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] divided or undivided, transverse [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] undivided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] absent. Front of hypopharynx [**14**] not entirely covered with setae, a row of setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate with central stick not reaching the end of the plate. Last palpomere of maxillary palp [**17**] reduced to a stick, digitiform sensillae [**18** and **19**] absent. Labial palp [**20**] not hairy. Antennae [**21**] straight and [**22**] moderately elongated. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] not exposing protrochantins. – Legs. Tibia [**26**] with mid-tibial spur(s) and [**27**] spines or rows of stiff setae. Tarsal segmentation [**28**] 3–3–3 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] absent, carina [**41**] not present on any sternites. Fimbriate edge [**42**] on tergite VII sometimes modified into comb. Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its basolateral parts [**45**] fused to tergum IX leaving behind rhomboid shape. – Secondary sexual characters. Macrocephaly [**46**] present, macrothoracy [**47**] absent. Sternum VII without spines [**48**] or row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX [51] present, with setae [52] on apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] well developed or sometimes simplified, not modified into clasping structure. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, without extra lobe [**59**] or membranous region [**60**], with one or without setae [**61**]. With visible pump and flagellum [**62**]. – Female terminalia. Female genital appendages [**63**] are divided into coxites, valvifers but no styli. Sclerites (possible remnant of sternum X) [**64**] appear as small ring. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided, not associated with invisible [**67**] spermathecal gland, tubular portion [**68**] not penetrating distal bulb, umbilicus [**69**] present. Sclerotized "tube" [**70**] cannot be found.

Diversity and distribution – *Xerophygus* is currently known from the Afrotropical and Oriental regions, and is represented by approximately 10 species. Very little is known about their life habits, the majority of the studied material is from different traps, but a few are labelled as collected on stream banks in rainforests, where they supposedly live in mud and plant debris accumulating on the bank.

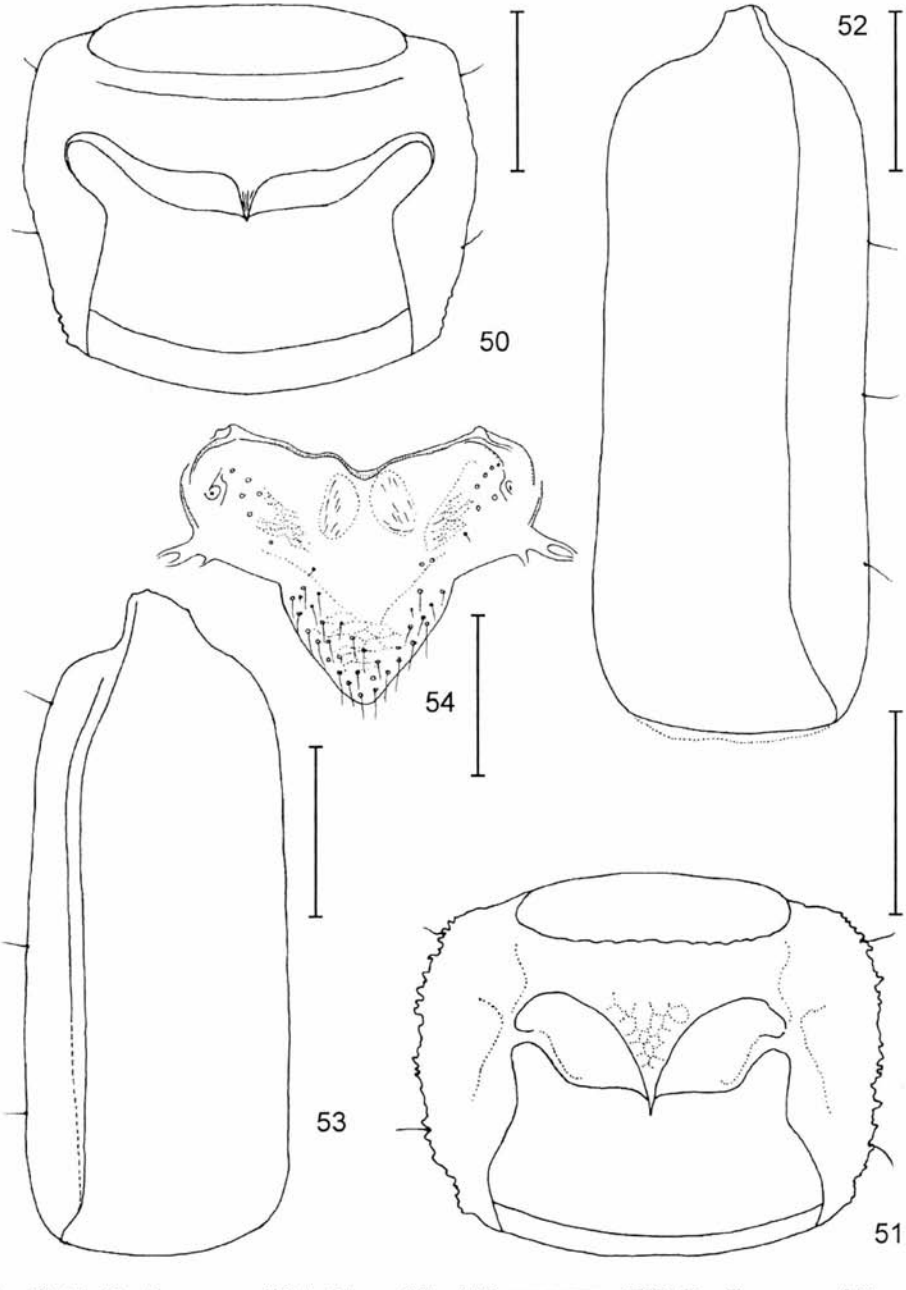


Figs 44–49. 44 = Maxillary palp of *Ochthephilus flexuosus* MULSANT et REY, 1856 (scale 0.05 mm). 45 = Last segment of maxillary palp of *Manda mandibularis* (GYLLENHAL, 1827); 46 = same of *Coprophilus longicollis* CAMERON, 1941 (lateral view); 47 = same of *Thinodromus chagosanus* (BERNHAUER, 1922) (scales on all three 0.05 mm). 48 = Penultimate segment of maxillary palp of *Trogactus ocellatus* sp. n.; 49 = same of *Thinodromus singularis* (FAUVEL, 1907) (scales on both 0.05 mm).

Carpelimus LEACH, 1819

Carpelimus LEACH, 1819 (type species: *Oxytelus fuliginosus* GRAVENHORST, 1802)
Trogophloeus MANNERHEIM, 1830 (type species: *Oxytelus corticinus* GRAVENHORST, 1806)
Taenosoma MANNERHEIM, 1830 (type species: *Aleochara pusilla* GRAVENHORST, 1802)
Batychrus GISTEL, 1834 (type species: *Oxytelus corticinus* GRAVENHORST, 1806)
Glomus GISTEL, 1848 (type species: *Oxytelus pusillus* GRAVENHORST, 1802)
Troginus MULSANT et REY, 1878 (type species: *Trogophloeus exiguus* ERICHSON, 1839)
Boopinus KLIMA, 1904 (type species: *Trogophloeus memnonius* ERICHSON, 1840)
Oxytrogus WENDELER, 1930 (type species: *Oxytrogus oculatus* WENDELER, 1930, unavailable)
Nanolobus CAMERON, 1933 (type species: *Nanolobus pacificus* MOTSCHULSKY, 1857)
Bucephalinus C. KOCH, 1934 (type species: *Trogophloeus priesneri* C. KOCH, 1934)
Paraboopinus SCHEERPELTZ, 1937 (type species: *Trogophloeus nitidus* BAUDI DI SELVE, 1848)
Myopinus SCHEERPELTZ, 1937 (type species: *Trogophloeus elongatulus* ERICHSON, 1839)
Thoracoplatynus SCHEERPELTZ, 1937 (type species: *Oxytelus fuliginosus* GRAVENHORST, 1802)
Paratrogophloeus HATCH, 1957 (type species: *Carpelimus bilineatus* STEPHENS, 1834)
Typhlopinus COIFFAIT, 1967 (type species: *Trogophloeus anophthalmus* COIFFAIT, 1967)
Stenoderophloeus SCHEERPELTZ, 1972 (type species: *Trogophloeus guttifer* SCHEERPELTZ, 1972)
Anopinus PACE, 1993 (type species: *Carpelinus*[sic] *caecus* PACE, 1993)

Description – Small to medium-sized (1.2–3.8 mm), usually dark brown, but some species reddish coloured, with the smallest ones pale yellowish brown. Pubescence on body varies, but usually sparse and short. Surface of pronotum either relatively smooth or has four shallow, oval impressions around tha basal half of the midline. Elytra parallel-sided, temples usually distinct, abdomen broadest at (or around) the 6th segment. The difference between sexes in the formation of Sternum VIII is often very small, sexes are hard to recognize (males usually have broader tip of terminalia). – Head. Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent at least anteriorly. Head [**5**] without dorsal midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] divided, transverse [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] undivided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] absent. Front of hypopharynx [**14**] entirely or not entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate with central stick either or not continuing till end. Last palpomere of maxillary palp [**17**] bulbous, but strongly desclerotized basally, digitiform sensillae [**18**] present on last palpomere, arranged [**19**] in parallel fashion. Labial palp [**20**] not hairy. Antennae [**21**] straight and [**22**] moderately elongated. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] not exposing protrochantins. – Legs. Tibia [**26**] with or without mid-tibial spur(s) but [**27**] without spines or rows of stiff setae. Tarsal segmentation [**28**] 3–3–3 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] absent, carina [**41**] not present on any sternites. Fimbriate edge [**42**] on tergite VII unmodified . Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its basolateral parts [**45**] not fused to tergum IX. – Secondary sexual characters. Macrocephaly [**46**] sometimes present, macrothoracy [**47**] absent. Sternum VII without spines [**48**] or row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but



Figs 50–54. 50 = Pronotum of *Thinobius apfelbecki* BERNHAUER, 1905. 51 = Pronotum of *Neoxus crassicornis* (CASEY, 1889) (scale 0.1 mm). 52 = Elytron of *Thinobius apfelbecki* BERNHAUER, 1905. 53 = Elytron of *Neoxus crassicornis* (CASEY, 1889) (all ventral view) (scales on all four 0.1 mm). 54 = Scutellum of *Thinobius longipennis* (HEER, 1841) (scale 0.05 mm).

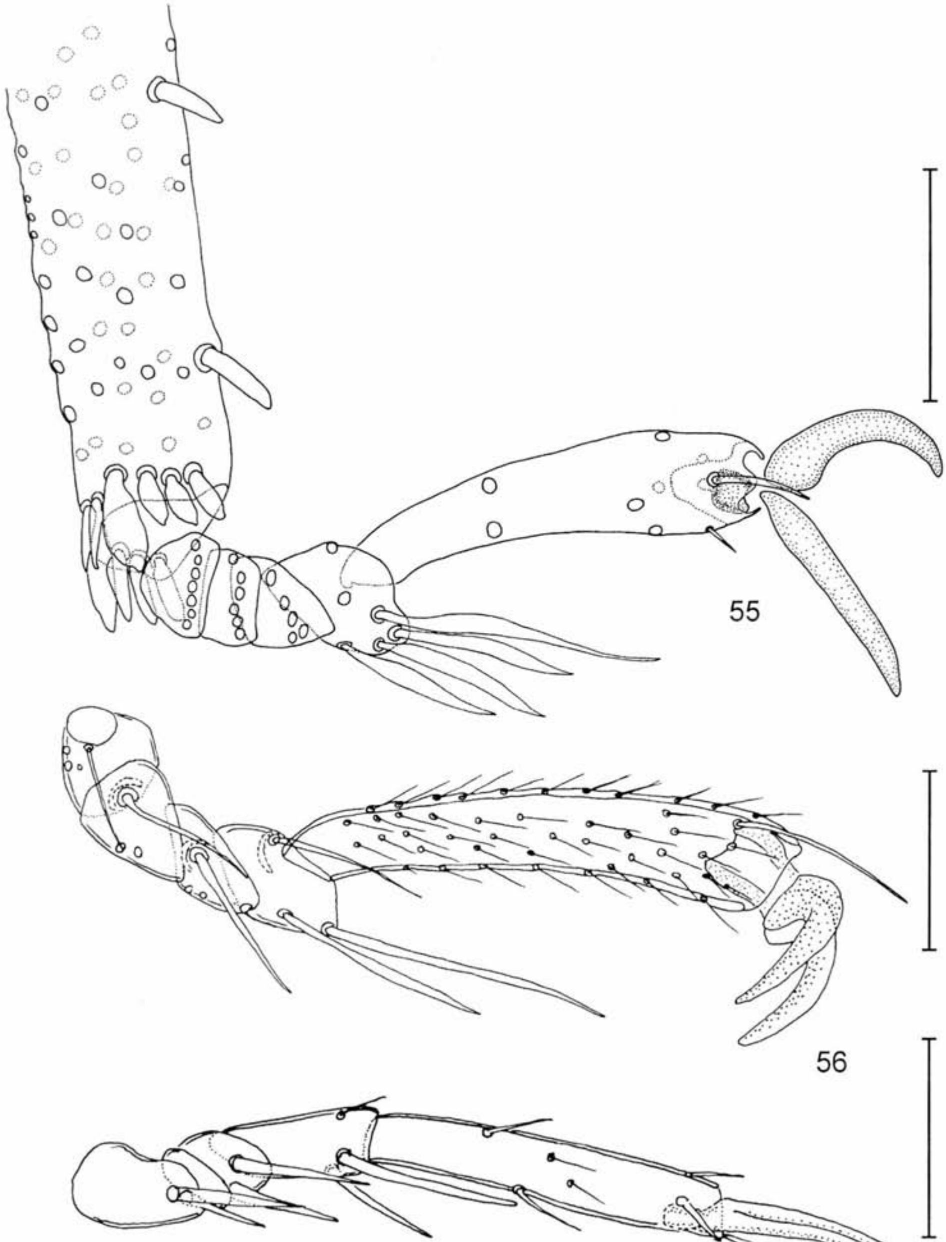
bears no tubercles. – Male terminalia. Sternum IX [**51** and **52**] absent. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] simplified, truncated. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, sometimes with extra lobe [**59**], often with membranous region [**60**], with one seta [**61**] each. Without visible pump and flagellum [**62**]. – Female terminalia. Female genital appendages [**63**] are lost. Sclerites (possible remnant of sternum X) [**64**] appear as small ring. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided, not associated with visible or invisible [**67**] spermathecal gland, tubular portion [**68**] not penetrating distal bulb, umbilicus [**69**] absent. Sclerotized "tube" [**70**] sometimes can be found.

Diversity and distribution – *Carpelimus* is a worldwide genus with a vast number of species (currently about 400 named and valid) and relatively little diversity (for the most part) and ubiquitous life habits. They characteristically live near slower running waters or muddy places, near ponds.

Thinodromus KRAATZ, 1857

Thinodromus KRAATZ, 1857 (type species: *Trogophloeus dilatatus* ERICHSON, 1839)
Amisammus DES GOZIS, 1886 (type species: *Carpelimus arcuatus* STEPHENS, 1834)
Warburtonia OKE, 1933 (type species: *Warburtonia inflatipes* OKE, 1933)
Paracarpalimus SCHEERPELTZ, 1937 (type species: *Homalotrichus luteipes* SOLIER, 1849)
Apocellagria CAMERON, 1920, **syn. n.** (type species: *Apocellagria indica* CAMERON, 1920)
Carpaliaceus GILDENKOV, 2000 (type species: *Carpaliaceus thoracicus* GILDENKOV, 2000)

Description – Medium to large sized (1.9–7.8 mm), usually dark brown to almost black, but some medium to yellowish brown (even if fully coloured). Body covered with sometimes rather long pubescence. Most species have a broad, transverse groove before the basal edge of pronotum. Elytra parallel-sided, sometimes reduced (wingless species), temples developed, abdomen broadest at (or around) the 6th segment. The difference in the formation of sternite VIII (not broadly rounded) helps recognizing the males; also, in several species groups the antennal segments of the male are more elongated than that of the female – this feature is, of course, easier to observe in those species where the antennal segments are otherwise longer than broad. – Head. Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent at least anteriorly. Head [**5**] without midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] divided, transverse [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] divided or undivided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] present or absent. Front of hypopharynx [**14**] entirely or not entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate with central stick either or not continuing till end. Last palpomere of maxillary palp [**17**] either bulbous basally or reduced to a stick, digitiform sensillae [**18**] present on last palpomere, fused to the apex or middle of penultimate, or completely missing; if present, arranged [**19**] in parallel fashion. Apex of penultimate segment of labial palp [**20**] hairy or not. Antennae [**21**] straight and [**22**] moderately elongated. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] not exposing protrochantins. – Legs. Tibia [**26**] with or without mid-tibial spur(s) but [**27**] without spines or rows



Figs 55–57. 55 = Tarsus of *Ochthephilus flexuosus* MULSANT et REY, 1856 (scale 0.1 mm). 56 = Tarsus of *Trogactus ocellatus* sp. n. (scale 0.05 mm). 57 = Tarsus of *Planeustomus palpalis* (ERICHSON, 1839) (on all only modified setae are shown, except on last tarsomeres on 56-57) (scale 0.1 mm).

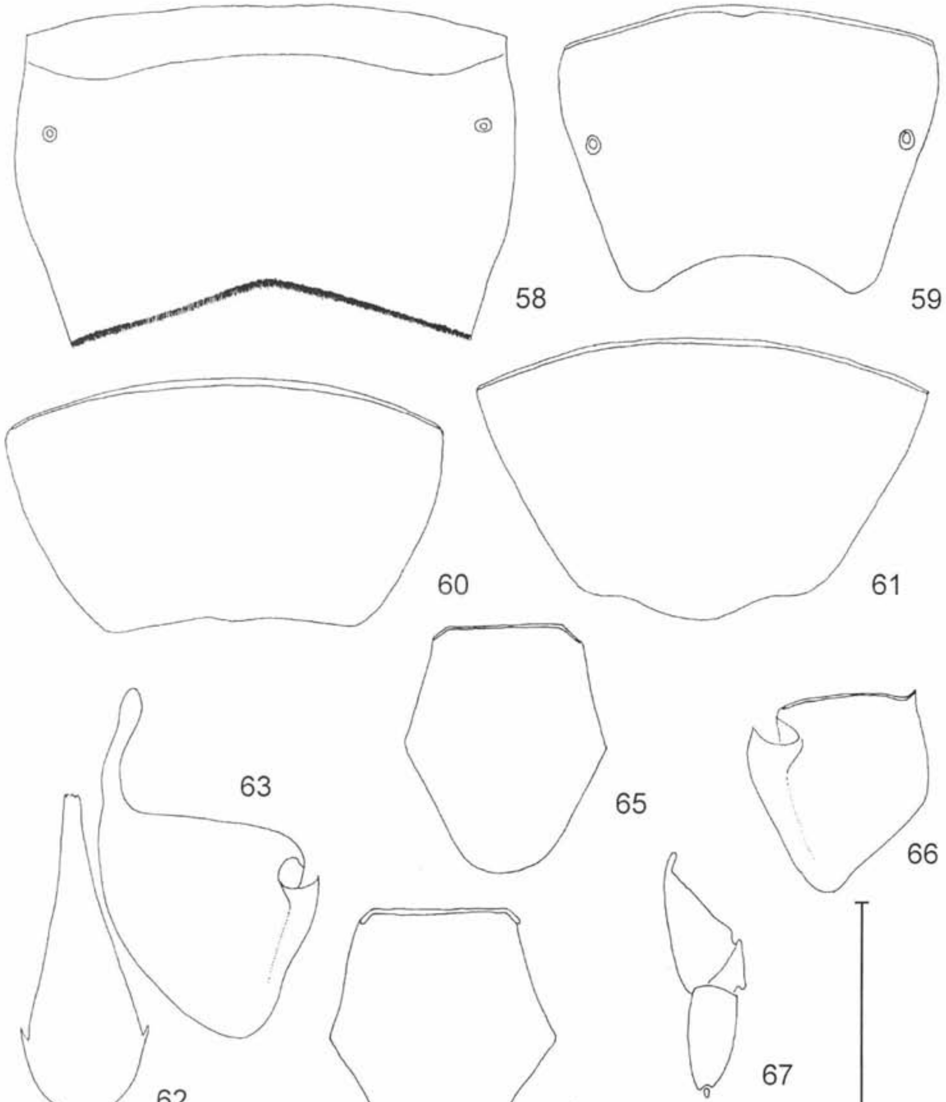
of stiff setae. Tarsal segmentation [**28**] 3–3–3 with no pseudosegment [**29**] and basal articles [**30**] compressed or sometimes uncompressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] absent, carina [**41**] not present on any sternites. Fimbriate edge [**42**] on tergite VII unmodified or modified into comb (in which case the fimbriate edge itself is lost). Tergum X [**43**] sometimes divided by transversal line, its dorsal struts [**44**] not developed, its basolateral parts [**45**] not fused to tergum IX. – Secondary sexual characters. Macrocephaly [**46**] sometimes present, macrothoracy [**47**] absent. Sternum VII sometimes with spines [48] or with a row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX [**51**] present, with or without setae [**52**] on apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like or laterally flattened, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] sometimes well developed (in this case not modified into clasping structure), but often simplified (truncated) or completely membraneous (amorphous). Median face membranous, apically bearing sclerotized edge or contains embedded sclerotized plates [**56**], without apicomedial hook [**57**]. Parameres [**58**] often wrapping around the middle of median lobe, sometimes with extra lobe [**59**], sometimes with membranous region [**60**], with none, or sometimes one or two setae [**61**] each. Without visible pump and flagellum [62]. – Female terminalia. Female genital appendages [**63**] lost. Sclerites (possible remnant of sternum X) [**64**] appear as small ring. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided, not associated with visible or invisible [**67**] spermathecal gland, tubular portion [**68**] sometimes penetrating distal bulb, umbilicus [**69**] present or absent. Sclerotized "tube" [**70**] sometimes can be found.

Diversity and distribution – *Thinodromus* is distributed worldwide, contains approximately 200 species and exhibits the most overwhelming diversity within this group of genera. Those species where habitats are known live in periaquatic situations, but always associated with running waters. The specimens often hide under stones and unlike other oxytelines move (and fly away) rather fast, making their collection a challenge. A range of species prefer living in mosses at streams.

Trogactus SHARP, 1887

Trogactus SHARP, 1887 (type species: *Trogactus championi* SHARP, 1887)

Description – Medium small to large sized (1.9–6.8 mm), usually dark brown, the smallest are medium to light brown (even if fully coloured). Body with sparse, weakly developed pubescence especially on the abdomen (besides few longer hairs in angles). Antennae extremely long and slender (mid-antennal segments always more than 3 times longer than broad). Elytra parallel-sided, often with tubercles or projections near the postero-lateral corners, temples developed, abdomen usually very narrow at base, broadest at (or around) the 6th segment. The difference in the formation of sternite VIII (not broadly rounded) helps recognizing the males. – Head. Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent at least anteriorly. Head [**5**] without midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] divided, transverse [**8**]. Setation behind front of labrum [**9**] in middle



Figs 58–67. The constitution of the last abdominal segments and terminalia of *Ochthephilus strandi* (SCHEERPELTZ, 1950), with differences between the sexes: 58 = tergum VII, 59 = tergum VIII, 60 = sternum VIII (male), 61 = sternum VIII (female), 62 = sternum IX (male), 63 = tergum IX (male), 64 = tergum X (male), 65 = tergum X (female), 66 = tergum IX (female), 67 = hemisternite, coxites and styli (female) (scale 0.2 mm).

much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] divided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] absent. Front of hypopharynx [**14**] entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate with central stick continuing till end. Last palpomere of maxillary palp [**17**] reduced to a stick, digitiform sensillae [**18**] fused to penultimate palpomere or absent, if present, arranged [**19**] in parallel fashion. Apex of penultimate segment of labial palp [**20**] hairy. Antennae [**21**] straight and [**22**] extremely elongated (mid-antennal segments more, than 3 times as long as broad). – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] without pubescence, hypomera [**25**] not exposing protrochantins. – Legs. Tibia [**26**] with mid-tibial spur(s) but [**27**] without spines or rows of stiff setae. Tarsal segmentation [**28**] 3–3–3 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] with dense pubescence. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] absent, carina [**41**] present at the base of second sternites. Fimbriate edge [**42**] on tergite VII unmodified. Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its basolateral parts [**45**] not fused to tergum IX. – Secondary sexual characters. Macrocephaly [**46**] absent, macrothoracy [**47**] absent. Sternum VII without spines [**48**] or row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX [**51**] present, with setae [**52**] on apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] well developed, not modified into clasping structure. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, without extra lobe [**59**], with membranous region [**60**], with one seta [**61**] each. Without visible pump and flagellum [**62**]. – Female terminalia. Female genital appendages [**63**] lost. Sclerites (possible remnant of sternum X) [**64**] lost. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided, not associated with visible [**67**] spermathecal gland, tubular portion [**68**] not penetrating distal bulb, umbilicus [**69**] absent. Sclerotized "tube" [**70**] cannot be found.

Diversity and distribution – *Trogactus* is presently only known from the Neotropical region, where it is represented with approximately 15 species. Most species are found in higher elevations, 1200–1800m, with a few occurring also on lower altitudes. A characteristic habitat for the species is leafpacks floating at the edge of mountain streams.

Thinobius group (*Thinobius*, *Sciotrogus*, *Neoxus*)

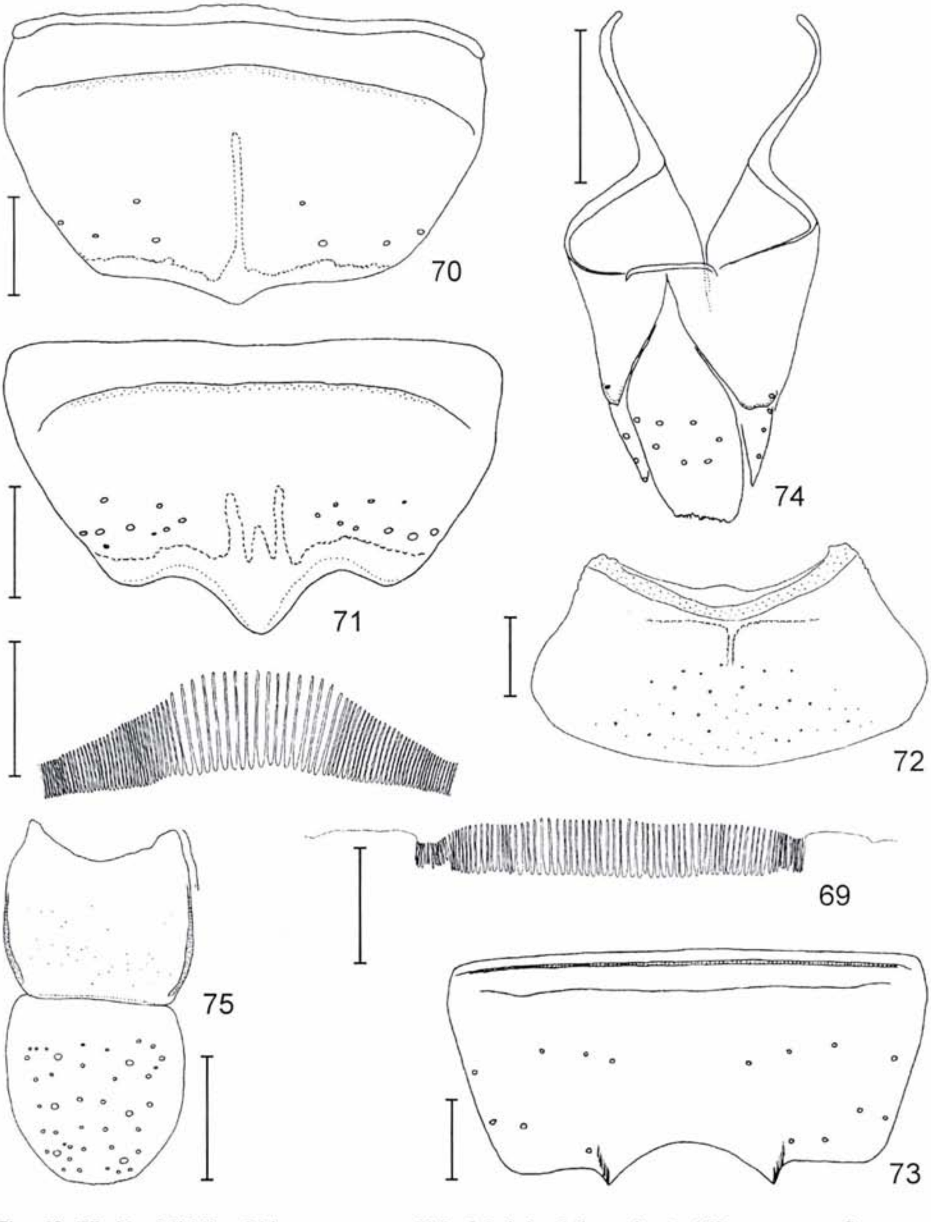
Thinobius KIESENWETTER, 1844 (type species: *Thinobius ciliatus* KIESENWETTER, 1844)
Thinobiellus BERNHAUER, 1909 (type species: *Thinobius rossicus* BERNHAUER, 1909)
Torrentomus BIERIG, 1934 (type species: *Thinobius torrei* BIERIG, 1934)
Thiphonilus TOTTENHAM, 1939 (type species: *Thinobius linearis* KRAATZ, 1857)
Platyderothinophilus SCHEERPELTZ, 1959 (type species: *Thinobius major* KRAATZ, 1857)
Myopothinophilus SCHEERPELTZ, 1959 (type species: *Thinobius klimai* BERNHAUER, 1902)
Oedarthrothinophilus SCHEERPELTZ, 1959 (type species: *Thinobius nodicornis* EPPELSHEIM, 1884)
Bracharthrothinophilus SCHEERPELTZ, 1959 (type species: *Thinobius nitens* FAUVEL, 1871)

Sciotrogus SHARP, 1887 (type species: *Sciotrogus opacus* SHARP, 1887)
Neoxus HERMAN, 1970 (type species: *Neoxus crassicornis* CASEY, 1889)

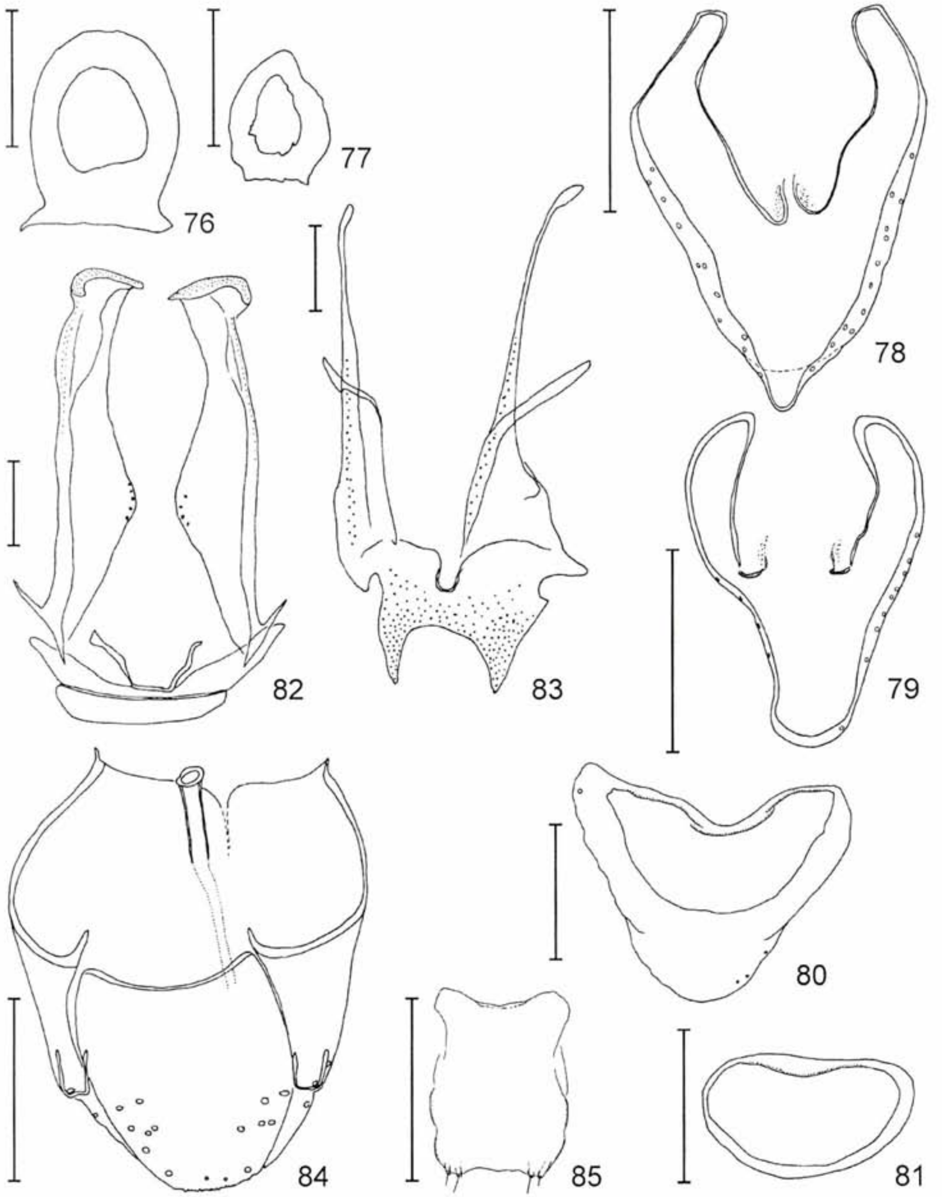
Description – Although this taxon/clade is not analyzed in detail, it must be dealt with here, since it is (at least according to the previous phylogenetic hypotheses) sister to the clade that is the subject of this revision.

Very small to medium-sized (0.6–3.5 mm), usually medium to light brown, but some species darker coloured. Body with dense but short pubescence. Elytra parallel-sided, suture dehiscent, temples developed, abdomen broadest at (or around) the 6th segment. Males of several species can be recognized by the tips of their elongated aedeagi or the flagella exposed at the abdominal apex. – Head. Clypeus [**1**] well developed, epistomal sulcus [**2**] present. Eyes [**3**] not extending to the ventral portion of the head. Gular sulci [**4**] confluent at least anteriorly. Head [**5**] without midline keel. The mola [**6**] on the mandibles separated, well developed. Labrum [**7**] undivided, rounded [**8**]. Setation behind front of labrum [**9**] in middle much smaller, irregular or missing. Dorsal seta [**10**] on epipharynx absent. Hypopharynx [**11**] undivided, without coriaceous field [**12**] on ventral side. Lateral row of bulbous setae [**13**] absent. Front of hypopharynx [**14**] not entirely covered with setae, no setae [**15**] on mid-line. Median sclerotized plate of hologlossa [**16**] anteriorly enlarged into a plate. Last palpomere of maxillary palp [**17**] fully formed, strongly bulbous basally, digitiform sensillae [**18**] present on last palpomere, arranged [**19**] in parallel fashion. Basal segment of labial palp [**20**] not hairy. Antennae [**21**] straight and [**22**] moderately elongated. – Thorax. Prosternal process [**23**] pointed, scutellum [**24**] sometimes with pubescence, hypomera [**25**] sometimes exposing protrochantins. – Legs. Tibia [**26**] with mid-tibial spur(s) but [**27**] without spines or rows of stiff setae. Tarsal segmentation [**28**] 2–2–2 with no pseudosegment [**29**] and basal articles [**30**] compressed. Ventral setae [**31**] modified to form tarsal lobes, last tarsomere [**32**] only with sparse setae. – Elytra. Elytra [**33**] without puncture-rows, elytral suture [**34**] parallel, epipleural ridge [**35**] present. – Abdomen. Abdomen [**36**] with two pairs of laterosclerites. Intersegmental membrane [**37**] without brickwall pattern. Second sternite [**38**] fully developed, first sternite [**39**] completely absent. Tergal basolateral ridges [**40**] present, carina [**41**] not present on any sternites. Fimbriate edge [**42**] on tergite VII unmodified. Tergum X [**43**] not divided, its dorsal struts [**44**] not developed, its basolateral parts [**45**] not fused to tergum IX. – Secondary sexual characters. Macrocephaly [**46**] absent, macrothoracy [**47**] absent. Sternum VII without spines [**48**] or row of modified setae [**49**]. The apical edge of sternite VIII [**50**] shows sexual dimorphism, but bears no tubercles. – Male terminalia. Sternum IX [**51**] present, with setae [**52**] on apex. – Male genitalia. Aedeagus median lobe [**53**] bulb-like, internal sclerites [**54**] present, symmetrical/paired. Apical opening [**55**] well developed, not modified into clasping structure. Median face membranous [**56**], without apicomedial hook [**57**]. Parameres [**58**] not wrapping, without extra lobe [**59**] or membranous region [**60**], with sometimes one seta [**61**] each. Sometimes with visible pump and flagellum [**62**]. – Female terminalia. Female genital appendages [**63**] are sometimes present. Sclerites (possible remnant of sternum X) [**64**] sometimes appear as small ring. – Female genitalia. Spermatheca [**65**] sclerotized. Receptacle [**66**] divided or undivided, associated with visible [**67**] spermathecal gland, tubular portion [**68**] penetrating distal bulb, umbilicus [**69**] present or absent. Sclerotized "tube" [**70**] cannot be found.

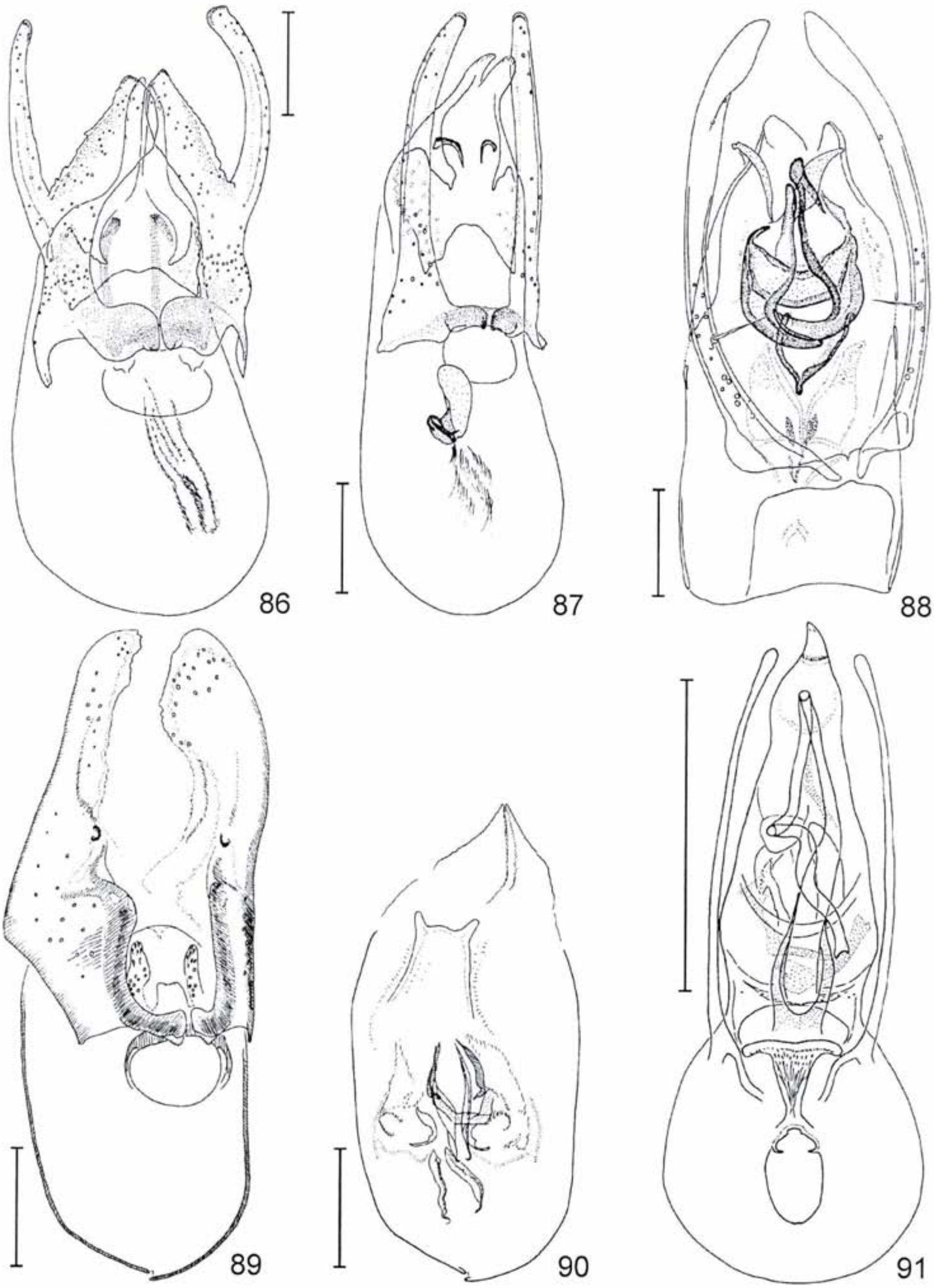
Diversity and distribution – *Thinobius* is distributed worldwide, although apparently not as abundant or specious in the tropics as in the temperate regions. *Thinobius* species are found mainly in periaquatic situations, near (fast running) streams or a small number of species near ponds and on intertidal mud flats. The genus at present contains about 120 named species. *Neoxus* and *Sciotrogus* pre-



Figs 68–75. 68 = Middle of fringe on tergum VII of *Ochthephilus vulgaris* (WATANABE et SHIBATA, 1961); 69 = same of *Thinodromus juanfernandezianus* sp. n. (scales on both 0.05 mm). 70 = Sternum VIII of *T. juanfernandezianus* sp. n.; 71 = same of *T. schillhammeri* sp. n. (scales on both 0.2 mm). 72 = Sternum II of *Mimopaederus insularis* CAMERON, 1936 (scale 0.1 mm). 73 = Sternum VII of *Thinodromus diffusus* (CASEY, 1889) (scale 0.1 mm). 74 = Rhomboid fusion of tergites IX and X in *Xerophygus hreblayi* sp. n. (male) (scale 0.2 mm). 75 = Tergum X of *Thinodromus caloderinus* (LECONTE, 1877) (scale 0.1 mm).



Figs 76–85. 76–77 = Female ring structures of two closely related *Ochthephilus* sp., illustrating usefulness in identification of species (scale 0.05 mm). 78–79 = Same of two closely related *Thinodromus* sp., illustrating usefulness in identification of species (scale 0.1 mm). 80 = Same of *Sciotrogus opacus* SHARP, 1887; 81 = same of *Thinobius apfelbecki* BERNHAUER, 1905; 82 = same of *Aploderus caelatus* (GRAVENHORST, 1802); 83 = same of *Anotylus seticornis* (FAUVEL, 1895) (scales on all four 0.05 mm). 84 = Tube in the terminalia of *Thinodromus priorus* GILDENKOV, in litt. (female) (scale 0.1 mm). 85 = Modified female genital appendages of *Thinobius crinifer* SMETANA, 1959 (scale 0.1 mm).



Figs 86–91. 86–87 = Aedeagi of *Ochthephilus* sp. 88 = Aedeagus of *Carpelimus asmarensis* (COIFFAIT, 1981). 89–90 = Aedeagus of *Thinodromus* sp. (outer shell and parameres shown separate from internal structures). 91 = Aedeagus of *Thinobius* sp. (all scales 0.1 mm).

sumably occur in the same habitat. Of *Sciotrogus*, 2 species, there are a handful of old specimens known, with little bionomical information. They are distributed in the Neotropical region, with one species known from Mexico and Panama, another (of dubious status) in the West Indies. Of *Neoxus*, 4 Nearctic and Neotropical species, previously only light trap specimens were available (or ones with no bionomical information), but a few specimens very recently collected by me in their original habitat, at a slower streamlet, in similar circumstances and habitat as for *Thinobius* species.

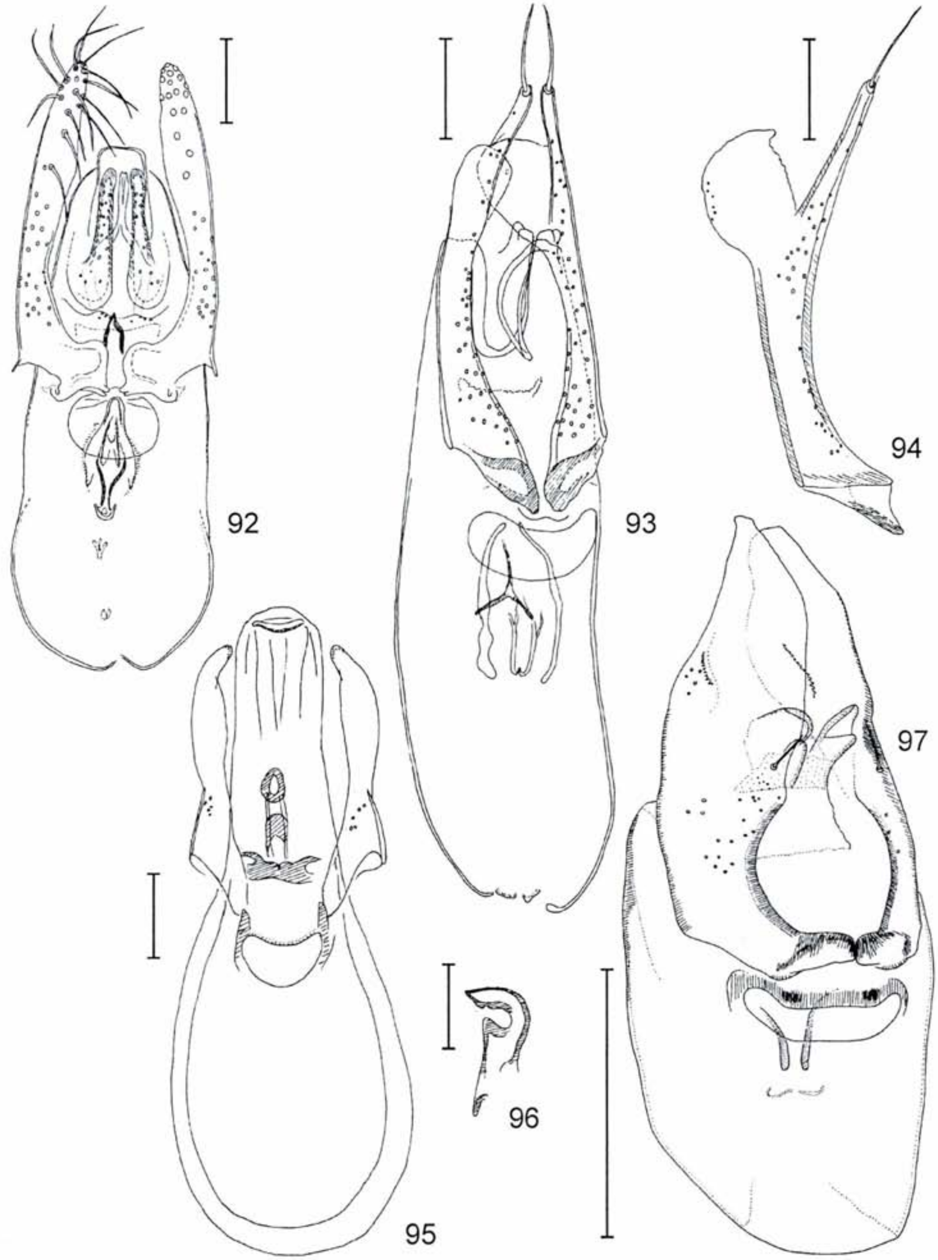
Problems in the current classification

The development of the current tribal classification was detailed in the second chapter. The tribal classification according to the Tree of Life webpage, with additions of the newly described or omitted taxa, is as follows:

1. Tribe Deleasterini REITTER, 1909
    - genus *Platydeleaster* SCHÜLKE, 2003
    - genus *Deleaster* ERICHSON, 1839
    - genus *Mitosynum* CAMPBELL, 1982
    - genus *Syntomium* CURTIS, 1828
    - genus *Oxypius* NEWTON, 1982
    - genus *Euphanias* FAIRMAIRE et LABOULBÈNE, 1856
2. Tribe Coprophilini HEER, 1839
    - genus *Coprophilus* LATREILLE, 1829
    - genus *Coprostygnus* SHARP, 1886
    - genus *Homalotrichus* SOLIER, 1849
3. Tribe Thinobiini J. SAHLBERG, 1876
    - genus *Manda* BLACKWELDER, 1952
    - genus *Planeustomus* JACQUELIN DU VAL, 1857
    - genus *Bledius* LEACH, 1819
    - genus *Eppelsheimius* BERNHAUER, 1915
    - genus *Crassodemus* HERMAN, 1968
    - genus *Aploderus* STEPHENS, 1833
        (= *Bledioschema* SMETANA, 1967, **syn. n.**)
    - genus *Blediotrogus* SHARP, 1900
    - genus *Pareiobledius* BERNHAUER, 1934
    - genus *Carpelimus* LEACH, 1819
    - genus *Xerophygus* KRAATZ, 1859
    - genus *Ochthephilus* MULSANT et REY, 1856
    - genus *Teropalpus* SOLIER, 1849

genus *Thinodromus* KRAATZ, 1857
  (= *Apocellagria* CAMERON, 1920, **syn. n.**)
genus *Trogactus* SHARP, 1887
genus *Thinobius* KIESENWETTER, 1844
genus *Neoxus* HERMAN, 1970
genus *Sciotrogus* SHARP, 1887
4. Tribe Oxytelini THOMSON, 1858
genus *Sartallus* SHARP, 1871
genus *Parosus* SHARP, 1887
genus *Paraploderus* HERMAN, 1970
genus *Ecitoclimax* BORGMEIER, 1934
genus *Jerozenia* HERMAN, 2004
genus *Platystethus* MANNERHEIM, 1830
genus *Oxytelus* GRAVENHORST, 1802
  (= *Paroxytelopsis* CAMERON, 1933, **syn. n.**,
  = *Anisopsidius* FAGEL, 1960, **syn. n.**,
  = *Anisopsis* FAUVEL, 1904, **syn. n.**,
  = *Hoplitodes* FAUVEL, 1904, **syn. n.**)
genus *Apocellus* ERICHSON, 1839
genus *Anotylus* THOMSON, 1859
  (= *Rimba* BLACKWELDER, 1952, **syn. n.**,
  = *Oxytelopsis* FAUVEL, 1895, **syn. n.**)

The roots of this classification are LEE HERMAN's original tree (HERMAN 1970) and character list. HERMAN did not present a character matrix; his data are inferred from the tree and character table. But even based on these data, the basal branch of the tree is at an incorrect place. It should also be noted here that HERMAN's phylogeny (HERMAN 1970) was not a quantitative phylogenetic analysis; it was merely a Hennigian argumentation (still revolutionary in the late 60s). A decade later, NEWTON reanalized the phylogenetic relationships of the basal genera (NEWTON 1982). He thought that HERMAN's "Character 34" should be reversed in polarity: the well developed second abdominal sternite is in fact the derived character state, not the ancestral one. This change had a profound effect: the tree was re-rooted. A related character, the presence of a long articulating membrane connecting the second and third sternites, is correlated with the presence of the well-developed second sternite. All non-oxytelines have the second sternite fused to the third and is narrowed and more lightly sclerotized than that. The taxa he studied (*Syntomium*, *Oxypius*, *Euphanias*) all had the character state possessed by other staphylinid subfamilies, i.e., the reduced, fused second sternite. Another

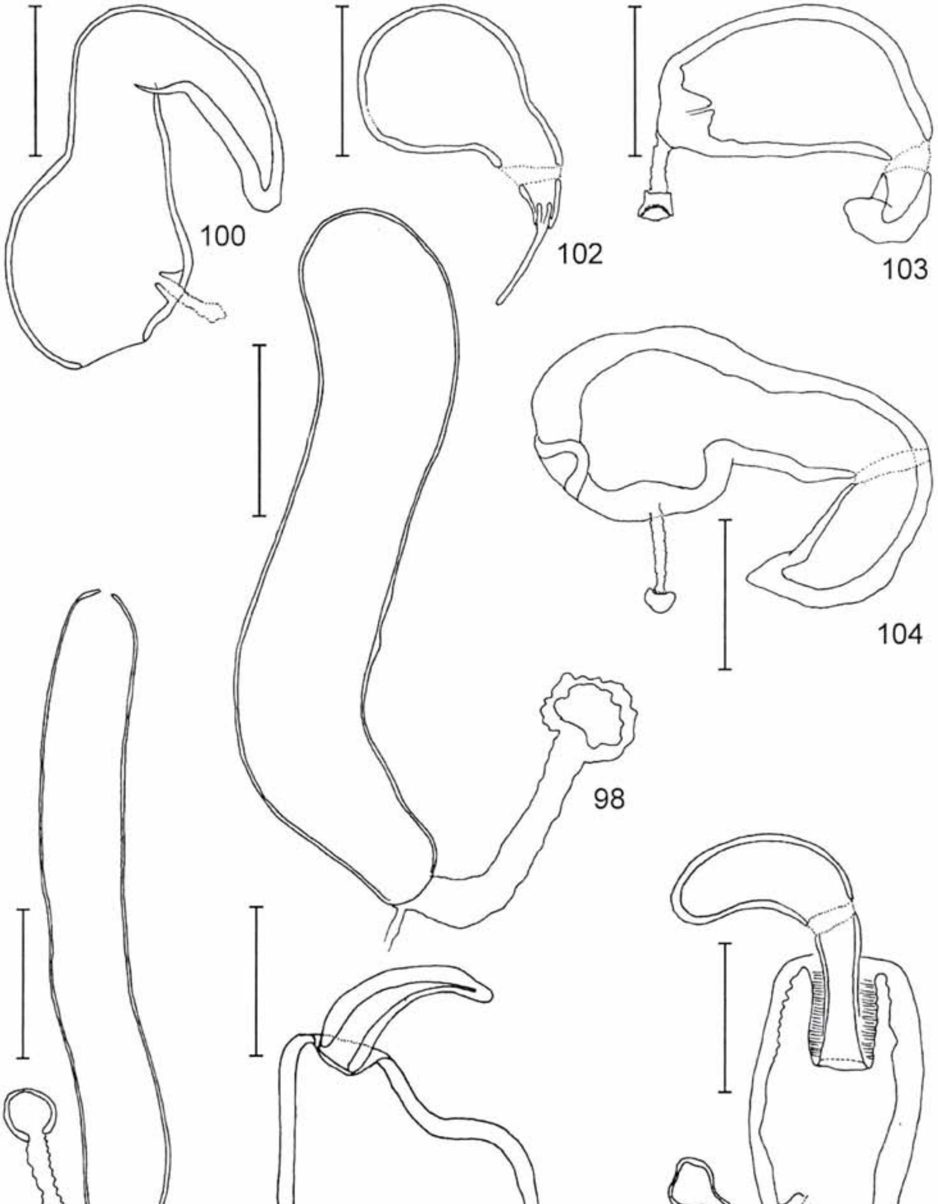


Figs 92–97. 92 = Aedeagus of *Paraploderus parcepunctus* (FAUVEL, 1905) (parameral setae shown only on one side). 93 = Aedeagus of *Carpelimus bifidus* sp. n. 94 = Paramere of *Carpelimus bifidus* sp. n. (side view). 95 = Aedeagus of *Oxytelus echidne* (FAUVEL, 1904). 96 = Apicomedial hook on the aedeagus of *Oxytelus echidne* (FAUVEL, 1904) (scales on all five 0.05 mm). 97 = Aedeagus of *Thinodromus juanfernandezianus* sp. n. (scale 0.2 mm).

group of oxyteline genera (*Deleaster* and the *Coprophilus* group) had an intermediate state: reduced second sternite with a short, immobile membranous connection to the third sternite. As it was stated in the introduction, the reexamination of the phylogeny of the *Carpelimus* group taxa was necessitated by the newly discovered characters and their expected influence on the classification of the involved genera. I anticipate that this work will bring a new approach to the study of these difficult, but character-rich beetles, and solves some problems that existed with outdated keys, old species descriptions, very regional revisions and many misidentified specimens in collections. In most cases good quality genital preparations unquestionably place taxa in the genera and species groups, and in most cases readily identify species. Such ease of identification is rather unique in any larger assemblage of staphylinids.

Treatment of subgeneric classification

A special part of this study must deal with the problem of subgenera and the subgeneric classification in oxytelines in general. For groups comprising hundreds of species, but even for smaller ones, the human mind searches for ways of subdivision. For centuries, the naming of subgenera was extremely popular and many such names were made available. In most instances, authors picked one or two characters that seemed distinctive and united all the species that possessed these particular character states under a newly given name. The drawbacks of such action are obvious: (1) such classification would not be based on phylogeny, (2) taxa that the author has not yet examined remained unplaced, (3) new taxa with intermediate character states cannot be placed in such a system, and (4) the variability of characters is poorly assessed (for example, in several instances the female of a species should go to one subgenus and the male to another). Ill-defined subgenera cause huge problems in the classification of the larger genera, *Carpelimus*, *Thinodromus* and *Bledius* are the three most important ones. The case with *Bledius* is discussed in detail by HERMAN (1986) and it illustrates problems with the others as well. In order to maintain the monophyly of named groups, either an unreasonable number of subgeneric names must be created, or the number of subgenera must be reduced. So a few very distinctive species with extreme characteristics are placed in the majority of the named groups, while the bulk of the species are placed together in one or two subgenera, so the goal of convenient subdivision is not met. HERMAN (1986) in the case of *Bledius* expressed his preference for a purely species group classification. For the aforementioned reasons, I take the same approach. The goal is to create a system where the yet undescribed species can be



Figs 98–105. Spermathecae of: 98 = *Platydeleaster bimaculatus* SCHÜLKE, 2003, 99 = *Manda mandibularis* (GYLLENHAL, 1827), 100 = *Aploderus caelatus* (GRAVENHORST, 1802), 101 = *Thinodromus diffusus* (CASEY, 1889), 102 = *T. chagosanus* (BERNHAUER, 1922), 103 = *T. schillhammeri* sp. n., 104 = *T. juanfernandezianus* sp. n., 105 = *Anotylus seticornis* (FAUVEL, 1895) (all scales 0.05 mm).

placed with a minimum of nomenclatural acts. This can only be achieved by the species group approach.

The *Anotylus* problem

Issues with the classification of the Anotylus and Oxytelus lineages

Although not strictly the subject of the paper, these groups have to be dealt with to some extent, because (1) some characters of this group occur within the *Carpelimus* group as well and (2) it is the most questionably resolved part of the phylogeny of Oxytelinae. These lineages have not only a large number of species, but a great degree of specialization. The latter usually (but not exclusively) appears in species associated with ants and those living in leaf litter. The appearance of the leaf-litter inhabiting species is characterized by their sculpture (and resulting detritus accumulation) on their bodies. Some species are corticolous (= live under bark). The taxa involved are numerous and poorly known. An estimated 80% of the species from the Neotropical region (one of the main diversity centers of the *Anotylus* group) are still undescribed, and many species-groups lack any specific names. However, in order to establish specific identities, the variability of characters has to be examined broadly, which is almost impossible to do within a reasonable amount of time and is clearly out of the scope of this work. So the approach used for this chapter is to search for characters that can identify larger assemblages of taxa and firmly establish genera, so that any future discoveries can be assigned to them. The majority of the species belong to either of two large lineages: the *Oxytelus* group and the *Anotylus* group. Within these lineages there are a great number of genus-group taxa, only a few of which are maintained today as valid genera. But even for these there are problems with the characters supporting them. A reevaluation of the generic characters is necessary to assure the unequivocal placement of the known species into genera and to create a stable nomenclature. While the tribe itself is well supported by a number of characters, most genera are weakly defined. The *Oxytelus* group consists of *Hoplitodes* (Fig. 129), *Anisopsis*, *Paroxytelopsis*, *Anisopsidius* and *Oxytelus*. The *Anotylus* group has *Oxytelopsis*, *Rimba*, *Anotylus* and *Apoçellus*. These two major clades are traditionally well characterized by the presence (*Oxytelus* group) or absence (*Anotylus* group) of the basolateral ridge on tergite II, and the different types of scutellar impressions: diamond-shaped for the *Oxytelus* group and crest-shaped for the *Anotylus* group (except *Apocellus*). Besides these, the genitalia and terminalia have modifications that are valuable for characterizing these lineages: a median lamellar formation on sternite VIII and an apicomedial hook on the median lobe of aedeagus characterizing the *Oxytelus* group, and a pointed, well developed apical opening structure of the aedeagus in case of the *Anotylus* group. Within these major lineage groups, the genera are defined by characters appearing in several other genera as well, or by characters showing a lot of variation and intermediate character states among the known species. Based on these characters it is quite impossible to place all species unequivocally into genera and account for the yet undescribed or undiscovered species as well. To solve these problems and give more support to genus-group taxa, new characters were sought.

The rhomboid fusion of tergite X

One of the potential characters (in terms of generic definition) was an interesting modification of tergite X, most prominently displayed in the species originally included in *Rimba* BLACKWELDER, 1952 (Figs 127–128), but present also in a few other taxa. In these species the basal and lateral parts of tergite X split from the apical (rhomboid) part (Fig. 12) along 2 oblique lines and fuse to the lateral regions of tergites IX. When dissecting a specimen the apical (remaining) region usually breaks off easily from the sheath-like formation of tergites IX (Fig. 13). This feature is here first referred to as rhomboid fusion. Throughout the *Oxytelus–Anotylus* clade, and in some outside this lineage (*Xerophygus*, most notably) the apical part of tergite X has further modifications: serrate, oblique lines and apicolateral flaps usually bending ventrally from the main plane. I initially hoped that this character would support and better define *Rimba*. In the course of the investigation, however, it appeared that from the complete absence of this modification to a rather small rhomboid tergite X, many intermediate states are also present, although in a small percentage of species. In a group of Neotropical *Anotylus*, the oblique lines delimitating the rhomboid remnant are so close to the basal edge of tergite X that it is impossible to decide whether this is actually a fragmented tergite X or just a basally-narrowed, full segment. Apart from the aforementioned *Xerophygus* (*Carpelimus* group), the rhomboid fusion was also found in *Oxytelus* (*Oxytelus* group). It became clear that this character does not support *Rimba*, and has evolved several times in apparently distantly related species groups.

Enlarged ventral struts on tergites IX

The species formerly included in *Oxytelopsis* have the ventral struts of their tergites IX enlarged into a broad, rounded plate, almost as large as the main parts of these plates (Fig. 15). The occurrence of such a modification was studied within the *Oxytelus–Anotylus* clade. One undescribed species (Fig. 126), that must be placed in *Oxytelopsis* based on external defining characters for the genus, does not have this modification. This species is from Kenya (East Africa), whereas all the other species of former *Oxytelopsis* are from the Oriental region. It is known that for historical reasons the East African fauna bears considerable resemblance to that of the Oriental region, so the find of an *Oxytelopsis*-like species in Kenya is not at all surprising. In its genital characteristics, the species from Kenya is a rather typical *Anotylus* (Fig. 14, 16); therefore its inclusion in *Oxytelopsis* makes no sense. It appears that the character states that traditionally define *Oxytelopsis* should not be used as generic characters. Certain Neotropical *Anotylus* species share features (and a genuine *Oxytelopsis*-like appearance) with the true Oriental *Oxytelopsis*, further emphasizing the thought that the defining characters are adaptive modifications, variously (depending on mode of life) expressed in lineages within *Anotylus*.

The *Oxytelus* group

A suite of similar character states are used for delimitation of genera in the *Oxytelus* group. The highly modified aedeagus and the very peculiar structures of the terminalia shared among the genera *Hoplitodes*, *Anisopsis*, *Paroxytelopsis*, *Anisopsidius* and *Oxytelus* suggested to specialists long ago that these taxa should be merged with *Oxytelus*. FAGEL, who focused on the study of the *Oxytelus* group in the Afrotropical region (where all these genera occur), published (FAGEL 1960) most of the important structural drawings that are necessary to draw this conclusion, yet he was content to describe even more genera rather than recognizing the similarities. Upon examination of the characters used for separation of the monobasic genera *Hoplitodes* (Fig. 129), *Anisopsis* and *Anisopsidius*, it becomes obvious that there is in fact a gradient including *Oxytelus* and *Paroxytelopsis*, with various adaptive characters (processes on various body parts, longitudinal carinae on the elytra, presence or absence of sensory setae on the antennae, modifications and spines on tibiae, carinae on mesosternal process), including perhaps the most extreme in the very specialized myrmecophile *Hoplitodes*. All these taxa, however, share the characteristics of the genitalia and male terminalia described under the *Oxytelus* group. There is no reason for the continued separation of these genera.

Perspectives of the classification of the lineages within the Oxytelus *and* Anotylus *groups*

As it was briefly touched in the introduction of this chapter, the most disturbing problem with the classification of Oxytelini is that the newly discovered taxa cannot be placed in the present system. Some possess features even more extreme than the species currently placed in their own genera today, so it is obvious, that recognition of these taxa as separate genera will eventually lead to the atomization of the Oxytelini. The derived problem with the atomization is the resulting paraphyly of the remaining parts of the genera, which cannot be overcome. As an alternative, lumping the taxa into less genera and recognizing them in a broader sense (with firm and stable delimiting characters) would at least stabilize their nomenclature and ensure the proper naming of the undescribed fauna. The enormous diversity can be dealt with on the level of species groups, which are informal and can be modified without greater nomenclatural consequences. It is hoped that with the consistent implementation of the species group concept throughout the tribe, the phylogeny and evolutionary tendencies of the ancient lineages of Oxytelini will be understood better. The proposed classification is outlined below.

Oxytelus GRAVENHORST, 1802
= *Caccoporus* THOMSON, 1859
= *Tanycraerus* THOMSON, 1859
= *Epomotylus* THOMSON, 1859
= *Hoplitodes* FAUVEL, 1904, **syn. n.**
= *Anisopsis* FAUVEL, 1904 **syn. n.**
= *Paroxytelopsis* CAMERON, 1933, **syn. n.**
= *Paranisopsis* CAMERON, 1938
= *Basilewskyorus* FAGEL, 1957
= *Anisopsidius* FAGEL, 1960, **syn. n.**
= *Anisopsodes* FAGEL, 1960

Characters: diamond shaped scutellar impression; apicomedial hook on aedeagus; lamellar formation on sternite VIII; basolateral ridge on tergite II (plesiomorph).

Apocellus ERICHSON, 1839
= *Ocaleomorpha* FLEISCHER, 1921
= *Pheidoloxenides* WASMANN, 1925

Characters: spade shaped scutellar impression; neck width less than half of postocular head width; croisant shaped upward projection on sternite VIII; basolateral ridge missing on tergite II.

Anotylus THOMSON, 1859
- = *Oxytelopsis* FAUVEL, 1895, **syn. n.**
- = *Rimba* BLACKWELDER, 1952, **syn. n.**
- = *Styloxys* DES GOZIS, 1886
- = *Oxytelodes* BERNHAUER, 1908
- = *Emopotylus* BERNHAUER, 1910
- = *Boettcherinus* BERNHAUER, 1936
- = *Oncoparia* BERNHAUER, 1936
- = *Paracaccoporus* STEEL, 1948
- = *Oxytelosus* CAMERON, 1950
- = *Microxytelus* FAGEL, 1956
- = *Oxytelops* FAGEL, 1956
- = *Pseudodelopsis* FAGEL, 1957
- = *Anotylops* FAGEL, 1957

Characters: crest shaped scutellar impression; basolateral ridge missing on tergite II.

PHYLOGENETIC ANALYSIS

Introduction and methods

In phylogenetic analyses that are made on large and very diverse groups, there can be two basic problems: the groups (and the species that represent them in the analysis) are not those that can answer questions; and the characters selected are not those that carry information on relatedness. Of course, the larger the group, the harder it is to avoid these difficulties. It is simply not possible for a specialist to dissect and study every single specimen in those specious groups and gain a complete understanding of variability and the potential phylogenetic value of characters. The data matrix (Table 1) was created in WINCLADA and was analyzed with the parsimony ratchet as implemented in NONA. With multistate characters considered nonadditive (Fitch parsimony), 32 most parsimonious trees are recovered (L=258, CI=37, RI=65). One of them is presented on Fig. 3. Bootstrap values and Bremer support for the branches are displayed on this tree. Bremer support values were calculated in NONA using the commands hold 15000, suboptimal 20, bsupport 10. Bootstrap values were calculated using NONA executed from Winclada, using 1000 replications.

The problem of representative taxa

As explained before, in this subfamily the type species of certain genera are not at all representative of the structural diversity of the included species. Therefore a species-group based approach was chosen, in which presumptive basal members of the most distinctive lineages were chosen as representatives to be used in the analysis, irrespective of the size of the taxon. This selection was done on the basis of ongoing or finished revisionary projects and the careful evaluation of character variation.

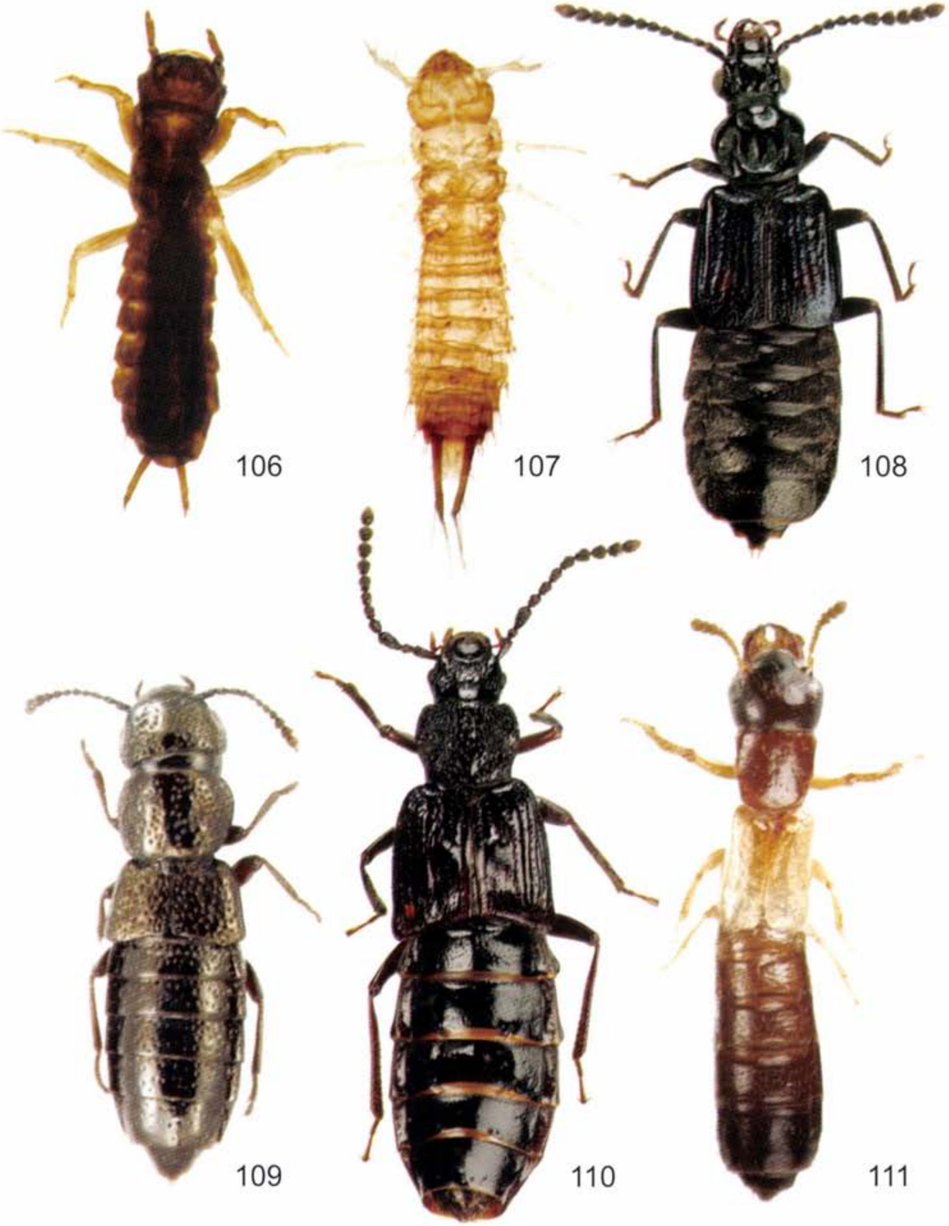
TAXON LIST

Outgroup taxa

1. *Platydeleaster bimaculatus* SCHÜLKE, 2003
2. *Deleaster dichrous* (GRAVENHORST, 1802)
3. *Coprophilus longicollis* CAMERON, 1941
4. *Manda mandibularis* (GYLLENHAL, 1827)
5. *Planeustomus palpalis* (ERICHSON, 1839)
6. *Crassodemus foraminosus* HERMAN, 1968
7. *Aploderus caelatus* (GRAVENHORST, 1802)
8. *Aploderus schweigeri* (SMETANA, 1967), formerly in *Bledioschema*
9. *Paraploderus parcepunctus* (FAUVEL, 1905)
10. *Oxytelus laqueatus* (MARSHAM, 1802)
11. *Anotylus seticornis* (FAUVEL, 1895)
12. *Bledius talpa* (GYLLENHAL, 1810)
13. *Eppelsheimius miricollis* (FAUVEL, 1898)
14. *Eppelsheimius pirazzolii* (EPPELSHEIM, 1885)
15. *Sciotrogus opacus* SHARP, 1887
16. *Thinobius apfelbecki* BERNHAUER, 1905
17. *Thinobius longipennis* (HEER, 1841)
18. *Neoxus crassicornis* (CASEY, 1889)

Ingroup taxa (*Carpelimus* group taxa)

1. *Blediotrogus guttiger* SHARP, 1900 [19]
2. *Pareiobledius alutellus* (BERNHAUER, 1934) [20]
3. *Teropalpus luniger* FAUVEL, 1867 [21]



Figs 106–111. 106 = Third instar larva of *Bledius talpa* (GYLLENHAL, 1810) (body length = 3.1 mm); 107 = same of *Thinodromus dilatatus* (ERICHSON, 1839) (2.4 mm). Habitus of: 108 = *Platydeleaster bimaculatus* SCHÜLKE, 2003 (♀) (7.4 mm), 109 = *Mitosynum vockerothi* CAMPBELL, 1982 (♀) (3.2 mm), 110 = *Coprostygnus optandus* BROUN, 1893 (♂) (7.1 mm), 111 = *Eppelsheimius pirazzolii* (EPPELSHEIM, 1885) (♀) (3.4 mm).

4. *Ochthephilus omalinus* (ERICHSON, 1840) [22]
5. *Ochthephilus monticola* (CAMERON, 1924) [23]
6. *Carpelimus similis* (SMETANA, 1967) [24]
7. *Carpelimus exiguus* (ERICHSON, 1839) [25]
8. *Carpelimus elongatulus* (ERICHSON, 1839) [26]
9. *Carpelimus bifidus* sp. n. [27]
10. *Xerophygus pallipes* MOTSCHULSKY, 1857 [28]
11. *Xerophygus hreblayi* sp. n. [29]
12. *Mimopaederus insularis* (CAMERON, 1936) [30]
13. *Thinodromus priorus* GILDENKOV sp. n., in litt. [31]
14. *Thinodromus dilatatus* (ERICHSON, 1839) [32]
15. *Thinodromus corvinus* (CASEY, 1889) [33]
16. *Thinodromus caloderinus* (LECONTE, 1877) [34]
17. *Teropalpus juanfernandezianus* sp. n. [35]
18. *Teropalpus skottsbergii* (BERNHAUER, 1921) [36]
19. *Thinodromus luteipes* (SOLIER, 1849) [37]
20. *Thinodromus diffusus* (CASEY, 1889) [38]
21. *Thinodromus chagosanus* (BERNHAUER, 1922) [39]
22. *Thinodromus thoracicus* GILDENKOV, 2000 [40]
23. *Thinodromus indicus* (CAMERON, 1920) [41], formerly in *Apocellagria*
24. *Thinodromus schillhammeri* sp. n. [42]
25. *Thinodromus singularis* (FAUVEL, 1907) [43], formerly in *Apocellagria*
26. *Trogactus ocellatus* sp. n. [44]
27. *Trogactus godmani* SHARP, 1887 [45]

About the selection of taxa – The selection of the most basal outgroup was a particularly difficult one. I picked both *Platydeleaster* and *Deleaster*, because they possess important features in different states. The inclusion of only one of them did not give a truthful representation of the primitive character states or would have hidden important facts. Both species of *Eppelsheimius* are included because the older literature associated these with a range of genera and some publications implied that they might differ in some features of key importance. The type species of all the genera synonymized herein (*A. indica* for *Apocellagria* and *B. schweigeri* for *Bledioschema*) are included in the analysis. For the outgroups, those taxa were chosen that share character states with the ingroups, therefore can resolve their relatedness. Particularly poorly sampled are the huge lineages of the *Thinobius* group, *Bledius* and the *Oxytelus*/*Anotylus* lineages, however, the diversity in these lineages does not greatly influence the larger phylogeny addressed in this study. Taxon sampling in the ingroup differs from the outgroup in density and method: all species groups possessing peculiar character states or combination of character states are represented. The proper representation of the diversity of the ingroups required inclusion of five species, which have not been previously named. With one exception these taxa were discovered in the course of revisionary work and will be included in the publications that revise these genera or species groups. However, in order to properly associate these unique taxa with an identity, the descriptions are lifted and published here as an appendix (Appendix B) to validate the names.

Character set and coding

The selection of the characters was done from the perspective of the phylogenetic information content of features in a higher level classification. Characters that may be useful in species-level identification provide no phylogenetic resolution for higher taxa. The phylogenetic information in characters might vary greatly between genera. HERMAN's (1970) character set was used as a basis, but many of his characters were either irrelevant for this analysis or proved to be highly variable and difficult to code. Therefore about two-thirds of his characters were modified, redefined or substituted by suites of characters almost completely omitted previously. The most important of these are the characters in the mouthparts, terminalia and genitalia. Characters and character states used to infer the phylogenetic relationships of the *Carpelimus* group (Oxytelinae) are as follows.

Head

01 clypeus: 0: well developed, more or less rectangular (Fig. 25), 1: reduced to narrow strip (Fig. 26).

02 epistomal suture: 0: present, 1: absent.

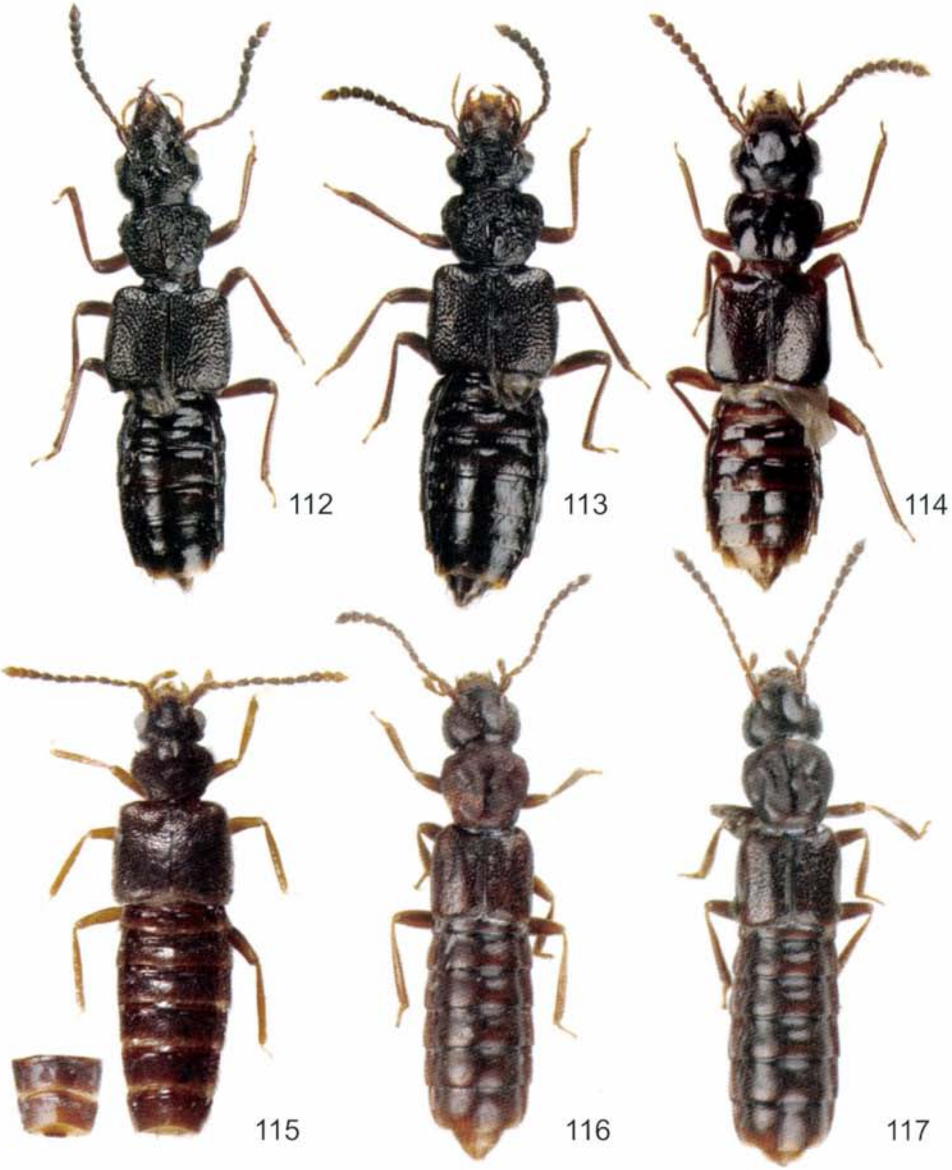
03 eyes: 0: not extending onto ventral portion of head (Fig. 25), 1: extending onto ventral portion of head (Fig. 26).

04 gular sulci: 0: entirely separated (although anterior portion may run very close) (Figs 26–27), 1: confluent at anterior portion (Fig. 25), 2: confluent in posterior portions, not anteriorly (Fig. 28).

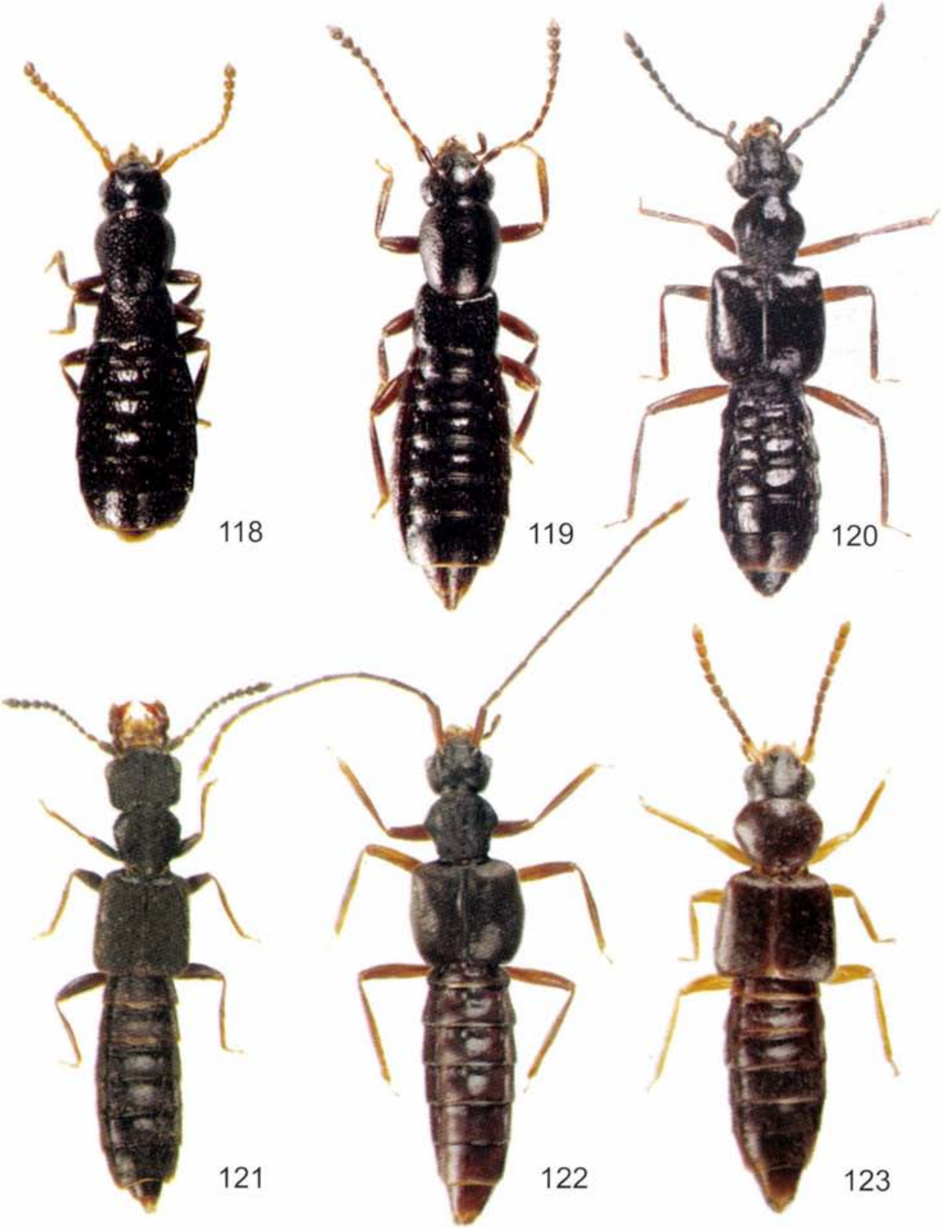
05 head dorsal midline keel: 0: absent, 1: present.

06 mandibular mola: 0: separated, well-developed (Fig. 29), 1: much reduced or absent (Figs 30–31).

07 labrum at mid-line: 0: undivided (Figs 24, 32–33, 35), 1: midlongitudinally divided (except perhaps at very base) (Fig. 34).



Figs 112–117. Habitus of: 112 = *Crassodemus foraminosus* HERMAN, 1968 (♂) (body length = 6.3 mm), 113 = *Crassodemus foraminosus* HERMAN, 1968 (♀) (6.5 mm), 114 = *Crassodemus* sp. (♂) (6.2 mm); 115 = *Thinodromus thoracicus* GILDENKOV, 2000 (♀, plus dissected abdominal tip of male, showing modification of sternum VII) (2.8 mm), 116 = *Thinodromus juanfernandezianus* sp. n. (♂) (4.3 mm), 117 = *Thinodromus juanfernandezianus* sp. n. (♀) (4.5 mm).



Figs 118–123. Habitus of: 118 = *Mimopaederus insularis* CAMERON, 1936 (♀) (body length = 2.9 mm), 119 = *Mimopaederus* sp. (♂) (4.1 mm), 120 = *Thinodromus schillhammeri* sp. n. (♂) (3.8 mm), 121 = *Xerophygus hreblayi* sp. n. (♀) (4.5 mm); 122 = *Trogactus ocellatus* sp. n. (♂) (4.7 mm), 123 = *Carpelimus bifidus* sp. n. (♀) (2.7 mm).

08 labrum shape: 0: transverse, concave at front (Figs 32–34), 1: rounded, convex at front (Fig. 35).

09 setation behind the front of labrum: 0: nearly equal sized and spaced setae, 1: nearly equal sized and spaced setae hyperdeveloped (reaching far beyond 2 times labrum length) (Fig. 33), 2: setae in the middle much smaller or missing (Fig. 32), 3: setae missing in middle, but lateral ones hyperdeveloped.

10 dorsal setae on epipharynx (interpreted differently from HERMAN 1970): 0: present (Fig. 33), 1: absent.

11 hypopharynx: 0: complete, undivided (Fig. 37) 1: anteriorly divided (=incised) (Figs 20–21).

12 hypopharynx: coriaceous field on ventral side: 0: present (often with setation) (Fig. 38) 1: absent.

13 hypopharynx: row of bulbous setae (inside setae on adoral margin): 0: no extra row, 1: row or field (sometimes sparse) of bulbous setae (Figs 20–21).

14 front of hypopharynx: 0: not entirely covered, bare in the middle (Fig. 37), 1: entirely covered by setae (Figs 20–21).

15 mid-line of hypopharynx: 0: without midlongitudinal row of setae (Fig. 37), 1: with midlongitudinal row of setae (Figs 20–21).

16 median sclerotized plate of hologlossa (term from NAOMI 1988*b*): 0: central stick with intermediate platelike enlargement (Figs 39–40), 1: central stick with large apical plate (stick continues till nearly the end of plate) (Figs 36, 41), 2: central stick shortened (not even nearly reaching apex), with large, lamellar apical plate (Figs 42–43).

17 maxillary palp last palpomere (term * conflicting with HERMAN's (1970) usage): 0: fully formed, not or only slightly asymmetrical (Fig. 45), 1: fully formed*, strongly enlarged (bulbous) on the side of digitiform sensilla (Fig. 44), 2: bulbous but strongly desclerotized at base (Fig. 47), 3: reduced to a stick ("acicular" by HERMAN) (Figs 23, 49).

18 digitiform sensilla of maxillary palp:, 0: present on last palpomere (Figs 44–46), 1: fused to apex of penultimate palpomere (Fig. 48), 2: on penultimate palpomere, towards middle (Fig. 49), 3: absent.

19 arrangement of digitiform sensilla on maxillary palp: 0: semi-circular or oval (Fig. 45), 1: transitional; parallel, but in a bit of a curve (Fig. 46), 2: parallel (Figs 44, 47–49).

20 vestiture of labial palp: 0: not setose or glabrous, 1: basal segment with setae mediad, 2: penultimate segment setose latero-apically.

21 antennae: 0: straight, 1: geniculate (flexes posteriorly), first segment elongated.

22 antennae: 0: antennomeres 3 times their width or less (Fig. 22), 1: antennomeres extremely elongated (midantennal segments more than 3 times their width).

Thorax

23 prosternal process: 0: pointed (Figs 50–51), 1: truncate.

24 scutellum: 0: without pubescence, 1: pubescent (at least on apex -posteriorly directed) (Fig. 54).

25 hypomera of pronotum (this character and the state definitions are in conflict with HERMAN's (1970) usage of terms): 0: moderately broad, exposing protrochantins (= wide open procoxal fissure) (Fig. 50), 1: greatly enlarged, concealing protrochantins (= closed or slightly open procoxal fissure) (Figs 19, 51).

Legs

26 mid-tibial spur(s): 0: absent, 1: present.

27 tibial spines or rows of stiff setae: 0: present, 1: absent.

28 tarsal segmentation: 0: 5–5–5, 1: reduced: 4–4–4, 2: reduced: 3–3–3, 3: reduced: 2–2–2.

29 presence of pseudo-segment (segment without its own setation): 0: does not have (asetose) pseudo-segment, 1: has (asetose) pseudo-segment (Fig. 57).

30 compression of basal tarsomeres: 0: not compressed, 1: compressed.

31 ventral tarsal setae: 0: unmodified, 1: on (usually) penultimate tarsomeres modified to form characteristic tarsal lobes (Figs 17–18, 55–56).

32 pubescence on last tarsomere: 0: sparse setae (Figs 55, 57), 1: dense pubescence (Fig. 56).

Elytra

33 elytral puncture-rows (striae): 0: present, 1: absent.

34 elytral suture: 0: normal (parallel), 1: dehiscent.

35 elytral epipleural ridge: 0: present (Fig. 53), 1: absent (Fig. 52).

Figs 124–129. Habitus of: 124 = *Neoxus crassicornis* (CASEY, 1889) (♀) (body length = 1.3 mm), 125 = *Sciotrogus opacus* SHARP, 1887 (♀) (1.8 mm), 126 = *Anotylus* sp. (♂) (3.8 mm), 127 = *Anotylus seticornis* (FAUVEL, 1895) (♂) (4.2 mm), 128 = *Anotylus seticornis* (FAUVEL, 1895) (♀) (3.7 mm); 129 = *Oxytelus echidne* (FAUVEL, 1904) (♂) (2.6 mm).

Abdomen

36 laterosclerites (on segments III-VII): 0: one pair per segment, 1: two pairs per segment.

37 intersegmental membranes: 0: with brickwall pattern, 1: without brickwall pattern.

38 second sternite: 0: not fully developed, anteriorly more membranous, 1: fully developed (sclerotized).

39 first sternite: 0: present as sclerite(s) embedded in basal membrane of sternite II, 1: absent.

40 tergal basolateral ridges: 0: absent, 1: present on tergites II-VII, 2: present on tergites III-VII.

41 basomedian carina on sternite II: 0: absent, 1: present (Fig. 72).

42 tergum VII apex with: 0: unmodified fimbriate edge (sometimes gradually enlarged in middle) (Fig. 58), 1: center of fimbriate edge modified into comb-like structure with sparser and elongated fimbriae (Fig. 68), 2: center modified into comb, fimbriae of edge otherwise lost (Fig. 69).

43 tergum X: 0: undivided, 1: divided by transverse line (Fig. 75).

44 dorsal strut between tergites IX and X: 0: present, attached to tergite X, 1: present, attached to tergite IX, 2: absent.

45 basal/lateral parts of tergum X fused to tergum IX: "rhomboid fusion": 0: no, 1: yes (Fig. 74)

Secondary sexual characters

46 macrocephaly: 0: males have heads similar to females, 1: males have heads with enlarged temples and/or broadened frons.

47 macrothoracy: 0: males have pronotum similar to females, 1: males have elongated pronotum.

48 spines on sternum VII: 0: absent, 1: present (apical edge is pulled out in 2 spines) (Fig. 73).

49 transverse row of modified setae on apical edge of sternum VII: 0: absent, 1: present (Fig. 115).

50 modification in sternum VIII: 0: males only have different shape of the apical edge of sternum VIII (Figs 70–71), 1: males have incisions, and/or appendices on sternum VIII, plus tubercules and hairs associated with them.

Male terminalia

51 sternum IX: 0: present (Fig. 62), 1: absent.

52 apex of sternum IX: 0: with setae, 1: without setae.

Male genitalia

53 aedeagus median lobe general shape: 0: bulb-like or slightly dorso-ventrally flattened, 1: laterally flattened.

54 internal sclerites of median lobe: 0: absent, 1: present, asymmetrical/unpaired, 2: present, symmetrical/paired.

55 aedeagus, apical opening: 0: distinct, well-developed apices (Figs 86–87), 1: simplified, truncated (Fig. 88), 2: completely membranous, amorphous (Fig. 90), 3: modified into sclerotized "clasping" structures, 4: frontally fused into triangular apex (Fig. 91).

56 aedeagus, median face: 0: only membranous surface (Figs 86–87), 1: present, with sclerotized edge (Fig. 92), 2: present, with embedded, strongly sclerotized plates (Fig. 89).

57 aedeagus with apicomedial hook (on frontal side) of median lobe, originating from base of parameres:, 0: absent, 1: present (weak, short or stronger, well-developed) (Figs 92, 95–96).

58 parameres: 0: not formed as wrapper (Figs 86–88), 1: wrapping around apical half of median lobe (Figs 89, 97).

59 parameres: 0: without projections, 1: bilobed (Figs 86, 93–94).

60 parameres: 0: without membranous region (Fig. 87), 1: with membranous regions towards apex (Fig. 89).

61 parameres: 0: without setae (Fig. 87), 1: with one seta each (Fig. 88), 2: with 2 setae each, 3: with many setae (Fig. 92).

62 visible pump and flagellum in median lobe: 0: absent (Figs 86–90), 1: present (Fig. 91).

Female terminalia

63 female genital appendages: 0: divided into coxites, valvifers and styli (Fig. 67), 1: coxites and valvifers only (styli absent), 2: coxites and valvifers fused (indistinguishable), 3: pair is fused to form a single plate (Fig. 85), 4: absent.

64 external sclerites (possibly remnant of sternum X), ring structure: 0: present, well-developed, attached to abdominal segments (Figs 82–83), 1: present, a (more or less) small ring, free from segments (Figs 76–79, 80–81), 2: absent.

Female genitalia

65 spermatheca: 0: sac-like (usually highly unsclerotized) (Figs 98–99), 1: characteristically shaped, sclerotized (Figs 100–105).

66 receptacle: 0: undivided (Fig. 100), 1: divided (Figs 101–105).

67 spermathecal gland: 0: visible (Figs 99, 101, 103), 1: invisible (Figs 98, 100).

68 introversion on spermatheca (tubular portion penetrating distal bulb): 0: absent, 1: present (Figs 101–102).

69 umbilicus on spermatheca: 0: absent, 1: present (Figs 104–105).

70 sclerotized "tube" apparently associated with female genital tract: 0: absent, 1: present (Fig. 84).

Results

The strict consensus tree (L=266, CI=36, RI=64) is shown on Fig. 2. Character states were distributed in the tree using Acctran optimization (favors reversals). For such an ancient group, the frequency of reversals might actually be high, therefore this optimization was favored against Deltran. As for the tribal classification of Oxytelinae, the following conclusions can be drawn: The tribe Deleasterini is likely not monophyletic, but as the basal clade of the subfamily with obviously great disparity, it makes sense to maintain it, pending further phylogenetic analysis. The tribe includes relict genera *Mitosynum*, *Oxypius* and *Euphanias*. None of the included 6 genera exceeds 10 species, and 3 of them monobasic. The clade is apparently very ancient and has suffered a lot of extinctions. The tribe Coprophilini is sampled by a single taxon. The tribe Planeustomini is revalidated herein to include genera *Planeustomus* and *Manda*. The clade is supported by 3 unique synapomorphies: Clypeus reduced to narrow strip (**1**–1), eyes extending on ventral portion of head (**3**–1), mandibular mola much reduced or absent (**6**–1). The monophyly of this group is very likely. There is some difference in opinion on whether the name Planeustomini published originally in non-latinized form should be regarded available from JACQUELIN DU VAL, but since at this time it cannot be said for sure exactly how many times this extremely old name can be found (there is at least one in ÁDÁM and HEGYESSY 2001), it is considered the valid name here.

NEWTON and THAYER (1992*a*), following the suggestion of MADGE (1989), accepted as available all the non-latinized names from well-known publications, if there has been at least one subsequent mention since the original publication (citing it from that particular author and date). The same treatment is followed here. Also, the suffix "-ites" (means "-like"), if applies to extant taxa, is generally accepted as an available family-group name. In this analysis the genera *Bledius* and *Eppelsheimius* appear as a monophyletic clade, distinguished from the rest of the taxa by one unique synapomorphy: the geniculate antennae (**21**–1). I propose the recognition of these genera in a separate tribe: Blediini ÁDÁM, 2001. The remaining branches of the tree have very weak support (many homoplasious characters), except for some terminal branches: characters **8**–1, **28**–3 and **35**–1 supporting *Sciotrogus+Thinobius+Neoxus*, characters **22**–1 and **32**–1 for *Trogactus*. The situation with the former tribes Thinobiini and Oxytelini is more complex. It is obvious, that none of these are monophyletic as currently recognized, although they do form a monophyletic clade together. With the recognition of Blediini, there are two remaining large clades; the separation between them has very weak support. One contains the former Oxytelini plus two genera (*Aploderus* and *Crassodemus*) from former Thinobiini. The other contains the *Carpelimus* and *Thinobius* groups of genera, only the latter is likely monophyletic. To resolve these problems, there are the following two options: (1) move *Aploderus* and *Crassodemus* into Oxytelini and redefine both Thinobiini and Oxytelini. Since the separation between the two is very weak and the contained diversity enormous, this is almost impossible to do. *Aploderus* and *Crassodemus* do not share those features (tarsal formula 3–3–3; broad metasternal process, tarsal lobes) upon which Oxytelini was previously based. In the other clade the only unique synapomorphy is the loss of a feature, the tibial spines and modified rows of setae. This character is rather difficult to determine in certain taxa, and its consistency in all related genera has not been tested. Also it is not clearly agreed between specialists what exactly constitutes of "modified setae" – throughout this work the term is used to differentaiate scattered, occasional setae from arranged, symmetrical formations. In my opinion, tribes without clearly defined, unique synapomorphies should not be maintained or created. (2) merging the Oxytelini with Thinobiini (the former name taking priority) less Blediini. This is the preferred solution, as it allows better characterization of the tribe.

Within the tribe Oxytelini (sensu novo) the generic limits are also investigated. The problems with the monophyly and delimitation of *Thinodromus* were hypothesized prior to the detailed study. The analysis confirmed this hypothesis. Two genera, *Carpelimus* and *Trogactus* appear within the clade of *Thinodromus*, meaning that the latter is not monophyletic. However, since the clades have such weak support, no taxonomic action is proposed, pending additional phylogenetic analysis with different suites of characters, possibly molecular data or larval characters. Apart from the homoplasious characters and lack of unique synapomorphies for the clades, the genera in the current sense can be unambiguously characterized by combinations of character states: *Carpelimus* (three segmented tarsi with compressed basal segments and tarsal lobes), *Trogactus* (densely pubescent last tarsomere, extremely elongated antennae), *Thinodromus* (five segmented tarsi with compressed basal segments and presence of sternite IX in males), *Xerophygus* (pump and flagellum in aedeagi and the unique combination of rhomboid fusion between tergites IX and X plus presence of fully developed sternite IX in males), *Teropalpus* (five segmented tarsi with tarsal lobes, narrowly separated gular sutures), *Blediotrogus* (frontally separated gular sutures, five segmented tarsi), *Pareiobledius* (four segmented tarsi with tarsal lobes), *Ochthephilus* (five segmented tarsi with tarsal lobes and presence of first sternite embedded in the basal membrane of the second sternite), *Mimopaederus* (five segmented tarsi with tarsal lobes, highly elongated, conical pronotum with margins dorsally invisible). Based on this information, the continued recognition of *Trogactus* and *Carpelimus* is suggested. However, former genera *Apocellagria* and *Bledioschema* are synonymized with *Thinodromus* and *Aploderus*, respectively. This conclusion is based on the almost total agreement with the generic characters of the senior taxa and the high variability in the characters that were used to delimit the 2 former genera. In case of *Aploderus* and *Bledioschema*, not only the adult characters, but also the larval ones agree in all important details (the larva of *Bledioschema* is described in LÖBL & KODADA 1996). In recent years, micropterous, microphthalmous *Aploderus* species were found on multiple occasions. The issues with the generic limits in the *Oxytelus* and *Anotylus* groups are discussed in a separate chapter and not repeated here, since these were not investigated in detail by cladistic analysis. The target of the study, the *Carpelimus* group does not appear to be monophyletic. The *Thinobius* group of genera resides within a clade with some members of the *Carpelimus* group. Since the *Thinobius* group itself was not the target of the study and was not sampled adequately for answering such a question, the exact relationships between these two groups of genera cannot be hypothesized from the results of the outlined analysis alone. Further investigation of the *Thinobius* group is needed. One conclusion, however, cannot be avoided: the genus *Neoxus* is likely a derived lineage within *Thinobius*, therefore the monophyly of the latter is at least questionable. The genus *Ochthephilus* is very challenging, for possessing a series of ancestral character states (undivided labrum, fully developed female genital appendages, sac-like unsclerotized spermatheca) together with fairly derived ones (tarsal lobes, compressed basal tarsomeres). The phylogenetic position of this group is still dubious as its placement is weakly supported (no unique synapomorphies). The primary result of this analysis, is that all the characters used for Oxytelini as recognized earlier either (1) vary within the tribe or (2) occur scattered in other genera outside the tribe. I am also guessing that the larval characters will confirm this conclusion, as well, but they definitely require further study. As the analysis concentrates primarily on the group of genera that was previously considered to be a monophyletic group within the former Thinobiini, the taxon sampling is limited for the *Bledius*, *Thinobius*, *Oxytelus* and *Anotylus* groups of genera. Therefore relationships among these taxa cannot be reliably inferred from the phylogenetic hypothesis depicted on the trees presented (Figs 2–3). The sampling of these taxa was only aimed at inclusion of characters and character states that might give information on the relatedness of the ingroups. This refers to the relationships of *Neoxus* and *Thinobius*, the genera of the former Oxytelini among each other, the species groups within *Bledius* (it was discussed in HERMAN 1986) and the basal clades of Deleasterini and Coprophilini. The sizes and diversities of some of these taxa is such, that their adequate sampling was impossible within the present study.

SCHEERPELTZ in 1944 erected a new tribe, Trigonobregmini, and described the genus *Trigonobregma*, based on the species *Thinobius ocularis* FAUVEL, 1902. HERMAN (2001) listed the genus and species in Oxytelinae and in a further paper (HERMAN 2003) explained that it was overlooked at the time of his 1970 generic revision and he erroneously included *T. ocularis* in *Thinobius*. Upon examination of the single syntype specimen it is obvious that it is not a member of the Oxytelinae, because there are not seven visible abdominal sternites, not even a trace of a developed second sternite. The species belongs in the tribe Aphaenostemmini (subfamily Omaliinae), but transferring the name is outside the scope of this work, so will be dealt with elsewhere.

The situation with the *Oxytelus* and *Anotylus* groups of genera (although only represented by 3 species in the analysis, was studied extensively on a worldwide basis) is dealt with in a separate chapter. The characters used in the analysis of the *Carpelimus* group do not provide resolution for these clades – in fact, probably no known morphological characters would.

THE PROPOSED NEW TRIBAL CLASSIFICATION

1. Tribe Deleasterini REITTER, 1909 (type: *Deleaster*)
    = Pholidiens MULSANT et REY, 1877 (type: *Pholidus*)
    = Pholidini ACLOQUE, 1896 (type: *Pholidus*)
    = Euphaniae REITTER, 1909 (type: *Euphanias*)

        - = Syntomiinae BÖVING et CRAIGHEAD, 1931
    - genus *Platydeleaster* SCHÜLKE, 2003
    - genus *Deleaster* ERICHSON, 1839
    - genus *Mitosynum* CAMPBELL, 1982
    - genus *Syntomium* CURTIS, 1828
    - genus *Oxypius* NEWTON, 1982
    - genus *Euphanias* FAIRMAIRE et LABOULBÈNE, 1856
2. Tribe Coprophilini HEER, 1839 (type: *Coprophilus*)
        - = Homalotriquitos SOLIER, 1849 (type: *Homalotrichus*)
        - = Homalotrichites LACORDAIRE, 1854 (type: *Homalotrichus*)
        - = Toxoderi BERNHAUER et SCHUBERT, 1911 (type: *Toxoderus*)
    - genus *Coprophilus* LATREILLE, 1829
    - genus *Coprostygnus* SHARP, 1886
    - genus *Homalotrichus* SOLIER, 1849
3. Tribe Planeustomini JACQUELIN DU VAL, 1857 (type: *Planeustomus*)
        - = Mandini GILDENKOV, 2003 (type: *Manda*)
    - genus *Manda* BLACKWELDER, 1952
    - genus *Planeustomus* JACQUELIN DU VAL, 1857
4. Tribe Blediini ÁDÁM, 2001 (type: *Bledius*)
    - genus *Bledius* LEACH, 1819
    - genus *Eppelsheimius* BERNHAUER, 1915
5. Tribe Oxytelini THOMSON, 1858 (type: *Oxytelus*)
        - = Trogophléaires MULSANT et REY, 1878 (type: *Trogophloeus*)
        - = Trogophloeini REITTER, 1909 (type: *Trogophloeus*)
        - = Thinobiides J. SAHLBERG, 1876 (type: *Thinobius*)
        - = Torrentomini BIERIG, 1934 (type: *Torrentomus*)
        - = Carpelimini HATCH, 1957 (type: *Carpelimus*)
        - = Apocellaria LYNCH, 1884 (type: *Apocellus*)
        - = Ecitoclimacini BORGMEIER, 1934 (type: *Ecitoclimax*)
        - = Apocellini HATCH, 1957 (type: *Apocellus*)
        - = Aploderini ÁDÁM, 2001 (type: *Aploderus*)
    - genus *Crassodemus* HERMAN, 1968
    - genus *Aploderus* STEPHENS, 1833
        - (= *Bledioschema* SMETANA, 1967, **syn. n.**)
    - genus *Blediotrogus* SHARP, 1900
    - genus *Pareiobledius* BERNHAUER, 1934
    - genus *Teropalpus* SOLIER, 1849
    - genus *Mimopaederus* CAMERON, 1936
    - genus *Ochthephilus* MULSANT et REY, 1856

genus *Xerophygus* KRAATZ, 1859
genus *Carpelimus* LEACH, 1819
genus *Thinodromus* KRAATZ, 1857
 (= *Apocellagria* CAMERON, 1920, **syn. n.**)
genus *Trogactus* SHARP, 1887
genus *Thinobius* KIESENWETTER, 1844
genus *Neoxus* HERMAN, 1970
genus *Sciotrogus* SHARP, 1887
genus *Sartallus* SHARP, 1871
genus *Parosus* SHARP, 1887
genus *Paraploderus* HERMAN, 1970
genus *Ecitoclimax* BORGMEIER, 1934
genus *Jerozenia* HERMAN, 2003
genus *Platystethus* MANNERHEIM, 1830
genus *Oxytelus* GRAVENHORST, 1802
 (= *Paroxytelopsis* CAMERON, 1933, **syn. n.**,
 = *Hoplitodes* FAUVEL, 1904, **syn. n.**,
 = *Anisopsis* FAUVEL, 1904, **syn. n.**,
 = *Anisopsidius* FAGEL, 1960, **syn. n.**)
genus *Apocellus* ERICHSON, 1839
genus *Anotylus* THOMSON, 1859
 (= *Oxytelopsis* FAUVEL, 1895, **syn. n.**,
 = *Rimba* BLACKWELDER, 1952, **syn. n.**)

Using the results of this phylogenetic analysis, certain individual problems can be addressed. One is the homologies of the structures within the internal sac of the male genitalia. These play a critical role in the identification of species, therefore their correct naming and consistent usage of the names is urgent and desirable. It is believed that the results of the analysis provide at least some clues on the evolution of these characters and will help naming and homologizing the structures. Just as interesting is the evolution and the origin of sclerites found in the female terminalia (and associated with the genitalia). Since these structures often provide very valuable identification tools, they require more attention. Another field of interest may be the larval characters. At this point we only have very basic information and the larvae of many, critically important, taxa are unknown.

LARVAE OF THE CARPELIMUS GROUP

Although immatures of certain genera (e.g. *Bledius*) are frequently encountered, descriptions of larval stages of Oxytelinae are sparse in the literature. There are only a few works devoted to the immatures of this subfamily (e.g. STANIEC 2001). Descriptions of the larvae of the most important genera can be found in POTOTSKAYA 1967, KASULE 1968, BOURNE 1975, GILDENKOV 1996 and STANIEC 1997, 1999. The larvae of Staphylinidae are distinguished from other Coleoptera by the (1) urogomphi on tergum IX, (2) mandibles without contiguous molar lobes at bases, (3) maxilla with a simple, undevided inner lobe (fixed or articulated). In most situations the larvae of Staphylinidae can be found together with those of Carabidae (riparian habitats) and Hydrophilidae (dung). They are distinguished from Carabidae by (1) articulated urogomphi, (2) having only a single segment without claws (tarsungulus) beyond the tibia of the legs. They are distinguished from Hydrophilidae by articulated appendage at the apex of the stipes of the maxilla, rather than on the first apparent palpal segment. Larvae of the subfamily Oxytelinae (Figs 106–107) are characterized by (1) left and right mandibles (rather wide at apex) approximately symmetrical (with similar number of subapical teeth), (2) penultimate segment of maxillary palp as long or shorter than preceding segment or urogomphus falciform, (3) urogomphus one-segmented, (4) four or less stemma, (5) ligula transverse, truncate. Within Oxytelinae, the larvae of Deleasterini (1) have more than one stemmata (4 or 3) in a curve and (2) urogomphi clubbed. The larvae of Coprophilini are distinguished by their (1) stemma absent and (2) urogomphi strongly falcate. For the tribe Planeustomini, there are no larvae known (NEWTON, pers. comm.). For Blediini, larvae are known only for *Bledius* (NEWTON, pers. comm.); since the life habits of these are rather similar to adults and they frequently appear together with them in large numbers (MAKRANCZY, pers. obs.), their collection and association to adults is relatively easy (does not require rearing or special collecting techniques) and descriptions are many. Although earlier literature mentioned a "brush" of stiff setae at the apex of the maxillary mala, this does not appear consistently throughout the genus. The larvae of Oxytelini are characterized by (1) stemmata one to three in a curve, (2) urogomphus (frequently) concavely pointed at apex. All the known larvae of the *Carpelimus* group have distinctive dark stretch marks in abdominal intersegmental membranes (Fig. 101). Most other Oxytelinae lack this feature (Fig. 100). Although the larvae of the genera *Blediotrogus*, *Pareiobledius* and *Teropalpus* were not studied personally by the author, the occurrence of these dark stretch marks in *Blediotrogus* and *Teropalpus* were confirmed by NEWTON (pers. comm.) and in *Pareiobledius* implied in a letter (2000) from HAMMOND (pers. comm.), who collected them. Apart from these aforementioned genera, the only known oxyteline larva with this character state is *Crassodemus*.

KEY TO GENERA OF OXYTELINAE

This key is not intended to be a practical identification guide, rather a systematic one, which helps workers determine whether a particular species belongs to a given genus or not. This goal can only be achieved by often relying on anatomical characters (necessitating permanent preparations or dissections). Since the superficial similarity between unrelated taxa can be great, it is unavoidable that less experienced workers examine at least a few of the key features of the genital segments, which can unequivocally determine the placement of a specimen. A more practical approach would require the use of external morphological characters that can vary and result in confusion – not counting the (great) possibility of previously unseen species possessing yet undiscovered character states.

1 Abdominal segments III to VI with one pair of laterosclerites per segment. (Deleasterini) 2

– Abdominal segments III to VI with two pairs of laterosclerites per segment 7

2 Procoxal fissure fully open. Tibia with longitudinal row of spines 3

– Procoxal fissure nearly or quite closed. Tibia without longitudinal row of spines absent 4

3 Pronotum distinctly convex in cross-section, laterally not margined; elytra without rows of punctures. Tergite VIII with serrate posterior margin. Body surface more or less dull *Deleaster*

– Pronotum flat and distinctly margined laterally; elytra with rows of punctures. Tergite VIII with smooth posterior margin. Body surface shining, except for the impressions and rows of punctures on head, pronotum, and elytra (Fig. 108) *Platydeleaster*

4 Body, especially dorsum, with numerous scale-like setae 5

– Body without scale-like setae 6

5 Scale-like setae not plumose. Tarsal formula 5–5–5 *Oxypius*

– Scale-like setae plumose. Tarsal formula 3–3–3 *Euphanias*

6 Labrum with anterior margin emarginate. Elytra (from apex of scutellum) at least as long as pronotum *Syntomium*

– Labrum with anterior margin broadly convex; elytra (from apex of scutellum) distinctly shorter than pronotum (Fig. 109) *Mitosynum*

7 Reduced second sternite with a very short, immobile membranous connection to third sternite (hence only 6 complete sterna can be counted) (Coprophilini)

– Well developed second sternite articulated to third by a long connecting membrane (hence 7 complete sterna can be counted) 10

8 Gular sulci separated along entire length (Figs 26–27) *Coprophilus*

– Gular sulci confluent anteriorly 9

9 Epistomal sulcus present (Fig. 110) *Coprostygnus*

– Epistomal sulcus absent *Homalotrichus*

10 Eyes extending onto ventral portion of head (Planeustomini) (Fig. 26) 11

– Eyes not extending onto ventral portion of head 12

11 Five distinct tarsomeres. Brick-wall pattern in intersegmental membrane *Manda*

– Four tarsomeres with additional non-setose pseudoarticle (Fig. 56), brick-wall pattern in intersegmental membrane absent *Planeustomus*

12 Antennae geniculate (flexing posteriorly) (Blediini) 13

– Antennae not geniculate (Oxytelini) 14

13 Setation behind the front of labrum hyperdeveloped so that the lateral setae reach well beyond four times the length of labrum (Fig. 111) *Eppelsheimius*

– Setation behind the front of labrum is well developed but not reach beyond four times the length of labrum *Bledius*

14 Tarsomeres five 15

– Tarsomeres less than five 25

15 Elytra long, almost entirely covering abdomen *Sartallus*

– Elytra short, abdomen almost fully visible 16

16 Pronotum cylindrical, lateral margins invisible from dorsal view (Figs 118–119) *Mimopaederus*

– Pronotum with lateral margins always visible from dorsal view 17

17 Gular sulci narrowly separated anteriorly, more widely posteriorly (Fig. 27) *Teropalpus*

– Gular sulci fused at least partially 18

18 Gular sulci not fused anteriorly, but merged posteriorly *Blediotrogus*

– Gular sulci always fused anteriorly 19

19 Labrum undivided 20

– Labrum divided along mid-line (Fig. 34) 21

20 Basolateral portions of tergite X fused to tergites IX (rhomboid fusion) (Fig. 74) *Xerophygus*

– Tergite X always complete, unmodified *Ochthephilus*

21 Antennae not extremely elongated (mid-antennal segments less than three times as long as broad) *Thinodromus*

– Antennae extremely elongated (mid-antennal segments more than three times as long as broad) *Trogactus*

22 Tarsomeres four 23

– Tarsomeres less than four 24

23 Basal segment of labial palp with strong setation mediad. Distal segment of maxillary palp much longer than penultimate (Figs 112–114) *Crassodemus*

– Basal segment of labial palp without such setation. Distal segment of maxillar palp quite reduced, much smaller and thinner than penultimate *Pareiobledius*

24 Tarsomeres three 25

– Tarsomeres two 34

25 Basal two tarsomeres strongly compressed *Carpelimus*

– Basal two tarsomeres not compressed 26

26 Labrum medially divided (Fig. 34) 27

– Labrum not divided medially 28

27 Tergum X not bilobed. Tergal basolateral ridges absent, epistomal sulcus present, sometimes accentuated by dark line *Aploderus*

– Tergum X slightly bilobed at apex. Tergal basolateral ridges present, epistomal sulcus absent *Paraploderus*

28 Labrum anteriorly with a very conspicuous rounded incision *Parosus*

– Labrum without such incision 29

29 Pronotal lateral marginal bead absent *Ecitoclimax*

– Pronotal marginal bead present 30

30 Antennomeres nine *Jerozenia*

– Antennomeres eleven 31

31 Elytra slightly overlapping at suture *Platystethus*

– Elytra strictly parallel at suture 32

32 Scutellar impression distinctly diamond-shaped. Aedeagus with apicomedial hook *Oxytelus*

– Scutellar impression different. Aedeagus without apicomedial hook 33

33 Neck about half as wide as head at temples *Apocellus*

– Neck wider than half of head width at temples *Anotylus*

34 Elytral epipleural ridge present. Hypomeron of pronotum well developed, concealing most of protrochantin (Fig. 53) (Fig. 124) *Neoxus*

– Elytral epipleural ridge absent. Hypomeron of pronotum less extended mediad; protrochantin visible (Fig. 52) 35

35 Scutellum pubescent (to various degrees) *Thinobius*

– Scutellum without pubescence (Fig. 125) *Sciotrogus*

APPENDIX A: Specimens examined

For this section, the data of the specimens actually examined for the phylogenetic analysis are listed (i.e. not all specimens seen by the author), followed by the depositories and the numbers of specimens. The permanent slide preparations (usually one of each species, where possible) are also listed (as a general rule, these were made of damaged, incomplete beetles and are kept in the author's possession). For those species, where there were not enough specimens to make such slide preparations, the critically important parts (usually mouthparts) are embedded on a plastic microslide, pinned with the specimen, the same way as described for genital preparations.

Platydeleaster bimaculatus – RUSSIA: Primorie (S7/11), Schutzgebiet Sichote-Alin, Jasnaja-Mündung, 26.VI.–4.VII.1998, leg. J. SUNDUKOW (sSch, 1, Paratype ♀); Sakhalin Is., Mt. Chekhova, 30.V.1991, leg. M. NESTEROV (slide preparation, 1♂).

Deleaster dichrous – ITALY: (Bresc.) Idro, 3.VII.1973, leg. P. KANAAR (SEMC, 1♂, 1♀). NETHERLANDS(?): "457" (slide preparation, 1).

Coprophilus longicollis – KYRGIZSTAN: W. Tian-Shan, Fergansky Mts., Valley of riv. Semendykgai, 2300 m, 19–20.IV.1992, leg. V. SHCHUROV (NHMB, 1♂, 1♀).

Manda mandibularis – UNITED KINGDOM: Bookham, 22.VI.1940, leg. C.E.T[OTTENHAM]. (SEMC, 1♂). HUNGARY: Aggteleki N.P., Szin, Szelcepuszta, at light, 20.VI.1990, leg. O. MERKL (HNHM, 1♀); Nógrád county, Ipolytarnóc, Borókás-árok, at light, 30.V.1999, leg. O. MERKL (HNHM, 1♀).

Planeustomus palpalis – HUNGARY: Nógrád county, Ipolytarnóc, Borókás-árok, netting with car, 29.VII.2001, leg. O. MERKL (HNHM, 1♀); Nógrád county, Ipolytarnóc, Borókás-árok, netting with car, 28.VI.2000, leg. O. MERKL (slide preparation, 1♂).

Crassodemus foraminosus – BRAZIL: Sao Paulo (NMPC, 2, Holotype ♂ and Paratype ♀); AM, Salesopolis, Biol. Stn. Boraceia, 14–17.VIII.1995, leg. ARNDT & GRÖGER (ZMHB, 1♂, 1♀).

Crassodemus sp., undescribed – ECUADOR: Zamora-Chinchipe, Rio Bombuscaro, 1100m, 26. VI.–4.VII. 1996, leg. P. HIBBS (SEMC, 1♂).

Aploderus caelatus – SLOVAKIA: Carpathian Mts., Trencsén [Trenčín], leg. BRANCSIK (SEMC, 1♂) (slide preparation, 1♀).

Aploderus schweigeri – TURKEY: Zonguldak, Eregli-Baliköy, 15.V.1976, leg. Cl. BESUCHET & I. LÖBL (MHNG, 1♂, 1♀, 3).

Paraploderus parcepunctus – KENYA, Mt. Elgon, 2380 m, 17.I.1979, leg Th. PALM (MZLU, 2♂, 1♀); Kakamega Forest, Udo's Bandas, under bark, 14.XI.2001, leg. V. GREBENNIKOV (FMNH, 2).

Oxytelus laqueatus – NETHERLANDS: Heeswijk (N.B.), ex: horse dung, 1.V.1975, leg. P. KANAAR (SEMC, 1♂). ITALY, (Brescia), Dosso Alto, 4km SW of Bagolino, 1950 m, VII.1972, leg. P. KANAAR (SEMC, 1♀). NORWAY, Austmarka, Ronningen, VII.1975, leg. P. KANAAR (slide preparation, 1).

Anotylus seticornis – BURMA: Carin, Asciuii Ghecu, 1400–1500 m, III-IV.1888, leg. L. FEA (ISNB, 1, Syntype of *Delopsis seticornis*, ♂); N. East Burma, Sadon, 1200 m, 28.VI.–5.VII., leg. MALAISE (NHRS, 1, Holotype of *Delopsis birmana*, ♂). NEPAL: East Nepal, Rolwaling Himal, Tama Koshi Tal, unterh. Simigaon, 1300 m, 03.VI.2000, leg. A. KLEEBERG (cKle, 1♀).

Bledius talpa – SLOVAKIA: Vysoké Tatry, Belá potok, near Podbanské, on gravelly-sandy bank, 900 m, 17.VII.1999, leg. MAKRANCZY (SEMC, 1♂); Vysoké Tatry, Kôprova dolina, Kôprovský potok, on gravel bank in wide valley, 1100 m, 17.VII.1999, leg. MAKRANCZY (SEMC, 1) (slide preparation, 1♀).

Eppelsheimius miricollis – TUNISIA: Kebili, V.1952., leg. J. OCHS (MHNG, 1♂, 1♀, 2).

Eppelsheimius pirazzolii – KAZAKHSTAN: ec. Džambul, VI.1964, leg. GOTTWALD (NHMB, 1♂, 1♀, 1). TUNISIA: Gabes, 18.II.1959, leg. PALM (ZMLU, 2).

Sciotrogus opacus – MEXICO: Tamaulipas, Gomez Farias, Nacimiento Rio frio, UV light, 29.VI.1969, leg. S. PECK (AMNH, 1♂); Sonora, Alamos, 12.VIII.1960, leg. P. H. ARNAUD, jr, E. H. ROSS, D. C. RENTZ (CASC, 1♀).

Thinobius apfelbecki – BOSNIA-HERCEGOVINA: Sarajevo, hochwasser (cSch, 1); Ilidže, hochwasser, V.1897, leg. APFELBECK (NHMW, 1♀, FMNH, 1♂, Syntype); Ilidže, 1902, leg. APFELBECK (NHMW, 1, Syntype). CZECH REPUBLIC: Moravia, O. Znaim [Znojmo], Sandbank a.d. Th. v. Trausnitz-mühl, leg. O. SCHEERPELTZ (NHMW, 1♀). AUSTRIA: O. Oe., Grünburg, Sand., leg. BERNHAUER (NHMW, 1♀).

Thinobius longipennis – GERMANY: Brandenb., LKr. Spree-Neiße, Zelz Schotterbank, geschwemmt, geklopft, 20.VIII.2000, M. SCHÜLKE (SEMC, 6) (slide preparation, 1).

"*Thinobius ocularis*" – ALGERIA: Barral, au bord de la Seybouse (ISNB, 1, Syntype, ♀).

Neoxus crassicornis – USA, Texas, Lampasas Co., 24 km NWW Lampasas, Hwy. 580, (Browns+Lynch) Creek, 370 m, creek bank, 25.IV.2003, leg. Gy. MAKRANCZY (HNHM, 1♂, 1); Nebraska, Knox Co. 6mi S Niobrara, Verdigre Creek, black light, 23.VI.1968, leg. L. HERMAN (AMNH, 1♀).

Blediotrogus guttiger – NEW ZEALAND: ND, Omapere, in & under moist high-tide beach wreck, 26.XI.1984, leg. A. NEWTON & M. THAYER (FMNH, 1♂, 1♀, 3) (slide preparation, 1); ND, Aranga Beach, in & under moist high-tide beach wreck, 3.XII.1984, leg. A. NEWTON & M. THAYER (FMNH, 2).

Pareiobledius alutellus – SOUTH AFRICA: Cape Prov., Cape Point, 19.VIII.1984, leg. G. MINET (NHMB, 1♀, 4) (slide preparation, 1). NAMIBIA: Lüderitz, Guano Bay, sandy Atlantic beach, under kelp, 27.III.1998, leg. M. & B. UHLIG (ZMHB, 1); Lüderitz, Grosse Bucht, sandy Atlantic beach, under kelp, 27.III.1998, leg. M. & B. UHLIG (ZMHB, 2♂).

Teropalpus luniger – CHILE: Atacama, Puerto Viejo (SEMC, 1♂, 1♀, 4) (slide preparation, 1).

Ochthephilus omalinus – HUNGARY: Gergelyiugornya, bank of Tisza, from debris on sandy bank, 18.IV.2002, leg. Gy. MAKRANCZY (HNHM, 1). GERMANY: Sachsen, LKr. Delitzsch, Mulde Zw. Gruna u.Laußig, schotterbank, 6.V.2000, leg. M. SCHÜLKE (SEMC, 1♂, 1♀).

Ochthephilus monticola – INDIA: Simla Hills, Gahan, IX.1921, leg. M. CAMERON (BMNH, 1). NEPAL: Dolakha distr., SW Kalinchok Mt., 3100 m, 19–23.IV.1995, leg. MARTENS & SCHAWALLER (SMNS, 1♂, 1♀).

Carpelimus similis – ROMANIA: jud. Vîlcea/Sibiu, Valea Fratelui, confluence of Olt and stream Vadul, gravelbank of Olt under bridge, 350 m, from plant debris on rocks, fine gravel on bank, flotation, 16.VII.2003, leg. Gy. MAKRANCZY (HNHM, 1♀). BULGARIA: Mac., Mittl Struma, Kresana-Defilé, 13.VI.1937, leg. J. BREIT (NHMW, 1♂).

Carpelimus exiguus – ROMANIA: Danube River, Cama Islet, 29.IV.2004, leg. M. STAN (MGAB, 1♂) (slide preparation, 1♀).

Carpelimus elongatulus – IRELAND: Killarnay, 21.V.?, leg. E. BULLOCH (SEMC, 1♂, 1♀, 2).

Carpelimus bifidus – See description.

Xerophygus pallipes – LAOS: Louangphrabang pr., BanSong Cha (5km W), 1200m, 1–16.V.1999, leg. Vít Kubáň (NHMB, 1♂, 4) (slide preparation, 1). INDONESIA: Seram, 10km NW Waisarisa, Maluku Univ. Pattimura Forest Area, 984ft, ex malaise trap, 17–25.I.1995, leg. D. C. DARLING (SEMC, 1♀). CHINA, Zheijang, Tienmushan, 2.IX.1994, leg. G. DE ROUGEMONT (cGdR, 1)

Xerophygus hreblayi – See description.

Mimopaederus insularis – RAPA ISLAND (FRENCH POLYNESIA): Maugaoa, 950ft, collected from *Freycinatia* leaf axils, 11.XII.1963, leg. J. P. G. & T. M. CLARKE (USNM, 1♂, 1♀) (slide preparation, 1♂)

Thinodromus priorus – ZAIRE: Kivu, Sanghe, Pl. Ruzizi, (à la lumière) XII.1951, leg. H. BOMANS (MRAC, 1♂, Paratype of *Mendaxinus priorus*); Elisabethville (à la lumière) 17.XII.1949, leg. Ch. SEYDEL (MRAC, 1♀, Paratype of *Mendaxinus priorus*); Elisabethville (à la lumière) 16.XII.1950, leg. Ch. SEYDEL (MRAC, 1♀, Paratype of *Mendaxinus priorus*). KENYA: Elgon, cratere, Maji Ya Moto, 3460 m, sous des pierres en prairie, XII.1953, leg. N. LELEUP (MRAC, 2♂, Paratypes of *Mendaxinus priorus*).

Thinodromus dilatatus – ITALY, Rivalta, Fiume Adige, gravelly/sandy riverbank, 120 m, 28.V.2003, leg. Gy. MAKRANCZY (HNHM, 1♂, 1♀).

Thinodromus corvinus – USA: North Carolina, Avery Co., Linville Falls, ex: washing moss by stream, 27.VII.1991, leg. J.S. & A.K. ASHE (SEMC, 1♂, 1♀, 1).

Thinodromus caloderinus – USA: Missouri, Crawford Co., Red Bluff Campgrounds, Huzzah River, 13–15.IX.1996, leg. D.L. WOOD (FMNH, 1♂, 1); Texas (USNM, 1♀).

Thinodromus luteipes – CHILE: Huanta, Coquimbo, Ri Sadavia, 16.V.1953, leg. L. PEÑA (FMNH, 1♀); Q., San Andrews, 2300 m, 22.VI.1955, leg. L. PEÑA (FMNH, 3); Huanta, Rivadavia, Coquimbo, 16.V.1953, leg. L. PEÑA (FMNH, 1♂, 1♀, 10) (slide preparation, 1).

Thinodromus skottsbergii – CHILE/JUAN FERNANDEZ ISLANDS: Robinson Crusoe Island, El Yungue Trail, open forest, berlese, 4.I.1993, leg. S.A. MARSHALL (SEMC, 1♂, 1♀, 4) (slide preparation, 1); Robinson Crusoe Island, Damajuana, 6.I.1993, leg. S.A. MARSHALL (SEMC, 1); JUAN FERNANDEZ ISLANDS: Robinson Crusoe Island, Quebrada on S side Mirador, 20PT, fern forest, 1–10.I.1993, leg. S.A. MARSHALL (SEMC, 2).

Thinodromus juanfernandezianus – See description.

Thinodromus diffusus – USA, Wash. (SEMC, 2♂, 1♀). USA, Wash., Spokane Falls, leg. C.W. LENG (FMNH, 1♂, 1♀, 1); CA, Los Angeles Co., Angeles NF, Buckhorn Spring at Angeles Crest Hwy, 1980 m, mixed conifer & hardwood forest in ravine, in damp & wet debris, edge of tiny stream, 20.VII.2000, leg. A.F. NEWTON & M.K. THAYER (FMNH, 1); Cal., Laguna, 26.VIII.1926, leg. BLAISDELL? (CASC, 1).

Thinodromus chagosanus – CHAGOS ARCH.: Diego Garcia, de Moulin, at light, 26.IV.1971, leg. A. M. HUTSON (BMNH, 1♂, 1); Diego Garcia, de Moulin, at light, 27.IV.1971, leg. A. M. HUTSON (BMNH, 1♀); Diego Garcia, Pointe Marianne, 12.IV.1971, leg. A. M. HUTSON (slide preparation, 1).

Thinodromus thoracicus – SIERRA LEONE: (no label data) (BMNH, 2♂, 2♀, Paratypes of *Thinodromus thoracicus*).

Thinodromus indicus – INDIA: S. India, Nilgiris (BMNH, 2♂, 1♀, 5, Syntypes of *Apocellagria indica*) (FMNH, 1, Syntype of *Apocellagria indica*).

Thinodromus schillhammeri – See description.

Thinodromus singularis – KENYA: Naromoru, Naromoru River, 31.I.1980, leg. T. POLHEMUS (CASC, 1♂, 1♀, 10). TANZANIA: Mts. Uluguru, Chenzema, 1700 m, 2–22.VII.1971, leg. L. BERGER, N. LELEUP & J. DEBECKER (MRAC, 1); West Usambara, II.1912, leg. METHNER (FMNH, 1). SUDAN: Aequatoria, Imatong Gebirge (NHMW, 1).

Trogactus ocellatus – COSTA RICA: San Jose, km. 117 Pan-Am. Hwy, 19km N San Isidro, 1800 m, ex berlese forest litter, 25.VI.1997, leg. R. ANDERSON (slide preparation, 1). For other specimens, see description.

Trogactus godmani – COSTA RICA: Puntarenas Prov., Las Cruces Biol. Sta., 1330 m, ex leaf packs in stream, 29.V.2004, leg. J.S. ASHE, Z. FALIN & I. HINOJOSA (slide preparation, 1); Puntarenas, OTS Sta, finca Las Cruces, 4000ft, San Vito, Berlese, leaf litter in stream bed, away from flowing water, steep banks, Virgin forest cover, 18.III.1973, leg. J. WAGNER & J. KETHLEY (FMNH, 1♂, 1♀); Alajuela, Esac. Biol. San Ramon, 900m, malaise trap, 1.VII.–30.IX.1995, leg. P. HANSON (SEMC, 1♀).

APPENDIX B: Descriptions of new species

Codes used for the measurements – HW = head width with eyes; TW = head width at temples; PW = maximum width of pronotum; SW = approximate width of shoulders; AW = maximum width of abdomen; HL = head length from front margin of clypeus to the beginning of neck; EL = length of eye; TL = length of temple; PL = length of pronotum in the middle-line; SL = length of elytra from shoulder; SC = length of elytra from hind apex of scutellum; hpe = combined length of head, pronotum and elytra; BL = approximate body length. All measured from dorsal view.

Xerophygus hreblayi sp. n.

(Fig. 121)

Type material – Holotype (♂): "Papua Nlle Guinée/PNG [PAPUA NEW GUINEA]: EHProv. [Eastern Highlands prov.], Onerunka, umg.[near] Kaimantu [6°20'41"N, 145°47'41"W], 5.IX.[19]79, [leg.] W.G. Ullrich" (MNHG). Paratypes (13): same data as holotype (MNHG, 3, SEMC, 1, NHMW, 1, FMNH, 1, BMNH, 1), same, but 18.V.1979 (MNHG, 3), same, but V.1979 (MNHG, 1), same, but IX.1979 (MNHG, 2).

Description – Measurements (in mm, n=10): HW = 0.72 (0.70–0.76); TW = 0.69 (0.66–0.73); PW = 0.63 (0.60–0.66); SW = 0.74 (0.69–0.78); AW = 0.78 (0.74–0.82); HL = 0.58 (0.56–0.60); EL = 0.17 (0.16–0.19); TL = 0.28 (0.26–0.29); PL = 0.54 (0.52–0.56); SL = 0.93 (0.87–0.96); SC = 0.88 (0.84–0.94); BL = 4.50 (4.04–4.88); Head+pronotum+elytra = 2.18 (2.04–2.38) mm. – Colour. Head and pronotum uniformly dark brown, eyes appear dark, but slightly silvery. Elytra bicoloured: the central parts of discs are yellowish light brown, the rest (lateral edges, apical margin and a triangular area around the tip of the scutellum) are darker brown. Abdomen dark brown. Mouthparts and legs are light to medium brown, central parts of antennal segments 3–11 usually darker. – Shape and sculpture. Vertex has 2 shallow impressions (at the sides of the center of midline). The pronotum bears fully developed but rather slightly elevated anchor-like ridge, with 2 straight depressions starting from the corners of the anchor heading anterio-laterad. The elevated areas don't differ in shininess or punctation, therefore giving the pronotum a rather flat and dull appearance, devoid of characteristic markings. Pronotum has well-formed and simple posterior angles (cca. 95°), sides and posterior edge bear thin and slightly visible rim. – Punctation and microsculpture. Head, pronotum and abdomen finely but distinctly microsculptured. The punctation on the head is distinct and dense, apparent microsculpture in the interspaces (1/2 of puncture diameters). On the pronotum similarly distinct punctures, interspaces 1/1–1/3 puncture diameters (slightly uneven puncture sizes); microsculpture prominent in the interspaces. Elytra has shallow and irregularly sized punctation, interspaces generally about one-fourth of diameters of largest punctures; on the surface between the punctures microsculpture is only slightly apparent. – Pubescence. The body has irregular pubescence, most prominently on the elytra. Elytral a- and b-setae are non-distinct. Tergum VII has medium wide, even fringe. Tarsal lobes are thin. – Secondary sexual features: The males differ from females very slightly, only in the shape of the temples; but their maximum width is right after the eyes then very slightly (♂) or more strongly (♀) converging, this is not reflected in the measurements.

Comparative notes – This species differs from all other described species of the genus by having a midline keel on the head (vertex). From two other undescribed species it can be distinguished by the head being square (length approximately equal to width) and the midline keel on it being well expressed, not just a slightly elevated, unsculptured (longitudinal) stripe.

Etymology – The species is named after Dr. MÁRTON HREBLAY, my childhood friend, a lepidopterist who died in Thailand in a road accident in October 2000.

Carpelimus bifidus sp. n.

(Fig. 123)

Type material – Holotype (♂): "PANAMA: Chiriquí, La Fortuna, 1200m, Continental Divide Trail 8°46'0"N, 82°12'0"W, ex: berlese forest litter, 9.VI.1995, [leg.] R. Anderson" (PAN 2A95 10C) (SEMC). Paratypes (16): PANAMA: Chiriquí, La Fortuna, 1200m, Continental Divide Trail 8°46'0"N, 82°12'0"W, ex: berlese forest litter, 9.VI.1995, leg. R. Anderson (PAN 2A95 10C) (SEMC) (SEMC, 1), same, but (PAN2A95 10B) (SEMC, 1), same, but (PAN2A95 10H) (SEMC, 3, BMNH, 1); Chiriquí, La Fortuna, 1100m, Hydrological Station Trail, 8°42'0"N, 82°12'0"W, ex: berlese forest litter, 9.VI.1995, leg. R. ANDERSON (PAN 2A95 13A) (SEMC, 1); Chiriquí, 6.0km NE Boquete, 1550m, 8°48'0"N, 82°26'0"W, ex: flight intercept trap, 14–19.VI.1996, leg. J. ASHE & R. BROOKS (PAN1AB96 179B) (SEMC, 2, FMNH, 1, MNHG, 1, NHMW, 1); Chiriquí, 6.0km NE Boquete, 1620m, 8°48'0"N, 82°26'0"W, ex: oak forest litter, 14.VI.1996, leg. R. ANDERSON (PAN2AB96 96–130A) (SEMC, 1), same, but (PAN2AB96 96–130D) (SEMC, 2); Chiriquí, 5.6km N Boquete, La Culebra Trail, 1800m, 8°49'23"N, 82°25'18"W, ex: cloud forest litter, 15.VI.1996, leg. R. ANDERSON (PAN2AB96 96–131C) (SEMC, 1).

Description – Measurements (in mm, n=10): HW = 0.44 (0.41–0.46); TW = 0.40 (0.38–0.43); PW = 0.51 (0.49–0.52); SW = 0.58 (0.57–0.60); AW = 0.64 (0.59–0.66); HL = 0.31 (0.30–0.32); EL = 0.12 (0.11–0.13); TL = 0.035 (0.03–0.04); PL = 0.39 (0.38–0.40); SL = 0.59 (0.57–0.62); SC = 0.55 (0.52–0.58); BL = 2.69 (2.28–3.28); Head+pronotum+elytra = 1.30 (1.26–1.38) mm. – Colour. Body uniformly dark brown, if there is a slight difference in the colouration of the main body parts, then the head is the darkest. Eyes appear dark, but slightly silvery. Mouthparts may be somewhat lighter. The basal segment of the antennae and the last 2 or 3 segments light brown, contrasting to the rest of the body. The legs and the tip of the abdomen (9th and 10th segments) and often 7th and 8th segments also light brown. The area laterad and anteriad of the scutellum (if exposed) may also be lighter brown. – Shape and sculpture. Vertex, midline of pronotum level, the latter may have traces of a very slight midline ridge (mostly just less dense puncturation marks it). The only impressions are those 4 impressions at both sides of the posterior half of the midline of pronutum, characteristic of *Carpelimus*, but so small and shallow that barely noticeable. The surface lacks microsculpture, so rather shiny. Neck and temples very poorly separated (therefore measurements above only approximate). Temples slightly longer than 1/3 of the eye length. Pronotum lateral edges convex, but unevenly curved, broadest at 2/5 of length, there 1.7 times broader than posterior edge. – Punctation and microsculpture. Head, pronotum and elytra densely but moderately punctured, interspaces half of the diameters of punctures. Punctures on the elytra may be oblong. The elytra have slight microsculpture, making it more dull than pronotum and head. The abdomen has very sparse punctation but moderately microsculptured. – Pubescence. Head and pronotum covered with dense, medium fine, but very uniform and short, outward directing setation. Setae on the elytra somewhat more irregular (but the same length as on pronotum), the setae on the abdomen are more sparse, but twice as long as on the elytra. Setae on the head and pronotum directed anteriad, on the elytra and abdomen posteriad. Tergum 7 has very thin, even fringe. Tarsal lobes are present, but non-distinct.

Comparative notes – This species is really distinctive out of all *Carpelimus*, not closely allied to any other known New World species of the genus. Slightly similar in build and size to species in the *C. memnonius* group, but can be easily distinguished by the head shape and antennal colouration.

Etymology – The specific epithet refers to the bilobed parameres, unique among *Carpelimus*.

Thinodromus juanfernandezianus sp. n.

(Figs 116–117)

Type material – Holotype (♂): "[CHILE:] Juan Fernandez [Islands], Masatierra, A[lto] Pangal (42/43), 600–650m, 5.3.[19]55, [leg.] P.G. Kuschel" (MNNC). Paratypes (11): CHILE/Juan Fernandez Islands: Masatierra, Alto Pangal (42/43), 600–650m, 5.III.1955, leg. P.G. KUSCHEL (BMNH, 2, MNNC, 2, NZAC 1, MNHG, 1, NHMW, 1, FMNH, 1, SEMC, 1); Masatierra, Alto Pangal, 600m, innerhalb sehr feuchten Dicksonia berteriana-Beständen, 8.II.1952, leg. P.G. KUSCHEL (NZAC, 2).

Description – Measurements (in mm, n=10): HW(♂) = 0.676 (0.67–0.68); HW(♀) = 0.69 (0.68–0.70); TW(♂) = 0.71 (0.70–0.72); TW(♀) = 0.716 (0.70–0.73) [n=3♂,7♀]; PW = 0.82 (0.78–0.84); SW = 0.87 (0.84–0.92); AW = 1.02 (0.96–1.06); HL = 0.50 (0.48–0.51); EL = 0.156 (0.15–0.16); TL = 0.23 (0.20–0.25); PL = 0.76 (0.74–0.79); SL = 0.82 (0.78–0.86); SC = 0.76 (0.72–0.80); BL = 4.40 (3.98–4.82); Head+pronotum+elytra = 2.17 (2.04–2.26) mm. – Colour. Body uniformly reddish brown. Head sometimes a little darker. Epistomal suture marked by dark brown line. – Shape and sculpture. Head rounded, posterior margin strongly arched. Pronotum and elytra with very uneven surface, latter with two broad and moderately deep longitudinal grooves. Pronotum with 2 small elevations in the middle of anterior half (on both sides), shinier than the surrounding areas. Shoulders are very weakly developed, broadly rounded. The head (except very base of vertex and tops of supraantennal ridges), posterior 1/3 of pronotum, a small area on the elytra immediately behind the scutellum, the 2nd tergite and partially the bases of the other tergites covered with very strong and rough scabrous sculpture, making them appear dull. Abdomen very strongly cylindrical, laterotergites very thin. Macrocephaly present but weakly expressed. – Punctation and microsculpture. Punctation on head fine, interspaces typically 0.5–1.5 times puncture diameters. On pronotum, punctures appear only tops of ridges, with larger but more sparse punctures (interspaces about 1.5

times puncture diameters. Elytra very strongly and deeply punctured. Interspaces 0.2–0.8 times diameters. Pronotum with slight microsculpture. Abdominal tergites have strong and dense coriaceous microsculpture, with sparse and very small punctures appearing at places. – Pubescence. Body with medium sparse, very short pubescence, therefore appears rather bare. The fringe of tergum VII is missing on most of the entire width, only the modified medial setae are left. This is another unique feature among *Thinodromus*. – Secondary sexual features. The males differ from females very slightly, only in the width of the temples relative to the head width at the eyes; temples are a little bit more (+1.4–3.0%) (♂) or less (+4.4–5.0%) (♀) exceeding the eye width.

Comparative notes – The species is closely allied to western South American *Thinodromus* species in the *Th. segnis* group, out of the Juan Fernandez Islands species *Th. skottsbergii* (Bernhauer, 1921), from which it differs by the absent fringe on the lateral parts of tergum VII.

Etymology – The species is named after its type locality.

Thinodromus schillhammeri sp. n.

(Fig. 120)

Type material – Holotype (♂): "CHINA: Yünnan, Xishuangbanna, ca. 10km NW Menglun [8°46'0"N, 82°12'0"W], ca. 700m, 7.XI.1999, leg. Jäch, et al. (CWBS 359)" (NHMW). Paratypes (8): CHINA: NW-Hunnan, Wulingyuan, N Dayong Suoxiyu, 400m, 31.X.1993, leg. SCHILLHAMMER (5) (NHMW, 2); Sichuan, ca. 14km N Ya'an City, rd. to Shangli [8°46'0"N, 82°12'0"W], 800m, 8.VI.1996, leg. JI & WANG (5) (CWBS 221) (NHMW, 1, SEMC, 1, FMNH, 1). N-LAOS, Prov. Lg. Nam Tha, ca. 20km SE Muang Sing [8°46'0"N, 82°12'0"W], 950m, 12–13.VI.1996, leg. SCHILLHAMMER (25) (NHMW, 1, MNHG, 1, BMNH, 1).

Description – Measurements (in mm, n=9): HW = 0.66 (0.62–0.70); TW = 0.59 (0.57–0.60); PW = 0.61 (0.58–0.64); SW = 0.87 (0.80–0.92); AW = 0.91 (0.84–0.94); HL = 0.43 (0.41–0.46); EL = 0.20 (0.19–0.22); TL = 0.12 (0.10–0.14); PL = 0.57 (0.53–0.60); SL = 0.97 (0.88–1.04); SC = 0.94 (0.86–1.00); BL = 3.80 (3.58–4.02); Head+pronotum+elytra = 2.09 (2.02–2.22) mm. – Colour. Body and antennae uniformly slightly reddish dark brown, almost black. Mouthparts and legs are medium to dark brown. – Shape and sculpture. The head (except very base of vertex and tops of supraantennal ridges), posterior 1/3 of pronotum, a small area on the elytra immediately behind the scutellum, the 2nd tergite and partially the bases of the other tergites covered with very strong and rough scabrous sculpture, making them appear dull. – Punctation and microsculpture. Punctation on the elytra strong and deep, but not even. Interspaces typically range from 0.5 to 2.0 times puncture diameters. T7 has medium wide, even fringe. Tarsal lobes are thin. – Pubescence. Medium dense, evenly sized, thin pubescence throughout. Sides of pronotum and abdomen have a couple of strong, dark, long spurs.

Comparative notes – The species is closely allied to *Th. assamensis* (CAMERON, 1930), but differs in size and sculpture: smaller and pronotum in the anterior half very shiny.

Etymology – The species is named after Dr. HARALD SCHILLHAMMER, curator of Staphylinidae in Naturhistorisches Museum, Wien, collector of part of the type series.

Trogactus ocellatus sp. n.

(Fig. 122)

Type material – Holotype (♂): "COSTA RICA: Puntarenas, Las Cruces Biol. Sta, San Vito, 5km SW 1400m, 08°47'13" N, 82°59'13" W, 22.VI.1998, [leg.] R. Anderson, ex: berlese leaf litter" (SEMC). Paratypes (100): COSTA RICA: Puntarenas, Las Cruces Biol. Sta., San Vito, 5km SW 1400m, 08°47'13" N, 82°59'13" W, 22.VI.1998, leg. R. ANDERSON (SEMC, 15); Puntarenas, Las Cruces Biol. Sta., San Vito, 5km SW 1425m, 08°46'59" N, 82°59'18" W, 22.VI.1998, leg. R. ANDERSON (SEMC, 1); Puntarenas, 11km SW Est. Biol. Las Cruces, 1450m, 08°46'43" N, 83°01'50" W, 09.VII.1999, leg. R. ANDERSON (SEMC, 32), (BMNH, 2), (FMNH, 2); Puntarenas, Est. Biol. Las Alturas, 2km NE, Alturas, 1520m, 08°56'56" N, 82°50'01" W, 10.VII.1999, leg. R. ANDERSON (SEMC, 1); San Jose, km117 Pan American Highway, 19km N San Isidro 1800m, 09°28'00" N, 83°42'20" W, 15.II.1998, leg. R. ANDERSON (SEMC, 1); San Jose, km117 Pan American Highway, 19km N San Isidro 1800m, 09°28'00" N, 83°42'20" W, 25.VI.1997, leg. R. ANDERSON (SEMC, 48); San Jose, km117 Pan American Highway, 19km N San Isidro 1800m, 09°28'00" N, 83°42'20" W, 20.VI.1997, leg. R. ANDERSON (SEMC, 6); San Jose, km117 Pan American Highway, 19km N San Isidro 1800m, 09°28'00" N, 83°42'20" W, 20–25.VI.1997, leg. S. & J. PECK (SEMC, 2); San Jose, km113 Pan American Highway, 23km N San Isidro 2000m, 09°28'00" N, 83°42'20" W, 20.VI.1997, leg. R. ANDERSON (SEMC, 2); San Jose, Zurqui de Moravia 1600m, 10°03'00" N, 84°01'00" W, 21.IV.1996, leg. P. HANSON (SEMC, 1). PANAMA: Chiriquí, 27.7km W Volcan, Hartmann's Finca, 1450m, 8°51'48" N, 82°44'36" W, 14.VI.1995, leg. R. ANDERSON (SEMC, 17); Panamá, Cerro Campana, near Capira, 950m, 8°44'0" N, 79°57'00" W, 5.VI.1995, leg. R. ANDERSON (SEMC, 1).

Description – Measurements (in mm, n=10): HW = 0.69 (0.67–0.72); TW = 0.65 (0.63–0.66); PW = 0.71 (0.70–0.73); SW = 0.98 (0.94–1.02); AW = 0.95 (0.90–1.02); HL = 0.52 (0.50–0.54); EL = 0.17 (0.15–0.18); TL = 0.22 (0.20–0.24); PL = 0.63 (0.60–0.64); SL = 0.99 (0.96–1.02); SC = 0.92 (0.86–0.98); BL = 4.74 (4.56–5.00); Head+pronotum+elytra = 2.25 (2.20–2.36) mm. – Colour. Head and pronotum uniformly dark brown, eyes appear dark, but slightly silvery. Elytra bicoloured: the central parts of discs are yellowish light brown, the rest (lateral edges, apical margin and a triangular area around the tip of the scutellum) are darker brown. Abdomen dark brown. Mouthparts and legs are light to medium brown, central parts of antennal segments 3–11 usually a little darker. – Shape and sculpture. Vertex has 2 shallow impressions (at the sides of the center of midline). The pronotum bears fully developed but rather slightly elevated anchor-like ridge, with 2 straight depressions starting from the corners of the anchor heading anterio-laterad. The elevated areas don't differ in shininess or punctation, therefore giving the pronotum a rather flat and dull appearance, devoid of characteristic markings. Pronotum has well-formed and simple posterior angles (cca. 95°), sides and posterior edge bear thin and slightly visible rim. – Punctation and microsculpture. Head, pronotum and abdomen finely but distinctly microsculptured. The punctation on the head is distinct and dense, apparent microsculpture in the interspaces (1/2 of puncture diameters). On the pronotum similarly distinct punctures, interspaces 1/1–1/3 puncture diameters (slightly uneven puncture sizes); microsculpture prominent in the interspaces. Elytra has shallow and irregularly sized punctation, interspaces generally about one-fourth of diameters of largest punctures; on the surface between the punctures microsculpture is only slightly apparent. – Pubescence. Forebody with rather uniformly sized and medium dense setation, albeit with a few larger setae on the sides, most prominently on the elytra. Abdomen has much longer and dense, somewhat irregular pubescence than forebody.

Comparative notes – The species is closely allied to *T. elegans* SHARP, 1887 and *T. funebris* SHARP, 1887, differs in the smaller (less than 0.5 times temples) eyes unusually protruding.

Etymology – The specific epithet refers to the unusually protruding eyes.

*

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