

Towards a phylogenetic system of derelomine flower weevils (Coleoptera: Curculionidae)

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Abstract. A revised phylogenetic classification for derelomine flower weevils (Coleoptera: Curculionidae: Curculioninae: Derelomini Lacordaire) is proposed, based on a cladistic analysis of 115 outgroup and ingroup taxa and 155 primarily morphological characters. The single most-parsimonious cladogram (length = 271, consistency index = 65, retention index = 95) indicates that several genera must be excluded from the tribe, as they lack certain modifications of the mouthparts and a primary reproductive association with the inflorescences of palms. These include *Araucarietus* Kuschel, *Eisingius* Kuschel, and *Planus* Kuschel, **new placements** (now all Trypetidini); *Euryscapoides* Wibmer & O'Brien, **new placement** (Curculioninae incertae sedis); *Neopsilorhinus* Bovie, **new placement** (Eriirhinidae: Eriirhinini); and *Pedetinus* Faust, **new placement** (Eugnomini). Five subtribes are recognized within Derelomini. The oldest African and South American Derelomina have a carinate rostrum and lamellate dorsal scales. *Grasidius* Champion (previously Eriirhinini) and *Terires* Champion (Storeini) are placed therein, **new placements**. *Neoderelomus* Hoffmann is nested within *Derelomus* Schoenherr, **syn.n.**, and its only species is therefore renamed as *D. piriformis* (Hoffmann), **comb.n.** The predominantly Asian Acalyptina are reduced from tribal status, **stat.n.**, to now be part of Derelomini, **new placement**. They are defined (inter alia) by truncate elytra. They also contain *Eudela* Pascoe and *Eudelodes* Zimmermann, **new placements** (previously Curculioninae incertae sedis). The New World Notolomina, **subtr.n.**, are distinguished by bifurcate maxillary lacinial teeth and other mouthpart characters. *Andranthobius mariahelena* (Bondar) (formerly *Derelomus*), **comb.n.**, is added to this entity. Phyllostrogina, **subtr.n.**, are a very diverse and mostly Neotropical lineage. They have two-segmented maxillary palps, a densely pubescent prosternum, and long macrosetae along the basal fifth of the posterior wing margin. Within the subtribe there are independent transitions to host plant associations with various dicots (*Phyllostrox* Schoenherr), Cyclanthaceae (e.g. *Perelleschus* Wibmer & O'Brien and *Systemotelus* Anderson & Gómez), and Araceae (*Cyclanthura* Franz). Their life history traits show related changes, including losses of the ability to pollinate, and more detrimental (herbivorous, seed-predating) larval developments (e.g. *Cotithene* Voss). *Phyllostrox tatarianae* (Bondar) (formerly *Derelomus*), **comb.n.**, is assigned to Phyllostrogina. *Hypolesschus* Fall is nested within *Phyllostrox*, **syn.n.**, and thereby the latter now contains *P. atratus* (Fall), **comb.n.** The Central American palm-associated *Androtrox* Franz, **gen.n.**, is proposed to accommodate *A. megalops* (Champion) (formerly *Phyllostrox*), **comb.n.**, a species with large

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contiguous eyes and a set of mouthpart attributes convergently present in *Andranthobius* Kuschel (Notolomina) and *Phyllotrox*. The Neotropical Staminodeina, **subtr.n.**, with a labial prementum with two triangular projections and a large anal lobe on the wing, probably represent a young clade of weevils specialized to oviposit into the ephemeral staminodes of Cyclanthaceae inflorescences. The apparent phylogenetic sequence of the subtribes is (Derelomina ((Acalyptina, Staminodeina) (Notolomina, Phyllotrogina))), with a Juanorhinini–Trypetidini clade as the most immediate outgroup, followed by various curculionine lineages. The revised system thus improves the taxonomy of derelomine weevils, and clarifies our understanding of their roles in the evolution of several tropical plant lineages – palms and cyclanths in particular.

Introduction

A revised phylogenetic classification for derelomine flower weevils (Coleoptera: Curculionidae: Curculioninae: Derelomini) is proposed. The new system is intended to serve a dual purpose. First, it improves the taxonomy of a poorly circumscribed tribe of pantropical weevils. When this study began, Derelomini comprised approximately 240 species. They were allocated in forty genera, half of them monotypic (Alonso-Zarazaga & Lyal, 1999; Franz, 2003a). It appeared that the tribe as a whole, and several of its constituent taxa, were not monophyletic. Second, a phylogenetic system for derelomines contributes to understanding the roles they have played in the evolution of several tropical plant lineages; palms (Arecaceae) and cyclanths (Cyclanthaceae) in particular.

As early as 1823, von Martius described the attraction of weevils to palm inflorescences. Henderson (1986) provided a summary of palm pollination studies (see Uhl & Dransfield, 1987; Moore, 2001). Therein he rejected the received view, according to which anemophily is the plesiomorphic state in this plant lineage. Instead, the predominance of cantharophily in members of both older and younger palm clades, and the specificity of their reproductive interactions, suggested that derelomines were among the initial pollinators of palms some 65 million years ago. These associations continue until today, with important economic and ecological ramifications (e.g. Mora-Urpí & Solís, 1980; Syed *et al.*, 1982; Listabarth, 1996; KÜchmeister *et al.*, 1998). A more complete picture will emerge once the life histories are viewed in a phylogenetic context.

Although less well documented, interactions among Derelomini and the Neotropical cyclanths are just as interesting. Accounts of the pollination biology of cyclanth inflorescences are relatively recent (Gottsberger, 1991; Eriksson, 1994a) and are compromised by a lack of precise identifications for the weevil species, most of which remain undescribed. More recently there are reports on derelomines pollinating aroids (Araceae), especially members of the diverse genus *Anthurium* Schott (Franz, 2003a). Other species from montane or temperate New World regions have been observed on the flowering organs of araucarias (Kuschel, 2000) and dicots (Table 1). Do the associations

with each plant clade correspond to one or several independent colonization events? What kinds of adaptive transformation have occurred along the way? To answer such questions convincingly, a phylogenetic system for derelomines is required.

A survey of derelomine biogeography, morphology, and behaviour reveals additional topics for inquiry. For instance, certain taxa have southern disjunct distributions (Kuschel, 1952) and others are restricted to tropical Central America (Anderson & Gómez, 1997), suggesting a considerable range of ages and conditions for speciation. Remarkable adaptations related to host plant use, oviposition, and male reproductive conflicts have evolved in apparently unrelated clades (Franz, 2003b). Independent transitions are presumed from adult pollen consumption to feeding on other floral organs, and from detritivorous to seed-predating larvae (Franz, 2004). The present study aspired to organize these observations more clearly. Due to practical constraints, this analysis focused primarily on New World derelomines, which make up over 75% of the described species. It was based on morphological as well as relevant behavioural and ecological character information. An exemplar approach was used to represent the diversity of all named clades above the species level. With the exception of the mouthparts, selective illustrations of apomorphies were emphasized over complete morphological accounts for each taxon.

The results will affect the continuity of reference from the traditional to the revised phylogenetic system of derelomines. As a convention internal to this paper, the classification of Alonso-Zarazaga & Lyal (1999) is considered valid throughout the ‘Taxonomic history’, ‘Methods’, and ‘Results’ sections. Thereafter, the current relationships and names are used.

Taxonomic history

Past characterizations of derelomine flower weevils have been largely unsatisfactory. Their overall appearance is that of relatively undifferentiated weevils, Curculionidae *sensu stricto*. Often they are recognized by an elongate shape, a small to moderate size, light to dark-brownish

colour, and procoxae that are inserted posteriorly on the prosternum. Throughout the years, a variety of taxa have been added to and subtracted from the tribe. At times the rearrangements were based on conceptions of a general *Gestalt*, individual external characters, or ecological similarities. The result has been a certain level of nomenclatural instability, and an increasing difficulty to assign new species to appropriate taxonomic entities. A review of the classificatory history of Derelomini serves as an introduction to these challenges.

Fabricius (1798) described the first species of Derelomini, then named *Curculio chamaeropsis*, from specimens collected in Morocco on inflorescences of the palm *Chamaerops humilis* Linnaeus (Anstett, 1999). Schoenherr (1825, 1826, 1844) placed it within the eventual type genus *Derelomus*. He also described such diverse derelomine genera as *Anchylorhynchus* Schoenherr (1835), *Celetes* Schoenherr (1836), *Phyllotrox* Schoenherr (1843), and *Phytotribus* Schoenherr (1843). According to recent checklists, these four taxa include at least 60% of all derelomine species (O'Brien & Wibmer, 1982, 1984; Wibmer & O'Brien, 1986, 1989). In retrospect, it is unfortunate that the collaborators of the *Genera et Species Curculionidum* (1833–1845) never presented a synthesis of their detailed and generally accurate descriptions.

The history of the tribe itself started with Lacordaire (1866), who considered *Derelomus*, *Everges* (Schoenherr, 1844; later synonymized with *Celetes*), and possibly *Psilorhinus* (Blanchard, 1851; later renamed as *Neopsilorhinus* Bovie, 1907; due to homonymy) to be members of the Déréloides. Previously they had been classified within the Eirrhinides and the Cholidés (Schoenherr, 1825). Lacordaire (1866) proposed the following diagnostic attributes for derelomines: geniculate antennae, funicle seven-segmented, prosternum long, mesosternum retracted from ventral plane, procoxal cavities slightly separated, femora inermous or with only small teeth, tibiae apically inermous, tarsal claws paired and simple, and elytra covering the abdomen. From a contemporary perspective – and in the absence of actual specimens – this description applies to many unrelated entities within and outside the Curculioninae. In a sense, it made the creation of a non-monophyletic set of taxa easier.

It is not surprising when an ambiguously defined tribe is assigned to more than one subfamily over the years. Most early authors included derelomines partly or entirely within the Eirrhininae (e.g. LeConte & Horn, 1876; Champion, 1902; von Heyden *et al.*, 1906; Blatchley & Leng, 1916; Hustache, 1930). This classificatory tradition was summarized by Klima (1934), who listed seventeen genera and ninety-three species of Derelomini. Among them were ten monotypic genera, seven from the Old World. Species of *Celetes* and *Phytotribus* were placed in the Eirrhinini. Voss (1937, 1940, 1954) attributed these and other derelomine species to the Trypetinae. In accordance with Voss (1935, in Dalla Torre & Voss, 1935), Bondar (1940, 1941, 1942) and Vaurie (1954) classified *Anchylorhynchus* within the Petalochilinae. A substantial analysis and revision of these

inconsistent taxonomies was presented by Kuschel (1952). Until now, this work constituted the most comprehensive summary of New World derelomines.

Another step towards a phylogenetic system was achieved when Kuschel (1964, 1971) re-examined the characters of the Eirrhininae (e.g. *Notaris* Germar). He separated the former from the Acalyptini and Derelomini on the basis of their orthocerous-type genitalia (see also Thompson, 1992). An updated account of derelomines as members of the Curculioninae (Curculionidae, *sensu stricto*) was provided by Kuschel in Wibmer & O'Brien's (1986) South American checklist of weevils. This placement has been reaffirmed in subsequent publications (Thompson, 1992; Kuschel, 1995; Anderson *et al.* 1997). Derelomini are classified as Curculioninae in the recent catalogue of the Curculionoidea of the world by Alonso-Zarazaga & Lyal (1999; a placement within the Molytinae is a reasonable alternative; see also Kuschel, 1987). Moreover, the removal of the tribe from the Eirrhininae is consistent with evidence from 18S ribosomal DNA (Marvaldi *et al.*, 2002).

The focus on New World derelomines presents an opportunity to discuss these taxa in more detail. Shortly after Lacordaire (1866), LeConte published an extensive treatment of North American Curculionoidea. Therein he offered an analysis of derelomine attributes (LeConte, 1876 in LeConte & Horn, 1876). LeConte evidently had examined species from the New World (e.g. *Celetes* and *Notolomus* LeConte, 1876), as well as such Old World genera as *Derelomus*. Complementing the then existing characterization, he noted *inter alia* a constriction in the anterior region of the pronotum, the indistinctness of the prosternal sutures, and the length relationships of the ventral segments. This description was slightly more discriminatory. It excluded *Phyllotrox*, however, which LeConte recognized as a eugnomine. Champion (1902) amended this and transferred *Phyllotrox* to the derelomines. In continuation, North American authors have adopted these concepts in keys and checklists without much refinement (e.g. Fall & Cockerell, 1907; Blatchley & Leng, 1916; Blackwelder, 1947; Kissinger, 1964; O'Brien & Wibmer, 1982; Anderson, 2002).

Champion (1902, 1903, 1909, 1910) made significant contributions to the knowledge of Central American derelomines. As part of the *Biologia Centrali-Americana*, he named three new genera and twenty-two new species, assigning eleven of them to *Phyllotrox*. The only major supplements to this work have come recently (Anderson & Gómez, 1997; Franz & O'Brien, 2001a, b; Franz, 2001, 2003a), reporting on a total of four new genera and thirty-six new species associated with the inflorescences of cyclanths and aroids. Two additional genera with (at least) three species each were included in the present analysis, but will be named formally on another occasion.

Various South American derelomines were described by nineteenth-century taxonomists, although mostly in non-specific regional treatments of weevils. In the first half of the twentieth century, many species – particularly of *Anchylorhynchus*, *Celetes*, and *Phytotribus* – were named

in a series of papers by Bondar (1940, 1941, 1942, 1943, 1949, 1950; for a total of forty new species), and by Hustache (1924, 1929, 1934, 1937, 1939, 1940; in Bondar, 1940; twenty species). The former also offered valuable information on the interactions of many derelomines with palms. Voss (1954) described several new species of *Phyllotrox* from Peru. As many as twenty-five new species of *Celetes* have been identified in an ongoing revision of this genus (R. Valente, Museu Paraense Emílio Goeldi, Brazil, pers. comm.).

As mentioned above, Kuschel (1952) provided the most recent synthesis of New World derelomines. Specifically, he transferred taxa from various tribes (e.g. Amalactini, Juanorhinini, and Trypetidini) to the Petalochilinae, partly on the basis of their associations with palms. He characterized the latter entity by the presence of an externally positioned mucron on the tibial apices (only in some taxa), and the merging of striae III and VI (instead of III and VIII) near the posterior margin of the elytra (in all taxa). Several synonymies were proposed, e.g. *Hoplorhinoides* Champion (1910) was subsumed under *Celetes*. Six new genera were named, four of them in a key that only excluded species from the Juan Fernández Islands. Certain (either unexamined or questionable) species of *Derelomus* were not transferred to the Petalochilinae at the time. Among the characteristics Kuschel (1952) used to identify sets of genera were the position of the mesosternum (on an even plane with the prosternum or retracted), the shape of the eyes (subcircular or elliptical), the number of funicular segments (six or seven), and the presence of coarse setae along the tibiae, as can be seen in *Amalactus* Schoenherr (1835).

Kuschel's treatment was particularly well suited to diagnose South American taxa, but is less adequate for distinguishing among Neotropical genera of derelomines as a whole, most of which would be identified as *Phyllotrox* (see Franz, 2003a). Moreover, the classification of this original work has been amended by Kuschel in a series of papers (Kuschel, 1955, 1964, 1971, 1987; in Wibmer & O'Brien, 1986) and the validity of the 1952 publication has thus been reduced.

The situation is similar, or worse, for Old World Derelomini. With the exception of an unpublished manuscript on Asian acalyptines (H. Kojima & K. Morimoto, Kyushu University, Japan: Weevils of the tribe Acalyptini (Coleoptera: Curculionidae: Curculioninae), with taxonomic treatment of the Japanese, Korean, and Taiwanese species, 2000), no comprehensive analysis has been attempted since the *Coleopterorum Catalogus* (Klima, 1934). Derelomine flower weevils sensu Alonso-Zarazaga & Lyal (1999) are clearly in need of a revised phylogenetic classification.

Methods

Character analysis

The analysis included predominantly adult morphological characters. Behavioural and ecological information

was used as long as this information was amenable to traditional coding (see Wenzel, 1992; Miller & Wenzel, 1995). Published interpretations of characters and relationships were considered at various stages of the study, yet for the most part the character matrix is original.

The observations of externally visible attributes were made under a dissecting stereoscope (Wild M5A), at magnifications of 25–100×. A compound microscope (Leitz Dialux 20) was used to examine cleared internal organs at magnifications of 250–1000×. All illustrations were drafted with a drawing tube. The scanning electron micrographs were taken with a Hitachi S-4700 SEM (American Museum of Natural History). The line drawings precede the photographs. Each set was numbered alphabetically according to the traditional classification; not phylogenetically or in order of appearance. The exception was *Notaris*, the taxon used to orientate the cladogram (see details below).

The morphological terminology is in accordance with *Torre-Bueno* (Nichols, 1989). Additional references for Curculionoidea were consulted to assign correct names to structures of the mouthparts (Ting, 1936; Morimoto & Kojima, 2003), metendosternite (Velázquez de Castro, 1998), wings (Zherikhin & Gratshev, 1995), segments of the venter (Thompson, 1992), and the male and female genital complex (Burke, 1959; Clark, 1977; Howden, 1995).

Alternative ways were explored to translate the observations into '0s and 1s'. In several cases, additive binary coding with inapplicable entries ('-') was considered to be the most adequate solution (see Maddison, 1993; Wilkinson, 1995; Strong & Lipscomb, 1999). Additive multistate coding was preferred whenever a series of evolutionary transformations could be proposed (Mickevich & Weller, 1990; Lipscomb, 1992). A subset polymorphism was assigned in one case where multiple types of scales were present in the same species (see Nixon & Davis, 1991; Stevens, 1991). Finally, autapomorphies of terminal taxa were excluded from the analysis, in spite of their diagnostic and predictive value (Yeates, 1992) but are included in a generic key and species checklist to be published separately (N. M. Franz & C. W. O'Brien, unpubl. data).

Examined taxa

An exemplar approach was used to infer the relationships among the principal lineages of Derelomini. The ingroup taxa were selected primarily to test the classification in Alonso-Zarazaga & Lyal (1999). Efforts were made to represent twenty-one of the twenty-five currently recognized New World genera of Derelomini (84%) in the matrix, including the postcatalogue additions *Staminodeus* Franz (2001), *Ganglionus* Franz & O'Brien (2001a), and *Cyclanthura* Franz (2003a). The two undescribed genera (see above) were also considered part of the ingroup. The individual types of *Euryscapoides* Wibmer & O'Brien (1986) and *Pygocetes* Kuschel (1955) were examined visually but excluded from the matrix. Various scanning

electron micrographs of *Planus* Kuschel (1952) were available for analysis (C. Ruiz Gouet, Universidad Austral de Chile, Chile, pers. comm.). The monotypic *Anthobius* Schoenherr (1833), the only unexamined New World genus, is apparently a eugnomine (G. Kuschel, Auckland, New Zealand, pers. comm.). The taxon selection was less representative with regards to Old World derelomines, in which no more than four out of fourteen genera were analysed. The extinct *Electrotribus* Hustache (1942) also could not be obtained.

Whenever specimens were available, published criteria for the selection of exemplar species were adopted to increase the reliability of the analysis (Yeates, 1995; Prendini, 2001). All designated type species were included for the ingroup genera (see Table 1). A special effort was made to identify twenty species of *Phyllotrox* (in collaboration with C. W. O'Brien, Florida A&M University, U.S.A.).

There was little reason to assume that the ingroup would be monophyletic. Molecular analyses had already indicated the absence of a close relationship among the Chilean *Araucarietus* Kuschel (1952) and *Eisingius* Kuschel (1952) on one hand, and the Neotropical *Perelleschus* Wibmer & O'Brien (1986) on the other (Marvaldi *et al.*, 2002). An adequate selection of outgroup taxa was thus required to avoid the creation of an 'artificially' monophyletic ingroup and unreliable character polarizations (Nixon & Carpenter, 1993; Bryant, 2001). Emphasis was placed on taxa previously considered to be relatives of derelomines (Kuschel, 1952). These included members of the Amalactini, Juanorhinini, and Trypetidini (Curculionidae: Molytinae), supplemented with species representing various tribes within the Curculioninae. Among them were the predominantly Asian Acalyptini, certain North American Ellescini and South American Eugnomini. *Grasidius* Champion (1902) and *Terires* Champion (1902) were added for their external resemblance to *Celetes*. The

cladograms were orientated with members of the aquatic Erihrinidae (i.e. *Notaris*; see Kuschel, 1971). As originally conceived, the matrix contained ninety-three and twenty-two species in the ingroup and outgroup, respectively (see Table 1). A synoptic collection of the examined taxa has been placed in the Cornell University Insect Collection (CUIC).

Identification of cladograms and support

The character matrix was compiled, edited, and refined using the visualization tools of the WINDADA and WINCLADOS interfaces in WINCLADA (Nixon, 2002). The characters were numbered in accordance with the sequence of description detailed in Franz (2003a). The most-parsimonious cladograms and character state optimizations were identified with NONA (Goloboff, 1999). Exploratory searches were performed using the parsimony ratchet (Nixon, 1999), as implemented in WINCLADA. Each time, fifty to 100 sequential ratchet runs were computed; with 200 iterations per replication, holding one tree per iteration, and sampling 8–12% of all characters (i.e. eighteen characters in the final analysis). Sometimes a strict consensus was calculated prior to examining the results. The analysis for the last set of cladograms was expanded to include 250 sequential ratchet runs. The obtained cladograms were resubmitted to NONA to identify additional islands with equally parsimonious solutions (Maddison, 1991). The commands entered were 'hold 50000', 'amb =', 'poly-', ad 'max*'; followed by 'amb-', 'poly =', and 'best'. The results were then saved and reviewed again in WINCLADA. This procedure was repeated three times to solidify the outcome. Bremer support values (Bremer, 1994) were calculated in NONA, with 'hold 50000', 'suboptimal 15', and 'bsupport 15'.

Table 1. List of ingroup and outgroup taxa included in the cladistic analysis of derelomine flower weevils, as named and placed (into tribes) according to the traditional classification (with complete citations), with host plant associations documented at the family level. Type species are marked with an asterisk.

Taxon	Classification	Host	Reference ^a
Ingroup			
<i>Anchylorhynchus aegrotus</i> Fähræus, 1843: 335 (in Schoenherr, 1843)	D	3	Vaurie (1954)
<i>Anchylorhynchus eriospathae</i> (Bondar, 1943: 364)	D	3	Vaurie (1954)
<i>Anchylorhynchus trapezicollis</i> (Hustache, 1940: 210; in Bondar, 1940)	D	3	Vaurie (1954)
<i>Anchylorhynchus tricarinatus</i> Vaurie, 1954: 21	D	3	Vaurie (1954)
<i>Anchylorhynchus variabilis</i> Gyllenhal, 1835: 451 (in Schoenherr, 1835)*	D	3	Vaurie (1954)
<i>Andranthobius argentinensis</i> (Hustache, 1939: 61)*	D	3	Bondar (1940)
<i>Andranthobius estriatus</i> (Champion, 1902: 140)	D	3	Spec. label (CWOB)
<i>Andranthobius palmarum</i> (Champion, 1902: 140)	D	3	Champion (1902)
<i>Araucarietus viridans</i> Kuschel, 1952: 275*	D	2	Kuschel (2000)
<i>Celetes binotatus</i> Gyllenhal, 1836: 635 (in Schoenherr, 1836)*	D	3	Spec. label (CMNC)
<i>Celetes cariniceps</i> (Hustache, 1934: 279)	D	3	Spec. label (CWOB)
<i>Celetes crispus</i> (Champion, 1903: 278)	D	3	Spec. label (CWOB)
<i>Celetes impar</i> Voss, 1940: 4	D	3	Spec. label (NMNH)

<i>Celetes landeroi</i> (Bondar, 1942: 456)	D	3	Bondar (1942)
<i>Celetes marizae</i> (Bondar, 1942: 452)	D	3	Bondar (1942)
<i>Celetes pallidus</i> (Champion, 1909: 7)	D	3	Spec. label (CWOB)
<i>Celetes tarsalis</i> (Hustache, 1934: 280)	D	3	Spec. label (CWOB)
<i>Cotithene globulicollis</i> Voss, 1940: 6*	D	4	Pers. obs.; Franz (1999)
<i>Cotithene</i> sp. 1	D	4	Pers. obs.; Franz (1999)
<i>Cyclanthura carinata</i> Franz, 2003a: 177	D	–	Franz (2003a)
<i>Cyclanthura crepidula</i> Franz, 2003a: 187	D	4	Franz (2003a)
<i>Cyclanthura laticola</i> Franz, 2003a: 166*	D	1	Franz (2003a)
<i>Cyclanthura pilosa</i> Franz, 2003a: 173	D	1	Franz (2003a)
<i>Cyclanthura striata</i> Franz, 2003a: 183	D	?	–
<i>Derelomini</i> gen. 1 sp. 1	D	4	Franz (1999)
<i>Derelomini</i> gen. 1 sp. 2	D	4	Franz (1999)
<i>Derelomini</i> gen. 1 sp. 3	D	4	Pers. obs.
<i>Derelomini</i> gen. 2 sp. 1	D	4	Franz (1999)
<i>Derelomini</i> gen. 2 sp. 2	D	4	Franz (1999)
<i>Derelomini</i> gen. 2 sp. 3	D	4	Pers. obs.
<i>Derelominus piceus</i> Champion, 1902: 141*	D	3	O'Brien, pers. comm.
<i>Derelomus abyssinicus</i> (Hustache, 1932: 78)	D	3	Spec. label (CWOB)
<i>Derelomus auberti</i> Hustache, 1932: 68	D	3	Spec. label (CWOB)
<i>Derelomus bicarinatus</i> Marshall, 1928: 545	D	3	Spec. label (NMNH)
<i>Derelomus chamaeropsis</i> (Fabricius, 1798: 167)*	D	3	Anstett (1999)
<i>Derelomus costifer</i> Fähræus, 1844: 93 (in Schoenherr, 1844)	D	3	Spec. label (CWOB)
<i>Derelomus mariaehelenae</i> Bondar, 1941: 281	D	3	Bondar (1941)
<i>Derelomus</i> sp. 1	D	3	Spec. label (AMNH)
<i>Derelomus tatiana</i> Bondar, 1941: 280	D	3	Bondar (1941)
<i>Diplothemiobius sternicornis</i> (Bondar, 1941: 277)*	D	3	Bondar (1941)
<i>Eisingius araucariae</i> Kuschel, 2000: 47	D	2	Kuschel (2000)
<i>Eisingius chusqueae</i> (Bondar, 1949: 182)*	D	2	Kuschel (2000)
<i>Elaeidobius kamerunicus</i> (Faust, 1898: 225)	D	3	Syed (1979)
<i>Elaeidobius subvittatus</i> (Faust, 1898: 224)*	D	3	Syed (1979)
<i>Ganglionus constrictus</i> Franz & O'Brien, 2001a: 847	D	4	Franz & O'Brien (2001a)
<i>Ganglionus mitigatus</i> Franz & O'Brien (2001a: 843	D	4	Franz & O'Brien (2001a)
<i>Ganglionus undulatus</i> Franz & O'Brien (2001a: 845*	D	4	Franz & O'Brien (2001a)
<i>Hypolesschus atratus</i> Fall, 1907: 266 (in Fall & Cockerell, 1907)*	D	5	Anderson (2002)
<i>Neoderelomus piriformis</i> (Hoffmann, 1938b: 47)*	D	3	Proches, pers. comm.
<i>Neopsilorhinus collaris</i> (Blanchard, 1851: 393)	D	0	Spec. label (CWOB)
<i>Neopsilorhinus modestus</i> (Blanchard, 1851: 394)	D	0	Spec. label (CWOB)
<i>Neopsilorhinus variegatus</i> (Blanchard, 1851: 393)	D	0	Kuschel (1952)
<i>Nodocnemus</i> sp. 1	D	3	Spec. label (CUIC)
<i>Notolomus basalis</i> LeConte, 1876: 222 (in LeConte & Horn, 1876)	D	3	Brown (1976)
<i>Notolomus bicolor</i> LeConte, 1876: 222 (in LeConte & Horn, 1876)	D	3	Brown (1976)
<i>Pedetinus flavipes</i> (Faust, 1894: 337)*	D	3	Spec. label (CMNC)
<i>Pedetinus halticoides</i> (Champion, 1903: 201)	D	3	Pers. obs.
<i>Perelleschus carludovicae</i> (Günther, 1936: 190)*	D	4	Franz & O'Brien (2001b)
<i>Perelleschus evelynae</i> Franz & O'Brien, 2001b: 264	D	4	Franz & O'Brien (2001b)
<i>Perelleschus rectirostris</i> Voss, 1954: 354	D	4	Franz & O'Brien (2001b)
<i>Phyllotrox aristidis</i> Voisin, 1986: 187	D	5	Voisin (1986)
<i>Phyllotrox ater</i> Champion, 1902: 142	D	5	Spec. label (NMNH)
<i>Phyllotrox canyonaceris</i> Warner, 1976: 463	D	5	Warner (1976)
<i>Phyllotrox crassipes</i> Champion, 1902: 143	D	5	Pers. obs.
<i>Phyllotrox derivatus</i> (Fall, 1913: 44)	D	5	Spec. label (CWOB)
<i>Phyllotrox ferrugineus</i> LeConte, 1876: 174 (in LeConte & Horn, 1876)	D	5	Spec. label (CMNC)
<i>Phyllotrox marcidus</i> Champion, 1902: 144	D	5	Spec. label (CWOB)
<i>Phyllotrox mecinoides</i> Champion, 1902: 142	D	5	Pers. obs.
<i>Phyllotrox megalops</i> Champion, 1902: 142	D	3	Spec. label (CWOB)
<i>Phyllotrox nubifer</i> LeConte, 1876: 174 (in LeConte & Horn, 1876)	D	5	Spec. label (CMNC)
<i>Phyllotrox pallidus</i> Fähræus, 1843: 191 (in Schoenherr, 1843)	D	3	Spec. label (CWOB)
<i>Phyllotrox quadricollis</i> Fall, 1907: 265 (in Fall & Cockerell, 1907)	D	5	Fall (1907)

Table 1. Continued.

Taxon	Classification	Host	Reference ^a
<i>Phyllotrox rubiginosus</i> Faust, 1894: 315	D	3	Spec. label (CWOB)
<i>Phyllotrox rufipes</i> Faust, 1894: 315	D	5	Spec. label (CWOB)
<i>Phyllotrox rutilus</i> (Fall, 1913: 43)	D	5	Fall (1913)
<i>Phyllotrox sejunctus</i> (Fall, 1913: 45)	D	5	Fall (1913)
<i>Phyllotrox semirufus</i> Boheman, 1843: 190 (in Schoenherr, 1843)*	D	5	Franz (2003a)
<i>Phyllotrox sericeus</i> Faust, 1894: 314	D	5	Spec. label (CWOB)
<i>Phyllotrox suturalis</i> (Boheman, 1844: 96; in Schoenherr, 1844)	D	5	Pers. obs.
<i>Phyllotrox variabilis</i> Schaufuss, 1866: 412	D	5	Spec. label (CWOB)
<i>Phytotribus lineatus</i> Chevrolat, 1879: cxliv	D	3	Spec. label (CWOB)
<i>Phytotribus</i> sp. 1	D	3	Spec. label (CMNC)
<i>Phytotribus unicolor</i> Boheman, 1843: 182 (in Schoenherr, 1843)*	D	3	Spec. label (CMNC)
<i>Pseudoderelomus baridiiformis</i> Champion, 1910: 184*	D	3	Spec. label (CMNC)
<i>Pseudoderelomus</i> sp. 1	D	3	Pers. obs.
<i>Staminodeus curvibialis</i> Franz, 2001: 420	D	4	Franz (2001)
<i>Staminodeus inermis</i> Franz, 2001: 419	D	4	Franz (2001)
<i>Staminodeus vectoris</i> Franz, 2001: 427*	D	4	Franz (2001)
<i>Systemotelus carلودovicae</i> Anderson & Gómez, 1997: 891*	D	4	Franz (2004)
<i>Systemotelus costaricensis</i> Anderson & Gómez, 1997: 893	D	4	Franz (2004)
<i>Systemotelus stockwelli</i> Anderson & Gómez, 1997: 894	D	4	Franz (2004)
<i>Terioltes circumdatus</i> Champion, 1903: 147	D	3	Spec. label. (INBC)
<i>Terioltes nigripennis</i> Champion, 1903: 147	D	3	Spec. label. (INBC)
Outgroup			
<i>Acalyptus carpini</i> (Fabricius), 1792: 409*	Acalyptini	5	Spec. label (CUIC)
<i>Amalactus nigritus</i> Gyllenhal, 1836: 252* (in Schoenherr, 1836)	Amalactini (M)	?	–
<i>Amorphoidea lata</i> Motschulsky, 1858: 79	Acalyptini	3	Spec. label (NMNH)
<i>Anthonomus corvulus</i> LeConte, 1876: 201 (in LeConte & Horn, 1876)	Anthonomini	5	Spec. label (CUIC)
<i>Curculio proboscideus</i> (Fabricius), 1775: 142	Curculionini	5	Spec. label (CUIC)
<i>Dorytomus hirtus</i> LeConte, 1876: 166 (in LeConte & Horn, 1876)	Ellescini	5	Spec. label (CUIC)
<i>Ellescus ephippiatus</i> (Say), 1831: 25	Ellescini	5	Spec. label (CUIC)
<i>Erodiscus tinamus</i> LeConte, 1884: 30	Erodiscini	5	Spec. label (CUIC)
<i>Grasidius</i> sp. 1	Erihrinini (E)	3	Spec. label (CWOB)
<i>Juanorhinus ruficeps</i> (Aurivillius), 1931: 467*	Juanorhinini (M)	5	Spec. label (CWOB)
<i>Nanus uniformis</i> Boheman, 1844: 90 (in Schoenherr, 1844)*	Trypetidini (M)	3	Spec. label (CWOB)
<i>Notaris acridulus</i> L. 1758* (preferred root)	Erihrinini (E)	0	Anderson (1993)
<i>Omoides humeralis</i> Boheman, 1859*	Eugnomini	5	Kuschel (1952)
<i>Parimera variabilis</i>	Acalyptini	3	Spec. label (NMNH)
<i>Platynanus sericatus</i> Aurivillius, 1931: 471	Trypetidini (M)	?	–
<i>Smicronyx griseus</i> LeConte, 1876: 171 (in LeConte & Horn, 1876)	Smicronychini	5	Spec. label (CWOB)
<i>Tadius erhinoides</i> Pascoe, 1885: 253*	Tadiini (E)	0	Spec. label (CWOB)
<i>Terires pilosus</i> Champion, 1902: 138*	Storeini	3	Spec. label (CWOB)
<i>Terires plurisetosus</i> Champion, 1910: 183	Storeini	3	Spec. label (CWOB)
<i>Trypetes politus</i> Pascoe, 1880: 180	Trypetidini (M)	3	Spec. label (CWOB)
<i>Tychius lineellus</i> LeConte, 1876: 217 (in LeConte & Horn, 1876)	Tychiini	5	Spec. label (CUIC)
<i>Udeus</i> sp. 1	Eugnomini	?	?

D, Derelomini; all tribes are part of Curculioninae, with the exceptions of M = Molytinae (Curculionidae), and E = Erihrinidae (all placements sensu Alonso-Zarazaga & Lyal, 1999); 0, aquatic monocotyledoneous plants; 1, Araceae; 2, Araucariaceae; 3, Arecaceae; 4, Cyclanthaceae; 5, dicotyledoneous plants; see also character 152.

^aCollection codons according to Arnett *et al.* (1993).

Results

Preferred cladogram and character state optimizations

The matrix for the final analysis included 155 characters (twenty are multistate, eleven of which were coded as nonadditive; see Appendix 1). It yielded a single most-parsimonious

cladogram, with a length of 271 steps, a consistency index (CI) of 65, and a retention index (RI) of 95 (see Farris, 1989). The unambiguous and preferred character state optimizations are shown in Fig. 1, which contains the reference cladogram for the remainder of the paper. Alternative, fast or slow optimizations are displayed in Figs. 2 and 3, respectively. The support values for individual clades are evaluated after the character analysis.

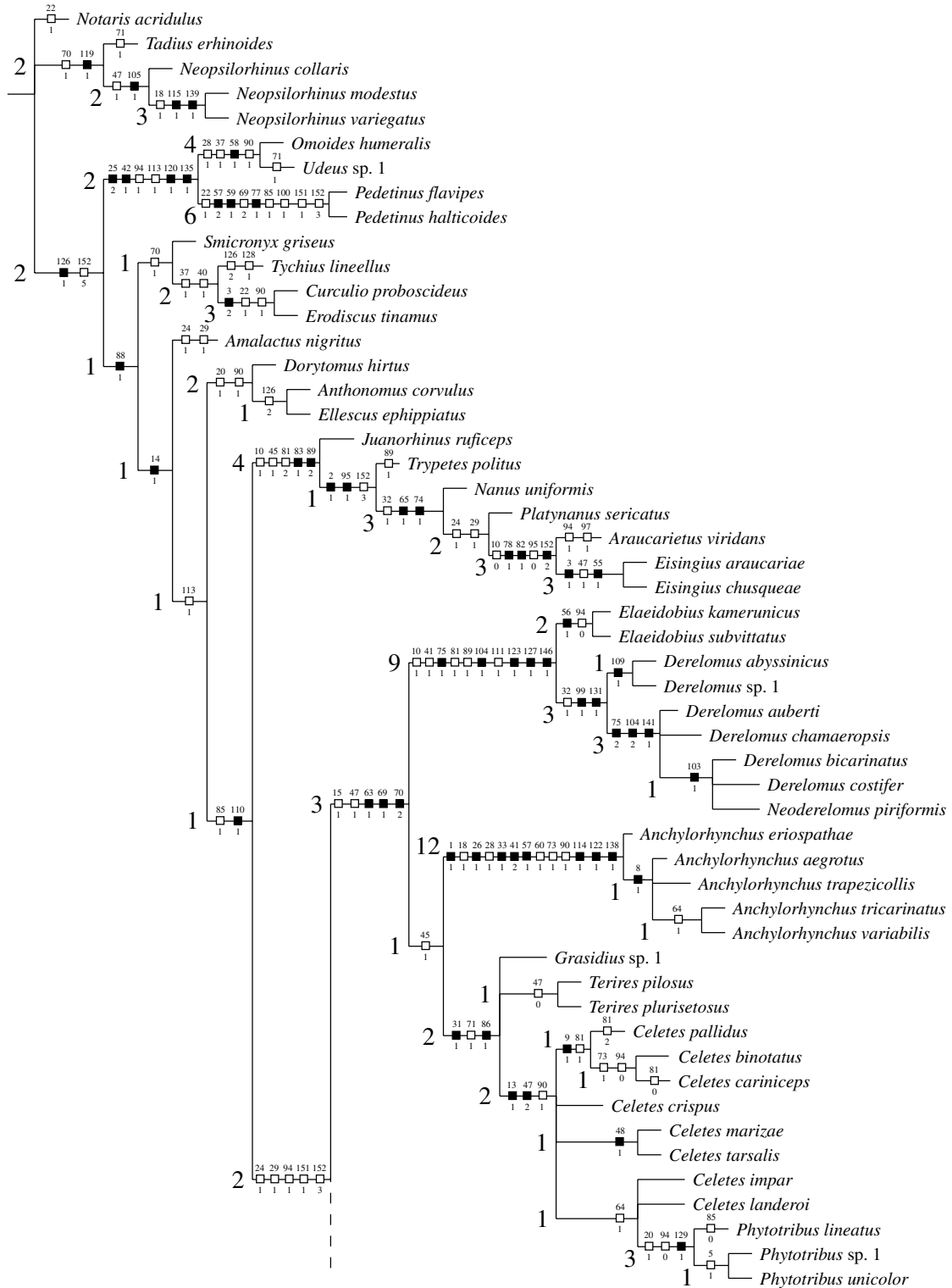


Fig. 1. Single most-parsimonious reference cladogram with preferred (unambiguous, fast, and slow; see text for details) character state optimizations (length = 271, consistency index = 65, retention index = 95). Black rectangles indicate (single) nonhomoplasious character state transformations, whereas the white rectangles indicate (multiple) homoplasious character state transformations. The numbers above and below each rectangle correspond to the coded characters and states, respectively. Bremer support values are situated near the left end of each node.

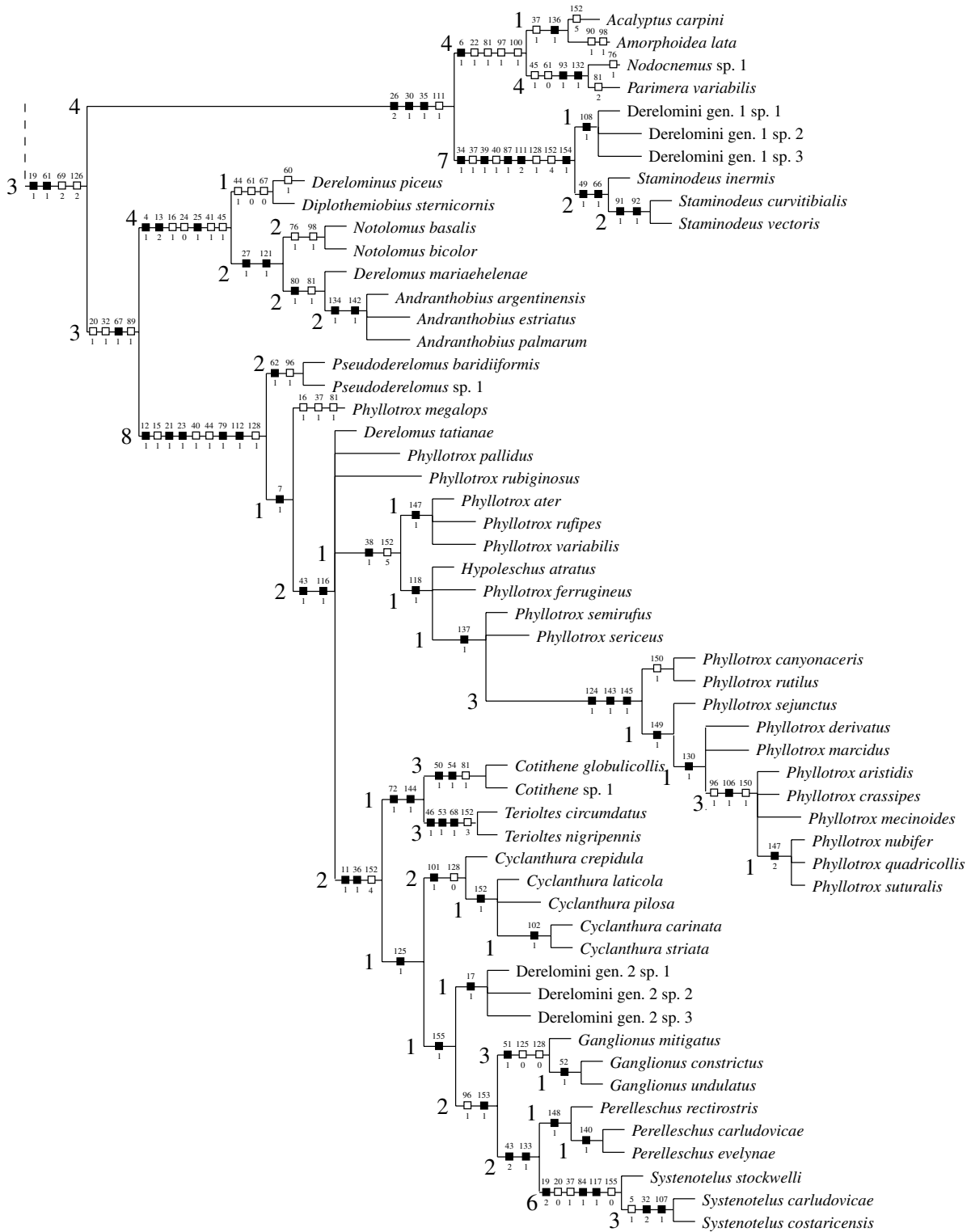


Fig. 1. (Continued) Single most-parsimonious reference cladogram with preferred (unambiguous, fast, and slow; see text for details) character state optimizations (length = 271, consistency index = 65, retention index = 95). Black rectangles indicate (single) nonhomoplasious character state transformations, whereas the white rectangles indicate (multiple) homoplasious character state transformations. The numbers above and below each rectangle correspond to the coded characters and states, respectively. Bremer support values are situated near the left end of each node.

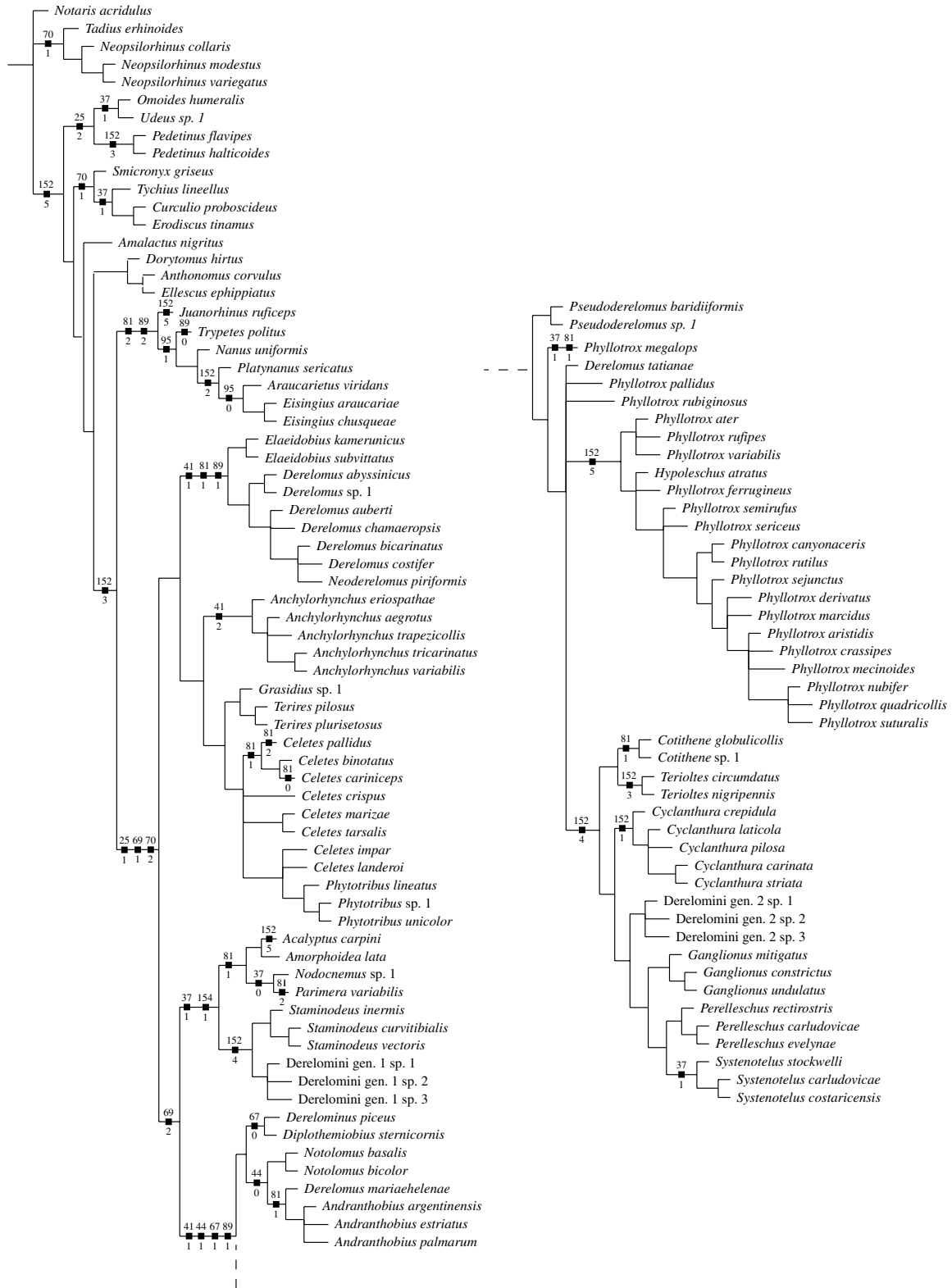


Fig. 2. Phylogeny of derelomine flower weevils; as in Fig. 1, yet character states mapped only according to fast (ACCTRAN) optimization (unambiguous characters omitted).



Fig. 3. Phylogeny of derelomine flower weevils; as in Fig. 1, yet character states mapped only according to slow (DELTRAN) optimization (unambiguous characters omitted).

Character analysis

Habitus

1. *Shape, dorsal view*: (0) elliptical to elongate (e.g. Fig. 56A); (1) oval (in lateral view globular).

Apomorphy for *Anchylorhynchus* (see also Vaurie, 1954: 7, fig. 1). The included species have a unique shape among all examined taxa, i.e. a comparatively lower length-to-width ratio and more convex elytra. This is also reflected in the transverse, trapezoidal (as opposed to variously elongate to equilateral) pronotum (Bondar, 1943; Voss, 1943; Vaurie, 1954). Unambiguous optimization (CI = 100; RI = 100).

2. *Shape, lateral view*: (0) moderately depressed to variously compressed (e.g. Fig. 64A); (1) dorsoventrally distinctly depressed (Fig. 48A).

Apomorphy for the *Trypetes*–*Eisingius* clade. The shape of certain species of *Andranthobius* Kuschel (1952), *Derelomus*, or *Notolomus* is also depressed yet still more convex, particularly along the ventral side, which is subplane in the apomorphic state (1). Unambiguous optimization (CI = 100; RI = 100).

Mandible

3. *Apical region, ventral view*: (0) bidentate: apically with two distinct, arcuate, variously separately acuminate (e.g. Fig. 37A) to rotundate (e.g. Fig. 9A) teeth; (1) monodentate: apically with one distinct, elongate, subrectate, apically narrowed-truncate tooth (see also Ting, 1936: 108, fig. 76; Morimoto & Kojima, 2003: 162, fig. 45); (2) 'monodentate' with two small, rotundate-triangular projections positioned subapically along larger central tooth (Fig. 18A).

Coded as nonadditive, as no two of the three character states appear similar to each other. State (1) is a synapomorphy for *Curculio* Linnaeus (1758) and *Erodiscus* Schoenherr (1825), whereas state (2) is an apomorphy for *Eisingius*. Individuals of *A. variabilis* Gyllenhal (1835; in Schoenherr, 1835) are polymorphic with respect to the number of teeth: smaller individuals are bidentate like the remaining members of *Anchylorhynchus*, yet in large individuals the outer tooth is more elongate and the inner tooth almost indistinct (Fig. 7A). Unambiguous optimization (CI = 100; RI = 100).

Maxilla

4. *Stipes, basal region, ventral view*: (0) one small seta absent (e.g. Fig. 10B); (1) basally in addition to the larger central seta(e) (see character 5) with one relatively small seta projecting to outer margin (e.g. Figs. 8B, 28B).

Apomorphy for the *Derelominus*–*Andranthobius* clade. *Diplothemiobius* Kuschel (1952) has two to four aligned, similarly positioned setae (Fig. 17B), which are considered homologous. Unambiguous optimization (CI = 100; RI = 100).

5. *Stipes, central region, ventral view*: (1) with one large seta projecting to outer margin (e.g. Fig. 12B); (2) with two large setae, presumably resulting from a secondary duplication (Figs. 34B, 38B).

Inapplicable in *Trypetes* Schoenherr (1836), which lacks setae on the stipes (Fig. 41B). Convergently present in a clade within *Phytotribus*, as well as in *S. carludovicae* Anderson & Gómez (1997) and *S. costaricensis* Anderson & Gómez (1997). In some individuals of *P. unicolor* Boheman (1843; in Schoenherr, 1843) the maxillae are asymmetrical in that only one of them has two large setae centrally on the stipes. Unambiguous optimization (CI = 50; RI = 66).

6. *Stipes, apical region, ventral view*: (0) one to two small setae absent (e.g. Fig. 39B); (1) apically and in addition to the larger central seta(e) (see character 5) with one (e.g. Fig. 6B) to two (e.g. Fig. 5B) relatively small seta(e) projecting to outer margin.

Apomorphy for the *Acalyptus*–*Parimera* clade. Unambiguous optimization (CI = 100; RI = 100).

7. *Galeo-lacinial complex (i.e. the 'mala' sensu Morimoto & Kojima, 2003: 140), apical region, ventral view*: (0) lacinia apically projecting along entire length of palpomere I (and typically extending to palpomere II, or even more, e.g. Figs. 26B, 40B); (1) lacinia apically truncate, not projecting beyond central region of palpomere I (e.g. Figs. 14B, 32B).

Apomorphy for the *P. megalops*–*Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).

8. *Galeo-lacinial complex, apical region, ventral view*: (0) lacinia apically gradually (and only slightly) narrowed to triangular in outline, rotundate (e.g. Figs. 21B, 35B); (1) lacinia apically distinctly projected, narrowly elongate to clavate, lateral margins subparallel, apically rotundate (Fig. 7B).

Coded as inapplicable in taxa in which the lacinia is apically truncate (see character 7). Apomorphy for a clade within *Anchylorhynchus*. Unambiguous optimization (CI = 100; RI = 100).

9. *Galeo-lacinial complex, apical region, ventral view*: (0) lacinia projecting subparallel to palpiger (e.g. Figs. 30B, 34B); (1) lacinia apically narrowed and distinctly angulate: projecting (slightly) across palpiger to outer margin of maxilla (Fig. 10B).

Apomorphy for a clade within *Celetes*, including *C. pallidus* (Champion, 1909), *C. cariniceps* (Hustache, 1934), and *C. binotatus* Gyllenhal (1836; in Schoenherr, 1836). Unambiguous optimization (CI = 100; RI = 100).

10. *Galeo-lacinial complex, region adjacent to stipes (setation), ventral view*: (0) bifurcate setae absent (e.g. Fig. 11B); (1) outer region adjacent to stipes with an isolated patch of one to two distinct, broad, yet relatively small, apically bifurcate setae (e.g. Fig. 23B).

Convergently present in the *Juanorhinus*–*Eisingius* clade, with an apparent reversal in *Araucarietis*–*Eisingius*, and in the *Elaeidobius*–*Derelomus* clade. Unambiguous optimization (CI = 33; RI = 83).

11. *Galeo-lacinal complex, central region (setation), ventral view*: (0) galeo-lacinal setae (sparsely to densely) aligned in various irregularly interlaced rows, not distinctly arranged along one continuous row (see, e.g. Ting, 1936: 109–111, figs 77–79); (1) galeo-lacinal setae regularly aligned along one contiguous, slightly arcuate row (see, e.g. Franz & O'Brien, 2001a: 838, fig. 2b; Franz, 2003a: 160, fig. 4B).
Apomorphy for the *Cotithene–Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).
12. *Galeo-lacinal complex, subapical region (setation), ventral view*: (0) one to two sclerotized setae absent (e.g. Figs. 8B, 13B); (1) with one to two small, arcuate, strongly sclerotized setae positioned in subapical region of lacinia, separate and distinct from lacinial teeth (e.g. Figs. 12B, 32B).
Apomorphy for the *Pseudoderelomus–Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).
13. *Galeo-lacinal complex, apical region (setation), ventral view*: (0) distinctly arcuate setae absent (e.g. Figs. 4B, 24B); (1) lacinia apically with one to three (very) large, distinctly arcuate (reflexed), strongly sclerotized setae (e.g. Fig. 10B); (2) lacinia apically with numerous (minimally five to ten) relatively large, distinctly arcuate (reflexed) yet only regularly sclerotized setae (e.g. Fig. 28B).
Coded as nonadditive. State (1) is an apomorphy for the *Celetes–Phytotribus* clade, whereas state (2) is a (presumably independent) apomorphy for the *Derelominus–Andranthobius* clade. Certain species in the *Elaeidobius–Derelomus* clade have slightly arcuate, unreflexed setae throughout the apical region of the lacinia. These were not considered homologous to state (2). Unambiguous optimization (CI = 100; RI = 100).
14. *Galeo-lacinal complex, inner margin (lacinial teeth), ventral view*: (0) lacinial teeth absent (e.g. Figs. 4B, 30B; see also Ting, 1936: 109–110, figs 77, 78); (1) in addition to regularly narrow setae with numerous (typically two to twenty) 'lacinial teeth' (sensu Ting, 1936: 101), i.e. relatively large, distinctly broadened, arcuate, strongly sclerotized setae arranged in one or more interlaced rows along inner margin of galeo-lacinal complex (e.g. Figs. 31B, 41B).
Apomorphy for the *Amalactus–Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).
15. *Galeo-lacinal complex, inner margin (lacinial teeth), ventral view*: (0) degree of sclerotization of lacinial teeth similar throughout (e.g. Figs. 6B, 18B); (1) inner margin subcentrally with one to two more strongly sclerotized lacinial teeth (in comparison with adjacent ones, e.g. Figs. 12B, 34B).
Inapplicable in taxa in which lacinial teeth are absent (see character 14). Convergently present in the *Elaeidobius–Phytotribus* clade and in the *Pseudoderelomus–Systemotelus* clade. The position of these distinct lacinial teeth within the entire row and the distance from the inner margin vary slightly among species. Unambiguous optimization (CI = 50; RI = 96).
16. *Galeo-lacinal complex, inner margin (lacinial teeth), ventral view*: (0) lacinial teeth apically acuminate, unific (e.g. Figs. 27B, 33B); (1) lacinial teeth apically (variously) bifurcate, terminating in two separate projections (e.g. Figs. 15B, 32B).
Inapplicable in taxa in which lacinial teeth are absent (see character 14). Convergently present in the *Derelominus–Andranthobius* clade, including *D. mariaehelena* Bondar (1941), and in *P. megalops* Champion (1902). Unambiguous optimization (CI = 50; RI = 87).
17. *Palpiger, central region, ventral view*: (0) glabrate and/or with sparsely to densely arranged setae (e.g. Figs. 20B, 36B); (1) variously denticulate: a significant (although variable) part of the central region of the palpiger is covered with numerous interlaced rows of densely arranged, microscopic teeth (Fig. 14B).
Apomorphy for *Derelomini* gen. 1. Unambiguous optimization (CI = 100; RI = 100).
18. *Palpiger, outer margin, region adjacent to stipes, ventral view*: (0) small setae absent (e.g. Fig. 21B); (1) with numerous relatively small setae positioned along larger setae (see character 19) of outer margin of palpiger (Figs. 7B, 26B).
Convergently present in a clade within *Neopsilorhinus* – entirely absent in *N. collaris* (Blanchard, 1851), most distinctive in *N. variegatus* (Blanchard, 1851) – and in *Anchylorhynchus* (therein also varying among species). Unambiguous optimization (CI = 50; RI = 83).
19. *Palpiger, outer margin, central region, ventral view*: (0) with (minimally) two large setae projecting beyond outer margin (e.g. Figs. 16B, 24B; up to four to six large setae are present in *Anchylorhynchus*; see Fig. 7B); (1) with one large seta projecting centrally from outer margin of palpiger (e.g. Figs. 22B, 37B); (2) with two large setae originating from the same position, presumably resulting from a secondary duplication (Fig. 38B).
Coded as additive. State (1) is an apomorphy for the *Acalyptus–Systemotelus* clade, whereas state (2) is an apomorphy for *Systemotelus* Anderson & Gómez (1997). The preferred coding implies that the state of having two setae – as present in various outgroup taxa – is the result of a reduction, not a duplication. The alternative interpretation, i.e. to assign state (0) to *Systemotelus*, would not affect the overall topology of the analysis. Unambiguous optimization (CI = 100; RI = 100).
20. *Palpiger, outer margin, subapical region, ventral view*: (0) small setae absent (e.g. Figs. 9B, 25B); (1) with an isolated patch of one to two(four) small setae projecting outward from subapical region of palpiger (e.g. Figs. 8B, 14B).
Convergently present in the *Dorytomus–Ellescus* clade, in *Phytotribus*, and in the *Derelominus–Systemotelus* clade, with an apparent reversal in *Systemotelus*. The transverse setal row in *Pedetinus* Faust (1895), *Acalyptus* Schoenherr (1833), and

related taxa (see character 22) is not immediately comparable with state (1) in its extension or in the size of the setae. Unambiguous optimization (CI = 25; RI = 94).

21. *Palpiger, outer margin, subapical region, ventral view*: (0) with two(four) small setae (e.g. Fig. 17B); (1) with one isolated, small seta (e.g. Fig. 31B).

Coded as inapplicable in taxa in which small setae are absent on the (subapical) outer margin of the palpiger (see character 20). Apomorphy for the *Pseudoderelomus–Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).

22. *Palpiger, apical region, ventral view*: (0) either (in the majority of examined taxa) glabrate (e.g. Fig. 34B) or with one to two isolated patches of one to two relatively small setae (e.g. Fig. 36B); (1) with one row of numerous, relatively large setae extending transversely from outer margin (almost) across entire apical region of palpiger (e.g. Figs. 5B, 29B).

Convergently present in *Notaris* (in spite of its current placement as sister to all remaining taxa in the analysis), *Curculio–Erodiscus*, *Pedetinus*, and in the *Acalyptus–Parimera* clade. Certain species of *Phyllotrox* have setal rows extending from the galeolacinial complex into the palpiger (e.g. Fig. 32B). This characteristic varies considerably among species within the *Phyllotrox–Systemotelus* clade and is not considered homologous to state (1). Unambiguous optimization (CI = 25; RI = 62).

23. *Maxillary palps, number of palpomeres, ventral view*: (0) three-segmented (e.g. Figs. 8B, 26B); (1) two-segmented (e.g. Figs. 31B, 33B).

Apomorphy for the *Pseudoderelomus–Systemotelus* clade. Up to four maxillary palpomeres are present in taxa pertaining to some of the oldest lineages of Curculionioidea (e.g. in *Cimberis* des Gozis, 1881, Nemonychidae; see Ting, 1936: 110, fig. 78), suggesting an ordered reduction in the number of maxillary palpomeres. The lost segments were presumably subapical, as the most apical palpomeres always display various small papillae. Unambiguous optimization (CI = 100; RI = 100).

24. *Maxillary palpomere I, central region (setation), ventral view*: (0) with one to various distinct setae present in centrolateral region (towards outer margin) of maxillary palpomere I (e.g. Figs. 4B, 15B); (1) centrolateral setae absent (e.g. Figs. 32B, 40B).

Convergently 'present' in *Amalactus*, in the *Platynanus–Eisingius* clade, and in the *Elaeidobius–Systemotelus* clade, with an apparent reversal in the *Derelominus–Andranthobius* clade (see character 25). Unambiguous optimization (CI = 25; RI = 88).

25. *Maxillary palpomere I, central region (setation), ventral view*: (0) with one distinct, relatively small seta present in centrolateral region (towards outer margin) of maxillary palpomere I (e.g. Figs. 4B, 24B); (1) with two distinct, large setae (e.g. Figs. 15B, 28B); (2) entire central region (i.e. extending from outer to inner

margin) of maxillary palpomere I with one row of (five to ten, or more) relatively large, regularly arranged setae (Fig. 30B).

Coded as nonadditive, which presumes states (1) and (2) to represent independent transformations from the plesiomorphic state (0) of character 24. Inapplicable in taxa in which centrolateral setae are absent (see character 24). State (1) is an apomorphy for the *Derelominus–Andranthobius* clade (including *D. maria-helenae*), whereas state (2) is an apomorphy for the *Omoides–Pedetinus* clade. In *Omoides* Boheman (1859) and *Udeus* Champion (1902) there are additional setae variously arranged throughout the central region of the maxillary palpomere I. Slow optimization preferred (compare Figs. 2 and 3; CI = 100; RI = 100).

26. *Maxillary palpomere I, apical region (setation), ventral view*: (0) with one small seta present on apicolateral edge of outer margin (e.g. Figs. 14B, 26B); (1) with two to three small apicolateral setae (Fig. 7B); (2) without apicolateral seta (e.g. Figs. 5B, 13B).

Coded as nonadditive. State (1) is an apomorphy for *Anchylorhynchus*, presumed to be the result of a secondary replication of setae. State (2) is an apomorphy for the *Acalyptus–Staminodeus* clade. The small apicolateral setae corresponding to states (0) and (1), and others with similar positions and shapes (see, e.g. characters 30 and 44), can easily become detached from the maxillary (or labial) palpomeres in the process of specimen preparation, in which case their presence is indicated by a setal socket. Unambiguous optimization (CI = 100; RI = 100).

27. *Maxillary palpomere II, size, ventral view*: (0) palpomere II smaller than or similar in size to palpomere I (e.g. Figs. 33B, 37B); (1) palpomere II larger (with respect to volume and also length) than palpomere I (Figs. 8B, 28B; see also character 28).

Apomorphy for the *Andranthobius–Notolomus* clade (including *D. maria-helenae*). Unambiguous optimization (CI = 100; RI = 100).

28. *Maxillary palpomere II, shape, ventral view*: (0) palpomere II transverse (e.g. Fig. 35B) to slightly elongate (e.g. Fig. 21B), shape not significantly different from that of palpomere I; (1) palpomere II distinctly more slender and elongate than shorter and stouter palpomere I (Fig. 7B).

Convergently present in the *Omoides–Udeus* clade and in *Anchylorhynchus*. Unambiguous optimization (CI = 50; RI = 83).

29. *Maxillary palpomere II, central region (setation), ventral view*: (0) with one to two relatively small setae present in centrolateral region (towards outer margin) of maxillary palpomere II (e.g. Figs. 4B, 24B); (1) centrolateral setae absent (e.g. Figs. 16B, 40B).

Inapplicable in taxa that have only two maxillary palpomeres (see character 23), assuming that their most apical palpomere is homologous to palpomere III and palpomere II is absent. Convergently 'present'

in *Amalactus*, the *Platynanus–Eisingius* clade, and in the *Elaeidobius–Systemotelus* clade; not entirely congruent with the setal pattern of maxillary palpomere I (see character 24). Unambiguous optimization (CI = 33; RI = 85).

30. *Maxillary palpomere II, apical region (setation), ventral view*: (0) with one small seta present on apicolateral edge of outer margin (e.g. Figs. 9B, 17B); (1) without apicolateral seta (e.g. Figs. 5B, 13B). Inapplicable in taxa that have only two maxillary palpomeres (see comments on character 23). Apomorphy for the *Acalyptus–Staminodeus* clade. Unambiguous optimization (CI = 100; RI = 100).

Labium

31. *Prementum, lateral margins (setation), ventral view*: (0) subbasal seta absent (e.g. Figs. 17C, 19C); (1) each lateral margin subbasally with one separate, very large seta in addition to those positioned along the subcentral region (e.g. Figs. 10C, 40C; see also character 32).

Inapplicable in *Tadius Pascoe* (1885) and *Erodiscus*, which (convergently) lack setae along the lateral margins of the prementum. Apomorphy for the *Grasidius–Phytotribus* clade. Unambiguous optimization (CI = 100; RI = 100).

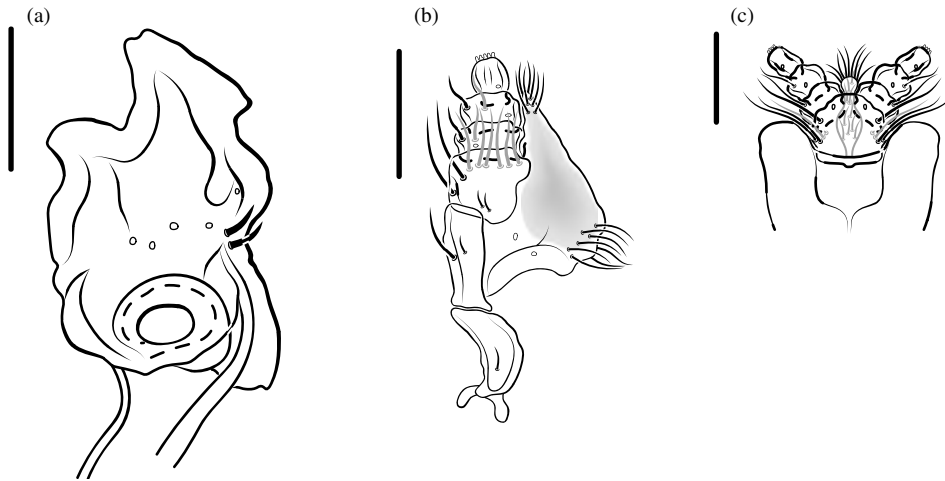


Fig. 4. *Notaris acridulus*. A, Left mandible; B, right maxilla; C, labium. Figures 4–41 illustrate the mouthparts of select taxa of derelomine flower weevils (emphasis on type species). The mouthparts are illustrated in ventral view and are typically of males; the variation among sexes was found to be insignificant when both were dissected. Scale bars 0.1 mm. All mouthpart drawings are interpretative, and intended to illustrate relevant apomorphies. On occasion, details (such as many small individual setae) are omitted for this purpose. Shaded areas indicate regions and/or structures with relatively fine setation, which is more dense in the darker areas. Different colours and broken (to dotted) lines are used to represent to various positions of setae and other structures. See text for details.

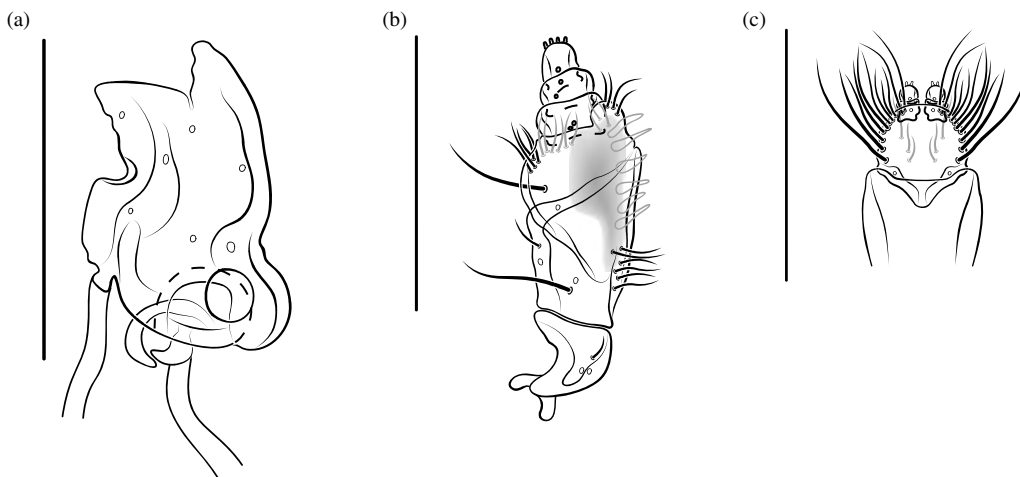


Fig. 5. *Acalyptus carpini*. A, Left mandible; B, right maxilla; C, labium.

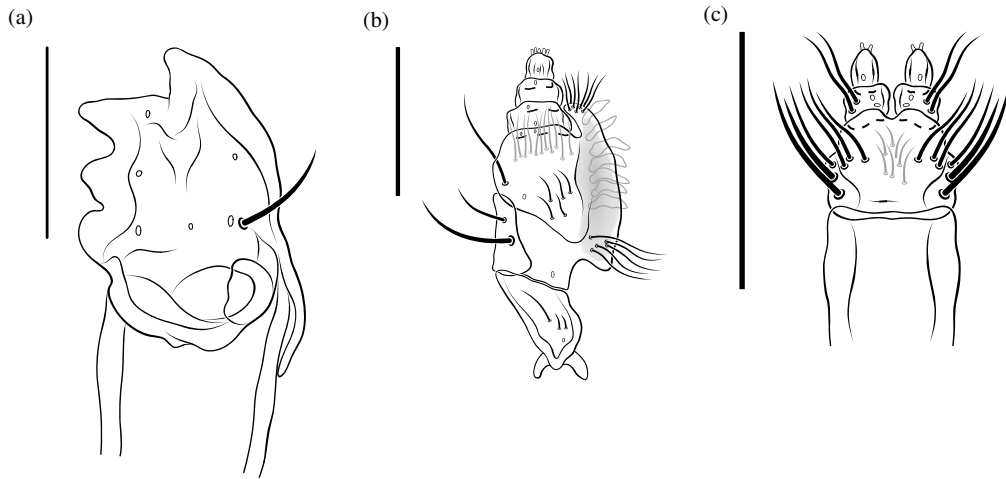


Fig. 6. *Amorrhoidea lata*. A, Left mandible; B, right maxilla; C, labium.

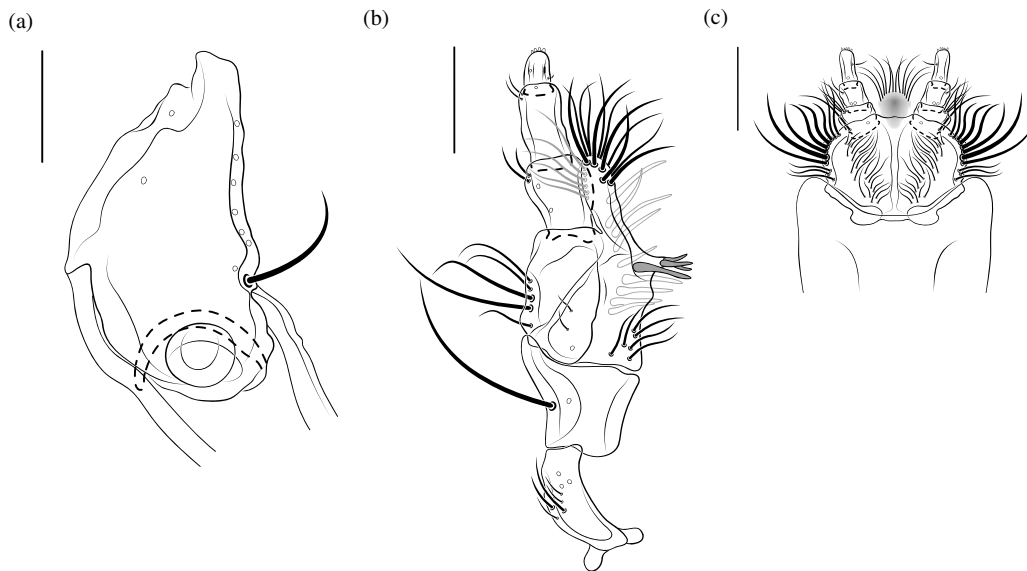


Fig. 7. *Anchylorhynchus variabilis*. A, Left mandible; B, right maxilla; C, labium.

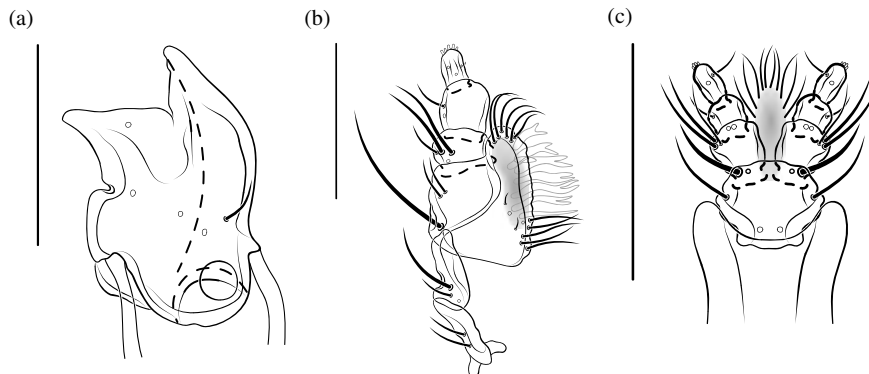


Fig. 8. *Andranthobius argentinensis*. A, Left mandible; B, right maxilla; C, labium.

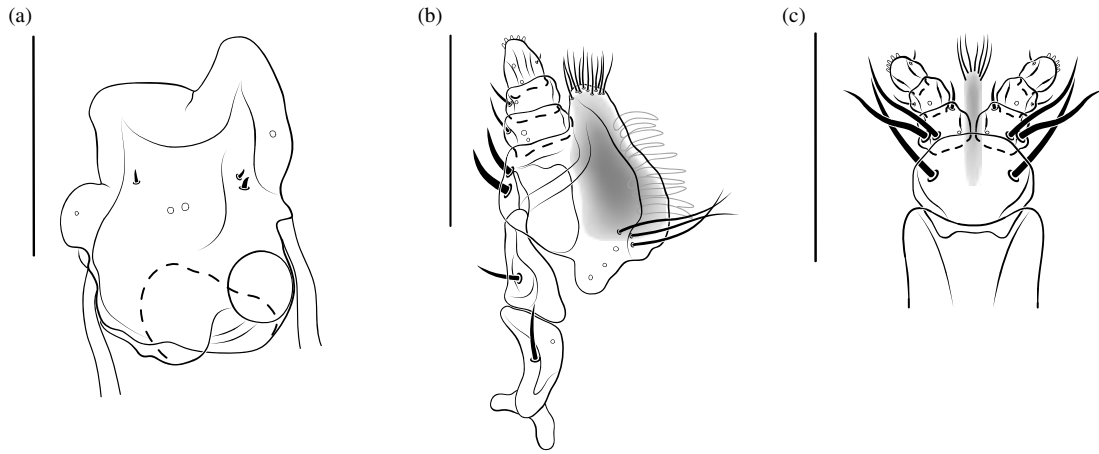


Fig. 9. *Araucarietus viridans*. A, Left mandible; B, right maxilla; C, labium.

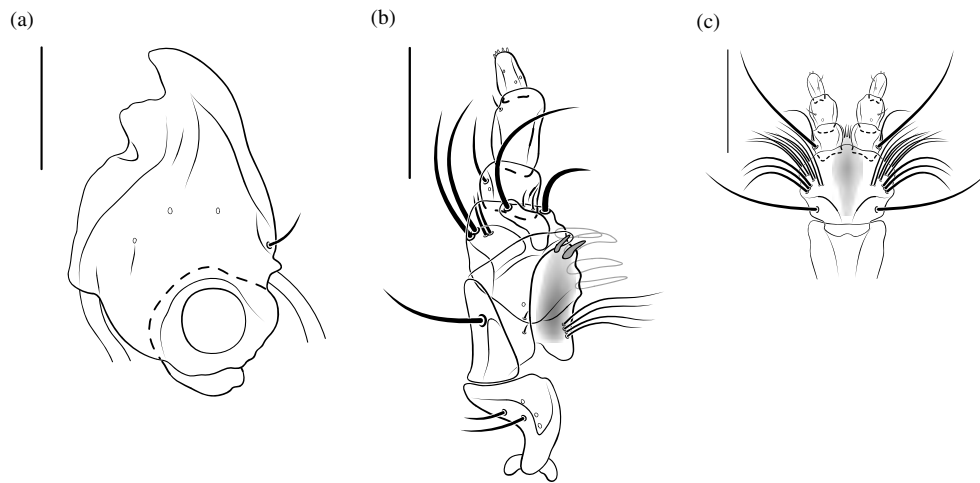


Fig. 10. *Celetes binotatus*. A, Left mandible; B, right maxilla; C, labium.

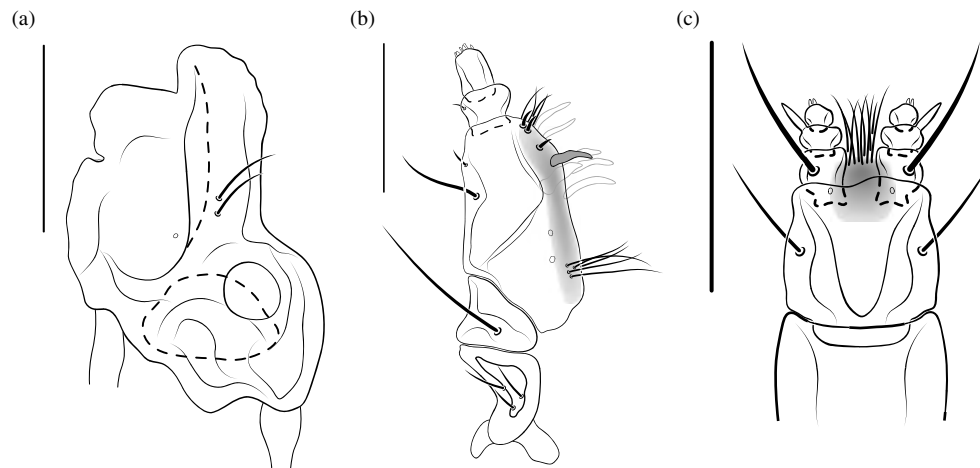


Fig. 11. *Cotithene globulicollis*. A, Left mandible; B, right maxilla; C, labium.

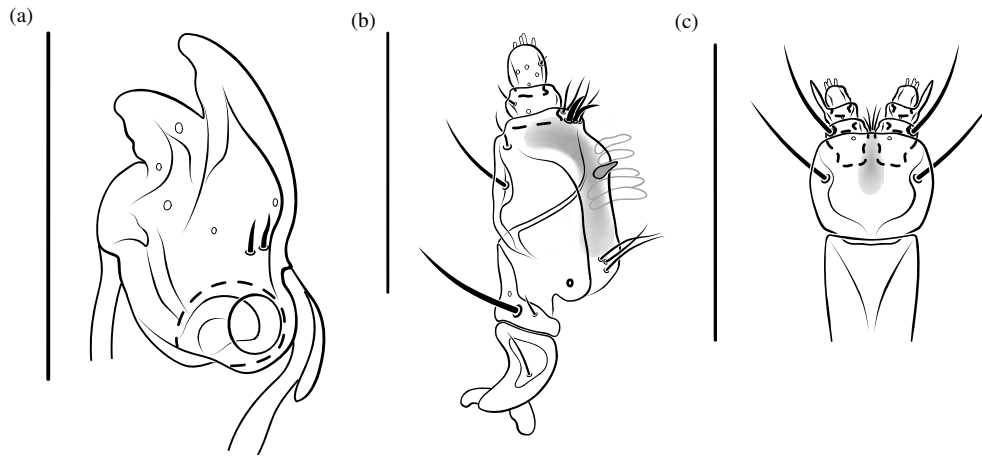


Fig. 12. *Cyclanthura laticola*. A, Left mandible; B, right maxilla; C, labium.

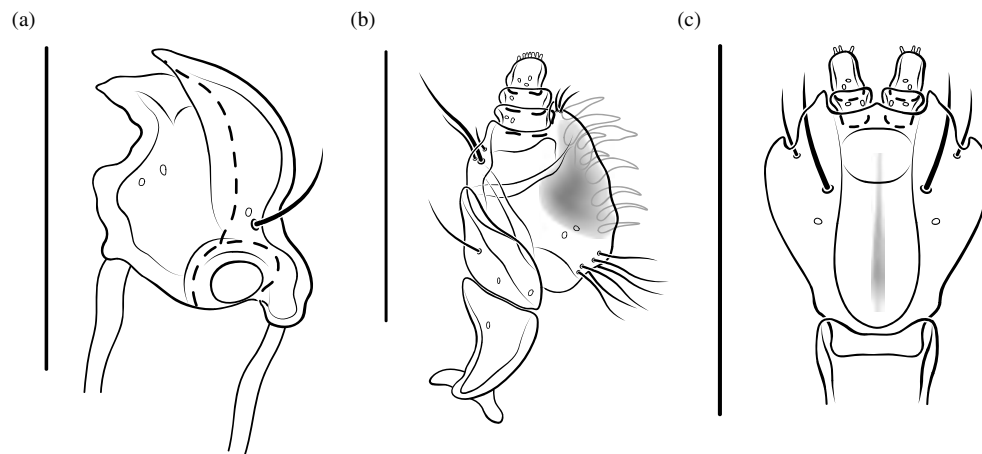


Fig. 13. *Derelomini* gen. 1. sp. 1. A, Left mandible; B, right maxilla; C, labium.

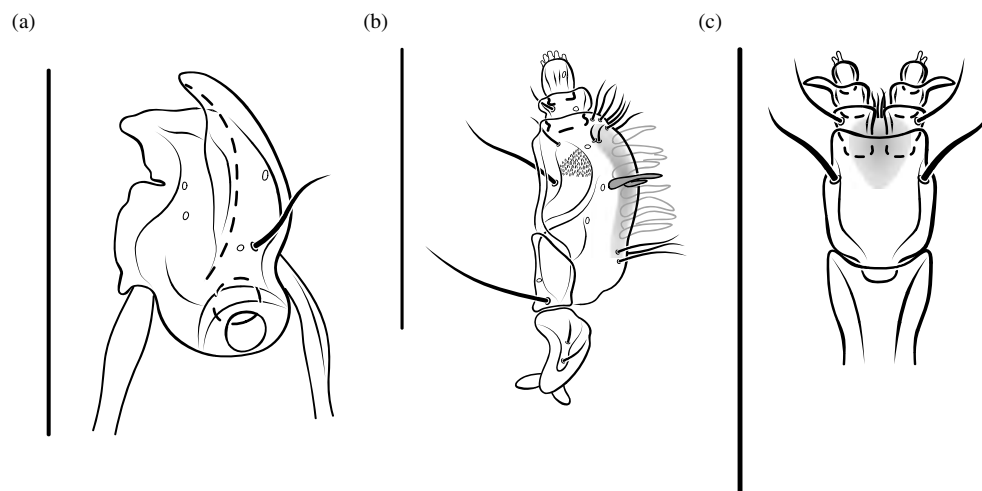


Fig. 14. *Derelomini* gen. 2. sp. 1. A, Left mandible; B, right maxilla; C, labium.

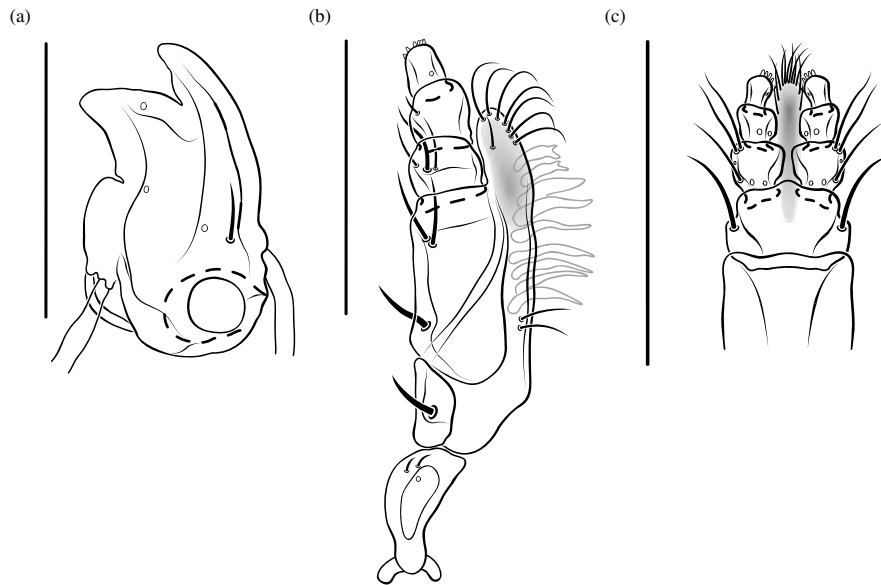


Fig. 15. *Derelominus piceus*. A, Left mandible; B, right maxilla; C, labium.

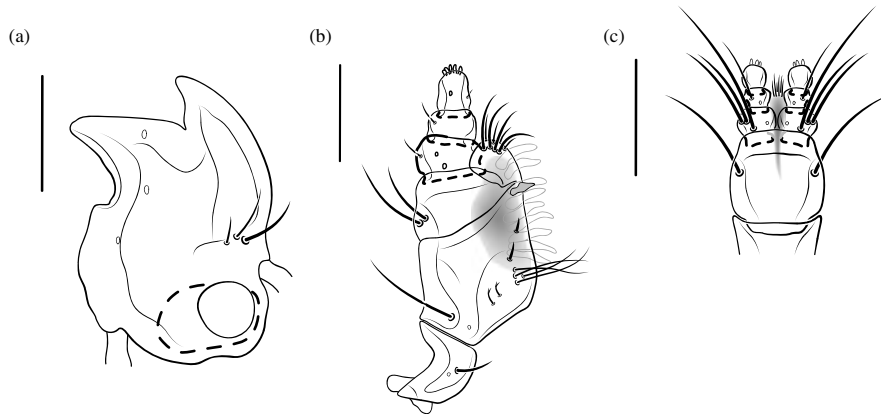


Fig. 16. *Derelomus chamaeropsis*. A, Left mandible; B, right maxilla; C, labium.

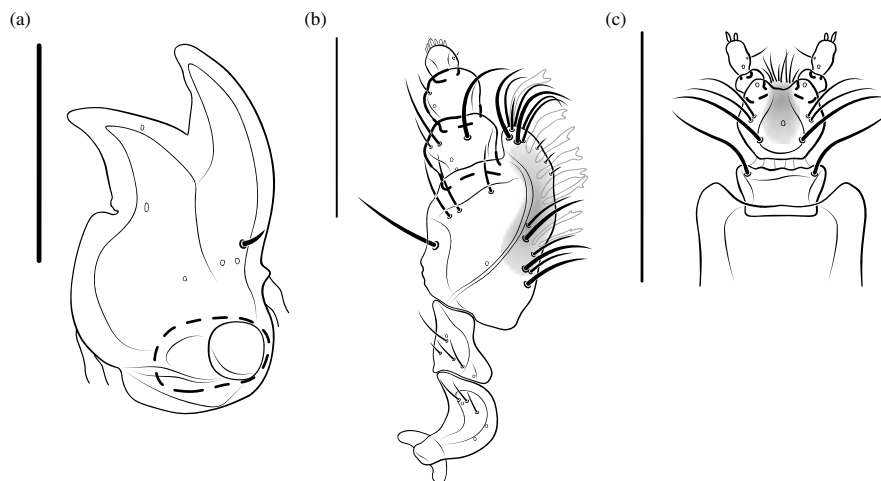


Fig. 17. *Diplothemiobius sternicornis*. A, Left mandible; B, right maxilla; C, labium.

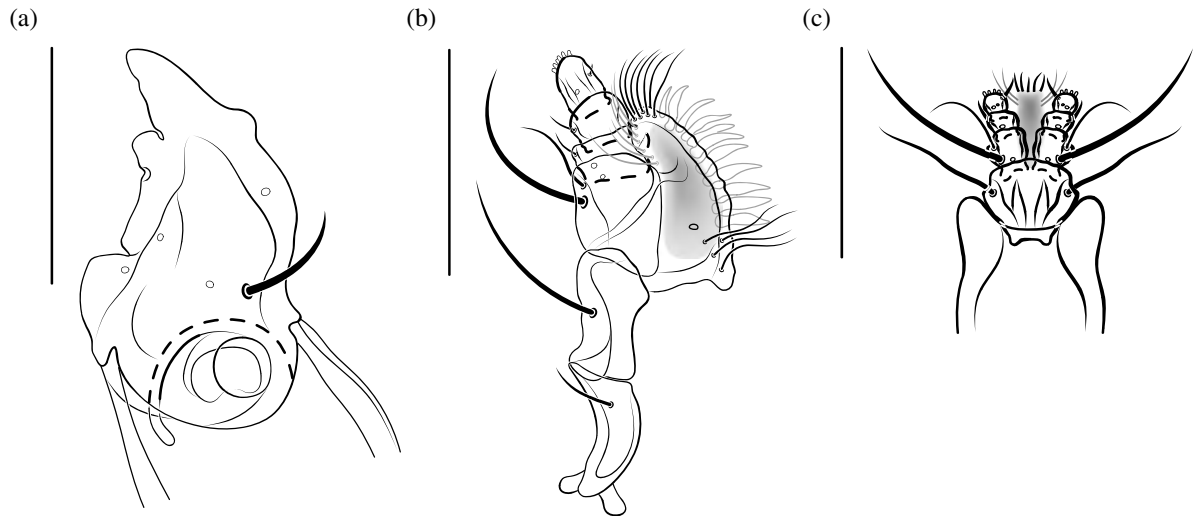


Fig. 18. *Eisingius chusqueae*. A, Left mandible; B, right maxilla; C, labium.

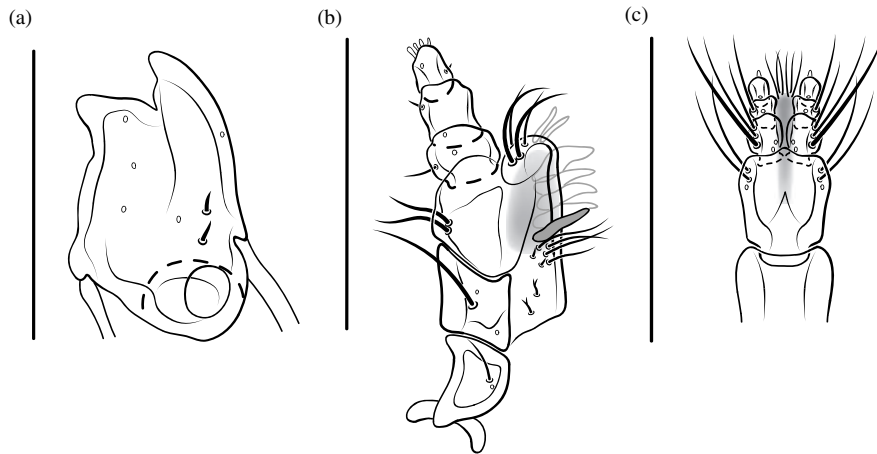


Fig. 19. *Elaeidobius subvittatus*. A, Left mandible; B, right maxilla; C, labium.

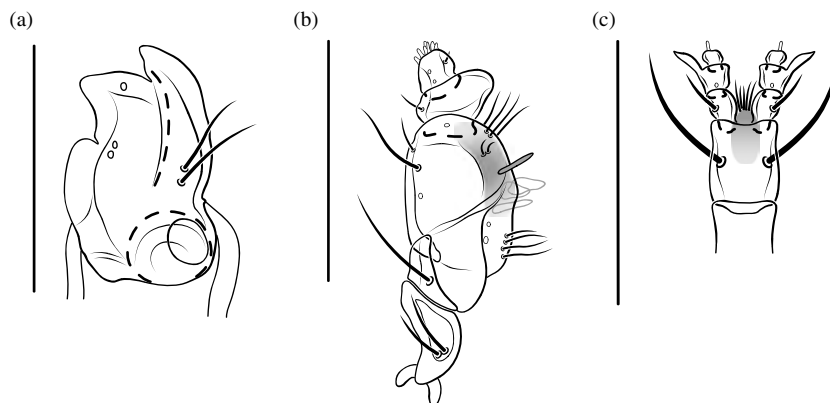


Fig. 20. *Ganglionus undulatus*. A, Left mandible; B, right maxilla; C, labium.

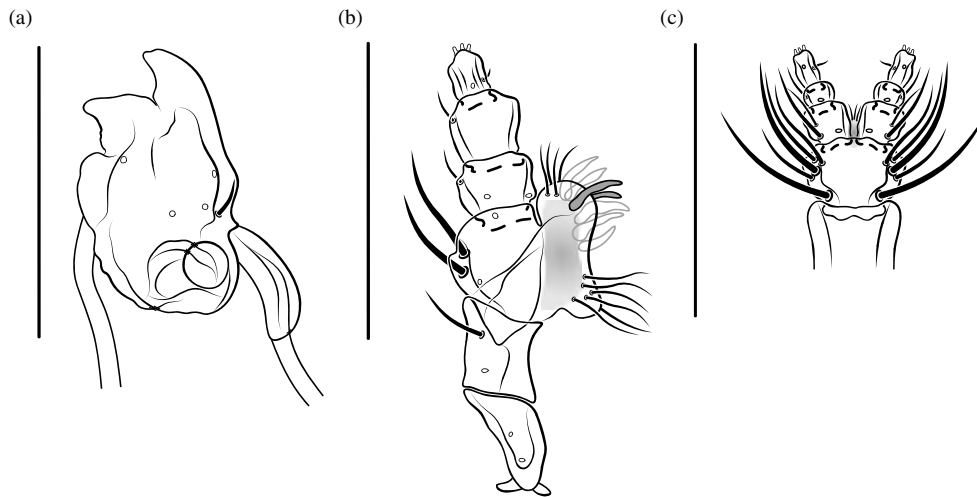


Fig. 21. *Grasiidius sp. 1.* A, Left mandible; B, right maxilla; C, labium.

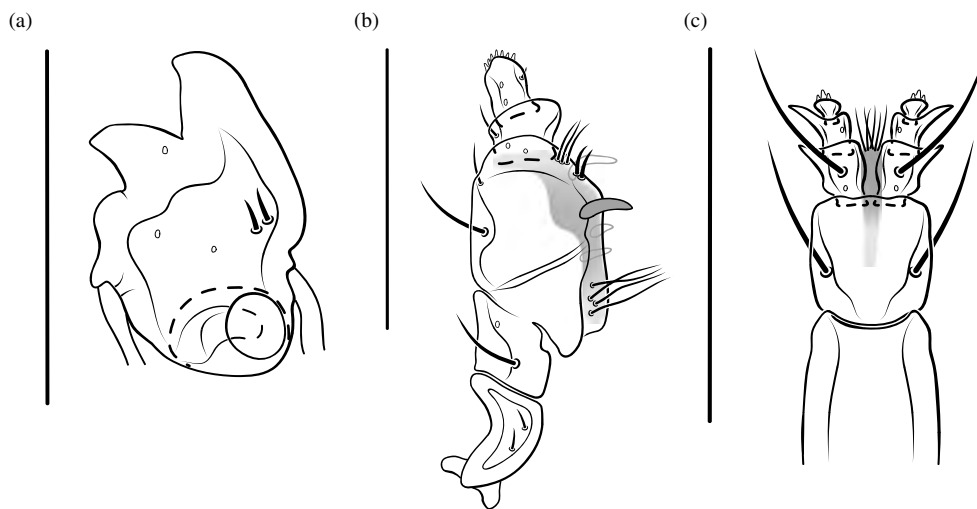


Fig. 22. *Hypoleschus atratus*. A, Left mandible; B, right maxilla; C, labium.

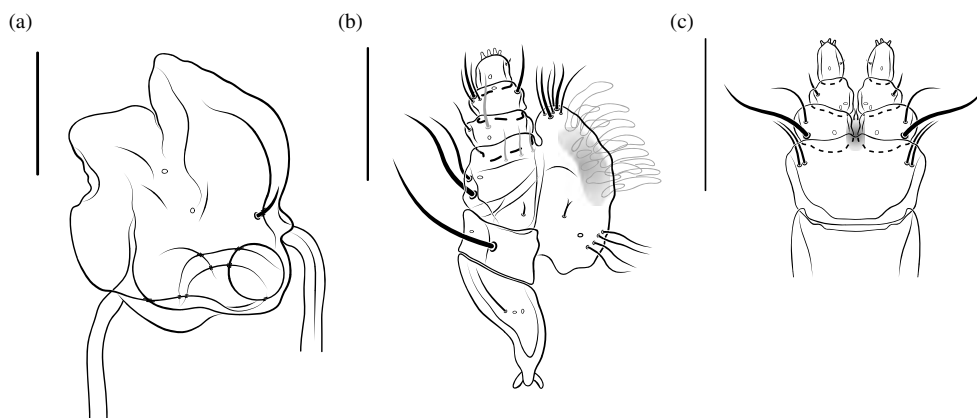


Fig. 23. *Juanorhinus ruficeps*. A, Left mandible; B, right maxilla; C, labium.

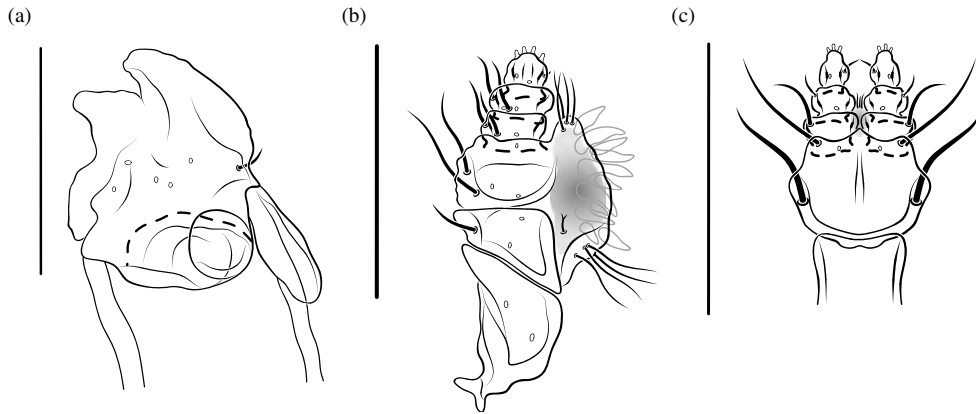


Fig. 24. *Nanus uniformis*. A, Left mandible; B, right maxilla; C, labium.

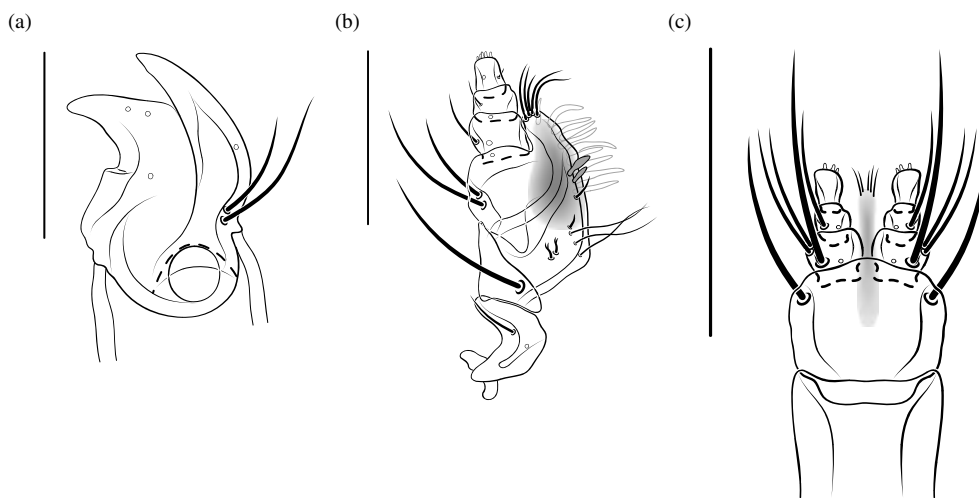


Fig. 25. *Neoderelomus piriformis*. A, Left mandible; B, right maxilla; C, labium.

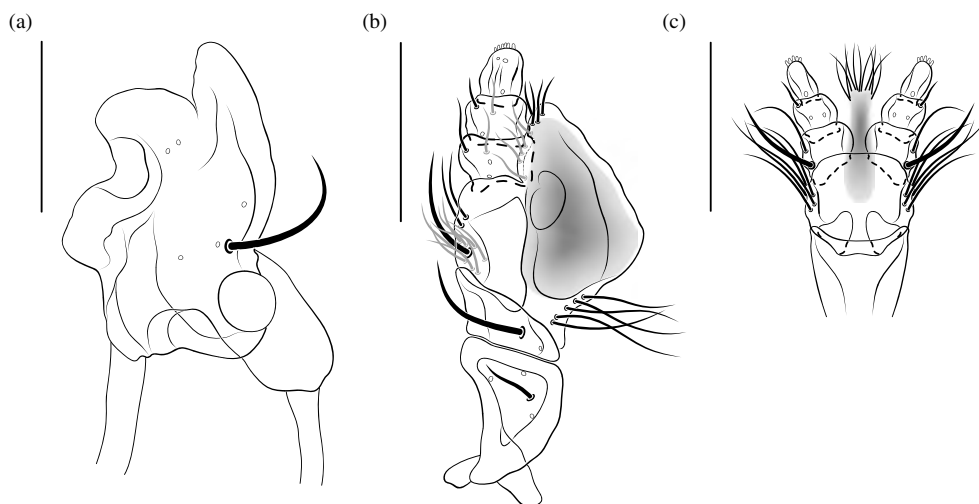


Fig. 26. *Neopsilorhinus variegatus*. A, Left mandible; B, right maxilla; C, labium.

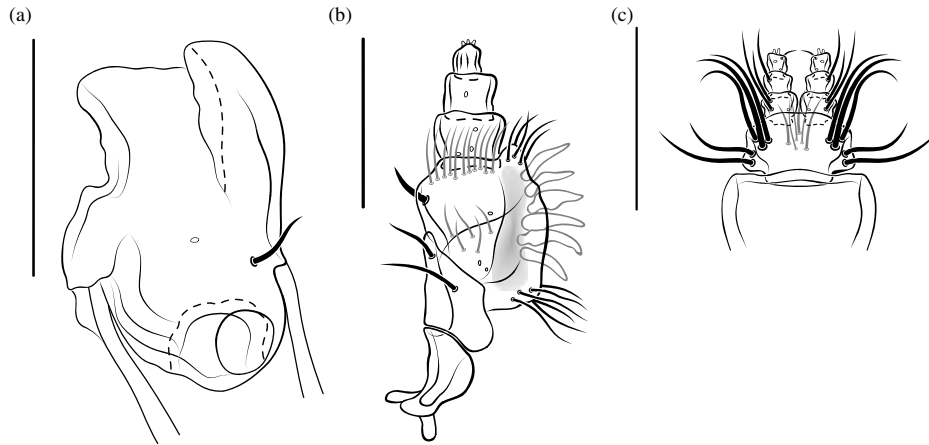


Fig. 27. *Nodocnemus* sp. 1. A, Left mandible; B, right maxilla; C, labium.

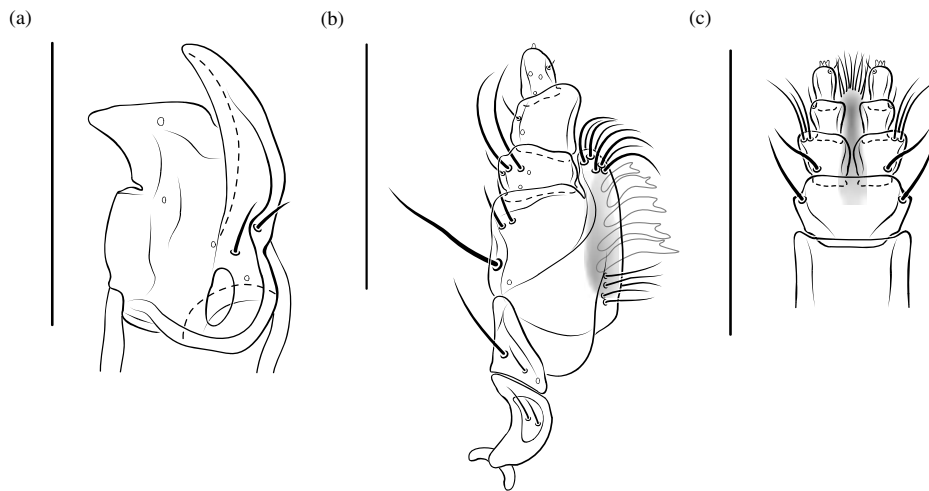


Fig. 28. *Notolomus basalis*. A, Left mandible; B, right maxilla; C, labium.

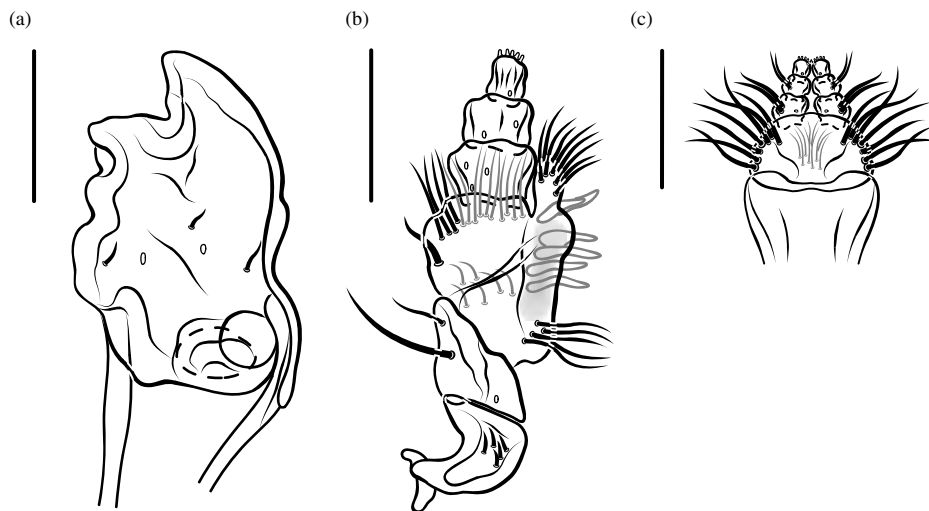


Fig. 29. *Parimera variabilis*. A, Left mandible; B, right maxilla; C, labium.

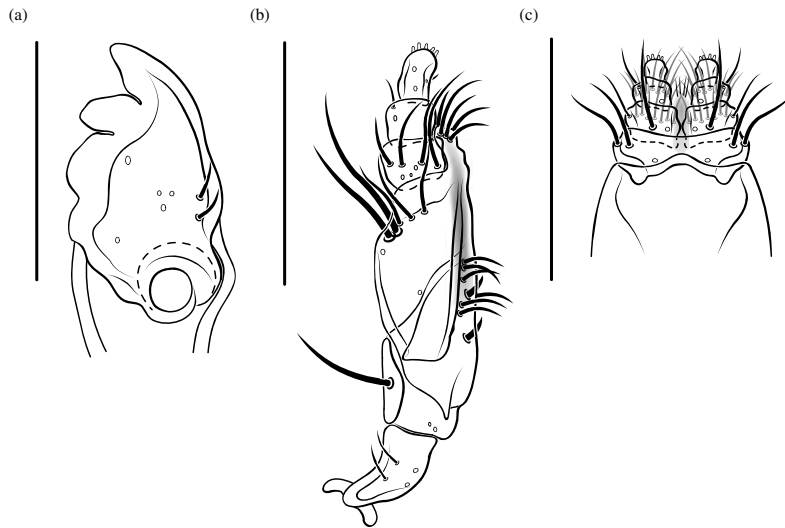


Fig. 30. *Pedetinus flavipes*. A, Left mandible; B, right maxilla; C, labium.

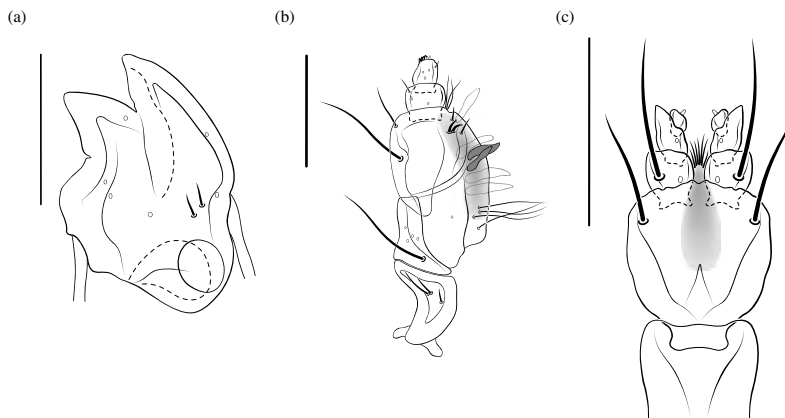


Fig. 31. *Perelleschus carludovicae*. A, Left mandible; B, right maxilla; C, labium.

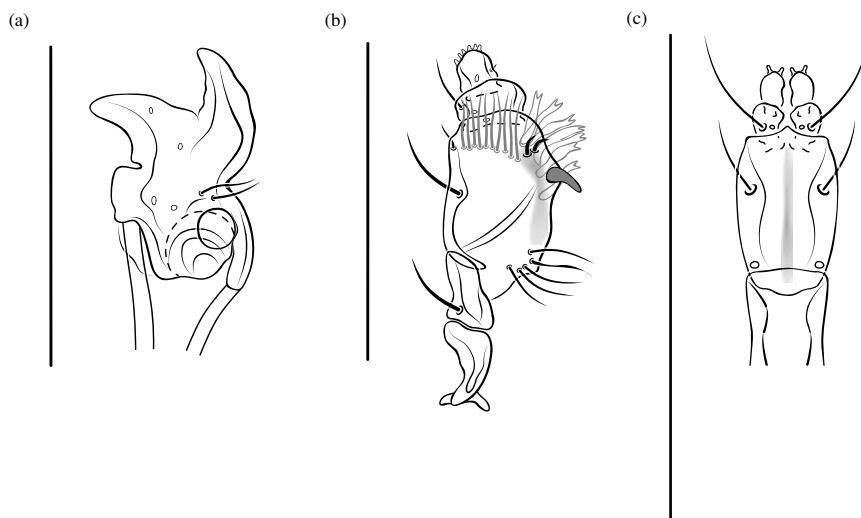


Fig. 32. *Phyllotrox megalops*. A, Left mandible; B, right maxilla; C, labium.

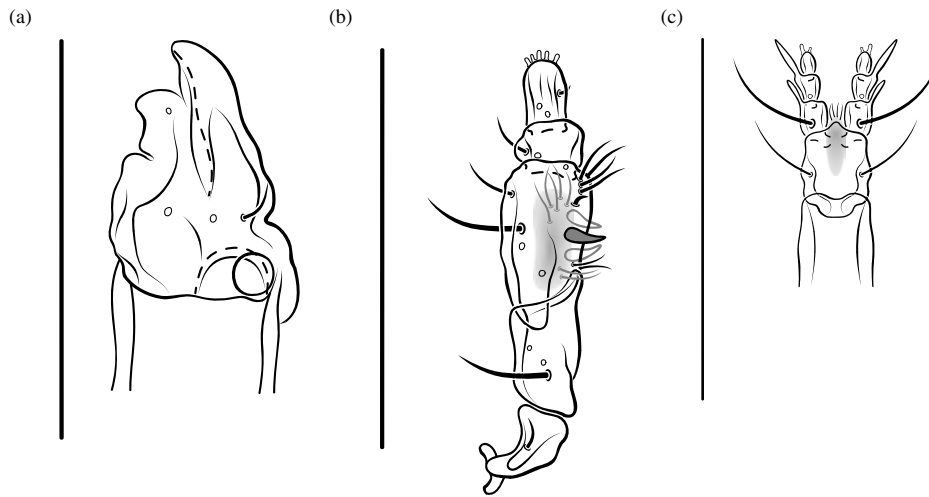


Fig. 33. *Phyllotrox semirufus*. A, Left mandible; B, right maxilla; C, labium.

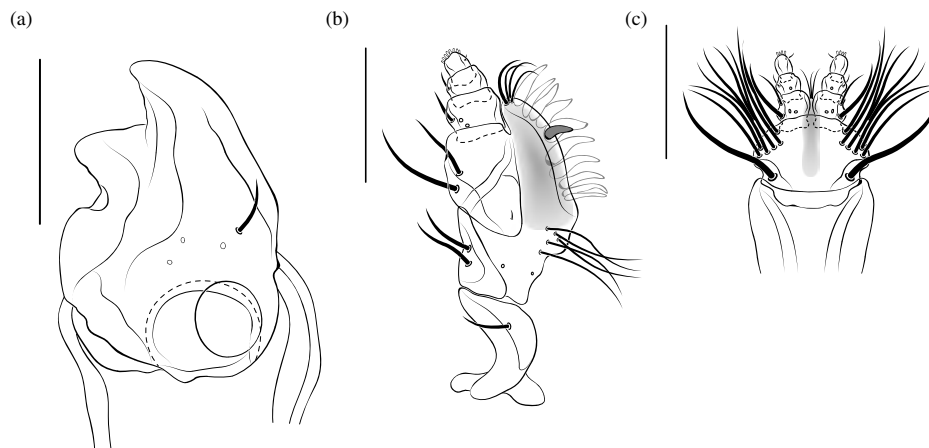


Fig. 34. *Phytotribus unicolor*. A, Left mandible; B, right maxilla; C, labium.

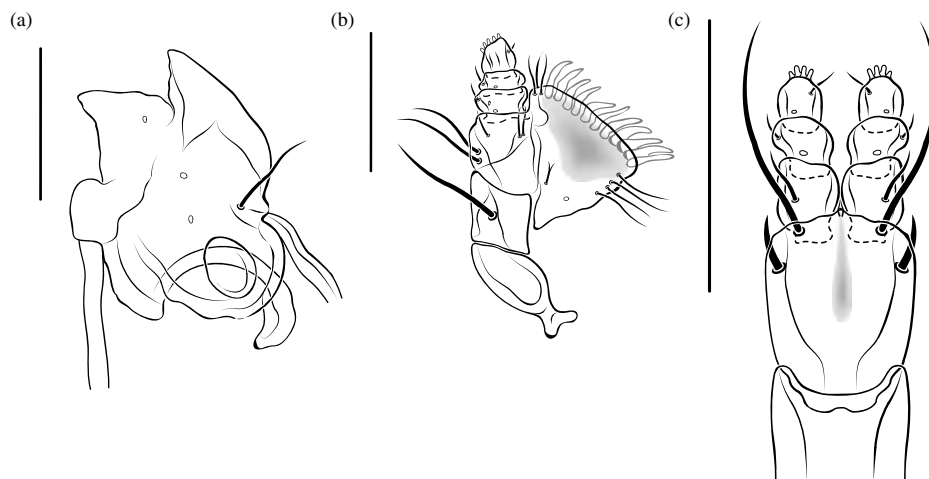


Fig. 35. *Platynanus sericatus*. A, Left mandible; B, right maxilla; C, labium.

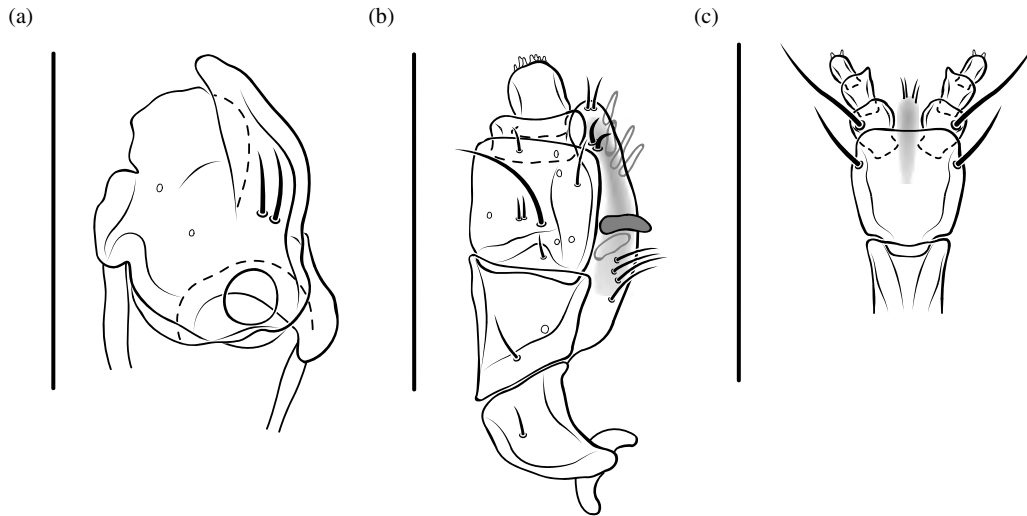


Fig. 36. *Pseudoderelomus baridiiformis*. A, Left mandible; B, right maxilla; C, labium.

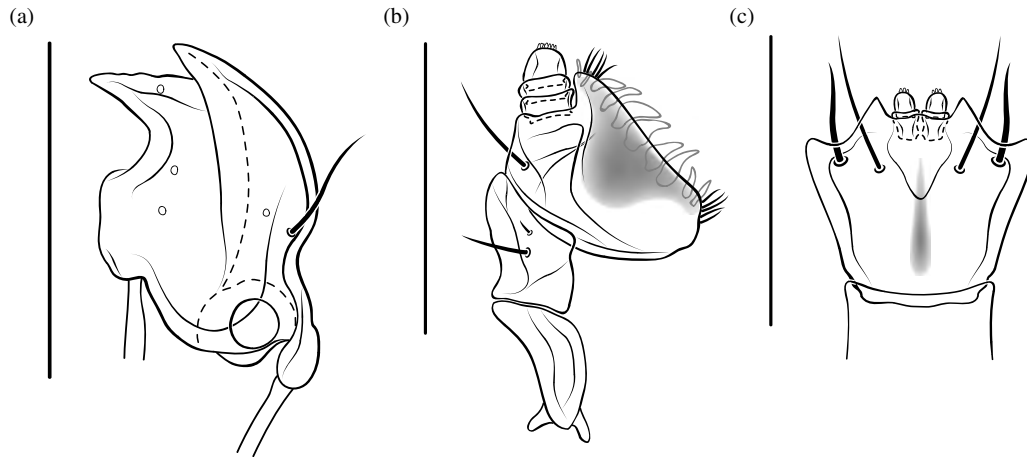


Fig. 37. *Staminodeus vectoris*. A, Left mandible; B, right maxilla; C, labium.

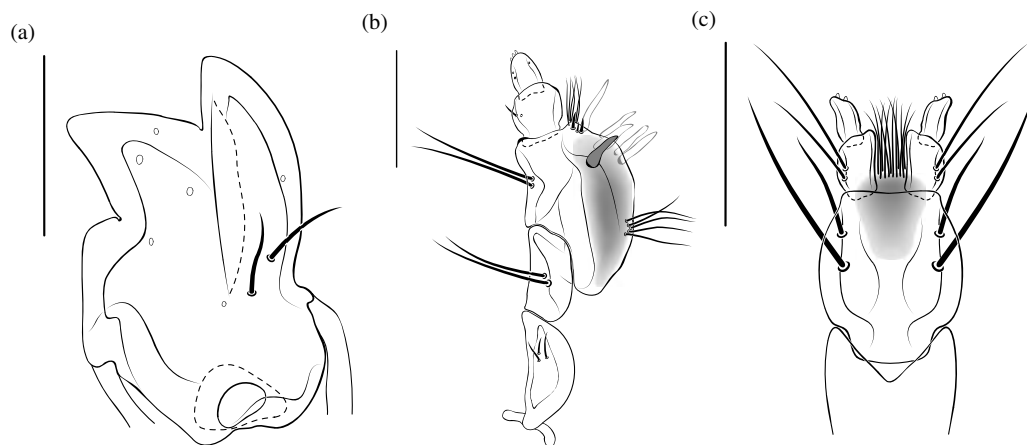


Fig. 38. *Systemotelus carludovicae*. A, Left mandible; B, right maxilla; C, labium.

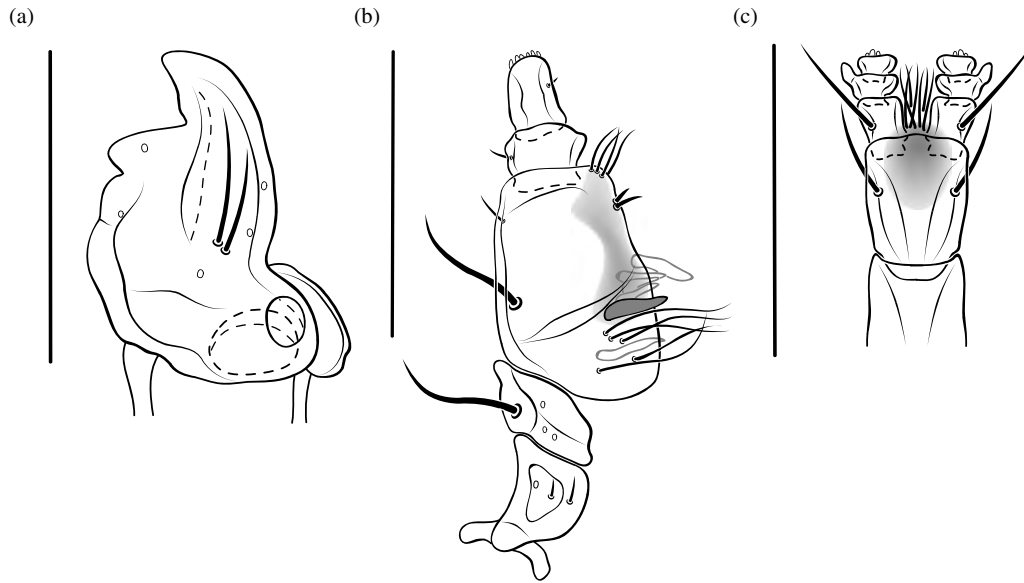


Fig. 39. *Terioltes circumdatatus*. A, Left mandible; B, right maxilla; C, labium.

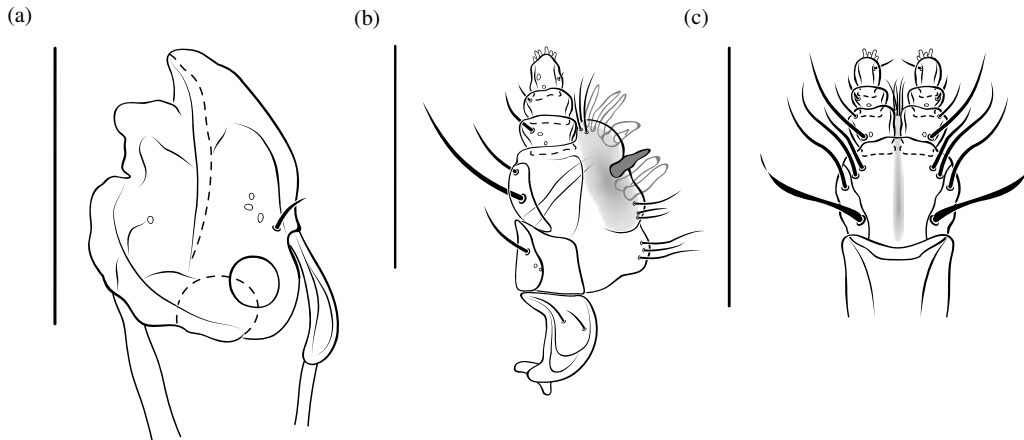


Fig. 40. *Terires pilosus*. A, Left mandible; B, right maxilla; C, labium.

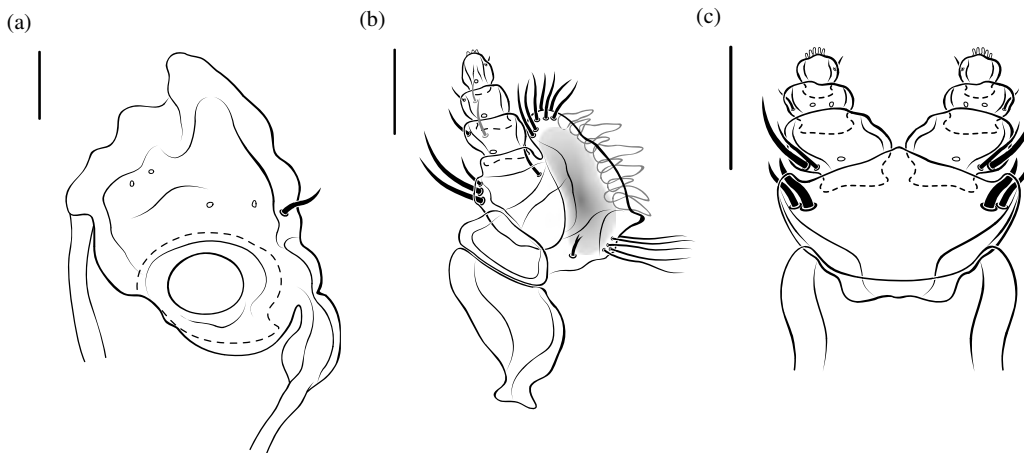


Fig. 41. *Trypetes politus*. A, Left mandible; B, right maxilla; C, labium.

32. *Prementum*, lateral margins (*setation*), ventral view: (0) each lateral margin subcentrally with multiple (two to ten, rarely more) large, variously arranged setae (e.g. Figs. 26C, 34C); (1) with only one large, subcentrally positioned seta (e.g. Figs. 9C, 15C); (2) with two large, closely associated setae, presumably resulting from a secondary duplication (Fig. 38C).
Coded as additive. Inapplicable in *Tadius* and *Erodiscus* (see comments on character 31). State (1) is convergently present in the *Nanus* Schoenherr (1844: 89)–*Eisingius* clade, in *Derelomus*, including *N. piriformis* (Hoffmann, 1938a), and in the *Derelominus*–*Systemotelus* clade. State (2) is a synapomorphy for *S. carludovicae*–*S. costaricensis*. As in character 19, the additive coding implies that state (2) within *Systemotelus* is phylogenetically less distant to state (1) than it is to state (0) in, e.g. *Trypetes* (Fig. 41C) and *Elaeidobius* Kuschel (1952; Fig. 19C). The latter taxa also have only two large setae on each lateral margin of the prementum. These are most-parsimoniously interpreted as the result of a reduction, not a replication as in *Systemotelus*. An alternative coding scheme would not affect the overall topology of the analysis. Unambiguous optimization (CI = 50; RI = 95).
33. *Prementum*, central region (*setation*), ventral view: (0) rows of setae absent (e.g. Fig. 21C); (1) with multiple interlaced rows of many relatively small, densely arranged setae extending obliquely from central to lateral region of prementum (Fig. 7C).
Apomorphy for *Anchylorhynchus*. Unambiguous optimization (CI = 100; RI = 100).
34. *Prementum*, apical margin (*shape*), ventral view: (0) apical margin variously slightly emarginate to rotundate, to irregular (e.g. Figs. 17C, 29C); (1) apical margin of prementum on each side, at a similar distance from centre and each lateral edge, with one distinct, triangular, acute projection extending beyond labial palpomere I (Figs. 13C, 37C; see also Franz, 2001).
Apomorphy for the *Derelomini* gen. 1–*Staminodeus* clade. Unambiguous optimization (CI = 100; RI = 100).
35. *Prementum*, anterior tendon (*'ligula'*; see also Ting, 1936: 103; Morimoto & Kojima, 2003: 141), dorsal view: (0) anterior tendon apically partly membranous, variously extending from apical margin of prementum (e.g. Figs. 4C, 16C) to labial palpomere III (e.g. Figs. 15C, 19C), with more or less numerous, sparsely or densely arranged, apically projecting setae; (1) anterior tendon strongly sclerotized throughout, narrow (resembling a triangular lamina in lateral view), not extending beyond apical margin of prementum, either with sparsely arranged setae positioned near central region of prementum (e.g. Fig. 27C) or lacking setae (e.g. Fig. 37C).
Apomorphy for the *Acalyptus*–*Staminodeus* clade. The taxa assigned to state (0) vary considerably with respect to the length and setation of the anterior tendon. At more inclusive levels, however, this variation almost turns into a continuum and thus becomes difficult to encode cladistically. Unambiguous optimization (CI = 100; RI = 100).
36. *Prementum*, anterior tendon (*setation*), dorsal view: (1) apical setae sparse to moderately dense, density increasing gradually towards apex of anterior tendon; (1) apical setae (very) densely arranged, density abruptly increasing (i.e. with a distinct, 'triangular' separation line) near apical half of anterior tendon. Inapplicable in taxa in which the anterior tendon does not extend beyond the apical margin of the prementum (see character 35). Apomorphy for the *Terioltes*–*Systemotelus* clade. Most distinctive in *Perelleschus* and *Systemotelus*, less so in certain species of *Cyclanthura*, e.g. *C. laticola* Franz (2003a) and *C. striata* Franz (2003a). Unambiguous optimization (CI = 100; RI = 100).
37. *Labial palps*, number of palpomeres, ventral view: (0) three-segmented (e.g. Figs. 4C, 12C); (1) two-segmented (e.g. Figs. 5C, 37C).
Convergently present in the *Omoides*–*Udeus* clade, the *Tychius*–*Erodiscus* clade, the *Acalyptus*–*Amorphoidea* de Motschulsky (1858) clade, the *Derelomini* gen. 1–*Staminodeus* clade, in *P. megalops*, and in *Systemotelus*. Under the preferred slow optimization, which does not assume a reversal in the *Nodocnemus*–*Parimera* clade, the cladogram proposes six independent reductions in the number of labial palpomeres. The oldest Curculionioidea lineages appear to have three-segmented labial palpi (see Ting, 1936: 103; Morimoto & Kojima, 2003: 141). The labial palpomeres in *Diplothemiobius* are congruently assigned to state (0). This implies that each palpomere I has become distinctly expanded and centrally fused (Fig. 17C). An alternative interpretation is that the prementum has undergone a transverse separation. Yet the setal pattern of the structure attached distad of the prementum in *Diplothemiobius* is similar to that of palpomere I in the closely related *Derelominus* Champion (1902; Fig. 15C; see also character 41), which supports only the current assignment. Slow optimization preferred (compare Figs. 2 and 3; CI = 16; RI = 68).
38. *Labial palpomere I*, shape (*apical region*), ventral view: (0) apically variously subrectate to (irregularly) rotundate, projection absent (e.g. Figs. 20C, 36C); (1) outer apical edge of labial palpomere I slightly to distinctly projected (Figs. 22C, 33C), shape and extension of projection variable, ranging from short and apically rotundate – e.g. *P. nubifer* LeConte, 1876 (in LeConte & Horn, 1876) and *P. sejunctus* (Fall, 1913) – to narrowly elongate, acute, and extending beyond labial palpomere II, e.g. *P. quadricollis* Fall (1907; in Fall & Cockerell, 1907) and *P. rufipes* Faust (1894).
Apomorphy for the *P. rufipes*–*P. suturalis* clade. Unambiguous optimization (CI = 100; RI = 100).

39. *Labial palpomere I, central region (setation), ventral view*: (0) with one (very) large seta positioned centrally (occasionally more basal, and/or close to outer margin) on labial palpomere I, typically extending along or (significantly) beyond apical palpomeres (e.g. Figs. 15C, 27C); (1) labial palpomere I lacking large setae (Figs. 13C, 37C).

Apomorphy for the Derelomini gen. 1–*Staminodeus* clade. Unambiguous optimization (CI = 100; RI = 100).

40. *Labial palpomere I, apical region (setation), ventral view*: (0) with one to three(eight) relatively large, closely associated setae present on apicolateral edge of outer margin of labial palpomere I (e.g. Figs. 24C, 40C; see also character 41); (1) without apicolateral setae (e.g. Figs. 14C, 32C).

Convergently 'present' in the *Tychius*–*Erodiscus* clade, in the Derelomini gen. 1–*Staminodeus* clade, and in the *Pseudoderelomus*–*Systemotelus* clade. Unambiguous optimization (CI = 33; RI = 96).

41. *Labial palpomere I, apical region (setation), ventral view*: (0) with one (relatively) large seta present on apicolateral edge of outer margin of labial palpomere I (e.g. Figs. 18C, 34C); (1) with two to three closely associated setae (e.g. Figs. 16C, 28C); (2) (typically) with more than three (and usually less than eight) closely aligned setae (Fig. 7C).

Coded as nonadditive, under the assumption that states (1) and (2) represent independent transformations. Inapplicable in taxa in which apicolateral setae are absent (see character 40). State (1) is convergently present in the *Elaeidobius*–*Derelominus* clade (including *N. piriformis*) and in the *Derelominus*–*Andranthobius* clade (including *D. mariahelena*). State (2) is an apomorphy for *Anchylorhynchus*; smaller species such as *A. tricarinatus* Vaurie (1954) tend to have less apicolateral setae on the labial palpomere I than larger ones like *A. aegrotus* Fåhræus (1843; in Schoenherr, 1843). Slow optimization preferred (compare Figs. 2 and 3; CI = 66; RI = 95).

42. *Labial palpomeres I and II, central region (setation), ventral view*: (0) transverse row of setae absent (e.g. Fig. 4C); (1) each labial palpomere with one (*Pedetinus*) to multiple (*Omoides* and *Udeus*) rows of distinct, relatively large, transversely aligned setae (Fig. 30C).

Apomorphy for the *Omoides*–*Pedetinus* clade. Unambiguous optimization (CI = 100; RI = 100).

43. *Labial palpomere II, shape (apical region), ventral view*: (0) apically variously subrectate to (irregularly) rotundate, projection absent (e.g. Figs. 8C, 32C); (1) outer apical edge of labial palpomere II distinctly projected, with relatively narrow, acuminate projection extending (at an oblique angle) along or (typically) beyond labial palpomere III (e.g. Figs. 11C, 33C); (2) apical margin of labial palpomere II distinctly oblique, outer apical edge significantly projected (e.g. Fig. 31C).

Coded as additive. State (1) is an apomorphy for the *D. tatiana*–*Systemotelus* clade (see also Franz, 2003a, 2004); whereas state (2) is an apomorphy – presumed to represent a secondary transformation – for the *Perelleschus*–*Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).

44. *Labial palpomere II, apical region (setation), ventral view*: (0) with one small (to relatively large) seta present on apicolateral edge of outer margin of labial palpomere II (e.g. Figs. 10C, 28C); (1) apicolateral seta absent (e.g. Figs. 12C, 22C).

In applicable in taxa that have only two labial palpomeres (see character 27), assuming that labial palpomere II is absent there. Convergently 'present' in the *Derelominus*–*Diplothemiochus* clade and in the *Pseudoderelomus*–*Systemotelus* clade. Slow optimization preferred (compare Figs. 2 and 3; CI = 50; RI = 97).

45. *Apical labial palpomere (either palpomere II or III, see character 37), central region (setation), ventral view*: (0) small seta absent (e.g. Figs. 25C, 30C); (1) with one (relatively) small seta present and positioned centrally (to apically) along inner margin of apical labial palpomere (e.g. Figs. 7C, 21C).

Convergently present in the *Juanorhinus*–*Eisingius* clade, the *Anchylorhynchus*–*Phytotribus* clade, the *Nodocnemus*–*Parimera* clade, and in the *Derelominus*–*Andranthobius* clade (including *D. mariahelena*). Unambiguous optimization (CI = 25; RI = 91).

Rostrum

46. *Rostrum, dorsal view; male*: (0) central impression absent (Fig. 51A); (1) centrally with elongate impression (or sulcus) extending along entire length of rostrum, and produced by slightly elevated (although not carinate) dorsolateral margins of rostrum (Fig. 71A; see also Champion, 1902: 147).

Apomorphy for *Terioltes* Champion (1903). Unambiguous optimization (CI = 100; RI = 100).

47. *Rostrum, dorsal view*: (0) central and lateral carinae absent; (1) with multiple (typically five, yet ranging from two to seven; see O'Brien, 1981: 501), centrally to laterally positioned, subparallel carinae extending from base to subapical region of rostrum (Figs. 45A, 59A); (2) similar to state (1) yet carinae in females less apically extended, not extending beyond insertion of antennae (to entirely absent, e.g. in *C. pallidus*), thus apical region of rostrum indistinct (Fig. 67A).

Coded as additive. State (1) is convergently present in *Neopsilorhinus*, in *Eisingius*, and in the *Elaeidobius*–*Phytotribus* clade, with an apparent reversal in *Terires*. State (2) is a synapomorphy for *Celetes* and *Phytotribus*, assuming a secondary transformation in females. Additional characteristics specifying the number of carinae were considered uninformative across species (see also Bondar, 1943; Vaurie, 1954; O'Brien, 1981). The

- obscure carinulae or elongate elevations in *Juanorhinus* Aurivillius (1931) and in *Nanus* Schoenherr (1844) were not included under state (1). Unambiguous optimization (CI = 40; RI = 92).
48. *Rostrum, dorsal view; male*: (0) carinae absent or contiguous, tubercles absent (e.g. Fig. 67A); (1) with dorsolateral carinae irregularly interrupted and (more regularly) expanded into (very) small, elongate tubercles, present along entire length of rostrum (Fig. 50A). Apomorphy for the *C. marizae*–*C. tarsalis* clade. Less distinctive in males of the latter species. Unambiguous optimization (CI = 100; RI = 100).
49. *Rostrum, dorsal view*: (0) combination of lateral carinae and central smaller carinae; (1) centrally with two small (to almost indistinct), basally connected and apically slightly diverging carinae (extending only to apical third of rostrum), and laterally with two larger, subparallel carinae, each extending from internal margin of eye to subapex of rostrum (ending along dorsolateral margin, thus also slightly diverging; Fig. 69A).
Apomorphy for *Staminodeus* (see also Franz, 2001). Differing from the carinate rostral projections in other taxa (see characters 46, 50) through the combination of two different kinds of carina, their slight apical divergence (beginning centrally and ending laterally), and similar presence in males and females. Unambiguous optimization (CI = 100; RI = 100).
50. *Rostrum, dorsolateral margins; male*: (0) carinae absent; (1) with one distinct, slightly elevated carina extending along entire length of rostrum (Fig. 51A), producing a rectangular (instead of subcircular) impression of the rostrum in cross-section.
Apomorphy for *Cotithene* Voss (1940: 5), and differing from character 49 by the exact dorsolateral position, degree of projection, and complete absence in females. Also differing from the noncarinate elevation along the dorsolateral margins of the rostrum in males of *Terioltes* (see character 46). Unambiguous optimization (CI = 100; RI = 100).
51. *Rostrum, dorsal region and dorsolateral margins; male*: (0) tubercles absent; (1) with numerous small, irregularly distributed tubercles along basal half of rostrum, and one small tubercle near inner margin of each eye (Fig. 56B).
Apomorphy for *Ganglionus* (see also Franz & O'Brien, 2001a). Unambiguous optimization (CI = 100; RI = 100).
52. *Rostrum, dorsolateral margins; male*: (0) tubercles absent near basal two-fifths; (1) with one distinct, laterally projecting tubercle along each margin, positioned near basal two-fifths of rostrum.
Apomorphy for a clade within *Ganglionus* (see Franz & O'Brien, 2001a). Unambiguous optimization (CI = 100; RI = 100).
53. *Rostrum, apical region, dorsal view; male*: (0) tubercles absent; (1) with one small, slightly arcuate-elongate, obliquely orientated tubercle along each apicolateral edge of rostrum (Fig. 71B).
Apomorphy for *Terioltes*. Unambiguous optimization (CI = 100; RI = 100).
54. *Rostrum, lateral view; male*: (0) breadth similar throughout or apically variously narrowed; (1) dorsally slightly broadened (tumescent) near central region, proximad of antennal insertion (Fig. 51A).
Apomorphy for *Cotithene*. The subapical region of the rostrum can be slightly broadened dorsally in larger males of *T. circumdatus* Champion (1903), although only distad of the antennal insertion. Unambiguous optimization (CI = 100; RI = 100).
55. *Rostrum, ventral view; male*: (0) carina absent; (1) with one carina, extending from central region to subapex of rostrum, apically gradually emerging and most visible near base of labium (Fig. 54A).
Apomorphy for *Eisingius* (see Kuschel, 1952: 277). The ventral carina is very apparent in males of *E. chusqueae* (Bondar, 1949; Fig. 54B), where it terminates apically in a triangular projection that could conceivably interact with the prosternal structures (see also character 78) in male reproductive conflicts. It is present only as a small subapical elevation in *E. araucariae* Kuschel (2000). Larger males of *A. viridans* Kuschel (1952) have two subparallel, irregularly nodulate elevations (or carinae) along the basal half of the rostrum, slightly removed from the ventral margin of the scrobe. These were not considered homologous with the ventral structures in *Eisingius*. Unambiguous optimization (CI = 100; RI = 100).
56. *Rostrum, subapical region, ventral view; male*: (0) tubercle absent; (1) with one small, centrally positioned tubercle, adjacent to base of labium (Fig. 55).
Apomorphy for *Elaeidobius*. The size of the tubercle appears to be allometrically correlated with that of individual males. Unambiguous optimization (CI = 100; RI = 100).
57. *Rostrum, position of antennal insertion, lateral view*: (0) central (i.e. ranging from apical fifth to basal third, e.g. Fig. 48A), antennal scape projecting to anterior margin of eye; (1) subapical (near apical sixth to eighth, Fig. 45A); (2) subbasal (near basal quarter to sixth, Fig. 63A), antennal to posterior margin of eye.
Coded as nonadditive. State (1) is an apomorphy for *Anchylorhynchus* (e.g. Vaurie, 1954: 9). Other taxa such as *Derelomus* or *Neopsilorhinus* also have apically inserted antennae (Fig. 59A), although the insertions are distinctly more basal in females (Fig. 53A). They display a kind of sexual dimorphism that is absent in *Anchylorhynchus*. State (2) is an apomorphy for *Pedetinus* (see Champion, 1903: 200). The plesiomorphic state (0) really circumscribes a range of various positions of the antennal insertion that can be used to recognize individual taxa. If more clades are considered, this variation becomes difficult to encode cladistically. Unambiguous optimization (CI = 100; RI = 100).
58. *Rostrum, position of scrobe, lateral view*: (0) exclusively or predominantly extending along lateral side of

rostrum (e.g. Fig. 66A); (1) predominantly extending along ventral side of rostrum (Fig. 73A).

Synapomorphy for *Omoides* and *Udeus* (see also Kuschel, 1952: 263–269). Other taxa included in the analysis also have the scrobe beginning laterally at the apex and ending ventrally at the base (e.g. *Anchylorhynchus*, *Eisingius*, *Phytotribus*, and *Tychius* Germar, 1817). There it invariably displays a distinct carina along its dorsal margin, positioned laterally on the rostrum throughout the length of the scrobe. In *Omoides* and *Udeus* the rostrum is continuously convex, from the dorsal to the ventral side, throughout the basal half of the scrobe. Unambiguous optimization (CI = 100; RI = 100).

Antenna

59. *Scape, lateral view*: (0) subrectate to (slightly) arcuate (e.g. Fig. 51A); (1) sinuate (Fig. 63A).

Apomorphy for *Pedetinus* (see also Champion, 1903: 200). Unambiguous optimization (CI = 100; RI = 100).

60. *Funicle, number of segments*: (0) seven-segmented (e.g. Fig. 64B); (1) six-segmented, apparently through a secondary fusion of segments II and III into one segment (Fig. 45B).

Convergently present in *Anchylorhynchus* and *Derelominus*. In each case an obscure suture or constriction may be visible near the central region of the elongate segment II, e.g. in *A. variabilis*. In disagreement with previous reports (e.g. Champion, 1910; Kuschel, 1952), a seven-segmented antennal funicle was observed in all species of *Celetes*, *Elaeidobius*, *Phytotribus*, and *Pseudoderelomus* Champion (1910). Unambiguous optimization (CI = 50; RI = 80).

61. *Club, number of segments*: (0) four-segmented (e.g. Fig. 42A); (1) three-segmented (e.g. Fig. 64C).

Apomorphy for the *Acalyptus*–*Systemotelus* clade, with two apparent reversals in the *Nodocnemus*–*Parimera* clade and in the *Derelominus*–*Diplothemiobius* clade. The sutures between segments are often difficult to identify (even under a compound microscope), and so the characteristic rows of suberect setae on each segment were used to reconfirm the counts. Unambiguous optimization (CI = 33; RI = 96).

62. *Club, shape, lateral view*: (0) oval to elongate, pubescence similar throughout (e.g. Fig. 66A); (1) oval to subcircular, compressed, segment I glabrate (to pubescent), pentagonal-triangular (apically narrowed), segments II and III annulate ('V-shaped'), densely pubescent (Fig. 68A).

Apomorphy for *Pseudoderelomus*. Unambiguous optimization (CI = 100; RI = 100).

63. *Segments I and II of club, shape, lateral view*: (0) transverse to slightly elongate, shorter to only slightly longer than apical segment(s) of club (i.e. segments III or III–

IV); (1) elongate-clavate (distinctly) longer than remaining segments combined.

Apomorphy for the *Elaeidobius*–*Phytotribus* clade, most distinctive in *Derelomus*. Unambiguous optimization (CI = 100; RI = 100).

Head

64. *Frons, anterodorsal view*: (0) central fovea absent (e.g. Fig. 64C); (1) anterocentral region of frons (centrally positioned between eyes) with one relatively large and deep fovea, typically more distinctive in (larger) males (Figs. 45A, 67B).

Convergently present in *A. tricarinatus* and *A. variabilis*, and in the *C. impar*–*Phytotribus* clade. Unambiguous optimization (CI = 50; RI = 83).

65. *Frons, dorsolateral view*: (0) suberect scales absent (e.g. Fig. 46A); (1) with one to three (five) distinct, relatively long, suberect scales near dorsal margin of each eye, elsewhere scales appressed (Fig. 48B).

Inapplicable in taxa whose head (and thus also the frontal region), pronotum, and elytra are regularly covered with similar suberect scales (see character 71). Apomorphy for the *Nanus*–*Eisingius* clade. The dorsal vestiture of *P. sericatus* Aurivillius (1931) is less coarse and more appressed in comparison with the other taxa. The frontal scales can still be homologized on the basis of their length, number, and position on the head. *Nanus* and *Trypetes* are dorsally for the most part without vestiture. They have isolated (possibly sensorial) setae on the anterior margin of the pronotum. The absence of frontal setae in *Trypetes* was therefore coded as pertaining to the plesiomorphic state (0), instead of being inapplicable. Unambiguous optimization (CI = 100; RI = 100).

66. *Frons, dorsolateral view; female*: (0) spine absent; (1) centrally (between posterior margins of eyes and anterior margin of pronotum) with one distinct, triangular, curved, acuminate, anteriorly directed spine (Fig. 69B). Apomorphy for *Staminodeus* (see Franz, 2001). Unambiguous optimization (CI = 100; RI = 100).

67. *Gena, near posterior margin of eye, lateral view (also visible in dorsal view of head)*: (0) sulcus absent (e.g. Fig. 49A); (1) with one (more or less) distinct sulcus, typically slightly removed from, yet extending parallel along entire posterior margin of eye, with the exception of its most dorsal and ventral parts, which are slightly less curved and thus more removed from the eye (e.g. Figs. 66A, 70A).

Apomorphy for the *Derelominus*–*Systemotelus* clade, with an apparent reversal in *Derelominus* and *Diplothemiobius*. The length, depth, and breadth of the postocular sulcus vary considerably within and among species. It is nevertheless characteristic for the apomorphic state (1) that the sulcus is slightly removed from the eye. In taxa assigned to the plesiomorphic state (0), the head margin posterior to the eye is

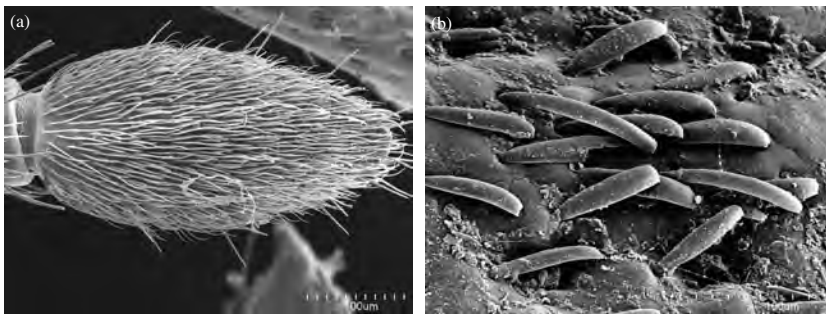


Fig. 42. *Notaris acridulus*. A, Antennal club, lateral view; B, elytral scales, dorsal view. Figures 42–73 show scanning electron micrographs of external morphological characters of select derelomine flower weevils (emphasis on type species and relevant apomorphies). The pictures were taken at various magnifications, as indicated by scale bars.

either planely adjacent (e.g. in *Acalyptus*) or (less commonly) slightly elevated (e.g. in *Eisingius*). Fast optimization preferred (compare Figs. 2 and 3; CI = 50; RI = 98).

68. *Gena* (central region), lateroventral view; male: (0) sulcus absent; (1) with one distinct, broad, vertically orientated sulcus, nearly as long as diameter of eye, and separated from it by a similar distance (Fig. 71C).

Apomorphy for *Terioltes*. The sulcus is absent in females and only visible in males when the rostrum is extended anteriorly. Unambiguous optimization (CI = 100; RI = 100).

69. *Head, pronotum, and elytra, vestiture, dorsal view*: (0) covered exclusively with (coloured) scales (e.g. Fig. 72); (1) covered with coarse scales as well as fine setae (e.g. Fig. 49B); (2) covered exclusively with setae (e.g. Fig. 44C).

Coded as nonadditive. Inapplicable in taxa whose dorsal surface is without vestiture. State (0) is present in most outgroup taxa that either lack macroscopic vestiture (e.g. *Amalactus*) or have variously shaped and coloured scales (e.g. *Curculio*; see also character 70). The relatively fine vestiture of *Platynanus* Aurivillius (1931) is congruently assigned to this state as well. State (1) is an apomorphy for the *Elaeidobius–Phytotribus* clade, whereas state (2) is convergently present in *Pedetinus* and in the *Acalyptus–Systenotelus* clade. Slow optimization preferred (compare Figs. 2 and 3; CI = 66; RI = 97).

70. *Head, pronotum, and elytra, shape (type) of scales, dorsal view*: (0) elongate (relatively) narrow, margins subparallel, variously coloured, surface not lamellate (e.g. *Notaris*; see also Fig. 42B); (1) relatively short, equilateral to subcircular, apical margins truncate to slightly rotundate, variously coloured, lamellate, apically truncate (e.g. *Neopsilorhinus*; see also Fig. 60A); (2) long, elongate, narrow, colour aurate, shiny, lamellate, apically slightly broadened, acute-rotundate, lamellae projecting terminally as small acute tips (e.g. *Celetes*; see also Fig. 50B).

Coded as nonadditive. Inapplicable in taxa in which scales are absent (see character 69). State (1) is convergently present in the *Tadius–Neopsilorhinus* clade and in the *Smicronyx–Erodiscus* clade. State (2) is an

apomorphy for the *Elaeidobius–Phytotribus* clade. In *P. lineatus* Chevrolat (1879) there appears to be a subset polymorphism, including type (1) and type (2) scales. The scales of *Anchylorhynchus* represent something like an ‘intermediate’ type (not to be interpreted phenetically). They were homologized with state (2) to maximize the overall congruence. Slow optimization preferred (compare Figs. 2 and 3; CI = 66; RI = 93).

71. *Head, pronotum, and elytra, orientation of scales, dorso-lateral view*: (0) appressed, subrectate, parallel to dorsal surface (e.g. Fig. 72); (1) suberect to slightly recurvate, orientated at an angle (ranging from 30 to 90°) to dorsal surface (e.g. Fig. 49C).



Fig. 43. *Amalactus nigratus*. A, Metatibial apex, ventrolateral view.

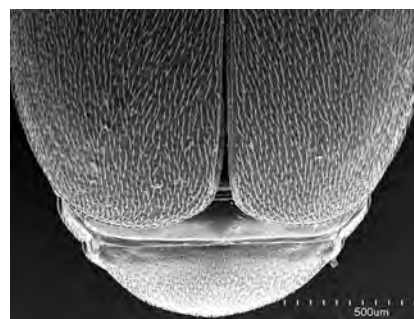


Fig. 44. *Amorphaidea lata*. A, Posterior half of elytra and pygidium, dorsal view.



Fig. 45. *Anchylorhynchus tricarinatus*. A, Rostrum and head, dorsal view; B, antennal funicle and club, lateral view; C, venter (female), ventral view.

Inapplicable in taxa in which scales are absent (see character 69). Convergent present in *Tadius* (elytra only), in *Udeus* (elytra only), and in the *Grasidius*–*Phytotribus* clade (head, pronotum, and elytra). In each of these taxa the suberect scales are characteristically aligned in regular rows along the stria intervals of the elytra. They vary from almost rectate (e.g. *C. binotatus*) to distinctly recurvate (or decumbent, e.g. *Grasidius*). The patchily arranged suberect scales in *Neopsilorhinus* (see character 105) are not considered homologous to the apomorphic state (1). Unambiguous optimization (CI = 33; RI = 85).

Pronotum

72. *Pronotum, shape and size (allometry), dorsal view; male*: (0) allometry largely similar among males and females; (1) males with pronotum expanded, larger, and more globular than in females, pronotal size and shape distinctly positively allometric.

Apomorphy for the *Cotithene*–*Terioltes* clade (see also Voss, 1940: 6). The only laterally expanded (i.e. not globular) pronotum in males of *Ganglionus* (see Franz & O'Brien, 2001a) was not homologized with state (1). Unambiguous optimization (CI = 100; RI = 100).

73. *Pronotum, anterior margin, region posterior to eye, lateral view*: (0) setae projecting from anterior margin of



Fig. 46. *Anchylorhynchus variabilis*. A, Rostrum, head, and pronotum, lateral view.

pronotum towards posterior margin of eye either indistinct (e.g. Fig. 66A) or relatively short, length more or less similar throughout (e.g. Fig. 50B); (1) 'postocular setae' distinctly longer than setae aligned dorsally and ventrally along anterior margin of pronotum, projecting to posteroventral margin of eye (Fig. 46).

Convergent present in *Anchylorhynchus* and in *C. binotatus*–*C. cariniceps*. The 'postocular setae' are relatively long in other species of *Celetes*, *Phytotribus*, and in certain outgroup taxa such as *Tadius*. In the latter case, however, they do not display a distinctive increase in length in the lateroventral region of the pronotal anterior margin. Unambiguous optimization (CI = 50; RI = 83).

74. *Pronotum, anterolateral region, dorsolateral view*: (0) tubercles absent (e.g. Fig. 46); (1) near anterior margin (occasionally extending to central region) with numerous very small, sparsely yet regularly distributed tubercles, larger towards the anterior margin (e.g. Figs. 48B, 54C).

Apomorphy for the *Nanus*–*Eisingius* clade. Most apparent in larger males of *E. chusqueae* (see Bondar, 1949: 182) and of *N. uniformis* Boheman (1844; in Schoenherr, 1844), less so in females of all examined species. Also present (particularly) in males of *Planus* (C. Ruiz Gouet, pers. comm.), suggesting that this taxon should be included in the aforementioned clade. Unambiguous optimization (CI = 100; RI = 100).

75. *Pronotum, dorsolateral margins, dorsal view*: (0) margins convex, carinae absent (e.g. Fig. 66B); (1) margins carinate, with one (small) carina projecting along entire length of each dorsolateral margin; (2) dorsolateral carinae in males interrupted near anterior margin, separating a small lobulate anterolateral projection in the constricted (tubulose) region of the pronotum from the posteriorly extending carina (e.g. Fig. 59B).

Coded as additive. State (1) is an apomorphy character for the *Elaeidobius*–*Derelomus* clade (including *N. piriformis*), whereas state (2) is an apomorphy, presumed to be a secondary transformation for a clade within *Derelomus*, excepting in each case *D. mariaeheleneae* and *D. tatianae* Bondar (1941). Unambiguous optimization (CI = 100; RI = 100).

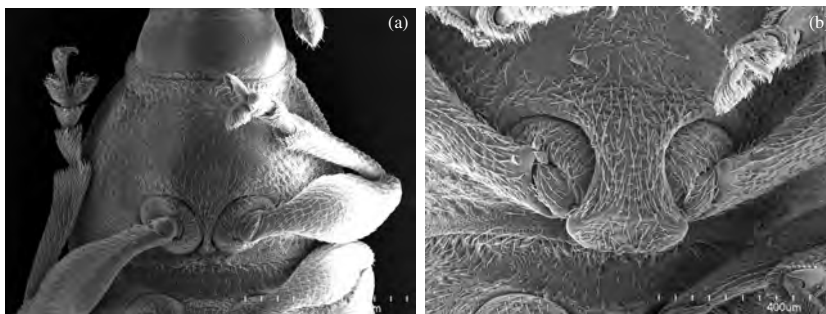


Fig. 47. *Andranthobius argentinensis*. A, Prosternum (female), ventral view; B, prosternum (male), ventral view.

76. *Pronotum, dorsolateral margins (anterior region)*; male: (0) projection absent (e.g. Fig. 56A); (1) with one small, carinate-cuspidate, laterally directed projection, positioned near anterior quarter of each dorsolateral pronotal margin (Fig. 62A).

Convergently present in *Nodocnemus* Marshall (1931) and in *Notolomus* (see LeConte, 1876: 221–223 in LeConte & Horn, 1876). The laminate, recurvate projections in males of *A. viridans* (see Fig. 48B) are positioned at the anterior margin of the pronotum, and thus not considered homologous. Unambiguous optimization (CI = 50; RI = 50).

Sterna

77. *Prosternum, length (in relation to mesosternum), ventral view*: (0) prosternum similar in length to or longer than mesosternum; (1) prosternum slightly shorter than mesosternum (Fig. 63B).

Apomorphy for *Pedetinus*, reflecting its unique shape among all examined taxa. Unambiguous optimization (CI = 100; RI = 100).

78. *Prosternum, antero-central region, ventral view*: (0) transverse carinae absent; (1) with various small, subparallel (lamellate), transversely aligned carinae, extending along entire anterior region of prosternum (Fig. 54B). Apomorphy for the *Araucarietus*–*Eisingius* clade. Most apparent in larger males, less so in females. Unambiguous optimization (CI = 100; RI = 100).

79. *Prosternum, central and lateral regions, vestiture, ventral view*: (0) either glabrate or scaled/setose, yet similar throughout entire prosternum (e.g. Fig. 53B); (1) central region of prosternum (anterior to procoxal cavities) with distinct, relatively long (occasionally shorter, pubescent), fine and densely arranged vestiture, absent in lateral prosteral region (Fig. 64B).

Apomorphy for the *Pseudoderelomus*–*Systemotelus* clade (see also Franz & O'Brien, 2001a, b; Franz, 2003a). Behavioural studies of cyclanth-associated derelomines (see Franz, 2004) would seem to support the inference that the prosteral pubescence can increase the amount of pollen transferred by the adult weevils from one inflorescence to another. Nevertheless, effective pollination can occur without this characteristic, e.g. in the closely related *Andranthobius* (see, e.g. Bondar, 1943: 364–366) and *Notolomus* (see Brown, 1976). Unambiguous optimization (CI = 100; RI = 100).

80. *Prosternum, central region (procoxal cavities), ventral view*: (0) posteriorly directed projection absent (e.g. Fig. 56D); (1) with one small (females) to (moderately) large (males), apically narrowly acute (females) or slightly to distinctly transversely expanded (lobulate to incudate, males), posteriorly directed projection, extending from central prosteral region to or beyond the separated procoxal cavities (Fig. 47A, female; Fig. 47B, male). Apomorphy for *Andranthobius* (see Kuschel, 1952: 272), including *D. mariahelena*. The prosteral projection is most impressive in larger males of *A. bondari* (Hustache,

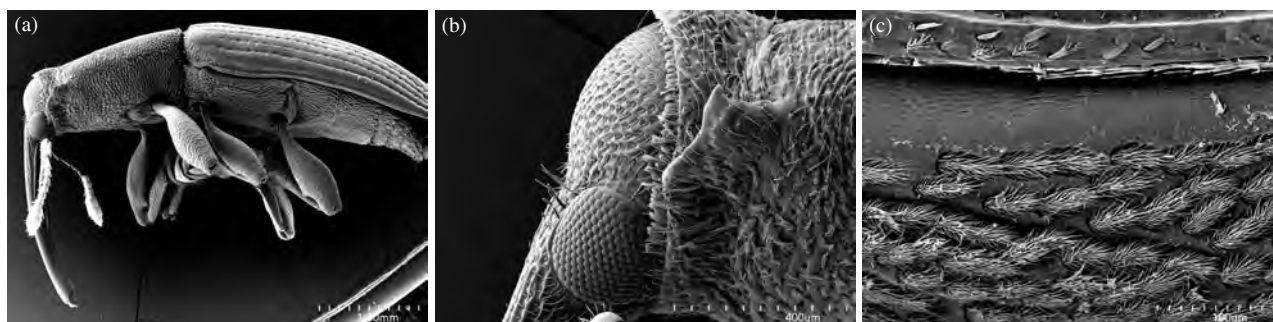


Fig. 48. *Araucarietus viridans*, male. A, Habitus, lateral view; B, head and pronotum, lateral view; C, epipleura, lateral view.

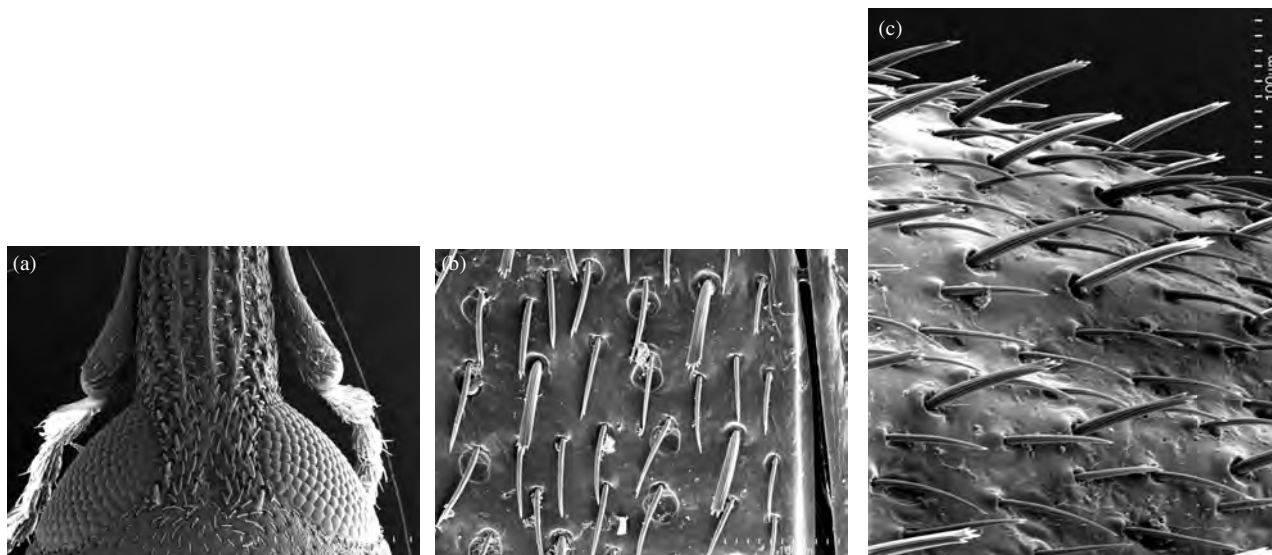


Fig. 49. *Celetes landeroi*. A, Rostrum and head, dorsal view; B, elytral vestiture, dorsal view; C, elytral vestiture, dorsolateral view.

1940; in Bondar, 1940; see also Hustache, 1940: 692; this species was examined but excluded from the analysis), where it terminates in a ventrally orientated, triangulate ('alate'), transverse lamina that extends as broadly as the distance between the lateral margins of the procoxal cavities. The females in this species have the smaller, acute, posteriorly directed projection that characterizes the females in other species as well. The dimorphism is least apparent in *D. mariahelena*. Prosternal projections in other, unrelated taxa such as *P. megalops* are less narrowly projected (or triangular) and not considered homologous to state (1). Unambiguous optimization (CI = 100; RI = 100).

81. *Prosternum, central region, separation of procoxal cavities, ventral view; female*: (0) procoxal cavities contiguous (i.e. centrally not separated by projection of prosternum, e.g. Fig. 56E); (1) procoxal cavities narrowly separated by distance not exceeding breadth of antennal club (e.g. Fig. 47A); (2) procoxal cavities broadly separated by distance exceeding breadth of antennal club (e.g. Fig. 58A).

Coded as additive. Inapplicable in *Tadius* in which the procoxal cavities are separated by a ventral rostral channel extending to the posterior margin of the mesosternum. State (0) is present in most outgroup and ingroup taxa. State (1) is convergently present in a variety of clades and individual species, among them the *Derelomus–Elaeidobius* clade, the *Acalyptus–Parimera* clade, *Andranthobius* (including *D. mariahelena*), and *Cotithene*. The additive coding preserves the homology of the procoxal separation among *Nodocnemus* (state 1) and *Parimera* Faust (1896; state 2). State (2) is convergently present in the *Juanorhinus–Eisingius* clade, in *C. pallidus*, and in *Parimera*. The slightly less separated procoxal cavities in *Platynanus*

are congruently assigned to state (2). The most extreme separation can be observed in *Trypetes*, where the distance exceeds the diameter of the procoxae. Fast optimization preferred (compare Figs. 2 and 3; CI = 18; RI = 75).

82. *Sterna and epipleura, vestiture, ventrolateral view*: (0) plumose scales absent; (1) prosternum (mostly posterior half), mesosternum, metasternum (anterior and lateral margins), and epipleura with relatively densely arranged, equilateral to elongate, appressed, whitish, plumose scales (Figs. 48C, 54D).

Apomorphy for the *Araucarietus–Eisingius* clade. Unambiguous optimization (CI = 100; RI = 100).

83. *Mesosternum, shape, ventrolateral view*: (0) concave (posteriorly angulate, incurvate), slightly to distinctly retracted from ventral plane constituted by prosternum and metasternum (e.g. Figs. 63B, 66C); (1) subplane (almost) equal with ventral plane (Fig. 48A).

Apomorphy for the *Juanorhinus–Eisingius* clade. State (1) is congruently interpreted to also be present in *Eisingius*; this is in contrast to Kuschel (1952: 271). Although the shape of certain species of *Derelomus* appears similarly depressed (see character 2) and ventrally subplane, there the posterior region of the mesosternum is plesiomorphically concave. Unambiguous optimization (CI = 100; RI = 100).

84. *Mesosternum, posterior region (centrally between mesocoxal cavities), shape, ventral view*: (0) posterior region slightly elevated, equal with anterior margin of metasternum; (1) with one large, ventrally distinctly protruding, convex to truncate, subquadrate tumescence (Fig. 70B).

Apomorphy for *Systemotelus*. The anteriorly directed, lobulate-triangular projection in males of *Derelominus*

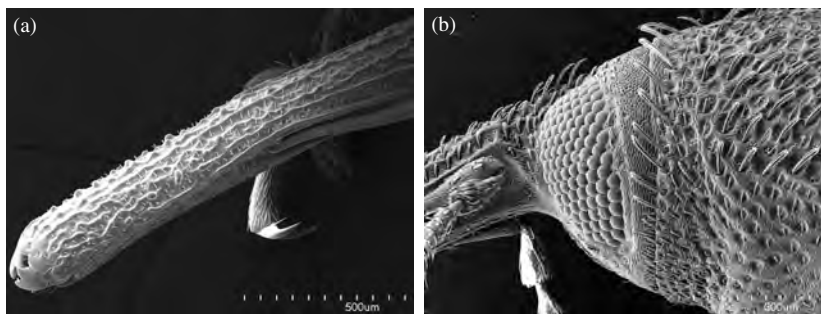


Fig. 50. *Celetes tarsalis*, male. A, Rostrum, anterior region, dorsolateral view; B, rostrum, head, and pronotum, lateral view.

is not considered homologous to state (1), nor is the smaller, more acute projection in *Pedetinus*. Unambiguous optimization (CI = 100; RI = 100).

85. *Metasternum, central region, ventral view*: (0) posteriorly with one distinct, small to relatively large fovea, positioned centrally between metacoxal cavities (Fig. 60B); (1) centrally with one small, linear canal extending along posterior half (concave region) to entire length of metasternum (Fig. 64D).

Convergently present in *Pedetinus* and in the *Juanorhinus–Systemotelus* clade. Apparently reversed in *P. lineatus*. Unambiguous optimization (CI = 33; RI = 86).

Metendosternite

86. *Stalk, shape (lateral margins), posterior view*: (0) lateral margins arcuate, variously slightly concave to convex (see character 87), subparallel to dorsally slightly converging; (1) lateral margins subrectate, dorsally distinctly converging (stalk dorsally very narrow), resulting in a triangular appearance of the stalk.

Apomorphy for the *Grasidius–Phytotribus* clade. Unambiguous optimization (CI = 100; RI = 100).

87. *Stalk, shape (lateral margins), posterior view*: (0) lateral margins subrectate to concave; (1) lateral margins slightly convex (see Franz, 2001: 415, fig. 2d).

Apomorphy for the *Derelomini* gen. 1–*Staminodeus* clade. Unambiguous optimization (CI = 100; RI = 100).

88. *Central sclerotization (lateral margins), lateral projections, posterior view*: (0) lateral projections equilateral to elongate, margins subparallel, apically slightly

narrowed, truncate; (1) lateral projections clavate, apically expanded, margins rotundate to obliquely truncate.

Apomorphy for the *Smicronyx–Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).

89. *Central sclerotization (lamina), insertion of anterior tendons, posterior view*: (0) anterior tendons inserted near central region between centre of lamina and furcal arms (e.g. Franz, 2001: 415, fig. 2d); (1) anterior tendons inserted centrolaterally along lamina, near (ventrally of) bases of furcal arms (e.g. Franz, 2003a: 162, fig. 5A); (2) anterior tendons inserted laterally on inner margins of furcal arms, at or dorsally of insertions of lateral projections.

Coded as nonadditive. State (0) is present in various outgroup and ingroup clades, and varies considerably among them (compare, e.g. *Neopsilorhinus* and *Pedetinus*). State (1) is convergently present in the *Elaeidobius–Derelomus* clade and in the *Derelominus–Systemotelus* clade. State (2) is interpreted as a phylogenetically independent apomorphy for the *Juanorhinus–Eisingius* clade, with a single reversal in *Trypetes*. Fast optimization preferred (compare Figs. 2 and 3; CI = 50; RI = 96).

Legs

90. *Pro-, meso-, and metafemur, ventral margin, lateral view*: (0) inermous (teeth absent, e.g. Fig. 64A; but see below); (1) each with one small to large, apicoventrally directed, acuminate tooth near apical quarter (e.g. Fig. 73B).

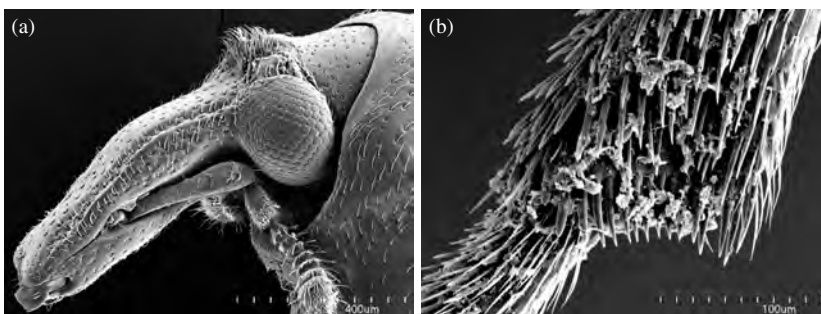


Fig. 51. *Cotithene* sp. 1, male. A, Rostrum, head, and pronotum, dorsolateral view; B, metatibial apex, lateral view.

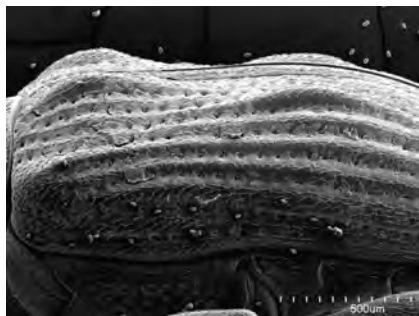


Fig. 52. *Cyclanthura laticola*. A, Elytra, dorsolateral view.

Convergently present in the *Omoides–Udeus* clade, the *Curculio–Erodiscus* clade, the *Dorytomus–Ellescus* clade, in *Anchylorhynchus*, and in the *Celetes–Phytotribus* clade. Similar (large) teeth are present only on the profemora of *Parimera* and of *Trypetes*. Smaller, triangular, and more centrally positioned projections can be observed on the metafemora of *Pedetinus*. Very small yet similarly positioned teeth occur in *Nanus*, although they are entirely absent on the female profemora. Particularly in males of *S. carludovicae*, the ventral margins of the femora are projected into a carina, which terminates subapically with an emargination, resulting in a toothed appearance. None of these modifications is considered homologous to the (1) condition. Unambiguous optimization (CI = 16; RI = 78).

91. *Profemur, ventral margin, ventrolateral view; male*: (0) tubercles absent; (1) with numerous very small, evenly distributed tubercles.

Apomorphy for a clade within *Staminodeus* (see Franz, 2001). Unambiguous optimization (CI = 100; RI = 100).

92. *Protibia, ventral margin, lateral view; male*: (0) teeth absent; (1) anteroventral margin with row of (three to ten) relatively large to (twelve to eighteen) very small, aligned, apically directed teeth, extending along entire length of protibia.

Apomorphy for a clade within *Staminodeus* (see Franz, 2001). Unambiguous optimization (CI = 100; RI = 100).

93. *Protibia, ventral margin, lateral view; male*: (0) long setae absent; (1) apical half of protibia ventrally with region of very long, suberect, fine, aurate setae, extending to protibial apex (Fig. 61A).

Apomorphy for the *Nodocnemus–Parimera* clade. Unambiguous optimization (CI = 100; RI = 100).

94. *Pro-, meso-, and metatibia, apex, ventral margin, lateral view*: (0) mucronate, ventral margin of each tibia apically with one small (e.g. *Elaeidobius*) to relatively large (e.g. *Amalactus*, see Fig. 43A), elongate-triangular, acuminate projection, extending parallel to apical margin; (1) inermous, apicoventral mucron absent (e.g. Fig. 70C).

State (0) occurs in most outgroup taxa, whereas state (1) is convergently 'present' in the *Omoides–Pedetinus* clade, in *Araucarietus*, and in the *Elaeidobius–Systemotelus* clade, with apparent reversals in

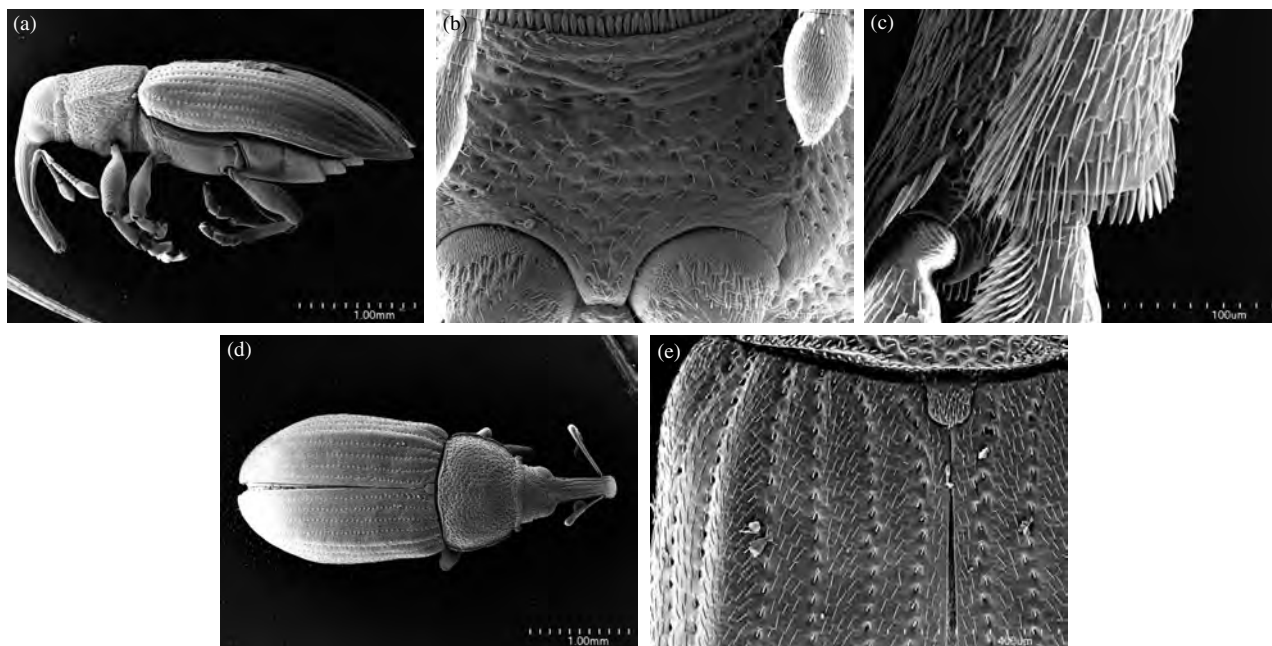


Fig. 53. *Derelomus chamaeropsis*, female. A, Habitus, lateral view; B, prosternum, ventral view; C, metatibial apex, lateral view; D, habitus, dorsal view; E, elytral vestiture, dorsal view.

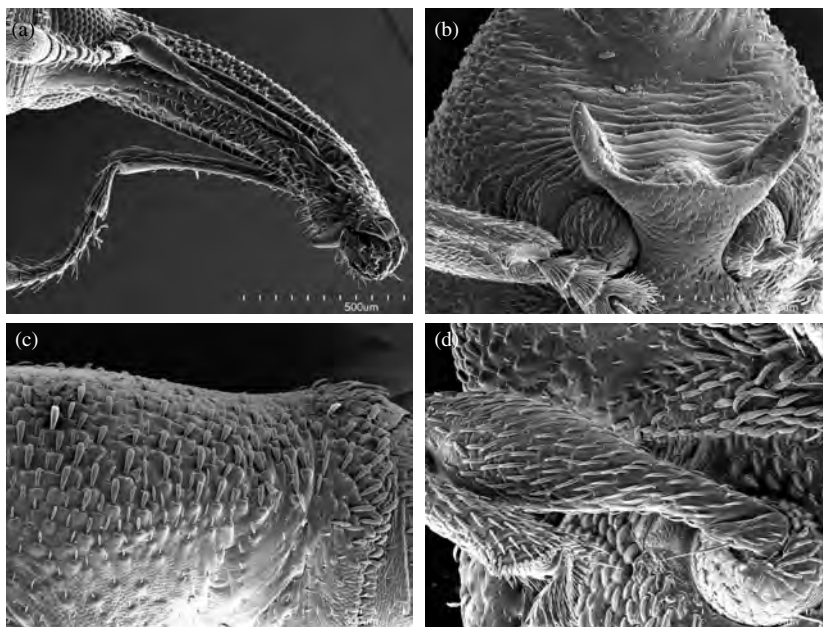


Fig. 54. *Eisingius chusqueae*, male. A, Rostrum and head, ventrolateral view; B, prosternum, ventral view; C, pronotum, lateral view; D, mesosternum, ventral view.

Elaeidobius, *C. binotatus*–*C. cariniceps*, and in *Phytotribus*. Unambiguous optimization (CI = 16; RI = 80).

95. *Pro-, meso-, and metatibia, apex, anteroventral margin (position of mucron), lateral view*: (0) mucron projecting terminally from ventral margin of each tibia; (1) mucron projecting centrally from anterior margin of each tibia, thus ventral margin appearing inermous and truncate (Fig. 58B).

Inapplicable in taxa that lack a mucron (see character 94). Apomorphy for the *Trypetes*–*Eisingius* clade; apparently secondarily absent in *Araucarietus* and *Eisingius*. The insertion of the large, slightly arcuate mucron in *Trypetes* is almost dorsal, with the anterior and ventral margins armed only with rows of very stout setae. Fast optimization preferred (compare Figs 2 and 3; CI = 50; RI = 50).



Fig. 55. *Elaeidobius subvitattus*, male. A, Apex of rostrum, lateral view.

96. *Pro-, meso-, and metatibia, apex, antero-/posteroventral margin (setal comb), lateral view*: (0) setal comb constituted by numerous (typically twenty to fifty) relatively fine, short to relatively long, densely arranged setae, extending from anterior to ventral to posterior apical margin of each tibia (e.g. Fig. 51B); (1) setal comb constituted by a smaller number (typically five to fifteen) of (very) stout, relatively short, sparsely arranged (evenly spaced, noncontiguous), spine-like setae, extending along posteroventral apical margin of protibia and anteroventral apical margins of meso- and metatibia (e.g. Fig. 64E; see also Franz & O'Brien, 2001a: 840, fig. 4b–d, 2001b: 280, fig. 3b).

Convergently present in *Pseudoderelomus*, in the *P. aristidis*–*P. suturalis* clade – somewhat ambiguously including *P. aristidis* Voisin (1986) – and in the *Ganglionus*–*Systemotelus* clade where it is most apparent. *Diplothemioobius* has longer, even more separated spine-like setae extending from the anterior to the posterior margin of each tibial apex. These were not considered homologous to state (1). Unambiguous optimization (CI = 33; RI = 87).

97. *Meso-, and metatibia, apex, anterodorsal margin (extension of setal comb), lateral view*: (0) setal comb extending along (to only slightly beyond) anterodorsal margin of tibial apex, not ascending beyond condyle and along dorsal tibial margin (e.g. Fig. 53C); (1) setal comb extending beyond anterodorsal margin of tibial apex to apical sixth (e.g. *Amorphoidea*) or even to apical third (e.g. *Parimera*) of dorsal tibial margin (Fig. 61B). Convergently present in *Araucarietus* and in the *Acalyptus*–*Parimera* clade. A similarly ascending setal comb can be observed in *Udeus*, where it is also present

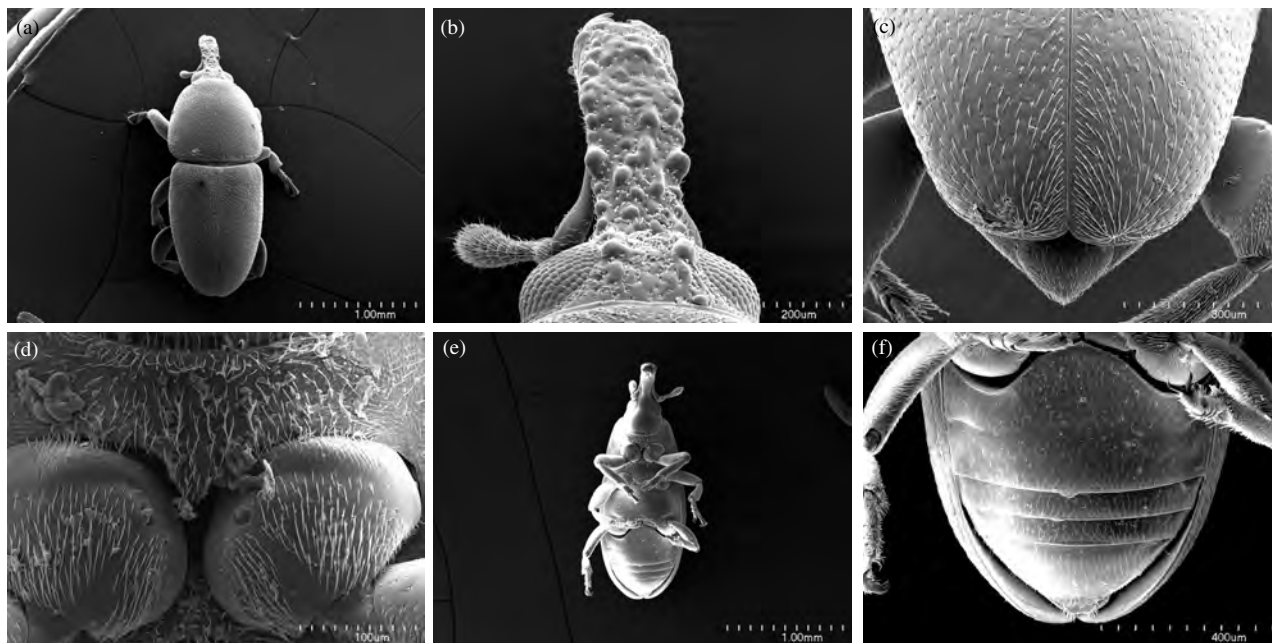


Fig. 56. *Ganglionus catenatus*. A, Habitus (male), dorsal view; B, rostrum and head (male), dorsal view; C, posterior half of elytra and pygidium (male), dorsal view; D, prosternum (male), ventral view; E, habitus (female), ventral view; F, venter (female), ventral view.

on the protibia. The metatibia of *Pedetinus* has setae ascending from the apex on both the antero- and posterodorsal edge of its dorsal margin. The pro- and mesotibiae lack this characteristic. In certain species of *Anchylorhynchus*, *Celetes*, and *Phytotribus* the setal comb appears to be ascending as well, yet the tibial apices are more expanded and obliquely rotundate-truncate. This contrasts with taxa assigned to state (1) where the setal comb ascends to the 'nonapical region' of the tibia. Unambiguous optimization (CI = 50; RI = 75).

98. *Tarsal claws, shape (dentation)*: (0) simple (triangular teeth absent, e.g. Fig. 68B); (1) toothed, with one distinct, triangular (apically acute) projection basally on each (paired) claw (Fig. 62B).

Convergently present in *Amorphoidea* and in *Notolomus* (see LeConte, 1876: 222; in LeConte & Horn, 1876). Similarly positioned yet smaller and apically more rotundate projections are present in *Hypoleschus* Fall (1907; in Fall & Cockerell, 1907; therein called 'appendiculate claws') and in *Omoides*. Longer and narrower structures occur in *Anthonomus* Germar (1817) and in *Tychius*. More laterally positioned and differently shaped teeth can be observed in *Curculio* and *Erodiscus*. None of these is considered homologous to the apomorphic state (1). Unambiguous optimization (CI = 50; RI = 50).

Elytra

99. *Elytra, shape, lateral margins (outline), dorsal view*: (0) shape oval to elongate, greatest width anterior to

or near central region of elytra (e.g. Fig. 66B); (1) shape slightly ovate, greatest width near posterior two-fifths of elytra (Fig. 53D).

Apomorphy for *Derelomus* (see Schoenherr, 1836: 629), including *Neoderelomus* Hoffmann (1938a), and excluding *D. mariaehelenae* and *D. tatiاناe*. The ovate elytral shape is most apparent in *D. auberti* Hustache (1932) and in *N. piriformis*, less so in *D. abyssinicus*. Unambiguous optimization (CI = 100; RI = 100).

100. *Elytra, shape, posterior margins (outline), dorsal view*: (0) margins of each elytron posteriorly gradually converging, subcontiguous (longest posterior extension of elytra near or at posterior point of contact), slightly to distinctly rotundate (e.g. Fig. 56C); (1) margins of each elytron posteriorly individually rotundate, separate ('truncate': longest posterior extension of elytra removed from posterior point of contact), outline connecting each margin in dorsal view broadly emarginate (Fig. 44A).

Convergently present in *Pedetinus* and in the *Acalyptus-Parimera* clade. The truncate appearance of the elytra is reinforced by the partly (e.g. *Acalyptus*) to entirely (e.g. *Amorphoidea*) exposed pygidium. Exposed pygidia are also present in taxa that have the (0) state (see character 116). In those cases, the posterior margins of the elytra do not form a broadly emarginate line. The posteriorly narrowly truncate elytra in *Trypetes* are not considered homologous to state (1). Unambiguous optimization (CI = 50; RI = 80).

101. *Elytra, shape, central region (sculpture), dorsolateral view*: (0) elytra evenly convex, undulations absent (e.g.



Fig. 57. *Hypoleschus atratus*, male. A, Posterior margin of elytra and pygidium, dorsal view.

Fig. 66C); (1) elytra undulate along anterior quarter: with one transverse, slightly convex elevation near anterior eighth of striae I–III, continuing posteriorly with one slight impression near anterior quarter of striae I–III (Fig. 52).

Apomorphy for *Cyclanthura* (see Franz, 2003a). More anteriorly positioned and similarly shaped elevations are present in *C. globulicollis* Voss (1940) and in *Nodocnemus* (only in males), although they are not posteriorly impressed. Conversely, slight depressions without anterior elevations are apparent on the elytra of *Derelomini* gen. 2. The slight, triangular, subplane elevations near the anterior elytral margins in males of *A. argentinensis* (Hustache, 1939) are also not considered homologous. Unambiguous optimization (CI = 100; RI = 100).

102. *Elytra, shape, central region (sculpture), dorsolateral view*: (0) carinate tumescences absent; (1) with two to three(five) distinct, elongate (length variable), convex, carinate tumescences (apparently positively allometric) extending along anterior sixth of strial interval II–III, central region of strial interval IV–V, and anterior half of strial interval VI–VII (see Franz, 2003a: 158, fig. 2B, 159, fig. 3A). Synapomorphy for *C. carinata* Franz (2003a) and *C. striata*. In the latter species, two additional carinate tumescences are present on strial intervals IV–V and VI–VII. Unambiguous optimization (CI = 100; RI = 100).

103. *Elytra, shape, central region (sculpture), dorsolateral view; male*: (0) tectate carinae absent; (1) with one small to moderately sized (apparently positively allometric), tectate (apically convex to triangular) carina extending along anterior three-quarters of strial interval IV–V of each elytron (see Marshall, 1928: 546). Apomorphy for a clade within *Derelomus* (including *N. piriformis*). Not considered homologous with character 104, due to differences in shape, length, and its exclusive presence in males. Unambiguous optimization (CI = 100; RI = 100).

104. *Elytra, shape, lateral region (sculpture) (postero) lateral view*: (0) lateral carinate projection/expansion absent; (1) with one distinct (although small), narrow, elongate, carinate projection extending along entire length of strial interval VIII–IX, more apparent in males; (2) strial interval in males broadly projected, distinctly convex, elevated, and expanded, resulting in an increased distance between striae VIII and IX. Coded as additive. State (1) is an apomorphy for the *Elaeiodobius–Derelomus* clade (including *N. piriformis*; excluding *D. mariaehelena* and *D. tatarica*). State (2) is an apomorphy, presumably a secondary transformation, for a less inclusive clade within the former. The additive coding preserves the positional and structural homology of the elytral modifications. Unambiguous optimization (CI = 100; RI = 100).

105. *Elytra, vestiture, scales (arrangement, orientation), dorsolateral view*: (0) arrangement and orientation of scales similar throughout entire elytral surface; (1) predominantly appressed scales interspersed with various small, symmetrically arranged (modelled) patches of distinctly projecting, suberect, variously coloured scales (less apparent on the pronotum, Fig. 60A).

Inapplicable in taxa that lack scales on the elytra (see character 69). Apomorphy for *Neopsilorhinus*. Unambiguous optimization (CI = 100; RI = 100).

106. *Elytra, anterior region, colour, dorsal view*: (0) colour similar throughout (but see below); (1) colour light to dark (reddish-)brown, anterior region with one small to relatively large, elongate-triangular, black maculation, extending laterally along anterior margin from stria I (e.g. *P. quadricollis*) to stria VII

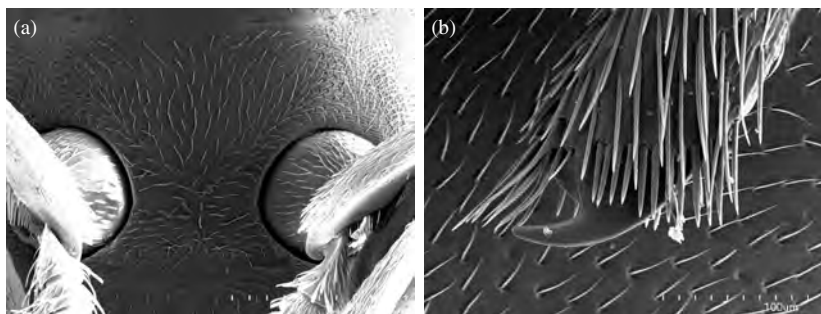


Fig. 58. *Nanus uniformis*, male. A, Prosternum, ventral view; B, metatibial apex, lateral view.

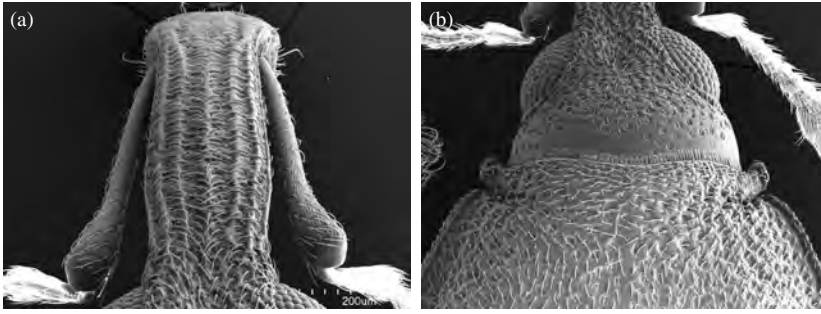


Fig. 59. *Neoderelomus piriformis*, male. A, Rostrum, dorsal view; B, head and pronotum, dorsal view.

(e.g. *P. mecinooides* Champion, 1902), and posteriorly to or beyond central region, posteriorly gradually narrowed and extending into inner margin of each elytron (e.g. see Champion, 1902: table 8, figs 27, 29). Apomorphy for the *P. aristidis*–*P. suturalis* clade. As described above, there is considerable variation within and among species in the extension of the triangular maculation, with *P. aristidis* (small) and *P. crassipes* Champion (1902; large) as extremes along a range of sizes. Unambiguous optimization (CI = 100; RI = 100).

107. *Elytra, anterior and central region, colour, dorsal view*: (0) colour similar throughout (but see below); (1) colour yellowish-brown, each elytron centrolaterally with two relatively small, narrowly elongate to irregularly subcircular, distinctly black maculations, each almost one-tenth as long as elytra, extending along anterior and central region of stria interval III–IV(–V) (see Anderson & Gómez, 1997: 898, figs 1, 4; 900, figs 14, 16).

Synapomorphy for *S. carludovicae* and *S. costaricensis*. The presence and extension of the maculations vary with the individual level of pigmentation. Unambiguous optimization (CI = 100; RI = 100).

108. *Elytra, central region, colour, dorsal view*: (0) colour similar throughout (but see below); (1) colour (light reddish-)brown, anterocentral region with one relatively large, elliptical, dark brown maculation, almost two-fifths as long as elytra, laterally extending to stria interval II–III (to III–IV).

Apomorphy for Derelomini gen. 1. The size and level of pigmentation of the anterocentral maculation vary

significantly within and among species. In teneral individuals it can be entirely absent. Unambiguous optimization (CI = 100; RI = 100).

109. *Elytra, central region, colour, dorsal view*: (0) colour similar throughout (but see below); (1) colour light (reddish-) brown, each elytron centrolaterally with one small, narrow, elongate, dark brown maculation, one-tenth to one-fifth as long as elytra, extending along central region of stria interval IV–V. Synapomorphy for *D. abyssinicus* and *D. sp. 1*. Unambiguous optimization (CI = 100; RI = 100).

Wings

110. *Wings, anterior margin, stigmal patch (setation)*: (0) small macrosetae absent (see, e.g. Zherikhin & Gratshev, 1995: 733, fig. 168); (1) with two(to four) distinct, small macrosetae projecting (on a slight elevation) from apicoposterior margin of stigmal patch (see Zherikhin & Gratshev, 1995: 756, figs 251–253). Inapplicable in taxa that lack wings. Apomorphy for the *Juanorhinus*–*Systemotelus* clade. See also Zherikhin & Gratshev (1995: 774); the Eugnomini were not examined therein, and should be excluded from the clade in light of the current observations. As many as four setae are present in certain species of *Anchylorhynchus* and *Celetes*. Various outgroup taxa (e.g. *Curculio*, *Notaris*, *Tadius*, and *Tychius*) have numerous very small, apparently nonhomologous macrosetae positioned more proximad (i.e. towards



Fig. 60. *Neopsilorhinus variegatus*. A, Elytral vestiture, dorsolateral view; B, metasternum, ventral view; C, venter (female), ventral view.

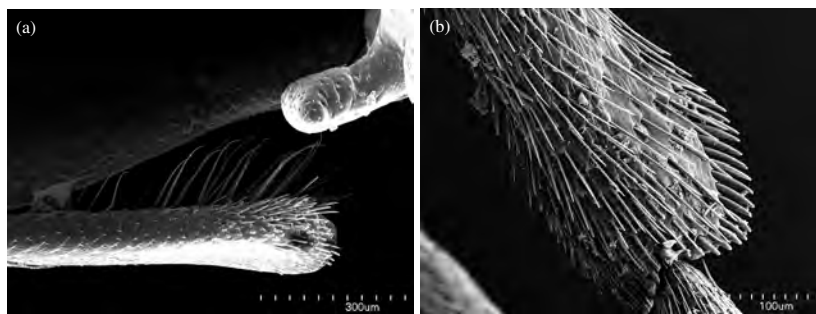


Fig. 61. *Nodocnemus* sp. 1, male. A, Protibia, ventrolateral view; B, metatibial apex, lateral view.

the base of the wing), on the stigmal patch. Unambiguous optimization (CI = 100; RI = 100).

111. *Wings, posterior margin, basal region (anal lobe)*: (0) posterior margin continuously rotundate, anal lobe absent (see, e.g. *A. aegrotus*, as illustrated in Zherikhin & Gratshev, 1995: 749, fig. 228); (1) anal lobe present, small; posterior margin subbasally with one small yet distinct, narrow (V-shaped) emargination (see, e.g. Zherikhin & Gratshev, 1995: 749, fig. 226: *Amorphoidea*, and fig. 227: *Derelomus*); (2) anal lobe present, large, posterior margin subbasally with one large, relatively narrow, V-shaped emargination, anal lobe equilateral to elongate, margin separately rotundate (see, e.g. Franz, 2001: 415, fig. 2e: *Staminodeus*).

Coded as additive. Inapplicable in taxa that lack wings. The presence of an anal lobe is considered to be plesiomorphic for Curculionoidea as a whole (see Zherikhin & Gratshev, 1995: 762). Within the present context, however, all outgroup and most ingroup taxa have state (0). State (1) is thus interpreted as convergently present in the *Elaeidobius*–*Derelomus* clade and in the *Acalyptus*–*Staminodeus* clade. State (2) is considered to represent an additional transformation in the Derelomini gen. 1–*Staminodeus* clade. Unambiguous optimization (CI = 100; RI = 100).

112. *Wings, posterior margin, basal region (length of setae)*: (0) length of macrosetae similar throughout entire posterior margin (see, e.g. Zherikhin & Gratshev, 1995: 749, fig. 228); (1) macrosetae along basal fifth distinctly longer (i.e. more than two to three (to five) times) than those positioned along apical four-fifths of posterior margin (see, e.g. Franz, 2003a: 162, fig. 5C).

Inapplicable in taxa that lack wings. Apomorphy for the *Pseudoderelomus*–*Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).

Venter

113. *Venter, shape, lateral margins (outline, particularly segments IV and V), ventral view*: (0) outline of lateral margins slightly emarginate, transition from segment IV to V (very) slightly angulate (appearing) constricted (Fig. 60C); (1) outline of lateral margins subrectate to slightly rotundate, continuously posteriorly converging, including transition from segment IV to V (Fig. 56F). Convergently present in the *Omoides*–*Pedetinus* clade and in the *Dorytomus*–*Systemotelus* clade (see also Thompson, 1992). The distinctly elongate and constricted venter in females of *Systemotelus* represents a secondary transformation; the males are congruently assigned to state (1). Unambiguous optimization (CI = 50; RI = 88).

114. *Venter, shape (length, orientation), segments III and IV; female*: (0) similar to male, often less concave; (1) ventral segments III and IV in females shorter than those of males, retracted and individually angulate, posterior margin of each segment distinctly posteroventrally projected, bisinuate (Fig. 45C; see also Vaurie, 1954: 7, fig. 1).

Apomorphy for *Anchylorhynchus*. Unambiguous optimization (CI = 100; RI = 100).

115. *Venter, shape (sculpture), segment VIII; female*: (0) subplane to slightly convex, similar to male; (1) ventral segment VII in females centrally with one

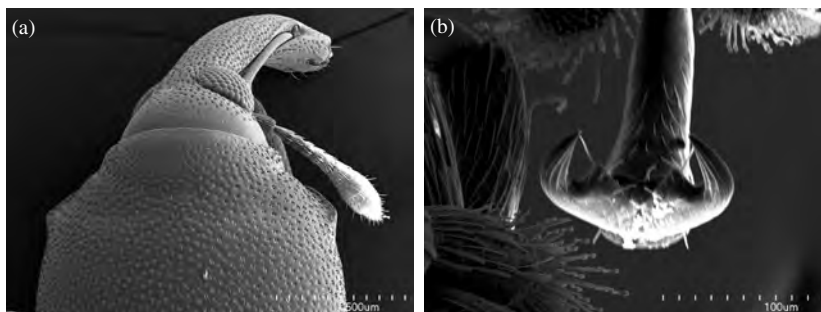


Fig. 62. *Notolomus bicolor*, male. A, Rostrum, head, and pronotum, dorsal view; B, metatarsal claw, ventrolateral view.

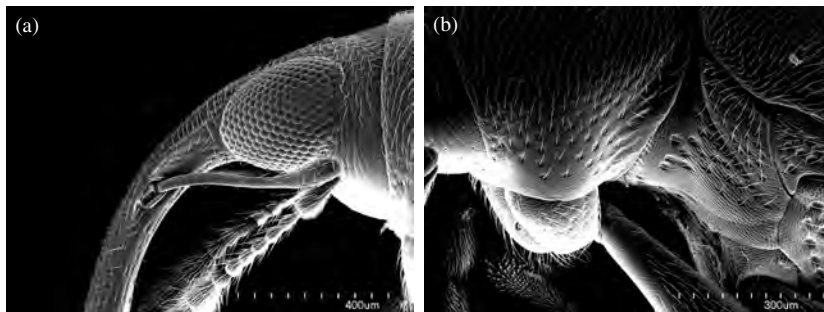


Fig. 63. *Pedetinus flavipes*. A, Rostrum and head, lateral view; B, pro- and mesosternum, lateral view.

(relatively) large, transverse (conical), apically narrowly convex tumescence (Fig. 60C).

Apomorphy for a clade within *Neopsilorhinus*. Unambiguous optimization (CI = 100; RI = 100).

Pygidium

116. *Pygidium, orientation (in relation to that of tergum and venter), lateral view*: (0) similarly orientated in males and females, either pygidium in each case subparallel to orientation of tergum (i.e. extending along a similar, slightly arcuate line in lateral view, e.g. *Pseudoderelomus*; Fig. 68C), or, if more angulate in relation to anterior tergal segments, then orientation of pygidium in males not differing significantly from that in females (e.g. *Udeus*, Fig. 73C); (1) significantly differing among males and females: pygidium almost perpendicular to orientation of venter in males, yet subparallel to orientation of tergum in females (e.g. *Perelleschus*, see Franz & O'Brien, 2001b; compare Figs 64A and 64F).

Apomorphy for the *D. tatiana*–*Systemotelus* clade. Almost perpendicularly orientated pygidia are present in various outgroup taxa (e.g. *Curculio*, *Pedetinus*, and *Tychius*). They lack the distinct sexual dimorphism associated with the apomorphic state (1). The orientation of the pygidium in *P. megalops* is more parallel. Unambiguous optimization (CI = 100; RI = 100).

117. *Pygidium, shape (lateral margins), posterior view; female*: (0) lateral margins subrectate to slightly rotundate or sinuate, posteriorly gradually converging (see, e.g. Franz, 2003a: 167, fig. 7A); (1) lateral margins emarginate-sinuate, pygidium (antero) centrally slightly (*S. stockwelli* Anderson & Gómez, 1997) to distinctly constricted (*S. carludovicae*; compare figs 12, 25, and 36 in Anderson & Gómez, 1997). Apomorphy for *Systemotelus*. The elongate and centrally constricted pygidium enables females of *Systemotelus* to oviposit 'from the outside' into the pistillate flowers of the inflorescences of the Panamahat palm *Carludovica* Ruiz & Pavón (Cyclanthaceae; see also Franz, 2004). Unambiguous optimization (CI = 100; RI = 100).

118. *Pygidium, shape (central region), posterior view; male*: (0) continuously subplane to (slightly) convex, fovea absent or (very) shallowly impressed, e.g. as in Franz (2003a: 162, fig. 5A); (1) centrally with one distinct, relatively large, deep, elliptical, dorsoventrally orientated fovea (Figs 57, 65).

Apomorphy for a clade within *Phyllotrox*, including *Hypoleschus* (see, e.g. Fall, 1907: 266; in Fall & Cockerell, 1907), and excluding (among others) *P. ater* Champion (1902), *P. rufipes*, and *P. variabilis* Schaufuss (1866). The shape of the central fovea varies among species. It is almost linear in *P. crassipes* and in closely related species, yet oval in males of the critical type species *P. semirufus* Boheman (1843; in Schoenherr, 1843). Unambiguous optimization (CI = 100; RI = 100).

Male terminalia

119. *Spiculum gastrale, posterior region, shape, dorsal view*: (0) posteriorly bifurcate, furcal arms distinct, narrow; (1) posterior region of spiculum gastrale complex, alate-explanate, each side basally and apically narrowed, thus furcal arms modified, indistinct. Apomorphy for the *Tadius*–*Neopsilorhinus* clade. Not considered homologous to the modified structures in *Anthonomus*. Unambiguous optimization (CI = 100; RI = 100).
120. *Spiculum gastrale, posterior region, shape, dorsal view*: (0) furcal arms region relatively long, arms diverging, Y-shaped; (1) furcal arms region very short, truncate, triangular-explanate, furcal arms indistinct. Apomorphy for the *Omoides*–*Pedetinus* clade. The posterior region of the spiculum gastrale in *Pedetinus* has a smaller basal projection on each side. Not homologous to character 119. Unambiguous optimization (CI = 100; RI = 100).
121. *Spiculum gastrale, posterior apical region, shape, dorsal view*: (0) furcal arms elongate, relatively slender, posteriorly narrow; (1) furcal arms region short, cordate: each arm slightly explanate, posteriorly rotundate. Apomorphy for the *Notolomus*–*Andranthobius* clade, including *D. mariahelena*. Not considered

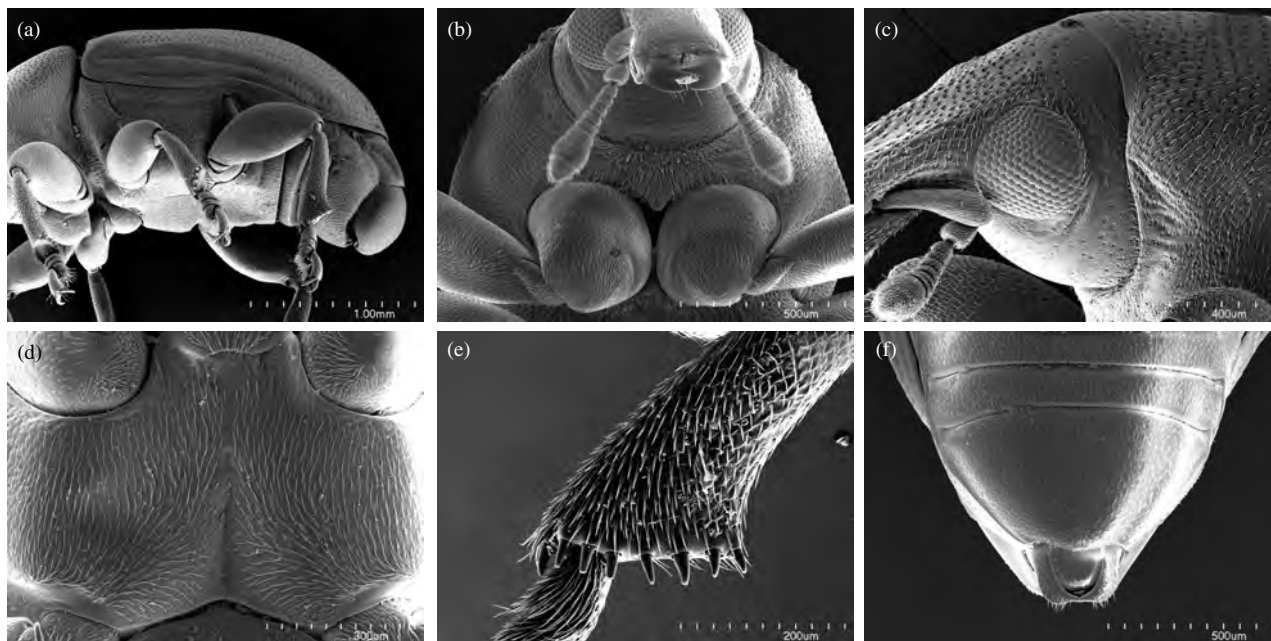


Fig. 64. *Perelleschus carlundovicae*. A, habitus (male), ventrolateral view; B, prosternum, ventral view; C, head and pronotum, lateral view; D, metasternum, ventral view; E, metatibial apex, lateral view; F, venter (female), ventral view.

homologous to either character 119 or character 120. Unambiguous optimization (CI = 100; RI = 100).

122. *Spiculum gastrale, posterior region, shape, dorsal view*: (0) furcal arms symmetrical, length similar on each side; (1) furcal arms asymmetrical, one slightly to distinctly shorter than the other.

Apomorphy for *Anchylorhynchus*. Unambiguous optimization (CI = 100; RI = 100).

123. *Spiculum gastrale, posterior region, shape and orientation, dorsal view*: (0) furcal arms similarly orientated, angle of divergence from central apodeme similar on each side; (1) furcal arms asymmetrically angulate with respect to central apodeme, one orientated slightly anteriorly and the other slightly posteriorly, also differing in length.

Apomorphy for the *Elaeidobius–Derelomus* clade (including *N. piriformis*). Unambiguous optimization (CI = 100; RI = 100).

124. *Spiculum gastrale, posterior region, shape and orientation, dorsal view*: (0) furcal arms Y-shaped, variously diverging and slightly arcuate; (1) furcal arms widely U-shaped, anterior two-thirds of each side projected from central apodeme at an angle of almost 90°, posterior third abruptly arcuate, projecting posteriorly (not laterally).

Apomorphy for a clade within *Phyllostrox*. Unambiguous optimization (CI = 100; RI = 100).

125. *Spiculum gastrale, furcal apices, shape, dorsal view*: (0) furcal apices either explanate (see characters 119–121) or variously narrowed; (1) furcal apices slightly expanded, clavate (see, e.g. Franz & O'Brien, 2001b: 281, fig. 4c; Franz, 2003a: 163, fig. 6C).

Apomorphy for the *Cyclanthura–Systemotelus* clade, with an apparent reversal in *Ganglionus*. Unambiguous optimization (CI = 50; RI = 92).

126. *Tegmen, posterior region, number of apodemes (processes), dorsal view*: (0) with one posterior, centrally positioned apodeme; (1) with two central to lateral, short to long, subparallel to posteriorly diverging processes; (2) posterior processes absent on the tegmen. Coded as additive. State (1) is an apomorphy for the *Omoides–Systemotelus* clade. State (2), presumably a secondary transformation, is convergently present in *Tychius*, *Anthonomus–Elleschus*, and in the *Acalyptus–Systemotelus* clade. Unambiguous optimization (CI = 50; RI = 96).

127. *Tegmen, posterior region, position and connection of apodemes (processes), dorsal view*: (0) processes centrally positioned along posterior margin of tegminal ring, variously close to each other (in the case of separation, relatively long), or connected; (1) each process positioned laterally along posterior margin of tegminal ring, short, widely separated.

Inapplicable in taxa in which the posterior tegminal processes are absent (see character 126). Apomorphy for the *Elaeidobius–Derelomus* clade, including *N. piriformis*. Unambiguous optimization (CI = 100; RI = 100).

128. *Tegmen, posterior region, tegminal ring, shape, dorsal view*: (0) tegminal arms completely arcuate, posteriorly connected, ring closed; (1) tegminal arms subrectate to (slightly) arcuate, diverging (often relatively short), posteriorly not connected, ring open.



Fig. 65. *Phyllotrox crassipes*, male. A, Posterior margin of elytra and pygidium, dorsal view.

Convergently present in *Tychius*, in the Derelomini gen. 1–*Staminodeus* clade, and in the *Pseudoderelomus*–*Systemotelus* clade, with two apparently independent reversals in *Cyclanthura* and in *Ganglionus*. Unambiguous optimization (CI = 20; RI = 90).

Aedeagus

129. *Aedeagal apodemes, insertion with median lobe, ventral view*: (0) aedeagal apodemes inserted laterally, on anterolateral edges of median lobe; (1) insertion of each aedeagal apodeme more internal, nearly one-half length towards the centre of anterior margin of median lobe, anterolateral edges thus fully apparent. Apomorphy for *Phytotribus*. Unambiguous optimization (CI = 100; RI = 100).
130. *Median lobe, anterior margin, shape, ventral view*: (0) anterior margin of median lobe variously convex to concave, to undulate or irregularly shaped; (1) anterior margin with two distinct, relatively large, narrowly triangular, acute, strongly sclerotized projections. Apomorphy for a clade within *Phyllotrox*. Unambiguous optimization (CI = 100; RI = 100).
131. *Median lobe, anterior margin, shape, ventral view*: (0) anterior margin of median variously shaped, not inflected, not strongly sclerotized; (1) anterior margin

subrectate, annulate: forming a regular, continuous ring from dorsal to ventral side of median lobe, strongly sclerotized, ventral margin projected, inflected.

Apomorphy for *Derelomus*, including *N. piriformis*. Unambiguous optimization (CI = 100; RI = 100).

132. *Median lobe, anterior region, shape, ventral view*: (0) anterior region of median lobe indistinct (but see above), lacking central projection; (1) anterior region on ventral side with one distinct, large, anteriorly directed projection, extending from anterior third of median lobe beyond anterior margin.

Apomorphy for the *Nodocnemus*–*Parimera* clade. Unambiguous optimization (CI = 100; RI = 100).

133. *Median lobe, lateral margins, sclerotization, ventral view*: (0) lateral margins relatively narrow and lightly sclerotized, only slightly more so than other regions of median lobe; (1) largely margins strongly sclerotized, broad and distinctly darker than internal regions of median lobe.

Apomorphy for the *Perelleschus*–*Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).

134. *Median lobe, posterior region, shape, ventral view male*: (0) median lobe posteriorly variously narrowed to rotundate, greatest breadth near central region; (1) median lobe distinctly broadened along posterior quarter, basally narrower, apex broadly rotundate.

Apomorphy for (a clade within) *Andranthobius* (i.e. excluding *D. mariahelena*). Unambiguous optimization (CI = 100; RI = 100).

135. *Median lobe, apex, shape, ventral view*: (0) apex of median lobe acute to rotundate; (1) apex narrowly truncate, apical margin subrectate.

Apomorphy for the *Omoides*–*Pedetinus* clade. Unambiguous optimization (CI = 100; RI = 100).

136. *Median lobe, apex, shape, ventral view*: (0) lobulate projection absent; (1) apex centrally with one distinct, small, separated, lobulate projection.

Apomorphy for the *Acalyptus*–*Amorphoidea* clade. Unambiguous optimization (CI = 100; RI = 100).

137. *Median lobe, apex, shape, ventral and lateral view*: (0) apex not capitate; (1) posterior region distinctly narrowed, apex small yet transversely expanded, capitate.



Fig. 66. *Phyllotrox semirufus*, male. A, Rostrum, head, and pronotum, lateral view; B, habitus, dorsal view; C, habitus, lateral view.

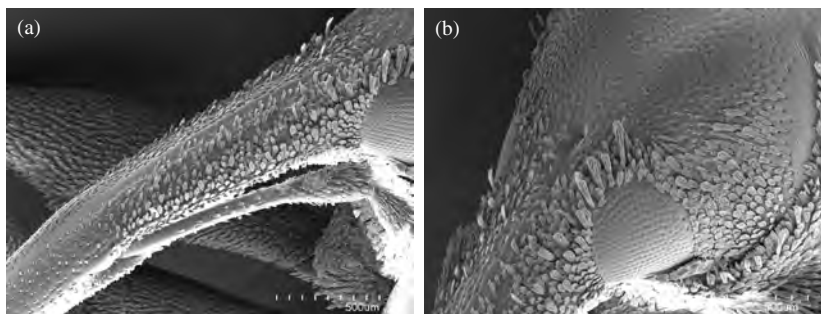


Fig. 67. *Phytotribus* sp. 1, female. A, Rostrum, dorsolateral view; B, head, dorso-lateral view.

- Apomorphy for a clade within *Phyllotrox*. Unambiguous optimization (CI = 100; RI = 100).
138. *Median lobe, internal sac (sclerites), anterior region, ventral view*: (0) internal sac anteriorly of anterior margin of median lobe indistinct, sclerites absent; (1) with one relatively large, very complex, symmetrical, variously connected and recurved, tubulose-uncinate sclerite. Apomorphy for *Anchylorhynchus*. Unambiguous optimization (CI = 100; RI = 100).
139. *Median lobe, internal sac (sclerites), anterior region, ventral view*: (0) anterior quarter of internal sac indistinct, tubulose sclerite absent; (1) with one relatively small, tubulose, posteriorly slightly narrowed sclerite. Apomorphy for a clade within *Neopsilorhinus*. Unambiguous optimization (CI = 100; RI = 100).
140. *Median lobe, internal sac (sclerites), central region, ventral view*: (0) paired sclerites absent; (1) subcentrally with two relatively large, elongate-narrow, subparallel sclerites. Apomorphy for a clade within *Perelleschus* (see also Franz & O'Brien, 2001b). Unambiguous optimization (CI = 100; RI = 100).
141. *Median lobe, internal sac (sclerites), posterior region, ventral view*: (0) long tubulose sclerite absent; (1) with one relatively large, weakly sclerotized, relatively narrow, elongate-tubulose sclerite, extending along posterior quarter of median lobe. Apomorphy for a clade within *Derelomus*, including *N. piriformis*. Unambiguous optimization (CI = 100; RI = 100).
142. *Median lobe, internal sac (sclerites), posterior region, ventral view*: (0) uncinatate sclerite absent; (1) subposteriorly with one small, very narrow, strongly reflexed (nearly 180°), uncinatate sclerite. Apomorphy for a clade within *Andranthobius*, excluding *D. mariahelena*. Unambiguous optimization (CI = 100; RI = 100).
143. *Median lobe, internal sac (sclerites), posterior region, ventral view*: (0) small tubulose sclerite absent; (1) subposteriorly, along centre of posterior orifice with one small, relatively narrow, weakly sclerotized, ampullate sclerite (see also character 145). Apomorphy for a clade within *Phyllotrox*. Unambiguous optimization (CI = 100; RI = 100).
144. *Median lobe, internal sac (sclerites), posterior region, ventral view*: (0) small paired sclerites absent; (1) subposteriorly, along (parts of) lateral margins of posterior orifice with two small, elongate, very narrow, subrectate, posteriorly converging sclerites. Apomorphy for the *Cotithene-Terioltes* clade. Not considered homologous to character 145. Unambiguous optimization (CI = 100; RI = 100).
145. *Median lobe, internal sac (sclerites), posterior region, ventral view*: (0) paired rami absent; (1) subposteriorly, along lateral margins of posterior orifice, with two small, narrow, slightly arcuate rami, adjacent to slightly shorter and centrally positioned ampullate sclerite (see character 143). Apomorphy for a clade within *Phyllotrox*. Unambiguous optimization (CI = 100; RI = 100).

Female terminalia

146. *Sternum VIII, posterior region, shape, ventral view*: (0) furcal arms variously shaped, anteriorly slightly diverging, subrectate to arcuate, posteriorly separate (U- or V-shaped) or connected (O-shaped); (1) furcal arms angulate: anteriorly distinctly diverging, yet subrectate and converging along posterior two-thirds, apices separate, rotundate. Apomorphy for the *Elaeidobius-Derelomus* clade, including *N. piriformis*. Unambiguous optimization (CI = 100; RI = 100).
147. *Sternum VIII, posterior region, shape, ventral view*: (0) furcal arms variously shaped, relatively narrow, typically broadly diverging; (1) furcal arms laminate-explanate, broad, anteriorly fused, posteriorly separate, slightly diverging, apices nearly truncate; (2) furcal arms, long, very narrow, completely separated yet subparallel in extension. Coded as nonadditive. State (1) is an apomorphy for a clade within *Phyllotrox*, including *P. variabilis*. State (2) is interpreted as an independent transformation in another clade within *Phyllotrox* that includes *P. suturalis* (Boheman 1884; in Schoenherr, 1844). Unambiguous optimization (CI = 100; RI = 100).



Fig. 68. *Pseudoderelomus baridiiformis*. A, Antennal club, lateral view; B, metatarsus, ventral view; C, abdomen (male), lateral view.

148. *Spermatheca, basal region, shape*: (0) appendix absent; (1) with one small, narrowly triangular, apically acute, sclerotized appendix, laterobasally inserted (i.e. opposed to reservoir) and directed (thus orientation similar to apex of spermatheca).

Apomorphy for *Perelleschus* (see Franz & O'Brien, 2001b). Unambiguous optimization (CI = 100; RI = 100).

149. *Spermatheca, basal region, shape*: (0) basal margin of spermatheca either subrectate or continuously rotundate (to irregular); (1) basal margin angulate, with two subrectate edges converging at a small angle (20–40°) centrally near insertion of spermathecal duct.

Apomorphy for a clade within *Phyllotrox*. Unambiguous optimization (CI = 100; RI = 100).

150. *Spermatheca, apical region, shape*: (0) apical half of spermatheca either subrectate or variously arcuate to reflexed; (1) apical half sinuate-undulate, alternately flexed and reflexed towards narrow apex.

Convergently present in the *P. canyonacris*–*P. rutilus* clade and in the *P. aristidis*–*P. suturalis* clade. Unambiguous optimization (CI = 50; RI = 85).

Host plant associations

151. *Adults, feeding*: (0) on various nonreproductive organs of angiosperms (including, e.g. cleaves and petioles; but see below); (1) adults feeding and reproducing only on angiosperm flowers and inflorescences, typically acting as pollinators (see also Table 1).

Convergently present in *Pedetinus* and in the *Elaeidobius*–*Systemotelus* clade. Adults in the *Araucarietus*–*Eisingius* clade reproduce on the cones of araucarias (Kuschel, 2000). This life history appears to reflect an independent transformation and was not included under state (1). Unambiguous optimization (CI = 50; RI = 94).

152. *Adults, plant range (for details see Table 1; as well as the 'Discussion')*: (0) associated with (i.e. feeding and reproducing on) aquatic monocots, e.g. Poaceae or Typhaceae (see in particular Kuschel, 1971: 244–247 for the various associations of Eirrhiniinae with aquatic host plants); (1) associated with (the inflorescences of) Araceae (*Anthurium* in particular); (2) associated with (the cones of) Araucariaceae; (3) associated with (the inflorescences of) Arecaceae; (4) associated with (the inflorescences of) Cyclanthaceae; (5) associated with (the flowers or inflorescences) of various (typically herbaceous or shrubby, tropical montane or subtropical to temperate) representatives of dicots, including Asteraceae and Rosaceae.

Coded as nonadditive, which reflects the assumption that host plant associations may evolve along various unordered paths. The necessary information was still absent in certain taxa when the analysis was completed (coded as "?"). State (1) is an apomorphy for *Cyclanthura* (see Franz, 2003a), whereas state (2) is an apomorphy (minimally) for the *Araucarietus*–*Eisingius* clade. State (3) is convergently present in a number of clades, including *Pedetinus*, the *Trypetes*–*Eisingius* clade (although see above), and the

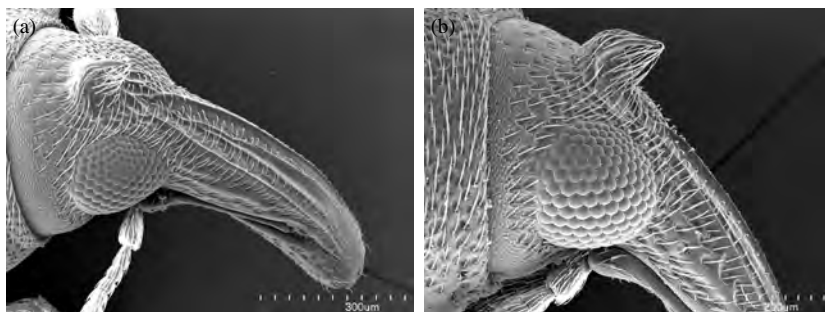


Fig. 69. *Staminodeus vectoris*, female. A, rostrum and head, dorsolateral view; B, head, lateral view.

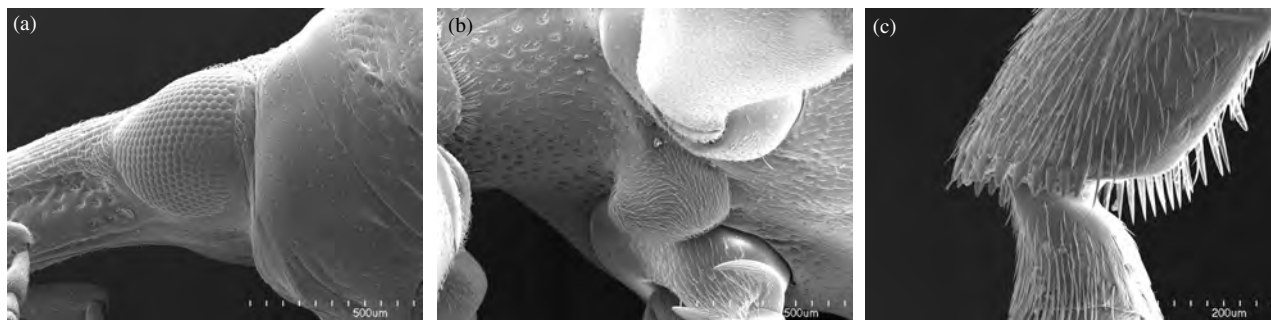


Fig. 70. *Systemotelus carludovicae*. A, head and pronotum, lateral view; B, mesosternum, ventrolateral view; C, metatibial apex, lateral view.

Elaeidobius–Systemotelus clade. In slow optimization, at least size-independent ‘reversals’ (additional transformations) are proposed. State (4) is convergently present in the Derelomini gen. 1–*Staminodeus* clade (see Franz, 2003b) and in the *Cotithene–Systemotelus* clade (see Franz, 2004), with two additional transformations apparent in the latter. State (5), as presently defined, represents an ambiguous homology assessment, according to which similar host plant associations occur in a number of outgroup taxa as well as in the more derived *Phyllotrox*. Further details would be useful to refine this character. Slow optimization preferred, except for within the *Cotithene–Systemotelus* clade (compare Figs 2 and 3; CI = 45; RI = 89).

153. *Adults and immature stages, associations with Cyclanthaceae (reproduction)*: (0) visiting and reproducing on various genera of Cyclanthaceae, e.g. *Asplundia* Harling, *Chorigyne* R. Eriksson, *Dicranopygium* Harling, and *Evodianthus* Oerst. (Franz, pers. obs.); (1) exclusively associated with the inflorescences of *Carludovica* (Franz, 2004). Inapplicable in taxa that are not associated with Cyclanthaceae (see character 152). Apomorphy for the *Ganglionus–Systemotelus* clade. Unambiguous optimization (CI = 100; RI = 100).
154. *Adults and immature stages, associations with Cyclanthaceae (reproduction)*: (0) oviposition and subsequent larval development in the staminate or

pistillate flowers of Cyclanthaceae inflorescences (see Franz, 2004); (1) exclusive reproductive association with the ephemeral staminodes (see Franz, 2003b). Inapplicable in taxa that are not associated with Cyclanthaceae (see character 152). Apomorphy for the Derelomini gen. 1–*Staminodeus* clade. Slow optimization preferred (due to abundance of inapplicables; compare Figs 2 and 3; CI = 100; RI = 100).

155. *Adults, reproductive and pollinating behaviour*: (0) reproducing on and/or pollinating host plants with largely open structures, ‘externally’; (1) adapted to enter the enclosed reproductive organs of Cyclanthaceae inflorescences, and thus capable of pollinating them (see Franz, 2004). Inapplicable in taxa that are not associated with angiosperm reproductive organs (see character 151). Apomorphy for the Derelomini gen. 2–*Systemotelus* clade, with an apparent (size-related) reversal in *Systemotelus* (see Franz, 2004). Unambiguous optimization (CI = 50; RI = 87).

Discussion

Character support for individual clades

The preferred cladogram shows much phylogenetic resolution along with mixed character support for individual taxa (Fig. 1). The evidence for the monophyly of a clade is



Fig. 71. *Terioltes circumdatus*, male. A, Rostrum, dorsolateral view; B, apex of rostrum, dorsolateral view; C, head, ventral view.

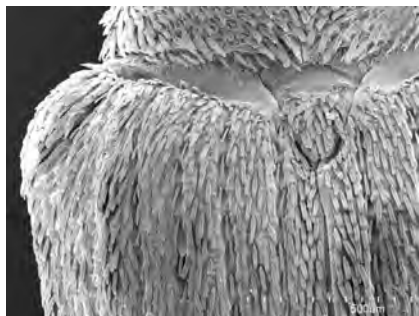


Fig. 72. *Tychius lineellus*. A, Elytral vestiture, dorsal view.

only overwhelming in select cases. Nevertheless, the proposed system contains a majority of unreversed apomorphies (110 out of 155 included characters). At 65 and 95%, respectively, CI and RI are high for an analysis of these dimensions. The numbers reflect a selective, successive-approximations approach to the task of assessing homologies.

Relatively weak support exists for most of the outgroup taxa and for the oldest splits among the represented lineages (Fig. 1). Often the taxon sampling and examined characters are insufficient to allow wide-ranging conclusions. Two exceptions are: the *Tadius*–*Neopsilorhinus* clade, with a complex apex of the male spiculum gastrale (char. 119), and the *Omoides*–*Pedetinus* clade, with a small, triangular apex (char. 120). In light of their ‘orthocerous’ male genitalia (char. 126; see also Kuschel, 1964, 1971; Thompson, 1992), *Notaris*, *Tadius*, and *Neopsilorhinus* are outside the Curculionidae sensu Alonso-Zarazaga & Lyal (1999). All members of the *Amalactus*–*Systemotelus* clade are well characterized by the presence of lacinial dentes on the inner margin of the maxilla (char. 14).

At the next less inclusive level there is notable support for the *Juanorhinus*–*Eisingius* clade on one hand, and for the *Elaeidobius*–*Systemotelus* clade on the other. The former includes *Juanorhinus* (Molytinae: Juanorhinini), as well as the phylogenetically more coherent *Trypetes*–*Eisingius* clade (Molytinae: Trypetidini; see also Kuschel, 1952, 1987; Marvaldi *et al.*, 2002). These weevils have a depressed shape (char. 10), separated procoxal cavities (char. 81), and

a subplane (noninflected) mesosternum (char. 83). *Araucarietus* and *Eisingius* share various additional chars, e.g. a transversely carinate prosternum (char. 78) and plumose epipleural scales (char. 82; see also Kuschel, 2000). The larger remaining clade represents Derelomini in the new sense. It is supported by five homoplasious characters, most prominently the absence of central setae on the maxillary palpomeres I and II (chars 24, 29) and the close reproductive association (originally) with the inflorescences of *Arecaceae* (chars 151, 152). The latter was also invoked by Bondar (1943) and Kuschel (1952).

None of the other attributes previously used for derelomines (see ‘Taxonomic history’) could be confirmed. They are either not specific to this tribe or they vary too much among taxa to be represented in a cladistic analysis. More conclusive evidence for the monophyly of Derelomini (in the present sense) should come from additional sources of characters, including studies of internal morphology, natural history, and of DNA sequence data. Until then, the characters examined herein – although neither unreversed nor unambiguous (see, e.g. char. 152) – remain the strongest evidence available for the monophyly of the tribe.

Most of the older clades within derelomines are well supported by the current analysis (Fig. 1). The first divergence appears to have separated the *Elaeidobius*–*Phytotribus* clade from the other lineages. The former has an African–South American distribution. It is characterized by a carinate rostrum (char. 15), an elongate segment I of the antennal club, and a unique pattern of dorsal scales and setae (chars 69, 70). The *Elaeidobius*–*Derelomus* clade and *Anchylorhynchus* represent the two most distinctive lineages in this analysis. There is much less support for the relationships among them, however, and with respect to the *Grasidius*–*Phytotribus* clade. Members of the latter have two large separated setae along the premental margins (char. 31), suberect elytral scales (char. 71), and dentate femora (char. 90). The monophyly of *Celetes* in relation to *Phytotribus* could not be confirmed. The effects of limited taxon sampling are probably most significant here. An in-depth analysis of these taxa is currently underway. It is likely to produce many new species and clarify their phylogeny (R. Valente, pers. comm.).

Within the *Acalyptus*–*Systemotelus* clade there are several well-circumscribed entities. Typically, all have only one

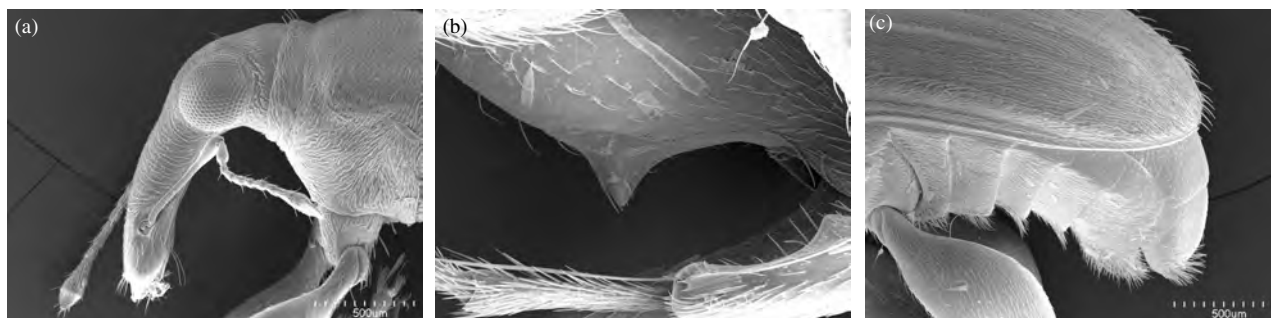


Fig. 73. *Udeus* sp. 1, male. A, Rostrum, head, and pronotum, lateral view; B, metafemur, lateral view; C, abdomen, lateral view.

large seta along the outer margin of the maxillary palpiger (char. 19), a three-segmented antennal club (char. 61), and a 'scale-less' dorsal vestiture (char. 69). Weevils placed in the succeeding *Acalyptus*–*Staminodeus* clade have no apicolateral setae on the maxillary palpomeres I and II (chars 26, 30), a nonprojecting ligula on the labial prementum (char. 35), and a small to large anal lobe on the wing (char. 111). The entailed lineages are each supported by multiple characteristics. The *Derelominus*–*Systemotelus* clade, on the other hand, is delimited best by the presence of a postocular sulcus (char. 67). It is separated further into two distinct lineages. The *Derelominus*–*Andranthobius* clade contains taxa with an 'additional' small seta on the maxillary stipes (char. 4), apically bifurcate lacinial dentes (char. 16), and two large setae positioned on the maxillary palpomere I (char. 25). The opposing *Pseudoderelomus*–*Systemotelus* clade is unique with respect to its two-segmented maxillary palps (char. 23), the ventrally densely pubescent prosternum (char. 79), and the long macrosetae along the reduced anal lobe region of the wing (char. 112), among other attributes. The immediately succeeding clade is supported by a single yet fairly distinctive apomorphy, i.e. an apically truncate mala on the maxilla (char. 7). The next less inclusive *Phyllotrox*–*Systemotelus* lineage is characterized by an apicolateral projection on the labial palpomere II (char. 43) and a perpendicular male pygidium (char. 116).

For *Phyllotrox*, in particular, the current analysis can identify only a number of apparent subclades. A more comprehensive picture will require increased taxon sampling and the examination of male and female genital characters. Meanwhile, the structure of the *Cotithene*–*Systemotelus* clade is defined much better: various parts of its phylogeny were diagnosed by Franz (2003a, 2004).

Evolutionary trends

The analysis uncovered many transformations in the mouthparts of derelomines (forty-three out of 155 characters), particular the maxillae and the labium. The results were somewhat unexpected; they are not easily explained by existing theories about the evolution of related taxa. Many of the examined mouthpart attributes constitute the core support for revised phylogenetic classification. Among them are: the apically truncate maxillary mala (char. 7), the presence of lacinial dentes (char. 14), the absence of centrolateral setae on the maxillary palpomeres I and II (chars 24, 29), the apicolateral projection on the labial palpomeres I and II (chars 38, 43), and the presence of a small centrolateral seta on the labial palpomere III (char. 45). These and other mouthpart transformations are sufficiently stable and unique to characterize various older clades. The appearances or losses of certain setae are often informative (see, e.g. chars 4, 6, 10, 12, 16, 30, 31, 40): curiously a reduction in the number of maxillary palpomeres (from three to two) occurred just once (char. 23), whereas a similar reduction in the labial palpomeres is

mapped six times on the preferred cladogram (char. 37). The present analysis indicates clearly that in-depth studies of mouthparts should be part of our overall evolutionary picture of derelomines (see also Morimoto & Kojima, 2003).

This study also provides insights into many phylogenetically independent occurrences of sexual dimorphisms in derelomines (Figs 1, 76). The list of modifications is long and diverse. At the moment, *Staminodeus* and *Systemotelus* are the only taxa for which there are adequate functional accounts. In the former, the armed fore legs in males (chars 91, 92) are used in male–male fights to have access to reproductively active females. The females apply their frontal spine (char. 66) during a complex process of cutting and transporting the staminodes of Cyclanthaceae inflorescences to oviposition sites (Franz, 2001, 2003b). In the latter, the females' narrow, extended reproductive structures (char. 117) allow them to oviposit into the otherwise inaccessible (well-protected) pistillate flowers of *Carludovica* inflorescences (Anderson & Gómez, 1997; Franz, 2004). The males of *Systemotelus* have relatively plesiomorphic morphologies. This stands in contrast with various other taxa where only the males have striking modifications. Examples are: the large size, conspicuous elytral projections and long setae in *Elaeidobius kamerunicus* (Faust, 1898: 225; see also O'Brien & Woodruff, 1986); the interrupted pronotal carinae (char. 75) and carinate-tectate elytra (char. 103) within *Derelomus*; the carinate-tuberculate rostral margins within *Celetes* (char. 48); the long setae on the protibiae of *Nodocnemus* and *Parimera* (char. 93; the former also has a small, lobulate prosternal projection); the impressive, arcuate, acute and anteriorly directed prosternal projection in *Diplothemobius* (see Bondar, 1941: 279, fig. 2); the small, cuspidate pronotal projections in *Notolomus* (char. 76); the variously expanded prosternal projections in *Andranthobius* (char. 80); the swollen (positively allometric) pronotum (char. 72) and various rostral modifications in *Cotithene* (chars 50, 54; see also the male frons in Fig. 51A) and in *Terioltes* (chars 46, 53; and also char. 68 representing a ventral head modification); and finally the unrelated rostral transformations in *Ganglionus* (chars 51, 52), in which the males also display a broader pronotum and darker pigmentation (see Franz & O'Brien, 2001a). Outside the derelomines in the new sense (see Fig. 75; Table 2), the males of *Eisingius* have remarkable rostral and prosternal attributes (chars 55, 78; see also Fig. 54A, B). Thus, a total of twenty external morphological traits in the matrix correspond to such exclusive male apomorphies. Most of them seem likely to function in male–male fights. To the extent that this number is 'unusually' high, it may be related to the frequent and dense aggregations of adult weevils on limited and ephemeral sites for oviposition. In any case, field studies should produce a wealth of interesting behavioural traits for these derelomines.

Significantly fewer modifications are manifested in females alone. Among them are the curiously transformed ventral segments III and IV in *Anchylorhynchus* (char. 114)



Fig. 74. Summary view of the phylogenetic analysis for derelomine flower weevils, indicating character state optimizations and support values for major lineages (see also Fig. 1). Lower-level taxa with proposed nomenclatural changes are marked with an asterisk.

and the tumescent ventral segment VII within *Neopsilorhinus* (char. 115; now placed in the outgroup). Most derelomines also display oviposition-related dimorphisms (in the rostral shapes and antennal insertions) typical for other weevil lineages (Anderson, 1995).

Finally, the analysis posits the occurrence of several major transformations in the host plant associations of derelomines (Figs 1, 76). The first and perhaps most important among them is a close reproductive interdependence with palms. This relationship was discovered over 200 years ago (Fabricius, 1798; von Martius, 1823), and was described further and analysed in the works of Bondar (1940, 1941, 1942, 1943, 1949, 1950), Kuschel (1952), and

Henderson (1986). These and many congruent studies provide reasons to think that the derelomine–palm association is indeed long-standing and unique among weevils. Once more detailed information is available about the various nonderelomines visiting palms, it should be possible to differentiate and homologize the associations more accurately than through the codings of characters 151 and 152. In other words, there is a still vague yet apparently exclusive quality to the palm–inflorescence associations of the *Elaeidiobius*–*Systemotelus* clade. It typically includes a combination of traits such as an efficient attraction to and pollination of the host plants, and the oviposition and larval development in more or less ‘dispensable’ floral organs, e.g.

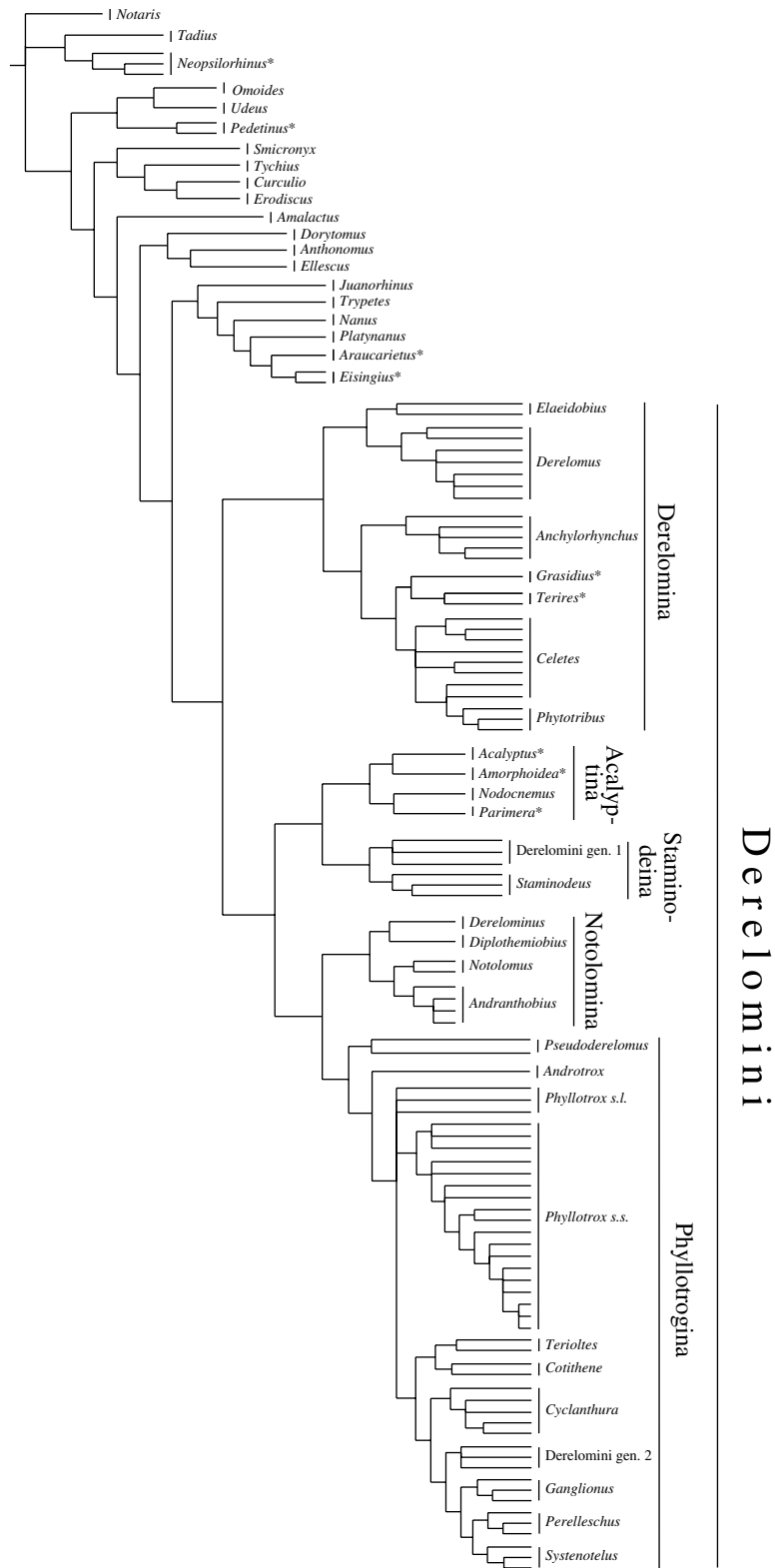


Fig. 75. Summary view of the phylogenetic analysis for derelomine flower weevils, indicating the revised higher-level classification (tribe and subtribes; also see text). Taxa previously classified within *Derelomini* and now placed outside the tribe, or vice versa, are marked with an asterisk.

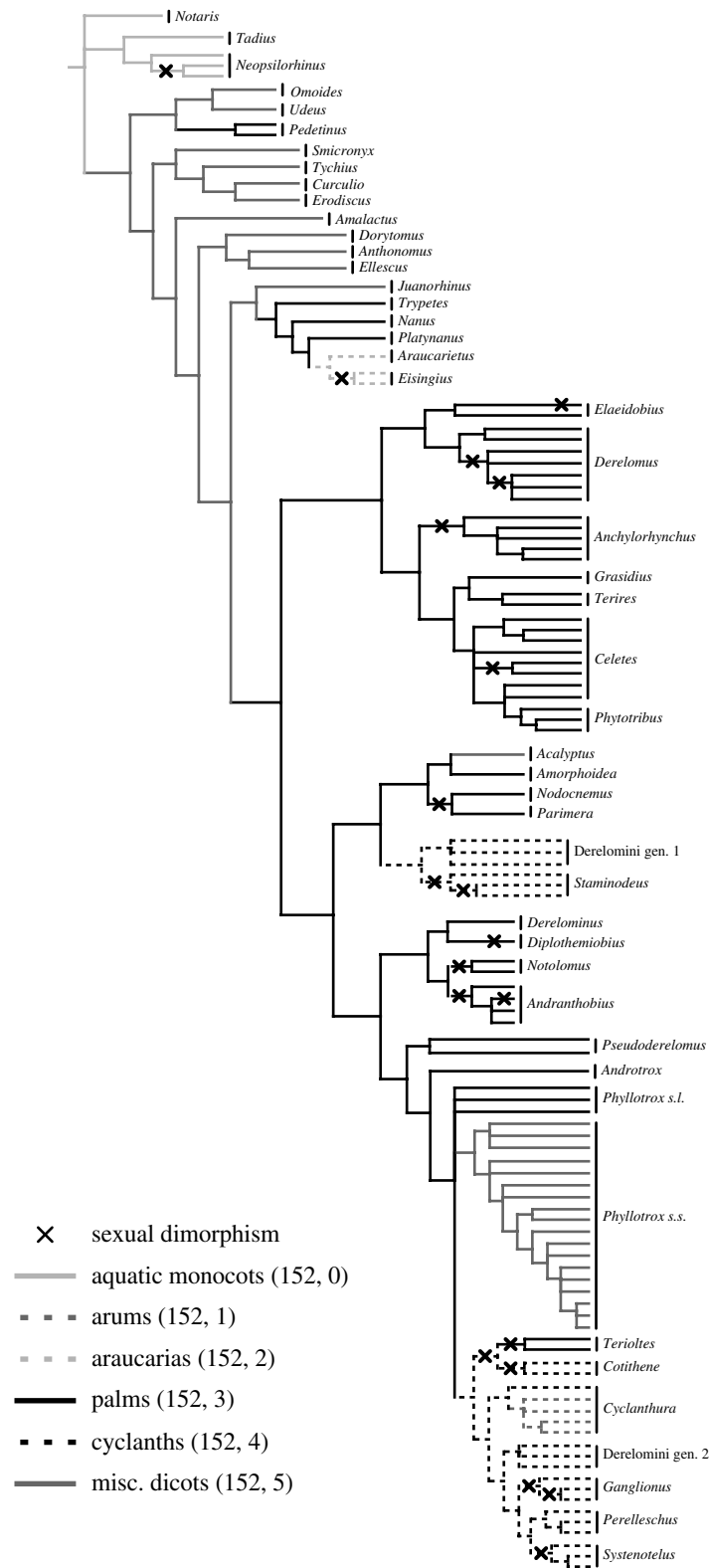


Fig. 76. Summary view of the significant occurrences of derelomine flower weevil sexual dimorphisms and major (higher-level) transformations in the host plant associations (character 152; see Table 1 and the text for further details).

the staminate flowers (see, e.g. Brown, 1976; Mora-Urpi & Solís, 1980; Syed *et al.*, 1982; Henderson, 1986; Eriksson, 1994a; Listabarth, 1996; Anstett, 1999; Franz & O'Brien, 2001a). Although their relative degrees of host specificity vary, as a whole derelomines may have shaped the evolution of palms more than any other insect taxon.

The close reciprocal interaction of derelomines and palms has nevertheless become dissociated in a number of lineages. The most critical secondary transformations have led to a shift onto various dicot hosts, and two independent colonizations of the inflorescences of Cyclanthaceae (Figs 1, 76). The former has taken place within a fairly well-characterized and species-rich clade of *Phyllotrox*. These weevils live on the flowers of a range of unrelated dicots such as Aceraceae, Asteraceae, Ericaceae, Geraniaceae, Melastomataceae, and several other families (Voss, 1954; Warner, 1976; C.W. O'Brien, pers. comm.). They often inhabit premontane or warmer temperate regions where palms are less abundant. The clade includes the type species *P. semirufus*, which occurs on the flowers of *Rubus* sp. (Rosaceae) in Colonia Tovar, Venezuela, at an altitude of 2000 m (Franz, 2003a). This observation is almost unfortunate, in that the existing palm pollination literature often references undescribed derelomines as '*Phyllotrox* sp.'. After a thorough revision, many of these entities might have to be placed elsewhere. *Phyllotrox* in the strict sense may then comprise only dicot-associated species.

Among the two independent colonizations of Cyclanthaceae, that of the *Terioltes*–*Systemotelus* clade appears older. It is also more biologically diverse and significant to the host plants' evolution. The corresponding palaeontological records are inconclusive, although they are not incompatible with an association that extends at least to the Eocene – some 40 million years ago (Kuschel, 1992; Eriksson, 1994b; Anderson & Gómez, 1997). The more than 230 species in the subfamily Carludovicoideae are all seemingly pollinated by this lineage of derelomines. The monotypic member of the remaining subfamily, *Cyclanthus* Poit., is visited (perhaps secondarily) by Cyclocephalini (Scarabaeidae) as well (Beach, 1982; Franz, 2003a).

The specialized inflorescence structures and phenologies in Cyclanthaceae suggest a long-standing co-evolutionary interaction. Within the derelomines there have been multiple independent transformations from pollinating to nonpollinating adults, and from mostly detritivorous to seed-predating larvae. *Cotithene* (Franz, pers. obs.) and *Systemotelus* (Anderson & Gómez, 1997) are two examples. Individual clades are specialized to oviposit into either the staminate (e.g. *Ganglionus*; Franz & O'Brien, 2001a) or the pistillate flowers (e.g. *Perelleschus*; Franz & O'Brien, 2001b). The unnamed *Derelomini* gen. 2 represents another diverse lineage. Some of its members reproduce exclusively on the staminodes of Cyclanthaceae. Much work remains to be carried out on the taxonomy and natural history of these weevils. Another recent phenomenon has evolved within *Cyclanthura*. Several of its species pollinate the inflorescences of *Anthurium* (Araceae; Franz, 2003a). The palm association of *Terioltes*, in turn, may constitute a reversal.

Lastly, a presumably younger lineage close to the acalyptines has also shifted from palms onto cyclanths. Their external appearance is similar enough to obscure the differences to the aforementioned taxa. Their reproductive behaviours are just as particular and synchronized, although the species of *Derelomini* gen. 1 and *Staminodeus* are exclusive parasites of the inflorescences' staminodes (Franz, 2003b). They will only feed on and oviposit into these organs without ever contacting the pistillate flowers. The larvae develop within less than 10 days in the decaying leaf litter. The ephemerality of the staminodes creates a competitive situation among multiple visiting species. Some can locate and infest the cyclanth inflorescences days before they open and become strongly fragrant. At this point no reversals or further dissociations of these interactions are reported.

In summary, the analysis favours a number of unexpected findings concerning the evolutionary history of derelomine host plant associations (Figs 1, 76). The 'special quality' of reproducing on palm inflorescences has been transformed on at least four occasions; twice through a shift onto Cyclanthaceae. The life history traits – particularly of derelomine larvae – have undergone significant changes. The ability to pollinate has been lost several times, leading to more antagonistic interactions (see also Franz, 2004). For the most part, the field observations are well accommodated by the preferred phylogenetic hypothesis. The entirety of these results provides a solid framework for future studies on derelomines.

Revised phylogenetic classification

In spite of its New World emphasis, the present study is judged comprehensive enough to propose a revised phylogenetic system for derelomines (see Figs 74, 75; Table 2). The previously accepted classifications of Kuschel (1952), O'Brien & Wibmer (1982, 1984), Wibmer & O'Brien (1986, 1989), and especially of Alonso-Zarazaga & Lyal (1999) are appropriate reference points. Only seven mostly Old World genera (with nine total species) could not be placed within the new subtribal arrangement. For the sake of completeness, they are listed here as *Derelomini* incertae sedis.

Another issue of uncertainty relates to the classification of several entities within or near the acalyptines sensu Alonso-Zarazaga & Lyal (1999). Many of these Old World taxa are treated in an unpublished manuscript (dated from 2000) by Kojima & Morimoto. In fairness to the authors, specific placements of acalyptines into the current system were made only if they could be confirmed independently of their findings (see notes in Table 2). Additional transfers are likely but will have to be delayed until their work is published.

Following the analysis, there was an option to delimit derelomines more broadly (including the *Juanorhinus*–*Eisingius* clade), or more narrowly (excluding the *Acalyptus*–*Systemotelus* clade). The former solution appeared undesirable as *Juanorhinus* or *Trypetes* clearly

lack the morphological traits and ecological roles that most authors have associated with derelomines. The latter definition, in turn, would have allocated such often-cited taxa as *Phyllotrox* and thirteen additional genera outside the tribe. The current proposal preserves the highest amount of referential continuity; now the most significant change is the inclusion of acalyptines as a subtribe within derelomines (see Table 2). The other subtribal definitions reflect four major biological and biogeographical transitions within the tribe. A finer separation is not required at this point, particularly as individual clades can also be referenced by their apomorphies or by their delimiting members, as depicted in Figs 1, 74 and 75. Even after this analysis, derelomines remain a challenging taxonomic entity. This is partly a reflection of their complex evolutionary history.

Tribe *Derelomini* Lacordaire, 1866

Type. *Derelomus* Schoenherr, 1825.

Diagnosis. Maxillary palpomere I lacking centrolateral setae (character 24:1), absent in notolomines (see details below); maxillary palpomere II lacking centrolateral setae (character 29:1); pro-, meso-, and metatibial apices inermous (character 94:1), absent in *Elaeidobius*, *C. binotatus* and *C. cariniceps*, as well as in *Phytotribus*; adults feeding and reproducing only on angiosperm flowers and inflorescences, typically acting as pollinators (character 151:1); and predominantly associated with the inflorescences of *Arecaceae* (character 152:3; but see Discussion for further transformations).

Discussion. Derelomini now include several taxa previously situated outside the tribe, particularly the acalyptines, with the closely related *Eudela* Pascoe (1885) and *Eudelodes* Zimmerman (1994), **new placements**; and *Grasidius* and *Terires*, **new placements**, which were previously assigned to the Eirrhiniini and the Storeini, respectively (see Table 2; all higher-level entities not treated herein are sensu Alonso-Zarazaga & Lyal, 1999). On the other hand, a number of genera formerly listed as derelomines have now to be located elsewhere. According to the preferred cladogram (Figs 1, 74, 75), *Neopsilorhinus* should be transferred to the Eirrhiniidae: Eirrhiniini, **new placement**. *Pedetinus* is shifted to the Eugnomini, **new placement**. *Araucarietus*, *Eisingius*, and *Planus* most conservatively are moved to the Trypetidini (see also Kuschel, 1952; the tribe is in need of revision), **new placements**. The latter has the apomorphic tuberculate pronotum of the *Nanus*–*Eisingius* clade (character 74) and occurs on *Araucariaceae* (character 152; see also Kuschel, 2000). Finally, *Euryscapoides* is provisionally treated as Curculioninae incertae sedis, **new placement**. The male holotype of the only described species *E. feisthameli* (Chevrolat, 1878) has a superficial resemblance to *Anchylorhynchus* or *Phytotribus*. At closer inspection, however, it lacks the relevant apomorphies of this or any

other derelomine subclade (see, e.g. characters 47, 69, 70). A more precise assignment will have to await further studies.

In total, the number of derelomine genera has increased from thirty-seven in Alonso-Zarazaga & Lyal (1999) to forty-one under the current system. Three genera had been described in the meantime: *Cyclanthura*, *Ganglionus*, and *Staminodeus*. Two unnamed genera are not yet included in the count. This analysis further proposes nine additions (eight transfers and one new taxon), together with eight subtractions (six transfers and two synonymizations). The new subtribal arrangement is detailed below (see also Table 2).

The most closely related outgroup is the Juanorhiniini–Trypetidini clade (Figs 1, 74, 75). The question thus arises whether derelomines should be transferred from the Curculioninae to the Molytinae. This move has been resisted, as the characterizations of these two higher entities remain highly unsatisfactory (M. A. Alonso-Zarazaga, pers. comm.; see also Kuschel, 1987, 1995; Thompson, 1992; Anderson, 1993; Marvaldi, 1997; Marvaldi *et al.*, 2002). The current placement of the tribe should be retained until we have a more complete picture of the relationships among major clades within the Curculionidae.

Subtribe *Derelomina* Lacordaire, 1866

Type. *Derelomus* Schoenherr, 1825.

Diagnosis. Inner margin of galeo-lacinal complex of maxilla subcentrally with one to two more strongly sclerotized lacinal dentes (character 15:1); rostrum dorsally with multiple (typically five, yet ranging from two to seven) subparallel carinae extending (at least in males) from base to subapical region of rostrum (character 47:1); segments I and II of antennal club elongate-clavate (distinctly) longer than remaining segments combined (character 63:1); head, pronotum, and elytra covered with coarse scales as well as fine setae (character 69:1); and scales elongate, with lamellae projecting terminally as small acute tips (character 70:2).

Discussion. This distinctive and possibly very old subtribe contains only African and South American taxa. It is sister to all remaining derelomines. *Anchylorhynchus*, *Celetes*, *Derelomus*, and *Phytotribus* are abundant, diverse, and widely distributed taxa. All known species in the clade appear to visit and pollinate palm inflorescences. The adults typically oviposit into the detaching staminate flowers. The larval development is then finalized in the upper layers of the soil.

Lomederus Marshall (1932) and *Prosoestus* Faust (1899) share the key pronotal synapomorphy (character 75) of the *Elaeidobius*–*Derelomus* clade. *Neoderelomus* has distinctive male autapomorphies (see Hoffmann, 1938b) but is otherwise well nested within *Derelomus* (Fig. 1), **syn.n.** Its only species must be renamed *D. piriformis* (Hoffmann, 1938b), **comb.n.** (see also Table 2). The unexamined *Adisius*

Table 2. Summary of revised classification for derelomine flower weevils (see also Figs 74 and 75; and main text for diagnoses of taxa above the genus level), including new subtribal assignments within Derelomini, new taxa, new combinations, and other new placements within and outside the tribe. All changes are proposed strictly in reference to the system of Alonso-Zarazaga & Lyal (1999). If not directly based on the cladistic analysis, then their motivations are commented on.

-
- Tribe Derelomini Lacordaire, 1866: 9 (*Curculionidae: Curculioninae* Latreille, 1802: 195)
- Subtribe Derelomina Lacordaire, 1866: 9
- Anchylorhynchus* Schoenherr, 1835: 450
 - Celetes* Schoenherr, 1836: 634
 - Derelomus* Schoenherr, 1825: 583; now including *Neoderelomus* Hoffmann, 1938a: 107, **syn.n.**
 - Elaeidobius* Kuschel, 1952: 272
 - Grasidius* Champion, 1902: 128, **new placement**, from Erihirinini Schoenherr, 1825: 582
 - Lomederus*^a Marshall, 1932: 219
 - Phytotribus* Schoenherr, 1843: 181
 - Prosoestus*^{a,b} Faust, 1899: 409
 - Terires* Champion, 1902: 138, **new placement**, from Storeini Lacordaire, 1863: 494
- Subtribe Acalyptina Thomson, 1859: 143, **stat.n., new placement**
- Acalyptus* Schoenherr, 1833: 20
 - Amorphoidea* de Motschulsky, 1858: 78
 - Derelomorplus*^{a,c} Marshall, 1928: 546
 - Eudela*^{a,c} Pascoe, 1885: 237, **new placement**, from Curculioninae Latreille, 1802 (incertae sedis)
 - Eudelodes*^{b,c} Zimmerman, 1994: 665, **new placement**, from Curculioninae Latreille, 1802 (incertae sedis)
 - Meredolus*^{b,c} Marshall, 1935: 140
 - Niseida*^c Pascoe, 1885: 236
 - Nodocnemus* Marshall, 1931: 260
 - Parimera* Faust, 1896: 146
 - Tithene*^c Pascoe, 1874: 25
- Subtribe Notolomina Franz, **subtr.n.**
- Andranthobius* Kuschel, 1952: 272
 - Derelominus* Champion, 1902: 141
 - Diplothemiobius* Kuschel, 1952: 272
 - Notolomus* LeConte, 1876: 222
- Subtribe Phyllotrogina Franz, **subtr.n.**
- Androtrox* Franz, **gen.n.**, to accommodate *A. megalops* (Champion, 1902: 142; therein *Phyllotrox*)
 - Cotithene* Voss, 1940: 5
 - Cyclanthura* Franz, 2003a: 155
 - (Derelomini gen. 2)
 - Ganglionus* Franz & O'Brien, 2001a: 836
 - Perelleschus* Wibmer & O'Brien, 1986: 197
 - Phyllotrox* Schoenherr, 1843: 189; now including *Hypolesschus* Fall, 1907: 265, **syn.n.**
 - Pseudoderelomus* Champion, 1910: 184
 - Pygocoteles*^b Kuschel, 1955: 310
 - Systemotelus* Anderson & Gómez, 1997: 888
 - Terioltes* Champion, 1903: 146
- Subtribe Staminodeina Franz, **subtr.n.**
- (Derelomini gen. 1)
 - Staminodeus* Franz, 2001: 413
- Derelomini Incertae Sedis
- Adisius* Fairmaire, 1903: 230
 - Anthobius* Schoenherr, 1833: 19 (possibly to Eugnomini Lacordaire, 1863: 499; G. Kuschel, pers. comm.)
 - Electrotribus* Hustache, 1942: 108
 - Liothenus* Fairmaire, 1901: 244
 - Ochrophoebe* Pascoe, 1872: 139
 - Psilocaulus* Fairmaire, 1901: 243
 - Stethelasma* Frivaldszky, 1884: 2
- I. New combinations
- Andranthobius mariaehelena* (Bondar, 1941: 281), **comb.n.** for *Derelomus mariaehelena*
 - Androtrox megalops* (Champion, 1902: 142), **comb.n.** for *Phyllotrox megalops*
 - Derelomus piriformis* (Hoffmann, 1938b: 47), **comb.n.** for *Neoderelomus piriformis*
 - Phyllotrox atratus* (Fall, 1907: 266; in Fall & Cockerell, 1907), **comb.n.** for *Hypolesschus atratus*
 - Phyllotrox tatiana* (Bondar, 1941: 280), **comb.n.** for *Derelomus tatiana*
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Table 2. Continued.

II. Taxa previously belonging to Derelomini and now placed elsewhere

Araucarietus Kuschel, 1952: 275, **new placement**, to Trypetidini Lacordaire, 1866: 177

Eisingius Kuschel, 1952: 277, **new placement**, to Trypetidini Lacordaire, 1866: 177

Euryscapoides^b Wibmer & O'Brien, 1986: 198, **new placement**, to Curculioninae Latreille, 1802 (incertae sedis)

Neopsilorhinus Bovie, 1907: 67, **new placement**, to Eirrhinidae: Eirrhinini Schoenherr, 1825: 582

Pedetinus Faust, 1895: 361, **new placement**, to Eugnomini Lacordaire, 1863: 499

Planus^b Kuschel, 1952: 273, **new placement**, to Trypetidini Lacordaire, 1866: 177

^aBased on a review of the pertinent literature (illustrations and circumscriptions), e.g. Ramamurthy & Ghai (1989) in the case of *Derelomorphus*.

^bBased on a personal examination of specimens.

^cIn agreement with an unpublished manuscript on Asian acalyptines by H. Kojima & K. Morimoto (Kyushu University, Japan; see also Kojima & Morimoto, 1995). That work also tentatively places *Sphincticraeropsis* Voss (1944: 50; formerly Acalyptini Thomson, 1859: 143) in the Tychiini Thomson (1859: 142).

Fairmaire (1903), *Liothenus* Fairmaire (1901), and *Psilocaulus* Fairmaire (1901) occur on Madagascar. They are probably part of this subtribe as well.

Subtribe Acalyptina Thomson, 1859; stat.n., new placement

Type. *Acalyptus* Schoenherr, 1833.

Diagnosis. Maxillary stipes apically (in addition to the larger central seta(e)) with one or two relatively small seta(e) projecting to outer margin (character 6:1); maxillary palpiger apically with one row of numerous, relatively large setae (character 22:1); procoxal cavities narrowly separated by distance not exceeding breadth of antennal club (character 81:1; broadly separated in Parimera); anterodorsal margins of meso- and metatibial apices with setal comb ascending to apical sixth to third of dorsal tibial margin (character 97:1); and each posterior margin of elytra individually rotundate, separate-truncate (character 100:1).

Discussion. The number of acalyptine genera has increased from five to ten through this study (see Table 2). All are now placed within the Derelomini. The new subtribe is quite diverse yet fairly easy to diagnose. With the exception of the holarctic *Acalyptus*, these weevils are pollinators (predominantly of palms) and distributed throughout much of tropical Asia and Australia. A completed, but unpublished manuscript by Kojima & Morimoto will contribute significantly to our knowledge of their morphology, taxonomy, and ecology. The unexamined *Ochrophoebe* Pascoe (1872; described from Australia) and *Stethelasma* Frivaldszky (1884; described from Turkey) may also be located here.

Subtribe Notolomina Franz, subtr.n

Type. *Notolomus* LeConte, 1876; by present designation.

Diagnosis. Maxillary stipes basally (in addition to the larger central seta(e)) with one (to two to four in *Diplothemobius*) relatively small seta(e) projecting to outer margin (character 4:1); apical region of galeo-

lacinial complex of maxilla with numerous (minimally five to ten) relatively large, distinctly arcuate (reflexed) yet only regularly sclerotized setae (character 13:2); lacinial dentes apically (variously) bifurcate, terminating in two separate projections (character 16:1); maxillary palpomere I with two distinct setae present in centrolateral region (character 24:0 and character 25:1); labial palpomere I apicolaterally with two to three closely associated setae (character 41:1); and labial palpomere III with one (relatively) small seta present and positioned centrally (to apically) along inner margin (character 45:1).

Discussion. The notolomines are a small yet apparently old New World lineage, and sister to the large *Pseudoderelomus*-*Systemotelus* clade (Figs 74, 75). *Diplothemobius* is highly distinctive and resembles only vaguely the related *Derelominus*. Perhaps 'intermediate' taxa will still be discovered in the future, or have become extinct. *Notolomus* is a North American palm-associated and palm-pollinating taxon (Brown, 1976). A number of undescribed species occur on Caribbean Islands (C. W. O'Brien, pers. comm.). The South American *Derelomus mariaehelena* is transferred to *Andranthobius*, as *A. mariaehelena* (Bondar, 1941), **comb.n.** Apparently, *Derelomus* is restricted to the Old World.

Subtribe Phyllotrogina Franz, subtr.n.

Type. *Phyllotrox* Schoenherr, 1843; by present designation.

Diagnosis. Galeo-lacinial complex of maxilla subapically with one to two small, arcuate, strongly sclerotized setae, separate and distinct from lacinial dentes (character 12:1); inner margin of galeo-lacinial complex subcentrally with one to two more strongly sclerotized lacinial dentes, in comparison with adjacent ones (character 15:1); outer margin of maxillary palpomere subapically with one isolated, small seta (character 21:1); maxillary palps two-segmented (character 23:1); labial palpomeres I and II without apicolateral setae (character 40:1 and character 44:1); prosternum ventrally (anterior to procoxal cavities) with distinct, relatively long (occasionally

shorter, pubescent), fine and densely arranged vestiture (character 79:1); posterior margin of wing with distinctly longer macrosetae along basal fifth (character 112:1); and male (genital) tegminal arms subrectate to (slightly) arcuate, diverging, apically not connected, ring open (character 128:1), reversed in *Cyclanthura* and in *Ganglionus*.

Discussion. This mostly Neotropical subtribe is relatively young, and sister to the Notolomina. It appears to be the most diverse among derelomines, outnumbering even the Derelomina in genera and species. It also includes many significant transitions to nonpalm host plants and more antagonistic life history traits, e.g. in *Cotithene*, *Cyclanthura*, and *Systemotelus*. Derelomini gen. 2 contains undescribed taxa that are the primary pollinators of species-rich members of Cyclanthaceae, such as *Asplundia*, *Dicranopygium*, and *Sphaeradenia* Harling (see Gottsberger, 1991; Eriksson, 1994a; Franz, 1999). The central South American cyclanth-associated weevils are still almost entirely unknown. *Pygoceletes* is probably most closely related to *Terioltes* and should occur on palms.

Phyllotrox remains by far the most problematic entity within derelomines. This analysis should be viewed merely as a framework for a future major revision. Again the taxon sampling is least comprehensive for South American species such as *P. rubiginosus* Faust (1894; see also Voss, 1954) or *P. tatianae* (Bondar, 1941), **comb.n.**, which was incorrectly placed in *Derelomus*. The North American *Hypolesschus* is nested within *Phyllotrox*, **syn.n.**, and its only species is thus renamed *P. atratus* (Fall, 1907), **comb.n.** It is part of the better-defined *P. ater*–*P. suturalis* clade that includes the type species *P. semirufus*, and is treated here as *Phyllotrox* in the strict sense (see Figs 74, 75). The wider notion of *Phyllotrox* also contains *P. pallidus* Fåhræus (1843; in Schoenherr, 1843), *P. rubiginosus*, and *P. tatianae*. Although the latter species render *Phyllotrox* paraphyletic, the current nomenclatural solution was judged more appropriate than erecting three new and poorly defined genera to accommodate them.

Androtrox Franz, **gen.n.**

Type. *Androtrox megalops* (Champion, 1902), **comb.n.** (for *Phyllotrox megalops*), by present designation.

Diagnosis. Small (c. 2.0 mm), light reddish-brown, similar to *Phyllotrox* and *Cyclanthura* (see also Champion, 1902: 142; Franz, 2003a for a more detailed description); although with rostrum narrower and more arcuate, eyes very large, completely contiguous along frons; apical margin of labial palpomere rotundate, not projected (character 43:0), and lacking a distinct male/female dimorphism in the shape and orientation of the pygidium (character 116:0). Moreover, maxillary lacinial dentes apically bifurcate (as convergently present in Notolomina; character 16:1), labial palps two-segmented

(character 37:1), and procoxal cavities narrowly separated (character 81:1); associated with the inflorescences of palms (character 152:3).

Discussion. This Central American taxon superficially resembles *P. pallidus*, but nevertheless displays a combination of traits not present in any other derelomine. The erection of a new genus for *A. megalops* is thus fully supported by the cladistic analysis (Figs 1, 74, 75).

Etymology. Named so as to express its 'sharing' of properties with other species assigned to *Andranthobius* ('*Andro-*') and *Phyllotrox* ('*-trox*'). The gender is masculine.

Subtribe *Staminodeina* Franz, **subtr.n.**

Type. *Staminodeus* Franz, 2001, by present designation.

Diagnosis. Apical margin of labial prementum with two distinct triangular projections (character 34:1); labial palps two-segmented (character 37:1); labial palpomere I centrally and apicolaterally without large setae (character 39:1 and character 40:1); lateral margins of stalk of metendosternite slightly convex (character 87:1); wing with large, well-developed anal lobe (character 111:2); male (genital) tegminal arms subrectate to (slightly) arcuate, diverging, apically not connected, ring open (character 128:1); exclusively associated with the inflorescences of Cyclanthaceae (character 152:4); and adults ovipositing only into the ephemeral staminodes (character 154:1).

Discussion. This exclusively Neotropical lineage is possibly the youngest among the newly recognized subtribes. Its presumed sister are the Acalyptina, and together they are sister to the Notolomina–Phyllotrogina clade (Fig. 75). Its species are specialized parasites whose adults oviposit into the staminodes of Cyclanthaceae. Derelomini gen. 1 contains at least five to ten undescribed species with considerable variations in size and rostral shapes.

Supplementary material

The data matrix is available at: <http://www.blackwell-synergy.com>

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Appendix 1. Character matrix for the cladistic analysis of derelomine flower weevils, with selected outgroup taxa (strictly alphabetical; also see text). In total, 155 characters and 115 taxa are represented (corresponding to 17 825 possible assignments of states). The twenty multistate characters are marked (on top of each column) with '+' (nine additive) and '-' (eleven nonadditive). Inapplicable and missing character states are represented (within the matrix) by '-' and '?', whereas a single asterisk stands for a '1, 2' subset polymorphism in *P. lineatus* (character 70). The matrix is available as Supplementary Material.

		10		20		30		40		50		60
	-	-	+	-	-	+	-	+	-	+	-	-
<i>Notaris acridulus</i>	00000	00000	0000-	-0000	-1000	00000	00000	00000	00000	00000	00000	00000
<i>Acalyptus carpini</i>	00000	10000	00010	00010	-101-	20011	00001	-1000	000-0	00000	00000	00000
<i>Amalactus nigritus</i>	00000	00000	00010	00000	-001-	00010	00000	00000	00000	00000	00000	00000
<i>Amorphoidea lata</i>	00000	10000	00010	00010	-101-	20011	00001	-1000	000-0	00000	00000	00000
<i>Anchylorhynchus aegrotus</i>	10000	00100	00011	00100	-001-	10110	00100	00000	20001	01000	00000	01001
<i>Anchylorhynchus eriospathae</i>	10000	00000	00011	00100	-001-	10110	00100	00000	20001	01000	00000	01001
<i>Anchylorhynchus trapezicollis</i>	10000	00100	00011	00100	-001-	10110	00100	00000	20001	01000	00000	01001
<i>Anchylorhynchus tricarinatus</i>	10000	00100	00011	00100	-001-	10110	00100	00000	20001	01000	00000	01001
<i>Anchylorhynchus variabilis</i>	10000	00100	00011	00100	-001-	10110	00100	00000	20001	01000	00000	01001
<i>Andranthobius argentinensis</i>	00010	00000	00210	10011	00001	01010	01000	00000	10001	00000	00000	00000
<i>Andranthobius estriatus</i>	00010	00000	00210	10011	00001	01010	01000	00000	10001	00000	00000	00000
<i>Andranthobius palmarum</i>	00010	00000	00210	10011	00001	01010	01000	00000	10001	00000	00000	00000
<i>Anthonomus corvulus</i>	00000	00000	00010	00001	00000	00000	00000	00000	00000	00000	00000	00000
<i>Araucarietetus viridans</i>	01000	00000	00010	00000	-001-	00010	01000	00000	00001	00000	00000	00000
<i>Celetes binotatus</i>	00000	00010	00111	00000	-001-	00010	10000	00000	00001	02000	00000	00000
<i>Celetes cariniceps</i>	00000	00010	00111	00000	-001-	00010	10000	00000	00001	02000	00000	00000
<i>Celetes crispus</i>	00000	00000	00111	00000	-001-	00010	10000	00000	00001	02000	00000	00000
<i>Celetes impar</i>	00000	00000	00111	00000	-001-	00010	10000	00000	00001	02000	00000	00000
<i>Celetes landeroi</i>	00000	00000	00111	00000	-001-	00010	10000	00000	00001	02000	00000	00000
<i>Celetes marizae</i>	00000	00000	00111	00000	-001-	00010	10000	00000	00001	02100	00000	00000
<i>Celetes pallidus</i>	00000	00010	00111	00000	-001-	00010	10000	00000	00001	02000	00000	00000
<i>Celetes tarsalis</i>	00000	00000	00111	00000	-001-	00010	10000	00000	00001	02100	00000	00000
<i>Cotithene globulicollis</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00001	00010	00000
<i>Cotithene</i> sp. 1	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00001	00010	00000
<i>Curculio proboscideus</i>	00200	00000	0000-	-0000	-1000	00000	00000	01001	-00-0	00000	00000	00000
<i>Cyclanthura carinata</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Cyclanthura crepidula</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Cyclanthura laticola</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Cyclanthura pilosa</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Cyclanthura striata</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Derelomini</i> gen. 1 sp. 1	00000	00000	00010	00010	-001-	20011	00011	-1011	-00-0	00000	00000	00000
<i>Derelomini</i> gen. 1 sp. 2	00000	00000	00010	00010	-001-	20011	00011	-1011	-00-0	00000	00000	00000
<i>Derelomini</i> gen. 1 sp. 3	00000	00000	00010	00010	-001-	20011	00011	-1011	-00-0	00000	00000	00000
<i>Derelomini</i> gen. 2 sp. 1	00000	01-00	11011	01011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Derelomini</i> gen. 2 sp. 2	00000	01-00	11011	01011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Derelomini</i> gen. 2 sp. 3	00000	01-00	11011	01011	1011-	000--	01000	10001	-0110	00000	00000	00000
<i>Derelominus piceus</i>	00010	00000	00210	10011	00001	00010	01000	00000	10011	00000	00000	00001
<i>Derelomus abyssinicus</i>	00000	00001	00011	00000	-001-	00010	01000	00000	10000	01000	00000	00000
<i>Derelomus auberti</i>	00000	00001	00011	00000	-001-	00010	01000	00000	10000	01000	00000	00000
<i>Derelomus bicarinatus</i>	00000	00001	00011	00000	-001-	00010	01000	00000	10000	01000	00000	00000
<i>Derelomus chamaeropsis</i>	00000	00001	00011	00000	-001-	00010	01000	00000	10000	01000	00000	00000
<i>Derelomus costifer</i>	00000	00001	00011	00000	-001-	00010	01000	00000	10000	01000	00000	00000
<i>Derelomus mariaehelenae</i>	00010	00000	00210	10011	00001	01010	01000	00000	10001	00000	00000	00000
<i>Derelomus</i> sp. 1	00000	00001	00011	00000	-001-	00010	01000	00000	10000	01000	00000	00000
<i>Derelomus tatiannae</i>	00000	01-00	01011	00011	1011-	000--	01000	00001	-0110	00000	00000	00000
<i>Diplothemobius sternicornis</i>	00010	00000	00210	10011	00001	00010	01000	00000	10011	00000	00000	00000
<i>Dorytomus hirtus</i>	00000	00000	00010	00001	00000	00000	00000	00000	00000	00000	00000	00000
<i>Eisingius araucariae</i>	01100	00000	00010	00000	-001-	00010	01000	00000	00001	01000	00001	00000
<i>Eisingius chusqueae</i>	01100	00000	00010	00000	-001-	00010	01000	00000	00001	01000	00001	00000
<i>Elaeidobius kamerunicus</i>	00000	00001	00011	00000	-001-	00010	00000	00000	10000	01000	00000	10000
<i>Elaeidobius subvittatus</i>	00000	00001	00011	00000	-001-	00010	00000	00000	10000	01000	00000	10000
<i>Ellescus ephippiatus</i>	00000	00000	00010	00001	00000	00000	00000	00000	00000	00000	00000	00000
<i>Erodiscus tinamus</i>	00200	00000	0000-	-0000	-1000	00000	--000	01001	-00-0	00000	00000	00000
<i>Ganglionus constrictus</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	11000	00000
<i>Ganglionus mitigatus</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	10000	00000
<i>Ganglionus undulatus</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	00000	11000	00000

<i>Grasidius</i> sp. 1	00000	00000	00011	00000	-001-	00010	10000	00000	00001	01000	00000	00000
<i>Hypolesschus atratus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Juanorhinus ruficeps</i>	00000	00001	00010	00000	-0000	00000	00000	00000	00001	00000	00000	00000
<i>Nanus uniformis</i>	01000	00001	00010	00000	0000	00000	01000	00000	00001	00000	00000	00000
<i>Neoderelomus piriformis</i>	00000	00001	00011	00000	-001-	00010	01000	00000	10000	01000	00000	00000
<i>Neopsilorhinus collaris</i>	00000	00000	0000-	-0000	-0000	00000	00000	00000	00000	01000	00000	00000
<i>Neopsilorhinus modestus</i>	00000	00000	0000-	-0100	-0000	00000	00000	00000	00000	01000	00000	00000
<i>Neopsilorhinus variegatus</i>	00000	00000	0000-	-0100	-0000	00000	00000	00000	00000	01000	00000	00000
<i>Nodocnemus</i> sp. 1	00000	10000	00010	00010	-101-	20011	00001	-0000	00001	00000	00000	00000
<i>Notolomus basalis</i>	00010	00000	00210	10011	00001	01010	01000	00000	10001	00000	00000	00000
<i>Notolomus bicolor</i>	00010	00000	00210	10011	00001	01010	01000	00000	10001	00000	00000	00000
<i>Omoides humeralis</i>	00000	00000	0000-	-0000	-0002	001-0	00000	01000	010-0	00000	00000	00100
<i>Parimera variabilis</i>	00000	10000	00010	00010	-101-	20011	00001	-0000	00001	00000	00000	00000
<i>Pedetinus flavipes</i>	00000	00000	0000-	-0000	-1002	000-0	00000	00000	01000	00000	00000	02010
<i>Pedetinus halticoides</i>	00000	00000	0000-	-0000	-1002	000-0	00000	00000	01000	00000	00000	02010
<i>Perelleschus carludovicae</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0210	00000	00000	00000
<i>Perelleschus evelynae</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0210	00000	00000	00000
<i>Perelleschus rectirostris</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0210	00000	00000	00000
<i>Phyllotrox aristidis</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox ater</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox canyonaceris</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox crassipes</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox derivatus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox ferrugineus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox marcidus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox mecinooides</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox megalops</i>	00000	01-00	01011	10011	1011-	000--	01000	01001	-00-0	00000	00000	00000
<i>Phyllotrox nubifer</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox pallidus</i>	00000	01-00	01011	00011	1011-	000--	01000	00001	-0110	00000	00000	00000
<i>Phyllotrox quadricollis</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox rubiginosus</i>	00000	01-00	01011	00011	1011-	000--	01000	00001	-0110	00000	00000	00000
<i>Phyllotrox rufipes</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox rutilus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox sejunctus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox semirufus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox sericeus</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox suturalis</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phyllotrox variabilis</i>	00000	01-00	01011	00011	1011-	000--	01000	00101	-0110	00000	00000	00000
<i>Phytotribus lineatus</i>	00000	00000	00111	00001	0001-	00010	10000	00000	00001	02000	00000	00000
<i>Phytotribus</i> sp. 1	00001	00000	00111	00001	0001-	00010	10000	00000	00001	02000	00000	00000
<i>Phytotribus unicolor</i>	00001	00000	00111	00001	0001-	00010	10000	00000	00001	02000	00000	00000
<i>Platyanus sericatus</i>	01000	00001	00010	00000	-001-	00010	01000	00000	00001	00000	00000	00000
<i>Pseudoderelomus baridiiformis</i>	00000	00000	01011	00011	1011-	000--	01000	00001	-0010	00000	00000	00000
<i>Pseudoderelomus</i> sp. 1	00000	00000	01011	00011	1011-	000--	01000	00001	-0010	00000	00000	00000
<i>Smicronyx griseus</i>	00000	00000	0000-	-0000	-0000	00000	00000	00000	00000	00000	00000	00000
<i>Staminodeus curvibtibialis</i>	00000	00000	00010	00010	-001-	20011	00011	-1011	-00-0	00010	00000	00000
<i>Staminodeus inermis</i>	00000	00000	00010	00010	-001-	20011	00011	-1011	-00-0	00010	00000	00000
<i>Staminodeus vectoris</i>	00000	00000	00010	00010	-001-	20011	00011	-1011	-00-0	00010	00000	00000
<i>Systemotelus carludovicae</i>	00001	01-00	11011	00020	-011-	000--	02000	11001	-02-0	00000	00000	00000
<i>Systemotelus costaricensis</i>	00001	01-00	11011	00020	-011-	000--	02000	11001	-02-0	00000	00000	00000
<i>Systemotelus stockwelli</i>	00000	01-00	11011	00020	-011-	000--	01000	11001	-02-0	00000	00000	00000
<i>Tadius erhinoides</i>	00000	00000	0000-	-0000	-0000	00000	--000	00000	00000	00000	00000	00000
<i>Terioltes circumdatus</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	10000	00100	00000
<i>Terioltes nigripennis</i>	00000	01-00	11011	00011	1011-	000--	01000	10001	-0110	10000	00100	00000
<i>Terires pilosus</i>	00000	00000	00011	00000	-001-	00010	10000	00000	00001	00000	00000	00000
<i>Terires plurisetosus</i>	00000	00000	00011	00000	-001-	00010	10000	00000	00001	00000	00000	00000
<i>Trypetes politus</i>	0100-	00001	00010	00000	-0000	00000	00000	00000	00001	00000	00000	00000
<i>Tychius lineellus</i>	00000	00000	0000-	-0000	-0000	00000	00000	01001	-00-0	00000	00000	00000
<i>Udeus</i> sp. 1	00000	00000	0000-	-0000	-0002	001-0	00000	01000	010-0	00000	00000	00100

Appendix 1. Continued.

	70		80		90		100		110		120	
	--	+	--	+	--	+	--	+	--	+	--	+
<i>Notaris acridulus</i>	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000
<i>Acalyptus carpini</i>	10000	0002-	-0000	00000	10001	00100	0001-	01001	0000-	00001	10100	00000
<i>Amalactus nigritus</i>	00000	000--	-0000	00000	00000	00100	00000	00000	0000-	00000	00000	00000
<i>Amorphoidea lata</i>	10000	0002-	-0000	00000	10001	00101	0001-	01101	0000-	00001	10100	00000
<i>Anchylorhynchus aegrotus</i>	00100	00012	00100	00000	00001	00101	0001-	00000	00000	00001	00110	00000
<i>Anchylorhynchus eriospathae</i>	00100	00012	00100	00000	00001	00101	0001-	00000	00000	00001	00110	00000
<i>Anchylorhynchus trapezicollis</i>	00100	00012	00100	00000	00001	00101	0001-	00000	00000	00001	00110	00000
<i>Anchylorhynchus tricarinatus</i>	00110	00012	00100	00000	00001	00101	0001-	00000	00000	00001	00110	00000
<i>Anchylorhynchus variabilis</i>	00110	00012	00100	00000	00001	00101	0001-	00000	00000	00001	00110	00000
<i>Andranthobius argentinensis</i>	10000	0102-	-0000	00001	10001	00110	0001-	00000	0000-	00001	00100	00000
<i>Andranthobius estriatus</i>	10000	0102-	-0000	00001	10001	00110	0001-	00000	0000-	00001	00100	00000
<i>Andranthobius palmarum</i>	10000	0102-	-0000	00001	10001	00110	0001-	00000	0000-	00001	00100	00000
<i>Anthonomus corvulus</i>	00000	00000	00000	00000	00000	00101	00000	00000	00000	00000	00100	00000
<i>Araucarietius viridans</i>	00001	00000	00010	00100	21101	00120	0001-	01000	00000	00001	00100	00000
<i>Celetes binotatus</i>	0010-	00012	10100	00000	10001	10101	00000	00000	00000	00001	00100	00000
<i>Celetes cariniceps</i>	0010-	00012	10100	00000	00001	10101	00000	00000	00000	00001	00100	00000
<i>Celetes crispus</i>	0010-	00012	10000	00000	00001	10101	0001-	00000	00000	00001	00100	00000
<i>Celetes impar</i>	0011-	00012	10000	00000	00001	10101	0001-	00000	00000	00001	00100	00000
<i>Celetes landeroi</i>	0011-	00012	10000	00000	00001	10101	0001-	00000	00000	00001	00100	00000
<i>Celetes marizae</i>	0010-	00012	10000	00000	00001	10101	0001-	00000	00000	00001	00100	00000
<i>Celetes pallidus</i>	0010-	000--	-0000	00000	20001	10101	0001-	00000	00000	00001	00100	00000
<i>Celetes tarsalis</i>	0010-	00012	10000	00000	00001	10101	0001-	00000	00000	00001	00100	00000
<i>Cotithene globulicollis</i>	10000	0102-	-1000	00010	10001	00110	0001-	00000	0000-	00001	01100	10000
<i>Cotithene</i> sp. 1	10000	0102-	-1000	00010	10001	00110	0001-	00000	0000-	00001	01100	10000
<i>Curculio proboscideus</i>	00000	00001	00000	00000	00000	00101	00000	00000	00000	00000	00000	00000
<i>Cyclanthura carinata</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	1100-	00001	01100	10000
<i>Cyclanthura crepidula</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	1000-	00001	01100	10000
<i>Cyclanthura laticola</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	1000-	00001	01100	10000
<i>Cyclanthura pilosa</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	1000-	00001	01100	10000
<i>Cyclanthura striata</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	1100-	00001	01100	10000
<i>Derelomini</i> gen. 1 sp. 1	10000	0002-	-0000	00000	00001	01100	0001-	00000	0000-	00101	20100	00000
<i>Derelomini</i> gen. 1 sp. 2	10000	0002-	-0000	00000	00001	01100	0001-	00000	0000-	00101	20100	00000
<i>Derelomini</i> gen. 1 sp. 3	10000	0002-	-0000	00000	00001	01100	0001-	00000	0000-	00101	20100	00000
<i>Derelomini</i> gen. 2 sp. 1	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Derelomini</i> gen. 2 sp. 2	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Derelomini</i> gen. 2 sp. 3	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Derelominus piceus</i>	00000	0002-	-0000	00000	00001	00110	0001-	00000	0000-	00001	00100	00000
<i>Derelomus abyssinicus</i>	00100	00012	00001	00000	10001	00110	0001-	00010	00010	00011	10100	00000
<i>Derelomus auberti</i>	00100	00012	00002	00000	10001	00110	0001-	00010	00020	00001	10100	00000
<i>Derelomus bicarinatus</i>	00100	00012	00002	00000	10001	00110	0001-	00010	00120	00001	10100	00000
<i>Derelomus chamaeropsis</i>	00100	00012	00002	00000	10001	00110	0001-	00010	00020	00001	10100	00000
<i>Derelomus costifer</i>	00100	00012	00002	00000	10001	00110	0001-	00010	00120	00001	10100	00000
<i>Derelomus mariaehelenae</i>	10000	0102-	-0000	00001	10001	00110	0001-	00000	0000-	00001	00100	00000
<i>Derelomus</i> sp. 1	00100	00012	00001	00000	10001	00110	0001-	00010	00010	00011	10100	00000
<i>Derelomus tataniae</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Diplothemibius sternicornis</i>	00000	0002-	-0000	00000	00001	00110	0001-	00000	0000-	00001	00100	00000
<i>Dorytomus hirtus</i>	00000	00000	00000	00000	00000	00101	00000	00000	00000	00000	00100	00000
<i>Eisingius araucariae</i>	00001	00000	00010	00100	21101	00120	00000	00000	00000	00001	00100	00000
<i>Eisingius chusqueae</i>	00001	00000	00010	00100	21101	00120	00000	00000	00000	00001	00100	00000
<i>Elaeidobius kamerunicus</i>	00100	00012	00001	00000	10001	00110	00000	00000	00010	00001	10100	00000
<i>Elaeidobius subvittatus</i>	00100	00012	00001	00000	10001	00110	00000	00000	00010	00001	10100	00000
<i>Ellescus ephippiatus</i>	00000	00000	00000	00000	00000	00101	00000	00000	00000	00000	00100	00000
<i>Erodiscus tinamus</i>	00000	000--	-0000	00000	00000	00101	00000	00000	0000-	0000-	--000	00000
<i>Ganglionus constrictus</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	10000
<i>Ganglionus mitigatus</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	10000
<i>Ganglionus undulatus</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	10000
<i>Grasidius</i> sp. 1	0010-	00012	10000	00000	00001	10100	0001-	00000	00000	00001	00100	00000

<i>Hypoleschus atratus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Juanorhinus ruficeps</i>	00000	000--	-0000	00000	20101	00120	00000	00000	0000-	0000-	--100	00000
<i>Nanus uniformis</i>	00001	00000	00010	00000	20101	00120	00001	00000	00000	00001	00100	00000
<i>Neoderelomus piriformis</i>	00100	00012	00002	00000	10001	00110	0001-	00010	00120	00001	10100	00000
<i>Neopsilorhinus collaris</i>	00000	00001	00000	00000	00000	00000	00000	00000	00001	00000	00000	00010
<i>Neopsilorhinus modestus</i>	00000	00001	00000	00000	00000	00000	00000	00000	00001	00000	00001	00010
<i>Neopsilorhinus variegatus</i>	00000	00001	00000	00000	00000	00000	00000	00000	00001	00000	00001	00010
<i>Nodocnemus</i> sp. 1	00000	0002-	-0000	10000	10001	00100	0011-	01001	0000-	00001	10100	00000
<i>Notolomus basalis</i>	10000	0102-	-0000	10000	00001	00110	0001-	00100	0000-	00001	00100	00000
<i>Notolomus bicolor</i>	10000	0102-	-0000	10000	00001	00110	0001-	00100	0000-	00001	00100	00000
<i>Omoides humeralis</i>	00000	00000	00000	00000	00000	00001	0001-	00000	00000	00000	00100	00001
<i>Parimera variabilis</i>	00000	0002-	-0000	00000	20001	00100	0011-	01001	0000-	00001	10100	00000
<i>Pedetinus flavipes</i>	00000	0002-	-0000	01000	00001	00000	0001-	00001	0000-	00000	00100	00001
<i>Pedetinus halticoides</i>	00000	0002-	-0000	01000	00001	00000	0001-	00001	0000-	00000	00100	00001
<i>Perelleschus carludovicæ</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	10000
<i>Perelleschus evelynæ</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	10000
<i>Perelleschus rectirostris</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	10000
<i>Phyllotrox aristidis</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	10001	01100	10100
<i>Phyllotrox ater</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Phyllotrox canyonaceris</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox crassipes</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	10001	01100	10100
<i>Phyllotrox derivatus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox ferrugineus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox marcidus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox mecinoïdes</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	10001	01100	10100
<i>Phyllotrox megalops</i>	10000	0102-	-0000	00010	10001	00110	0001-	00000	0000-	00001	01100	00000
<i>Phyllotrox nubifer</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	10001	01100	10100
<i>Phyllotrox pallidus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Phyllotrox quadricollis</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	10001	01100	10100
<i>Phyllotrox rubiginosus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Phyllotrox rufipes</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Phyllotrox rutilus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox sejunctus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox semirufus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox sericeus</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10100
<i>Phyllotrox suturalis</i>	10000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	10001	01100	10100
<i>Phyllotrox variabilis</i>	10000	0102-	-0000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Phytotribus lineatus</i>	0011-	0001*	10000	00000	00000	10101	00000	00000	00000	00001	00100	00000
<i>Phytotribus</i> sp. 1	0011-	00012	10000	00000	00001	10101	00000	00000	00000	00001	00100	00000
<i>Phytotribus unicolor</i>	0011-	00012	10000	00000	00001	10101	00000	00000	00000	00001	00100	00000
<i>Platynanus sericatus</i>	00001	00000	00010	00000	20101	00120	00001	00000	00000	0000-	--100	00000
<i>Pseudoderelomus baridiiformis</i>	11000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	00000
<i>Pseudoderelomus</i> sp. 1	11000	0102-	-0000	00010	00001	00110	0001-	10000	0000-	00001	01100	00000
<i>Smicronyx griseus</i>	00000	00001	00000	00000	00000	00100	00000	00000	00000	00000	00000	00000
<i>Staminodeus curvitiibialis</i>	10000	1002-	-0000	00000	00001	01100	1101-	00000	0000-	00001	20100	00000
<i>Staminodeus inermis</i>	10000	1002-	-0000	00000	00001	01100	0001-	00000	0000-	00001	20100	00000
<i>Staminodeus vectoris</i>	10000	1002-	-0000	00000	00001	01100	1101-	00000	0000-	00001	20100	00000
<i>Systemotelus carludovicæ</i>	10000	0102-	-0000	00010	00011	00110	0001-	10000	0000-	01001	01100	11000
<i>Systemotelus costaricensis</i>	10000	0102-	-0000	00010	00011	00110	0001-	10000	0000-	01001	01100	11000
<i>Systemotelus stockwelli</i>	10000	0102-	-0000	00010	00011	00110	0001-	10000	0000-	00001	01100	11000
<i>Tadius erhinoïdes</i>	00000	00001	10000	00000	-0000	00000	00000	00000	00000	00000	00000	00010
<i>Terioltes circumdatus</i>	10000	0112-	-1000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Terioltes nigripennis</i>	10000	0112-	-1000	00010	00001	00110	0001-	00000	0000-	00001	01100	10000
<i>Terires pilosus</i>	0010-	00012	10000	00000	00001	10100	0001-	00000	00000	00001	00100	00000
<i>Terires plurisetosus</i>	0010-	00012	10000	00000	00001	10100	0001-	00000	00000	00001	00100	00000
<i>Trypetes politus</i>	00000	000--	-0000	00000	20101	00100	00001	00000	0000-	00001	00100	00000
<i>Tychius lineellus</i>	00000	00001	00000	00000	00000	00100	00000	00000	00000	00000	00000	00000
<i>Udeus</i> sp. 1	00000	00000	10000	00000	00000	00001	0001-	00000	00000	00000	00100	00001

Appendix 1. Continued.

	130	+	140		150	-	-
<i>Notaris acridulus</i>	00000	00000	00000	00000	00000	00000	00---
<i>Acalyptus carpini</i>	00000	2-000	00000	10000	00000	00000	15--0
<i>Amalactus nigritus</i>	00000	10000	00000	00000	00000	00000	??--?
<i>Amorphoidea lata</i>	00000	2-000	00000	10000	00000	00000	13--0
<i>Anchylorhynchus aegrotus</i>	01000	10000	00000	00100	00000	00000	13--0
<i>Anchylorhynchus eriospathae</i>	01000	10000	00000	00100	00000	00000	13--0
<i>Anchylorhynchus trapezicollis</i>	01000	10000	00000	00100	00000	00000	13--0
<i>Anchylorhynchus tricarinatus</i>	01000	10000	00000	00100	00000	00000	13--0
<i>Anchylorhynchus variabilis</i>	01000	10000	00000	00100	00000	00000	13--0
<i>Andranthobius argentinensis</i>	10000	2-000	00010	00000	01000	00000	13--0
<i>Andranthobius estriatus</i>	10000	2-000	00010	00000	01000	00000	13--0
<i>Andranthobius palmarum</i>	10000	2-000	00010	00000	01000	00000	13--0
<i>Anthonomus corvulus</i>	00000	2-000	00000	00000	00000	00000	05---
<i>Araucarietius viridans</i>	00000	2-000	00000	00000	00000	00000	05---
<i>Celetes binotatus</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Celetes cariniceps</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Celetes crispus</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Celetes impar</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Celetes landeroi</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Celetes marizae</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Celetes pallidus</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Celetes tarsalis</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Cotithene globulicollis</i>	00000	2-100	00000	00000	00010	00000	14000
<i>Cotithene</i> sp. 1	00000	2-100	00000	00000	00010	00000	14000
<i>Curculio proboscideus</i>	00000	10000	00000	00000	00000	00000	05---
<i>Cyclanthura carinata</i>	00001	2-000	00000	00000	00000	00000	11--0
<i>Cyclanthura crepidula</i>	00001	2-000	00000	00000	00000	00000	14000
<i>Cyclanthura laticola</i>	00001	2-000	00000	00000	00000	00000	11--0
<i>Cyclanthura pilosa</i>	00001	2-000	00000	00000	00000	00000	11--0
<i>Cyclanthura striata</i>	00001	2-000	00000	00000	00000	00000	??--?
<i>Derelomini</i> gen. 1 sp. 1	00000	2-100	00000	00000	00000	00000	14010
<i>Derelomini</i> gen. 1 sp. 2	00000	2-100	00000	00000	00000	00000	14010
<i>Derelomini</i> gen. 1 sp. 3	00000	2-100	00000	00000	00000	00000	14010
<i>Derelomini</i> gen. 2 sp. 1	00001	2-100	00000	00000	00000	00000	14001
<i>Derelomini</i> gen. 2 sp. 2	00001	2-100	00000	00000	00000	00000	14001
<i>Derelomini</i> gen. 2 sp. 3	00001	2-100	00000	00000	00000	00000	14001
<i>Derelominus piceus</i>	00000	2-000	00000	00000	00000	00000	13--0
<i>Derelomus abyssinicus</i>	00100	11000	10000	00000	00000	10000	13--0
<i>Derelomus auberti</i>	00100	11000	10000	00000	10000	10000	13--0
<i>Derelomus bicarinatus</i>	00100	11000	10000	00000	10000	10000	13--0
<i>Derelomus chamaeropsis</i>	00100	11000	10000	00000	10000	10000	13--0
<i>Derelomus costifer</i>	00100	11000	10000	00000	10000	10000	13--0
<i>Derelomus mariaehelenae</i>	10000	2-000	00000	00000	00000	00000	13--0
<i>Derelomus</i> sp. 1	00100	11000	10000	00000	00000	10000	13--0
<i>Derelomus tatianae</i>	00000	2-100	00000	00000	00000	00000	13--0
<i>Diplothemibius sternicornis</i>	00000	2-000	00000	00000	00000	00000	13--0
<i>Dorytomus hirtus</i>	00000	10000	00000	00000	00000	00000	05---
<i>Eisingius araucariae</i>	00000	10000	00000	00000	00000	00000	02---
<i>Eisingius chusqueae</i>	00000	10000	00000	00000	00000	00000	02---
<i>Elaeidobius kamerunicus</i>	00100	11000	00000	00000	00000	10000	13--0
<i>Elaeidobius subvittatus</i>	00100	11000	00000	00000	00000	10000	13--0
<i>Ellescus ephippiatus</i>	00000	2-000	00000	00000	00000	00000	05---
<i>Erodiscus tinamus</i>	00000	10000	00000	00000	00000	00000	05---
<i>Ganglionus constrictus</i>	00000	2-000	00000	00000	00000	00000	14101
<i>Ganglionus mitigatus</i>	00000	2-000	00000	00000	00000	00000	14101
<i>Ganglionus undulatus</i>	00000	2-000	00000	00000	00000	00000	14101
<i>Grasidius</i> sp. 1	00000	10000	00000	00000	00000	00000	13--0

<i>Hypoleschus atratus</i>	00000	2-100	00000	00000	00000	00000	15--0
<i>Juanorhinus ruficeps</i>	00000	10000	00000	00000	00000	00000	05---
<i>Nanus uniformis</i>	00000	10000	00000	00000	00000	00000	03---
<i>Neoderelomus piriformis</i>	00100	11000	10000	00000	10000	10000	13--0
<i>Neopsilorhinus collaris</i>	00000	00000	00000	00000	00000	00000	00---
<i>Neopsilorhinus modestus</i>	00000	00000	00000	00010	00000	00000	00---
<i>Neopsilorhinus variegatus</i>	00000	00000	00000	00010	00000	00000	00---
<i>Nodocnemus</i> sp. 1	00000	2-000	01000	00000	00000	00000	13--0
<i>Notolomus basalis</i>	10000	2-000	00000	00000	00000	00000	13--0
<i>Notolomus bicolor</i>	10000	2-000	00000	00000	00000	00000	13--0
<i>Omoides humeralis</i>	00000	10000	00001	00000	00000	00000	05---
<i>Parimera variabilis</i>	00000	2-000	01000	00000	00000	00000	13--0
<i>Pedetinus flavipes</i>	00000	10000	00001	00000	00000	00000	13--0
<i>Pedetinus halticoides</i>	00000	10000	00001	00000	00000	00000	13--0
<i>Perelleschus carludovicae</i>	00001	2-100	00100	00001	00000	00100	14101
<i>Perelleschus evelynae</i>	00001	2-100	00100	00001	00000	00100	14101
<i>Perelleschus rectirostris</i>	00001	2-100	00100	00000	00000	00100	14101
<i>Phyllotrox aristidis</i>	00010	2-101	00000	01000	00101	00011	15--0
<i>Phyllotrox ater</i>	00000	2-100	00000	00000	00000	01000	15--0
<i>Phyllotrox canyonaceris</i>	00010	2-100	00000	01000	00101	00001	15--0
<i>Phyllotrox crassipes</i>	00010	2-101	00000	01000	00101	00011	15--0
<i>Phyllotrox derivatus</i>	00010	2-101	00000	01000	00101	00010	15--0
<i>Phyllotrox ferrugineus</i>	00000	2-100	00000	00000	00000	00000	15--0
<i>Phyllotrox marcidus</i>	00010	2-101	00000	01000	00101	00010	15--0
<i>Phyllotrox mecinoides</i>	00010	2-101	00000	01000	00101	00011	15--0
<i>Phyllotrox megalops</i>	00000	2-100	00000	00000	00000	00000	13--0
<i>Phyllotrox nubifer</i>	00010	2-101	00000	01000	00101	02011	15--0
<i>Phyllotrox pallidus</i>	00000	2-100	00000	00000	00000	00000	13--0
<i>Phyllotrox quadricollis</i>	00010	2-101	00000	01000	00101	02011	15--0
<i>Phyllotrox rubiginosus</i>	00000	2-100	00000	00000	00000	00000	13--0
<i>Phyllotrox rufipes</i>	00000	2-100	00000	00000	00000	01000	15--0
<i>Phyllotrox rutilus</i>	00010	2-100	00000	01000	00101	00001	15--0
<i>Phyllotrox sejunctus</i>	00010	2-100	00000	01000	00101	00010	15--0
<i>Phyllotrox semirufus</i>	00000	2-100	00000	01000	00000	00000	15--0
<i>Phyllotrox sericeus</i>	00000	2-100	00000	01000	00000	00000	15--0
<i>Phyllotrox suturalis</i>	00010	2-101	00000	01000	00101	02011	15--0
<i>Phyllotrox variabilis</i>	00000	2-100	00000	00000	00000	01000	15--0
<i>Phytotribus lineatus</i>	00000	10010	00000	00000	00000	00000	13--0
<i>Phytotribus</i> sp. 1	00000	10010	00000	00000	00000	00000	13--0
<i>Phytotribus unicolor</i>	00000	10010	00000	00000	00000	00000	13--0
<i>Platynanus sericatus</i>	00000	10000	00000	00000	00000	00000	??--?
<i>Pseudoderelomus baridiiformis</i>	00000	2-100	00000	00000	00000	00000	13--0
<i>Pseudoderelomus</i> sp. 1	00000	2-100	00000	00000	00000	00000	13--0
<i>Smicronyx griseus</i>	00000	10000	00000	00000	00000	00000	05---
<i>Staminodeus curvitiibialis</i>	00000	2-100	00000	00000	00000	00000	14010
<i>Staminodeus inermis</i>	00000	2-100	00000	00000	00000	00000	14010
<i>Staminodeus vectoris</i>	00000	2-100	00000	00000	00000	00000	14010
<i>Systemotelus carludovicae</i>	00001	2-100	00100	00000	00000	00000	14100
<i>Systemotelus costaricensis</i>	00001	2-100	00100	00000	00000	00000	14100
<i>Systemotelus stockwelli</i>	00001	2-100	00100	00000	00000	00000	14100
<i>Tadius erhinoides</i>	00000	00000	00000	00000	00000	00000	00---
<i>Terioltes circumdatus</i>	00000	2-100	00000	00000	00010	00000	13--0
<i>Terioltes nigripennis</i>	00000	2-100	00000	00000	00010	00000	13--0
<i>Terires pilosus</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Terires plurisetosus</i>	00000	10000	00000	00000	00000	00000	13--0
<i>Trypetes politus</i>	00000	10000	00000	00000	00000	00000	03---
<i>Tychius lineellus</i>	00000	2-100	00000	00000	00000	00000	05---
<i>Udeus</i> sp. 1	00000	10000	00001	00000	00000	00000	??---