Systematic Entomology (1993) **18**, 57–92

A revision of *Eurysphindus* LeConte (Coleoptera: Cucujoidea: Sphindidae) and a review of sphindid classification and phylogeny

JOSEPH V. McHUGH Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, and Department of Entomology, Cornell University, Ithaca, New York

Abstract. *Eurysphindus* LeConte is revised and redescribed, *Genisphindus* gen.n. is described and a key to the species is given for each. Four new species of *Eurysphindus* are described: *E.comatulus* sp.n., *E.grandiclaviger* sp.n., *E.halli* sp.n. and *E.infuscus* sp.n. *Eurysphindus brasiliensis* Sen Gupta & Crowson, *Eurysphindus plaumanni* Sen Gupta & Crowson and *Eurysphindus hirtus* LeConte are redescribed. Four species of *Genisphindus* are described: *G.latisternus* sp.n., *G.minor* sp.n., *G.rotundus* sp.n. and *G.roxanneae* sp.n. *Eurysphindus laevicollis* Sen Gupta & Crowson is reassigned to *Genisphindus*. A tentative hypothesis of the phylogenetic relationships of sphindid genera is presented based on a cladistic analysis. A classification derived from the phylogenetic hypothesis is proposed and compared with that of Sen Gupta & Crowson (1977). A generic key to adult Sphindidae is provided. Known distributions for the genera of sphindids are considered in light of the phylogenetic hypothesis and various interpretations are proposed.

Introduction

Sphindid beetles, although inconspicuous, are found in all major biogeographic regions of the world. Although little is known about their biology, available data suggest that all species are myxomycophagous (slime mould feeding) as immatures and adults, an unusual association which makes the group of interest ecologically. Systematically, the position of the family within the Cucujoidea is uncertain, and studies are needed to resolve this problem.

The prime focus of this study is the subfamily Eurysphindinae, and its phylogenetic position within the Sphindidae. The resolution of the latter problem, through a cladistic analysis of sphindid genera, allows both a reclassification on phylogenetic principles and an assessment of the biogeography of the family. Thus this study incorporates a modification of the existing subfamilial classification (Sen Gupta & Crowson, 1977), and biogeographic hypotheses to explain the known distributions of sphindid genera.

Taxonomic background

Sphindidae is a small, poorly studied family including forty-three previously described species and eight genera. Sen Gupta & Crowson (1977) organize the family with a system of four subfamilies: Protosphindinae, Sphindinae, Eurysphindinae and Aspidiphorinae.

Protosphindinae (*sensu* Sen Gupta & Crowson, 1977) comprises the single genus, *Protosphindus* Sen Gupta & Crowson with two Chilean species.

Sphindinae (*sensu* Sen Gupta & Crowson, 1977) includes two genera: *Sphindus* Chevrolat and *Odontosphindus* LeConte. *Sphindus* includes sixteen species and has been reported in all major biogeographic regions except Australia. *Odontosphindus* contains three species, two from the Nearctic region and one from the Palearctic region. McHugh & Wheeler (1991) describe the monotypic Australian genus *Notosphindus** and place it in Sphindinae as circumscribed in the present paper.

Included in Aspidiphorinae (*sensu* Sen Gupta & Crowson, 1977) is the monotypic South African genus *Sphindiphorus* Sen Gupta & Crowson and the Old World genus *Aspidiphorus* Latreille, which includes twelve species. Jacquelin du Val (1859–63) assigns *Aspidiphorus* to Sphindidae, subsuming the family Aspidiphoridae. Unfortunately, several subsequent works continue to recognize

Correspondence: Mr Joseph V. McHugh, Department of Entomology, Cornell University, Ithaca, New York 14853, U.S.A.

* The 'undescribed species' mentioned by McHugh & Wheeler (1991), with reference to this paper is *Notosphindus slateri*. The present paper is modified to reflect its later publication.

Aspidiphoridae (for references see Sen Gupta & Crowson, 1977; Sen Gupta & Pal, 1982).

Merkl (1986) points out that *Arpidiphorus* Dejean (1821) is a valid prior spelling of *Aspidiphorus* Latreille (1829), and should be used. This would also affect the family-group name, following the *International Code of Zoological Nomenclature* Art. 35(d)(i). The choice of stability or priority should be resolved by application to the Commission, but in this work the 'traditional' spelling and authorship of both the genus and subfamily — *Aspidiphorus* Latreille and Aspidiphorinae — will be used.

The subfamily Eurysphindinae (*sensu* Sen Gupta & Crowson) consists of a single genus, *Eurysphindus* LeConte, with four described species. The type species of the genus, *Eurysphindus hirtus* LeConte 1878, occurs throughout the eastern United States and southeastern Canada and is the only Nearctic representative. Sen Gupta & Crowson (1977) describe three Brasilian *Eurysphindus* species: *E.laevicollis*, *E.brasiliensis* and *E.plaumanni*. A Cuban species, *E.bicolor* Fisher 1936, is described with some concern as to its congeneric status with *E.hirtus*. Fisher's doubt is due to the fact that the hypomera of *E.bicolor* are not anterolaterally concave and therefore are incapable of housing the antennal clubs.

McHugh (1990) places *E.bicolor* in a new genus, *Carinisphindus*, with three new species, *C.isthmensis*, *C.platysphinctos* and *C.leptosphinctos*, but a subfamilial placement for *Carinisphindus* is not suggested.

The monotypic New Zealand genus *Cyclaxyra* is assigned to Sphindidae by Crowson (1967). It is now thought to form a new family related to Phalacridae or Laemophloeidae but not closely related to Sphindidae (Crowson, personal communication).

Biology of the Eurysphindinae

Little is known about the biology of the sphindid beetles. This point may be illustrated by the common name of the family 'the dry-fungus beetles'. The Sphindidae are in fact myxomycophagous (slime mould eating) (Figs 49–52) and the only coleopteran family thought to be exclusively so. The origin of the common name may stem from a broad usage of the word 'fungus' to include myxomycetes.

However, some authors clearly believe sphindids feed on higher fungi. For example, Bradley (1939) and Arnett (1963) report that sphindids feed on 'fungi' and 'shelf fungi' in particular. LeConte (1866) describes *Sphindus americanus* as 'not rare, in woody fungi'. A large enough body of sphindid-host literature now exists (see Benick, 1952; Crowson, 1967; Sen Gupta & Crowson, 1977; Russell, 1979; Lawrence & Newton, 1980; Lawrence, 1989) to suggest that these reports were based on an observation of either a casual fungus association with the beetles, or one coincident with an undetected slime mould fruiting body. One other possible explanation is that some beetles associated with the 'woody' or 'shelf' fungi were misidentified in the field and that this observation was perpetuated in the literature.

Records of Coleoptera feeding on slime mould plasmodia (Fig. 52) exist for a few beetle taxa (Lawrence & Newton, 1980; Wheeler, 1980, 1984; Ślipiński, 1988; Lawrence, 1989; Newton & Stephenson, 1990), but not Sphindidae. As far as is known, both larvae and adults feed only on supporting structures (Burakowski & Ślipiński, 1987) and spores of slime mould sporocarps or 'fruiting bodies' (see Lawrence & Newton, 1980).

To date, Burakowski & Ślipiński (1987) provide the only detailed life history notes on a sphindid, *Aspidiphorus orbiculatus*.

If little is known about the biology of sphindids in general, our knowledge of eurysphindine biology is almost nonexistent. *Eurysphindus* species are relatively rarely collected. Although *E.hirtus* has a wide distribution in eastern North America and has been found on a variety of common slime mould species, it is collected less often than other members of the family (e.g. *Sphindus americanus* and *S.trinifer*) with the same potential hosts and from the same region.

For a few of the more commonly collected sphindids, the data indicate a broad range of potential slime mould host species. The list of presumed hosts for *E.hirtus* is also diverse, including *Diachea thomasii*, *Fuligo septica* (Fig. 49), *Stemonitis axifera* (Fig. 50) and *Tubifera ferruginosa* (Fig. 51) (Lawrence & Newton, 1980 ; personal unpublished observations). These four hosts represent three of four orders (Liceales, Physarales and Stemonitales) in the Myxomycete subclass Myxogastromycetidae (Alexopoulos & Mims, 1979).

Eurysphindus species may prefer less conspicuous or rarer slime mould host species and feed only facultatively on the more obvious species. Blackwell (1984) points out that insect and slime mould collectors tend to concentrate on the lignicolous myxomycetes while overlooking the corticolous, foliicolous and coprophilous species. Curiously, *Eurysphindus* species have been collected more often in sifted leaf litter and flight intercept traps than directly from slime mould fruiting bodies. Perhaps a leaf litter slime mould species is preferred.

Given the above circumstances, it is not surprising that there has not been a larval description of a *Eurysphindus* species. Much could be gained in understanding the phylogenetic relationships of the Sphindidae were sufficient data available from other developmental stages. Burakowski & Ślipiński (1987) summarize the literature on larval Sphindidae and provide a key and descriptions of immature stages of *Sphindus dubius*, *Aspidiphorus orbiculatus*, *Odontosphindus clavicornis* and *Protosphindus chilensis*. Lawrence (1991) provides a generalized description of sphindid larvae.

Much of the ecology of this group also remains unknown. Crowson (1981) suggests that the characteristic cavities in the mandibles of Sphindidae serve as mycangia — pits with associated glands for transportation of fungi (Batra, 1963; Beaver, 1989). Studies of sphindid anatomy reveal a wealth of potentially mycangial punctures and depressions (Figs 3, 11, 12, 34, 75). The lateral pockets on the mesosternum of *Sphindiphorus natalensis* Sen Gupta &

Crowson are particularly curious. There is no doubt that sphindid beetles transport spores, since most specimens are at least partially covered with them.

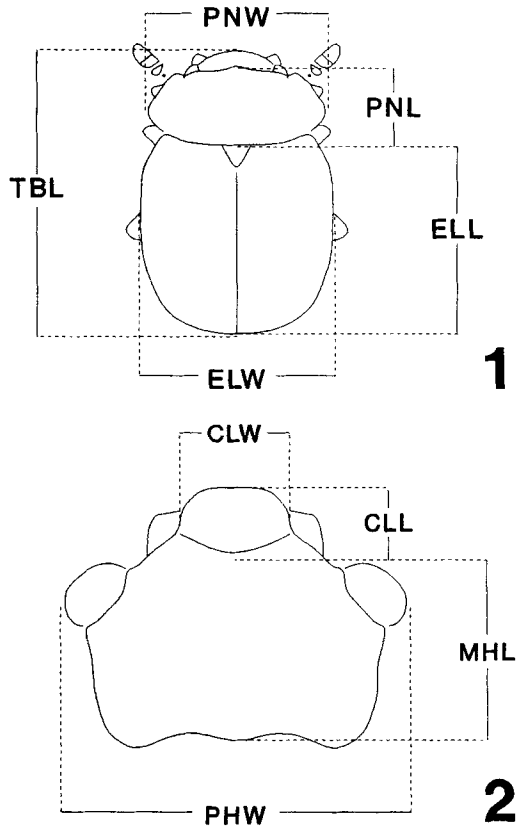
Whether some adaptive significance in spore transportation exists for either beetle or slime mould remains to be determined by ecological studies. Blackwell (1984) reports that spores of *F.septica* can pass through the gut of a sphindid beetle intact, but whether they are inactivated or in some way benefitted, perhaps by aiding germination through mechanical or chemical scarification, is unknown. Beetles may increase the chance of spores reaching appropriate substrates, although Myxomycetes unaided have few rivals for dispersal ability (see Blackwell, 1984). Finally, the beetles may be camouflaged from predators by the covering of spores; however, this does not explain the pits and depressions that are ventral or otherwise unexposed.

The following abbreviations are used in the text to indicate institutions and individuals who kindly provided material for this study: (ANC) Australian National Insect Collection, Canberra; (ANSP) Academy of Natural Sciences of Philadelphia; (BMNH) The Natural History Museum (London); (CAS) California Academy of Sciences, San Francisco; (CNC) Canadian National Collection, Biosystematics Research Institute, Ottawa; (CUIC) Cornell University Insect Collection, Ithaca, New York; (FMNH) Field Museum of Natural History, Chicago; (MANM) Manchester Museum, The University, Manchester; (MCZ) Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; (MEM) Mississippi Entomological Museum; (MHNG) Muséum d'Histoire naturelle, Geneva; (MIZA) Museo Del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay; (SEM) Snow Entomological Museum, University of Kansas, Lawrence; (UCB) University of California, Berkeley; (UCD) University of California, Davis; (UNH) Entomological Museum, University of New Hampshire, Durham; and (USNM) National Museum of Natural History, Smithsonian Institution, Washington, D.C. Additional specimens were provided by the following individuals from personal collections: (GKEN) G. G. Kennen; (JPAK) J. Pakaluk, University of Kansas, Lawrence; (JPAR) J. Parkinson, University of North Carolina; (KSTE) K. Stephan, Red Oak, Oklahoma; (MAIC) M. A. Ivie, Montana State University; (QWHE) Q. D. Wheeler, Cornell University; and (SPEC) S. Peck, Carleton University.

Methods and Materials

Computer graphic images (Figs 1, 2, 53–57, 93, 94 and part of Figs 58–60) were generated using Harvard Graphics, version 2.1 (Software Publishing Corp.). Standardized species descriptions were written using MDP (Monographic Database Program), a presently unreleased computer database system created by K. C. Nixon (Bailey Hortorium, Cornell University).

Morphometric data were taken using a ZIDAS image analyser (Zeiss, Inc.) to digitize images observed through a drawing tube. Measurements of the holotype are given in the type material section using the abbreviations shown in Figs 1 and 2. Measurements given in 'Description' sections are the arithmetic mean for all material examined. All measurements are in millimetres.



Figs 1–2. Dimensions used for morphometrics. 1, Whole insect; 2, Head; Abbreviations: TBL = Total body length, ELL = Elytral length, ELW = Elytral width, PNL = Pronotal length, PNW = Pronotal width, MHL = Median head length, PHW = Ocular head width, CLL = Clypeal length, CLW = Clypeal width.

In the phylogenetic analysis, cladograms were generated with HENNIG86 version 1.5 (J. S. Farris) using the 'ie*' function. To study character state transformations, K. Nixon's CLADOS program, version 0.9, was used.

Key to Genera of Sphindidae

1 Antenna 11-segmented, wing with third anal vein 2

– Antenna 10-segmented, wing lacking third anal vein .... (subfamily Sphindinae).....4

2 Dorsal surface of head lacking tubercles; pronotum not carinate, lateral margin crenulate; lateral margin of clypeus emarginate; head with at least one pair of dorsal longitudinal grooves extending posteriorly over eye from between antennal insertion and clypeus; apical segment of labial palp about as wide as other segments 3

– Head with tubercles over eye and one pair medially; pronotum carinate, lateral margin denticulate; lateral margin of clypeus straight to weakly arcuate; head lacking dorsal longitudinal grooves over eye; apical segment of labial palp strongly inflated (Chile) ..... *Protosphindus*

3 Elytra lacking raised carinae; head with single pair of dorsal grooves; antennal club two-segmented (antennomere IX ≪ X), antennomere III submoniliform; pygidium lacking dorsal median longitudinal groove; mesosternum lacking pair of large invaginations; wing with branched first anal vein; mandible tridentate but with one small ventral tooth not visible from dorsal view (Holarctic) ..... *Odontosphindus*

– Elytra with raised carinae; head with one pair of well-developed antennal grooves near eyes and several other weaker anterior grooves; antennal club three-segmented (antennomere IX about same size as X), antennomere III at least twice as long wide; pygidium with parallel-sided dorsal median longitudinal groove; mesosternum with pair of large deep invaginations anterior to mesocoxae; wing with unbranched first anal vein; mandible tridentate with all teeth visible from dorsal view (S. Africa) ..... *Sphindiphorus*

4 Body form oval, convex; procoxal cavities widely open exteriorly; pronotal hypomera anteroventrally concave; mesosternum with concave region to receive prosternal process; pronotal posterior margin sinuate 5

– Body form elongate-oval, parallel-sided; procoxal cavities externally closed by extensions of the hypomera and lateral flanges of the prosternal process; pronotal hypomera not anteroventrally concave; mesosternum with inflection but lacking concavity; pronotal posterior margin arcuate or nearly so 7

5 Pronotal lateral margin smooth 6

– Pronotal lateral margin crenulate (New World) ..... *Eurysphindus*

6 Femur with pointed apex (Figs 80–82); pygidium lacking median longitudinal groove; head with single pair of dorsolateral longitudinal grooves each extending posteriorly over eye from between antennal insertion and clypeus (Neotropics) ..... *Genisphindus*

– Femur with truncate or rounded apex; pygidium with median longitudinal groove; head often with more than one pair of dorsolateral grooves (Old World) ..... *Aspidiphorus*

7 Pronotum and scutellum with dorsal median longitudinal carina; pronotal lateral margin smooth (Caribbean and C. America) ..... *Carinisphindus*

– Pronotum and scutellum lacking a longitudinal carina; pronotal lateral margin crenulate (but may be feeble) 8

8 Pygidium lacking large impunctate patches; male metafemur with a posterior tooth; mandible tridentate; wing with three anal veins; pronotum abruptly depressed posteriorly and postero-laterally (S. Australia) ..... *Notosphindus*

– Pygidium with pair of large densely setulose impunctate patches; male metafemur lacking posterior tooth; mandible bidentate with one well-developed and one weak tooth; wing with a single anal vein; pronotum lacking abrupt posterior depression (Cosmopolitan except Australia) ..... *Sphindus*

Eurysphindus LeConte

Eurysphindus LeConte, 1878: 602. Type species: *Eurysphindus hirtus* LeConte, 1878, by monotypy.

Description. Body broadly oval, convex, head partially visible from above (Fig. 3). Length 1.0–2.2. Body uniformly black to reddish-brown or with dark brown to black head and pronotum, and lighter brown elytra. Setation (Fig. 3) of moderately-long to long, suberect to erect, moderately-dense setae.

Head with a pair of dorsal antennal grooves extending from between antennal insertions and clypeus to beyond top of eye (Figs 4, 8), ventrally with three pairs of antennal pits (Fig. 7), frontoclypeal suture arcuate (Fig. 8); dorsal surface with small, sparse punctules anteriorly gradually becoming larger, denser posteriorly (Fig. 8); clypeus emarginate laterally, arcuate apically, about as wide at base as long (Fig. 8); eye black to golden, small, finely facetted, not prominent, but convex (Figs 4, 7, 8); antenna 10-segmented, with enlarged, asymmetrical antennomeres I–II, III at least twice as long as wide (Figs 3, 4, 6, 8, 9), IV and sometimes V slightly elongate, VI and sometimes V submoniliform (Fig. 6), VII usually slightly enlarged, VIII–X enlarged in a densely pubescent club (Figs 4, 6, 9), VIII usually wedge-shaped (Figs 4, 6, 8), VIII–IX about same length, X 2–4 times as long as VIII or IX (Figs 4, 6, 8); labrum small and nearly completely concealed by clypeus (Fig. 4), weakly bilobed distally (Fig. 16); mandible flattened apically, bidentate (Figs 4, 5) with cavity and tubercle (Figs 5, 11, 12) and well-developed mola (Figs 11, 13).

Pronotum slightly narrowed in front, rounded at sides, flattened laterally with acute, crenulate edges (Figs 3, 20), hypomera concave anterolaterally, basal margin sinuate (Figs 3, 20), disc often with two lateral depressions (Fig. 3), procoxal cavities widely open (Fig. 21); dorsal surface with dense, fine punctules, becoming larger laterally and basolaterally (Fig. 20); prosternal process raised, densely punctate, with anterior keel (Figs 21, 53–55). Mesosternum posteriorly vertical, weakly convex to receive prosternal process (Fig. 30); mesosternal process narrow, knoblike (Figs 27, 30); trochantins exposed. Metasternum punctate, inflated (Fig. 27). Legs of moderate length, slender (Figs 3, 35–37). Coxae transverse (Fig. 27). Femora moderately setose, rounded at distal ends (Figs 3, 35–37). Tibiae narrowed basally, gradually dilated, lacking spurs (Figs 35–37), except for a crown of very short spurs at distal end (Figs 14, 35–38), distally with groove to receive tarsus (Figs 35–38). Tarsi 5-5-5 female, 5-5-4 male, tarsomeres simple, apical tarsomere about as long as others combined (Figs 35–38), tarsomeres with a sparse tuft of setae ventrally, claws simple. Scutellum large, quadrate to scutelliform (Figs 3, 26, 32), with distinct (Fig. 32) or confused shallow punctules, densely (Figs 3, 26) to sparsely setose. Elytra covering abdomen, broad, with prominent humeral calli (Fig. 3) and a weak to strong (Fig. 3) subhumeral depression, strongly depressed opposite lateral margins of scutellum (Fig. 3), epipleura rugulose and

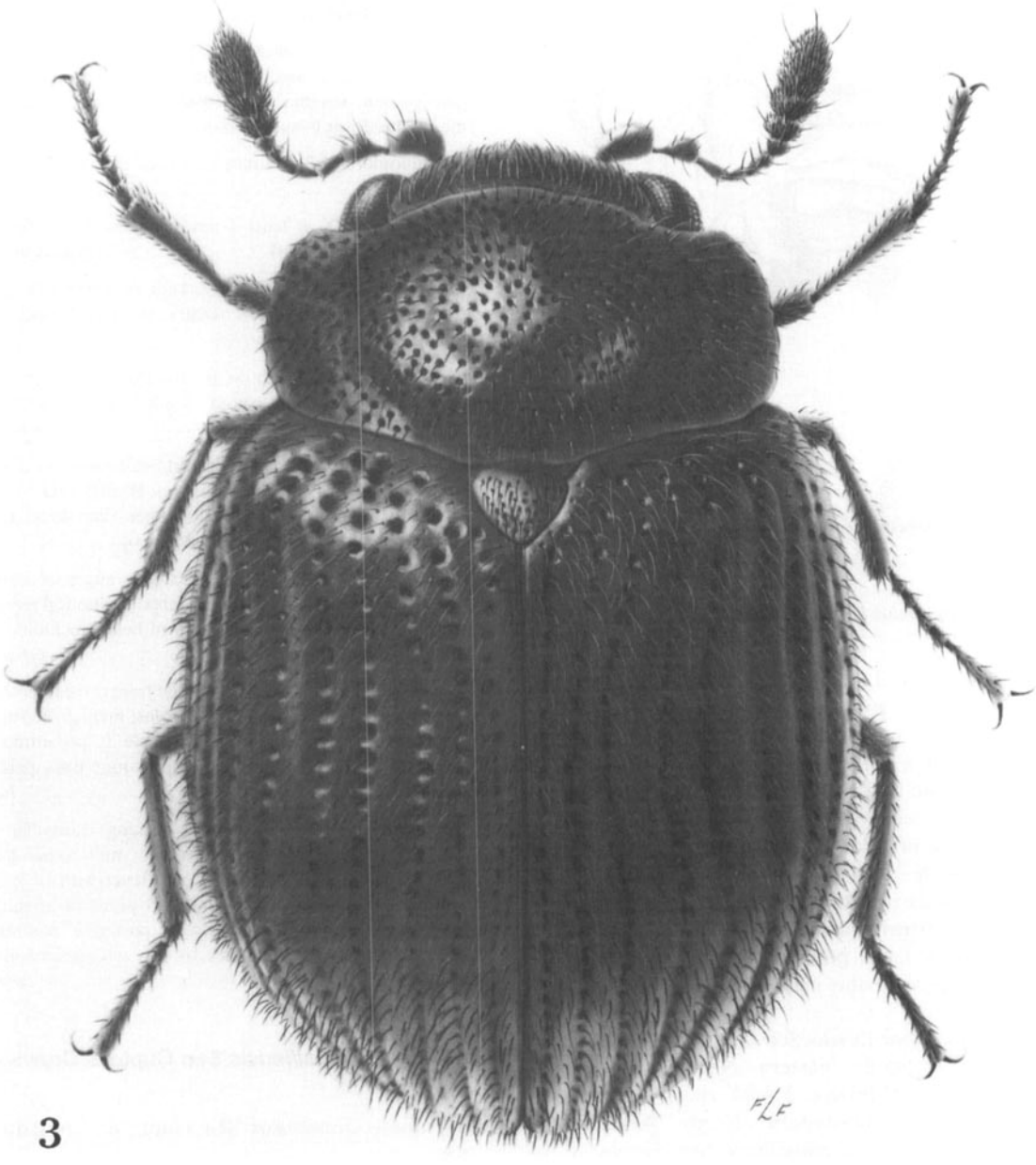


Fig. 3. *Eurysphindus halli*, holotype.

complete to between basal margins of abdominal sternites IV and V; dorsal surface with one scutellary and 10 long punctate strial 'interneurs' (Erwin, 1974) (Figs 3, 23), strial interspaces smooth (Fig. 3) to rugulose and flat to feebly convex (Fig. 3), with 1–2 rows of setae (Figs 3, 23, 33, 34).

Abdomen with five visible sternites, sternite I (minus intercoxal process) about 1.5–2 times as long as sternites II–V, II–V about same length and with a row of small (Fig. 24) to moderately large, basal depressions, sternites not in same plane giving shingled appearance. Intercoxal process narrow (Fig. 24). Pygidium densely and evenly punctulate (Fig. 39).

Natural history. All species presumably feed on myxomycetes.

Distribution. Nearctic and Neotropical.

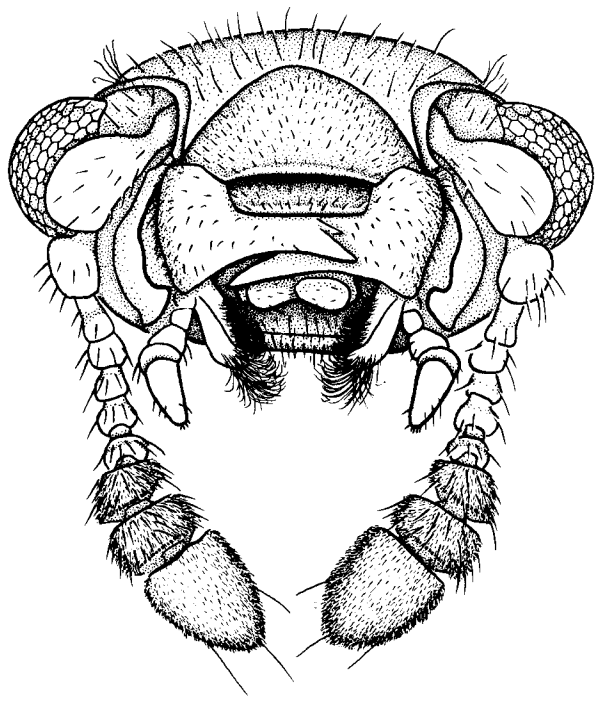


Fig. 4. *Eurysphindus hirtus*, head, anterior view.

Remarks. This genus is similar to *Aspidiphorus* and *Genisphindus* in having 10-segmented antennae, concave hypomera and a convex, oval body shape. It differs from both genera in having a keel on the prosternal process and dorsal head punctation that is more uniform in density and size basally (as opposed to having an impunctate region and a transverse row of enlarged punctures). In addition, it differs from *Aspidiphorus* by lacking a groove on the pygidium and has a narrow knoblike mesosternal process rather than a flat broad one. *Eurysphindus* has a less compact body form, lacks pointed femoral apices and the pair of large pits on the mesosternal process seen in *Genisphindus*.

Species included: *E.brasiliensis* Sen Gupta & Crowson, Brasil; *E.comatulus* sp.n., eastern North America; *E.grandiclaviger* sp.n., Mexico; *E.halli* sp.n., Mexico; *E.hirtus* LeConte, central-eastern North America; *E.infuscus* sp.n., Mexico; *E.plaumanni* Sen Gupta & Crowson, Brasil.

Key to *Eurysphindus* species

1 Scutellum with distinct punctures (Fig. 32) about same size and density as punctures on posteromedial region of pronotum; setae of head, pronotum and elytra long and erect; pronotum lacking posteromedial longitudinal depression 2

– Scutellum with punctules shallower, denser, smaller and less distinct than punctures on posteromedial region of pronotum (Fig. 26); setae of head, pronotum and elytra short and suberect; pronotum with or without posteromedial longitudinal depression 3

2 Body broadest near midpoint (Fig. 46B); prosternal process with small anterior ridge (Fig. 55); eyes black to grey; length 2 mm; pronotum and scutellum usually darker reddish-brown than elytra (central to eastern North America) ..... *hirtus*

– Body broadest at about 3/4 length (Fig. 46A); prosternal process with large anterior tooth-like projection (Fig. 54); eyes pale golden; length 2.2 mm; pronotum, scutellum and elytra medium reddish-brown (Brasil) ..... *brasiliensis*

3 Antennomere X 2–3 times length of IX; distal end of femur rounded 4

– Antennomere X at least 4 times length of IX; distal end of femur angled (Mexico) ..... *grandiclaviger* n.sp.

4 Prosternal process with large keel or tooth-like projection (Figs 53, 54); projection darker in colour than adjoining prosternal process; (Neotropics) 5

– Prosternal process with weak anterior projection (Fig. 55); projection about same colour as adjoining prosternal process (eastern North America) ..... *comatulus* n.sp.

5 Head, pronotum and elytra reddish-brown; antennal club long, abrupt, brown; antennomeres of club relatively loosely attached; pronotum appearing longer than head (including clypeus) in lateral view; (Brasil, Mexico) 6

– Head, pronotum and elytra piceous; antennal club short, gradual, black to grey; antennomeres of club tightly attached; pronotum appearing about length of head (including clypeus) (Mexico) ..... *infuscus* n.sp.

6 Scutellum triangular, with depressed transverse region at 1/3 its length and small but distinct punctules; metacoxae robust, not depressed opposite abdominal sternite I; pronotum lacking posterior median longitudinal depression; eyes pale golden (Mexico) ..... *halli* n.sp.

– Scutellum quadrate-scutelliform, lacking transverse depression, punctules confused and feeble; metacoxae depressed opposite abdominal sternite I, only level with or protruding beyond abdominal sternite I around point of attachment of trochanter; pronotum with weak posterior median longitudinal depression; eyes black to grey with golden highlights (Brasil) ..... *plaumanni*

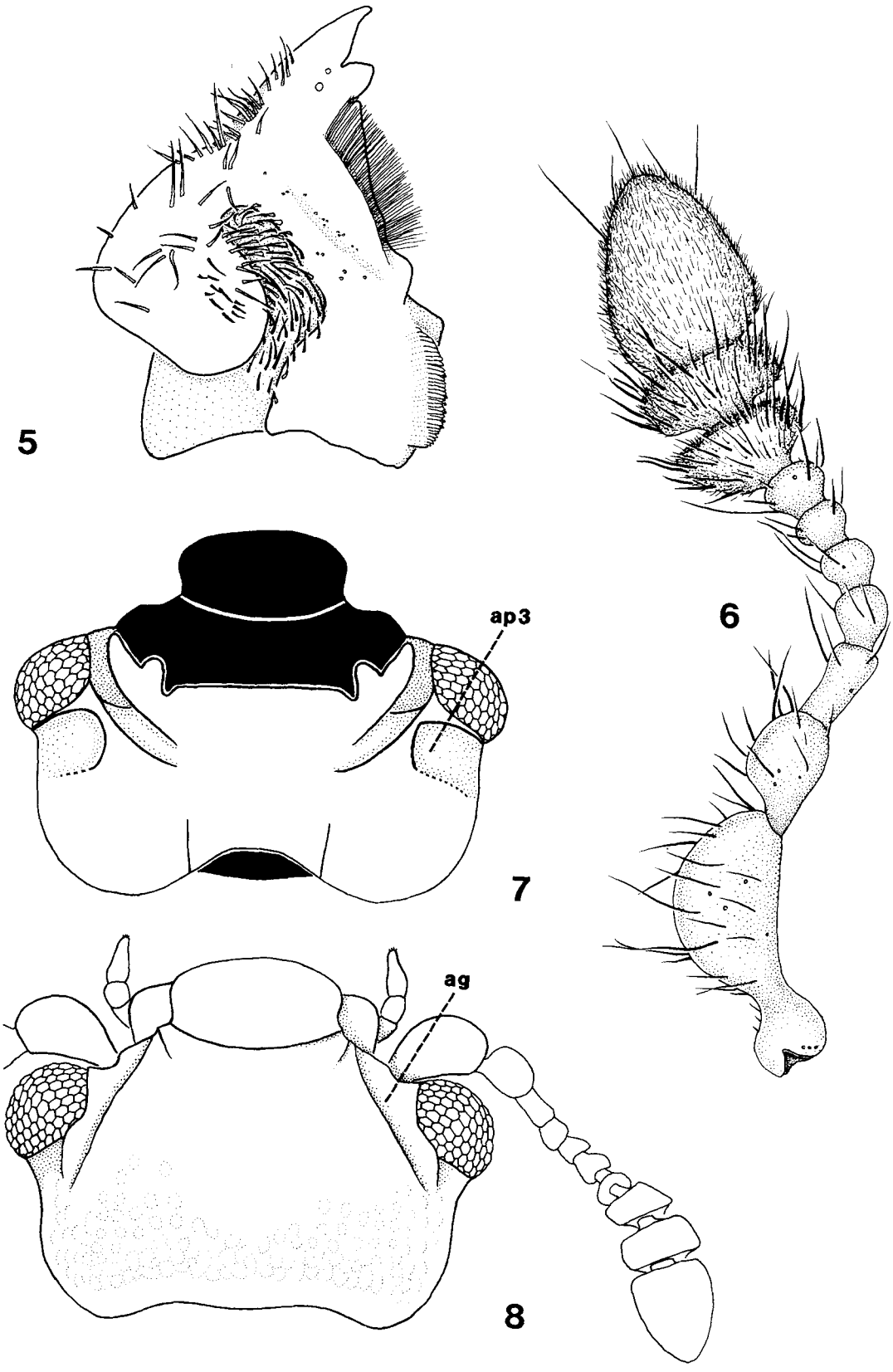
Eurysphindus brasiliensis Sen Gupta & Crowson
(Figs 54, 60)

Eurysphindus brasiliensis Sen Gupta & Crowson, 1977: 184.

Description. Head, pronotum, prosternum, mesosternum, metasternum and elytra dark reddish-brown, antennae, legs and abdomen lighter reddish-brown; body broad, elytra tapering abruptly posteriorly. Length 2.2.

Head depressed opposite frontoclypeal suture; dorsal surface densely and evenly punctulate; clypeus length 0.2, width 0.2; eyes pale golden; antennomere IV slightly elongate, V–VI submoniliform, VII slightly wider than III–VI, segment VIII slightly asymmetrical, IX wider than VIII, IX–X symmetrical, more compact than VIII–IX, X about twice length of either VIII or IX.

Pronotum with weakly crenulate lateral margin, basal margin weakly sinuate–arcuate; disc lacking paired de-



Figs 5–8. *Eurysphindus hirtus*. 5, Left mandible, dorsal; 6, Right antenna, dorsal; 7–8, Head; 7, Ventral, ap3 = antennal pit III; 8, Dorsal, ag = antennal groove.

pressions; pronotal width 1.1, length 0.6; dorsal surface densely and evenly punctulate; prosternal process with anterior keel produced as tubercle (Fig. 54). Metasternum depressed opposite mesosternal process. Scutellum large, scutelliform, densely and evenly punctulate, sparsely setose. Elytra with weak subhumeral depression, epipleura rugulose and complete to about middle of abdominal sternite IV; elytral width 1.3, length 1.5; dorsal surface with strial interspaces rugulose, feebly convex.

Abdomen with sternite I densely and shallowly punctate, II–V with row of small, basal depressions nearly concealed by anterior sternite. Abdominal intercoxal process broad at base, acute anteriorly.

Holotype, ♀, BRASIL: with data: 'Chapada Brasil Acc.No.2966', 'Nov.', 'Eurysphindus brasiliensis sp nov det. R.A. Crowson' and 'HOLOTYPE det. R.A. Crowson' (MCZ); measurements: TBL 2.1, ELL 1.5, ELW 1.4, PNL 0.6, PNW 1.2, PHW 0.7, CLL 0.2, CLW 0.3.

Paratype, same date-locality data as holotype and 'PARATYPE det. R.A. Crowson' (1 ♂, MCZ).

Distribution. Known only from the type locality (Fig. 60).

Remarks. E.brasiliensis may be distinguished from *E.plaumanni* (also known from Brasil) by the following: in *E.brasiliensis* the pronotum is larger and lacks the posteromedian longitudinal depression and the pair of lateral depressions seen in *E.plaumanni*; the scutellar punctation of *E.brasiliensis* is much like that of the pronotum, while in *E.plaumanni* the scutellum is more confusedly and feebly punctate; and the dorsal setation of *E.brasiliensis* is longer and more erect than that of *E.plaumanni*. Both specimens of *E.brasiliensis* are large and robust (Fig. 46A) compared with congeners.

***Eurysphindus comatulus* sp.n.** (Figs 26, 41, 45, 47, 48, 55, 58)

Description. Head, pronotum, prosternum, mesosternum, metasternum, abdominal sternites and antennal clubs black to dark reddish-brown, elytra, legs and antennal stems dark brownish-black to reddish-brown, body shiny. Setation short suberect curled eyelash-like. Length 1.9.

Head with dorsal surface sparsely and feebly punctulate anteriorly, becoming densely punctulate posteriorly; clypeus width 0.2, length 0.2; eyes moderately large, pale golden to grey with golden highlights; antennomere III at least twice as long as wide, IV slightly elongate, V–VI submoniliform, VII wider than III–VI, VIII–X enlarged in a relatively small, gradual, pubescent, compact club, segment VIII wedge-shaped, VIII about same length as IX, IX wider than VIII, IX–X symmetrical, X over twice length of either segment VIII or IX.

Pronotum with weakly crenulate edge, basal margin sinuate opposite scutellum, disc usually with two lateral depressions and median longitudinal depression; pronotal width 0.9, length 0.5; dorsal surface with dense, fine punctures becoming larger laterally and basolaterally; prosternal process with weakly-developed anterior keel (Fig. 55). Scutellum large, scutelliform with feeble, confused punctation and dense, short setae (Fig. 26). Elytra with weak subhumeral depression, epipleura rugulose and complete to about basal margin of abdominal sternite IV; elytral width 1.1, length 1.3; dorsal surface with strial interspaces rugose and weakly to not at all convex.

Abdomen with sternite I shallowly punctate anteriorly, impunctate near posterior margin; segments II–V about equal in length and with basal row of small depressions partially hidden by anterior sternite. Abdominal intercoxal process narrow, with blunt apex.

Female. Genitalia with bilobed coxite (Figs 47, 48), sparsely covered with short setae; stylus short, preapical, with one apical seta and three arising from sides of stylus (Fig. 41); spermatheca as in Fig. 45.

Holotype, ♂, UNITED STATES; NEW HAMPSHIRE, Carroll Co., with following data: 'the Bowl, 2.5 mi. NW Wonalancet VIII-23/IX-1-1984 DSChandler, FITrap' (CUIC) measurements: TBL 1.8, ELL 1.4, ELW 1.1, PNL 0.51, PNW 0.89, PHW 0.65, CLL 0.22, CLW 0.20.

Paratypes, UNITED STATES: NEW HAMPSHIRE, Carroll Co., 1 mi N Wonalancet E FK. Spring Brk., 2–10. vii.1985, 1900', flight int. trap (*Chandler*) (1 ♂, 1 ♀, ANC; 1 ♂, 1 ♀, ANSP; 1 ♂, 1 ♀, BMNH; 2 ♀ ♀, CUIC; 8 ♀ ♀, UNH); The Bowl, 2.5 mi NW Wonalancet, 21–27. vi.1984 (*Chandler*) (1 ♂, UNH); 28.vi–4. vii.1984, flight int. trap (*Chandler*) (1 ♂, 1 ♀, CAS; 1 ♂, 1 ♀, CNC; 1 ♂, 4 ♀ ♀, CUIC; 1 ♂, 1 ♀, MEM; 1 ♂, 1 ♀, UCB; 1 ♂, 2 ♀ ♀, UNH); 5–11.vii.1984 (*Chandler*) (3 ♀ ♀, UNH); 11–16.viii.1984 (*Chandler*) (1 ♀, UNH); 20–26.vii.1984 (*Chandler*) (1 ♂, 1 ♀, MANM; 1 ♂, 1 ♀, UCD); 26.vii–1.viii.1984 (*Chandler*) (2 ♂ ♂, UNH); 27.vii–1.viii.1984 (*Chandler* (1 ♂, 1 ♀, MHNG; 1 ♂, 3 ♀ ♀, UNH); 2–10.viii.1984 (*Chandler*) (1 ♂, 1 ♀, FMNH; 1 ♂, 1 ♀, MCZ; 1 ♂, 1 ♀, SEM; 1 ♂, UNH); 11–16.viii.1984 (*Chandler*) (1 ♂, UNH); 23.viii–1.ix.1984 (*Chandler*) (1 ♂, 3 ♀ ♀, UNH); (1 ♂, 1 ♀, USNM); 2–17.ix.1984 (*Chandler*) (1 ♀, UNH).

Additional material, CANADA: ONTARIO, Leeds Co. Chaffey's Locks, 1.viii.1974 (*Smith*) (1 ♀, CNC); QUEBEC, Old Chelsea, 21.vi.1959 (*Vockeroth*) (1 ♂, CNC); UNITED STATES: MASSACHUSETTS, Hampshire Co., Mt Tom, nr Holyoke, vii.1973 (*Blanchard*) (1 ♀, MCZ); NEW HAMPSHIRE, Coos Co., 1 mi NE East Inlet Dam, 12–24.vi.1986, flight int. trap (*Chandler*) (1 ♂, 2 ♀ ♀, UNH); Abeniki Lake, Dixville Notch, 27. v.1986, 'sift maple/birch leaf litter' (*Chandler*) (1 ♀, UNH); Norton Pool, 3 mi NE East Inlet Dam, 10–24. vii.1986, flight int. trap (*Chandler*) (1 ♀, UNH); Rockingham Co., 1 mi SW Durham, 19.vi–1.vii.1987, flight int. trap (*Chandler*) (1 ♂, UNH); Strafford Co., Spruce Hole, 3 mi SW Durham, 2–9.vii.1987, flight int. trap (*Chandler*) (1 ♀, UNH); NEW YORK, Rensselaerville, 1.ix.1955, (1 ♂, USNM); NORTH CAROLINA, Avery Co., Linville Falls, 3500', Blue Ridge Pkwy mile 317, 16.viii.1981, 'for.intercept' (*Peck*) (3 ♂ ♂, 1 ♀, CNC); Buncombe Co., Great Craggy Mts, 4000', Blue Ridge Pkwy mile 371, 2.vi–15.viii.1981, 'for.intercept' (*Peck*) (1 ♂, CNC); Macon Co., Highlands nr California Gap, 3000–3500', 9.viii.1981, 'berlese Rhododendron hardwd. lf. litter,

JPakaluk 81241' (*Pakaluk*) 2 ♂ ♂, 1 ♀, JPAK); Highlands, Horse Cove, 14.vi.1981, 'ex: thin wht. myxo. plasmodium, in Rhododendron-hardwd. litter' (*Wheeler*) (1♂, JPAK); Transylvania Co., Mt Pisgah, 4300', Blue Ridge Pkwy mile 414, 3.vi–14.viii.1981, 'for.intercept' (*Peck*) (1 ♂, CNC); Wilkes Co., Jeffress Park, Blue Ridge Pkwy, 3500', 1. vi–17.viii.1981, 'intercept' (*Peck*) (1 ♂ and 1 ♀, CNC); PENNSYLVANIA, Allegeny Co., Upper St. Clair Twp., 25.iii.1951, (1 ♀, UCB); VIRGINIA, Giles Co., Mountain Lake Biological Station, 6.viii.83, 3700', SLS Lot 1920, ex. *Fuligo septica* (*Stephenson*) (1♀, 1?, CUIC) and same data for SLS Lot 2879, 8.ix.1984 (1♂, CUIC); WEST VIRGINIA, Mercer Co., Camp Creek St. For., Mash Fork Falls, 1970, 'litter rhododendron hardwoods' (*Bird*) (1♀, CNC).

Etymology. Latin, meaning 'with hair neatly curled' in reference to the neat arrangement of eyelash-like setae on the dorsum of these beetles.

Distribution. Known from the Great Smoky Mountains of North Carolina and from several more northern localities (Canada: Quebec, Ontario; U.S.A.: New York, Pennsylvania, West Virginia). Material from northern localities are lighter in colour than the Smoky Mountain material.

Remarks. This species is distinguishable from *E.hirtus* (also from eastern North America) by the short suberect eyelash-like setae covering the dorsum. The setae of *E.hirtus* are long, erect and relatively straight. Also the punctation of the scutellum differs between these species. The scutellum of *E.comatulus* has confused punctules smaller and denser than those on the posteromedial region of the pronotum. *E.hirtus* has scutellar punctures much like those on the posteromedial region of the pronotum.

***Eurysphindus grandiclaviger* sp.n.** (Fig. 59)

Description. Clypeus reddish-brown, head, pronotum, mesosternum and metasternum dark brownish-black, elytra and scutellum medium brownish-black; femur and tibia medium brown at base and apex and dark brownish-black between; tarsus and antennal stem light brown, antennal club medium brown with white pubescence. Dorsal setation on head, pronotum and elytra of medium length, golden, curved, suberect. Length. 1.79.

Head strongly deflexed, largely hidden beneath pronotum in dorsal aspect, with dorsal surface sparsely and feebly punctulate anteriorly and laterally, punctures becoming more distinct posteriorly; clypeus weakly emarginate, width 0.22, length 0.18; eyes moderately large, golden; antennomere III 2–3 times as long as wide; IV slightly longer and wider than V; V–VI submoniliform; VII broader than V–VI; VIII–X swollen into a relatively large pubescent compact club, segment VIII only weakly wedge-shaped; X relatively large, about 4 times length of VIII or IX.

Pronotum with weakly crenulate lateral margin and weakly sinuate posterior margin, disc with pair of strong lateral depressions and weaker single depression opposite scutellum, pronotal width 0.91, length 0.50; dorsal surface with fine punctures becoming larger laterally; hypomera weakly concave anterolaterally; prosternal process with moderately developed anterior keel (Fig. 55). Metasternum with well-developed fovea slightly anterior to midpoint. Femur with distal end sharply angled. Scutellum large, scutelliform with dense feeble confused punctulation and setae similar to that on pronotum. Elytra with weak subhumeral depression, epipleura rugulose and complete to about basal margin of abdominal sternite; elytral width 1.14, length 1.27; dorsal surface with strial interspaces rugose and weakly convex.

Abdomen with sternite I densely punctate; sternites II–V about equal in length and with basal row of small depressions partially hidden by anterior sternite. Abdominal intercoxal process projecting relatively abruptly ventrally and with a median longitudinal carina.

Holotype, ♂, MEXICO: TAMAULIPAS, with following data: 'Tamps, 1000 m nr Gomias Farias Rancho del Cielo 6-vi/7-vii 1983 cloud forest S&J.Peck' (ANIC); measurements: TBL 1.85, ELL 1.30, ELW 1.21, PNL 0.51, PNW 0.96, PHW 0.61, CLL 0.18, CLW 0.20.

Paratype, with same data as holotype (1♀, ANIC).

Etymology. Latin, meaning 'bearing a large club' in reference to the unusually large antennal club.

Distribution. Known only from type locality.

Remarks. This species is distinguished from all known congeners in that antennomere X is about 4 times the length of VIII or IX and the distal end of the femur is sharply angular. The head is also strongly deflexed and relatively difficult to see in dorsal aspect. These and some other general features of this species are somewhat reminiscent of *Genisphindus*. However, the femoral apex is not nearly as acute as is found in *Genisphindus* and when the other synapomorphies which define the two genera are considered, this species clearly falls within *Eurysphindus*.

***Eurysphindus halli* sp.n** (Figs 3, 59)

Description. Colour of head, pronotum, prosternum mesosternum and metasternum dark reddish-brown; scutellum and elytra medium reddish-brown, antennal stems, legs and abdominal sternites medium yellowish-brown, antennal club with dark brown antennomeres VIII–IX and lighter yellowish-brown antennomere X. Setation medium length, moderately dense, suberect (Fig. 3). Length 2.0.

Head with dorsal surface densely punctulate, punctules small and sparse anteriorly, larger and denser posteriorly; clypeus width 0.2, length 0.2; eyes small, gold; antennomere IV slightly elongate, V–VII submoniliform, VII slightly darker and broader than I–VI, VIII–X enlarged in a dark, densely pubescent club, VIII–IX darker than X, X about twice as long as VIII or IX; club covered with dense pale gold pubescence.

Pronotum with feebly crenulate lateral margin (Fig. 3), basal margin sinuate, disc with two lateral depressions (Fig. 3); pronotal width 1.0, length 0.5; dorsal surface with

dense, fine punctures, punctures becoming larger laterally, basolaterally and in depressions; prosternal process with large anterior keel (Fig. 53). Scutellum large, triangular-scutelliform, with depressed transverse region at about 1/3 length, punctation dense and minute but distinct; with setae similar to that on pronotum. Elytra with strong subhumeral depression, epipleura rugulose and complete to about basal margin of abdominal sternite IV; elytral width 1.5, length 1.6; dorsal surface with strial interspaces rugulose, feebly convex anteriorly and laterally, not convex at all posterodorsally.

Abdomen with sternite I densely punctate anteriorly, II–V about same length and with a row of small, basal depressions, abdominal intercoxal process broad basally, moderately blunt apically.

Holotype sex undetermined, MEXICO: NUEVO LEON, label data: 'Rio Linares, 20mi. West, Linares, Mex., Nov. 16, '48', 'H.B. Leech, Collector', 'Collection of the CALIFORNIA ACADEMY OF SCIENCES, San Francisco, Calif.' (CAS); measurements: TBL 2.1, ELL 1.4, ELW 1.4, PNL 0.6, PNW 1.1, PHW 0.7, CLL 0.2, CLW 0.3.

Paratype, none.

Etymology. A patronym for my friend and first Entomology teacher, James T. Hall of Ticonderoga High School, Ticonderoga, New York.

Distribution. Known only from the type locality.

Remarks. This species is distinct in that the punctation of the scutellum is neither like that of the pronotum (as in *E.hirtus*) nor confused (as in *E.comatulus*). Instead, the punctures are much smaller and denser than on the pronotum, but remain distinct. The scutellum is also somewhat triangular and has a weakly depressed transverse region anteriorly which is unknown in other *Eurysphindus* species. *E.halli* may be distinguished from other known Mexican species by its relatively large and flat pronotum (the other two species have a shorter more convex pronotum) and by the yellowish-brown elytra (the other two species have dark reddish-black elytra).

***Eurysphindus hirtus* LeConte** (Figs 4–25, 27–40, 42–44, 46B, 55, 58)

Eurysphindus hirtus LeConte, 1878: 602; Sen Gupta & Crowson, 1977: 183.

Description. Antennal clubs, elytra, abdominal sternites, prosternum, mesosternum and metasternum dark brown to reddish-brown; head, pronotum and scutellum black to reddish-brown; legs and antennal stems light yellowish-brown to reddish-brown. Body shiny; length 2.0.

Ocular head width 0.6, dorsal surface sparsely punctulate anteriorly, becoming densely but shallowly punctulate posteriorly (Fig. 8); eyes small, dark with gold highlights (Figs 4, 7–9); antennomere IV slightly elongate, V–VI submoniliform, VII wider than III–VI, segment VIII distinctly wedge-shaped, IX–X symmetrical and compact, X 2–3 times length of either VIII or IX (Figs 4, 6, 8, 9); mandible with prosthecal fringe inset from edge apically (Figs 5, 11); maxillae with slender galea and lacinia, densely setose at apices, lacking spines, with four-segmented palp, basal segment smallest, apical segment longest and with apical sensillae (Figs. 4, 17); labium with bilobed ligula, apical segment of palpi largest, distal end with sensillae (Figs 4, 10, 18, 19).

Pronotum with acute, crenulate edge (Figs 20, 21), basal margin weakly sinuate (Fig. 20); disc often with two lateral depressions; pronotal width 1.0, length 0.5; dorsal surface with dense, fine punctures, punctures becoming larger laterally (Figs 20, 31); hypomera strongly concave anterolaterally; prosternal process with small, anterior keel (Figs 21, 55). Metendosternite broad, anterior tendons widely separated, lamina long, narrow, tapering to recuspine apex, furcal arms widely separated and reaching enlarged, complex apex (Figs 25, 28). Wings with jugal lobe, weak recurrent radius, weak radial crossvein, cubitus, media, medio-cubital crossvein and one well-developed anal vein (Fig. 22). Scutellum large, quadrate to scutelliform, with coloration, punctation and setation similar to that on pronotum (Figs 26, 32). Elytra with a weak subhumeral depression (Fig. 23), epipleura rugulose and complete to about basal margin of abdominal sternite V; elytral width 1.2, length 1.4; dorsal surface with punctures darkened, strial interspaces smooth, feebly convex (Figs 23, 33, 34).

Abdomen with sternite I irregularly punctate, punctures becoming smaller posteriorly, sternites II–V about same length and with a row of small, basal depressions partially covered by preceding sternite (Fig. 24). Abdominal intercoxal process narrow (Fig. 24), with weak median longitudinal carina.

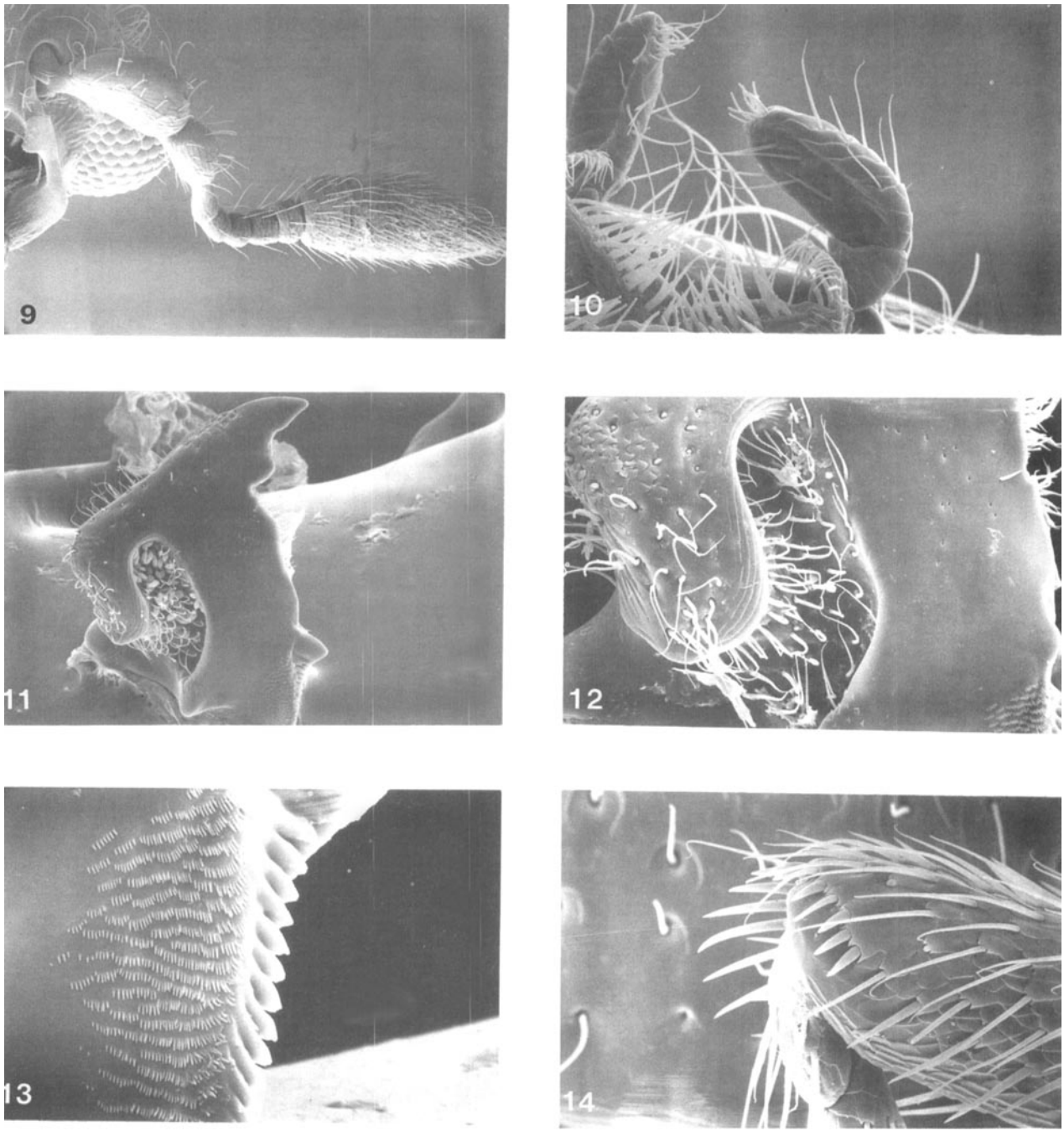
Male. Aedeagus turned on side when drawn into abdomen (Fig. 40), parameres fused and nonarticulated (Fig. 44), median lobe concave apically housing fused tip of parameres (Fig. 43).

Female. Genitalia with bilobed coxite, setae moderately dense at lateral margin; stylus short preapical, with cluster of five setigerous nodules, two setae longer than other three (Fig. 42).

Holotype, (sex undetermined), UNITED STATES: MICHIGAN, label data: 'Mic.', '9111', 'Type 3687', 'Eurysphindus hirtus *Lec.*', J.L. LeConte Coll. 230' (LeConte Collection, MCZ).

Paratype, none.

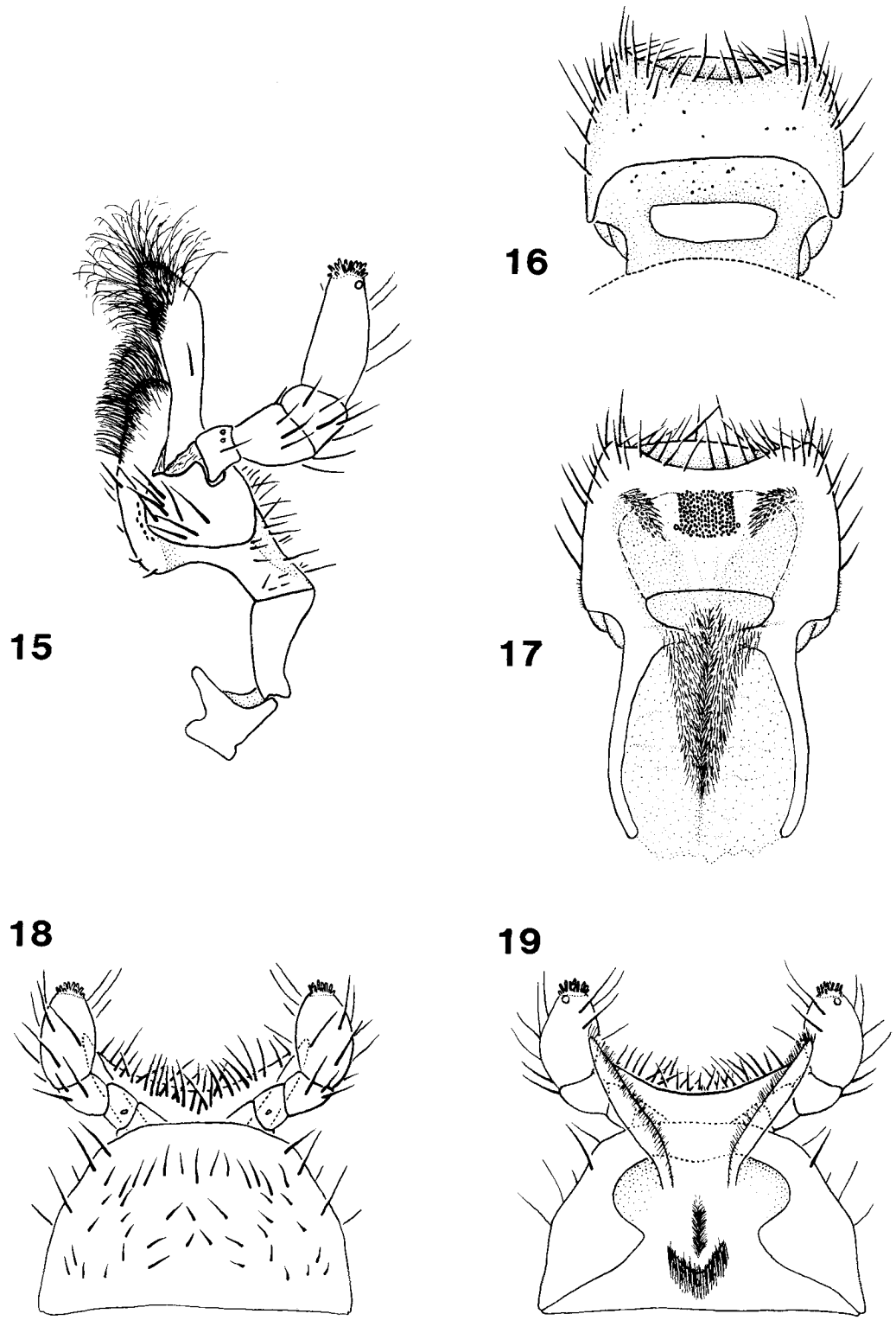
Additional material, CANADA: ONTARIO, Ottawa, Mer Bleu bog, 22.v.1953, 'berlese edge of swamp', (*Becker*) 1 ♀; MANITOBA, Aweme, 20.vii.1917 (*Criddle*) 1 ♂; QUEBEC, Montreal, 5.x.1979 (*Kiteley*) 1♂; UNITED STATES: CONNECTICUT, Cornwall, 6.vii.1925 (*Frost*) 1♀; ILLINOIS, Galesburg, (*Liebeck*) 1♂; no additional data, 1 (sex undet.); INDIANA, Mineral Springs, 1.ix. 1925 (*Montgomery*) 1♂; Porter Co., Dune Acres, 19.iv. 1942, 'by sifting', (*Dybas*) 1♀; IOWA, Iowa City, 29.vi. 1918 (*Wickham*) 1♀; MASSACHUSETTS, Middlesex Co., Estabrook Woods, Concord, 10.vii.1976, ex *Stemonitis axifera*, (*Lawrence*) 2♂♂; Pickman Area, Bedford, 26.vi.1974 (*Lawrence*): ex *Tubifera ferruginosa*, 1♂;



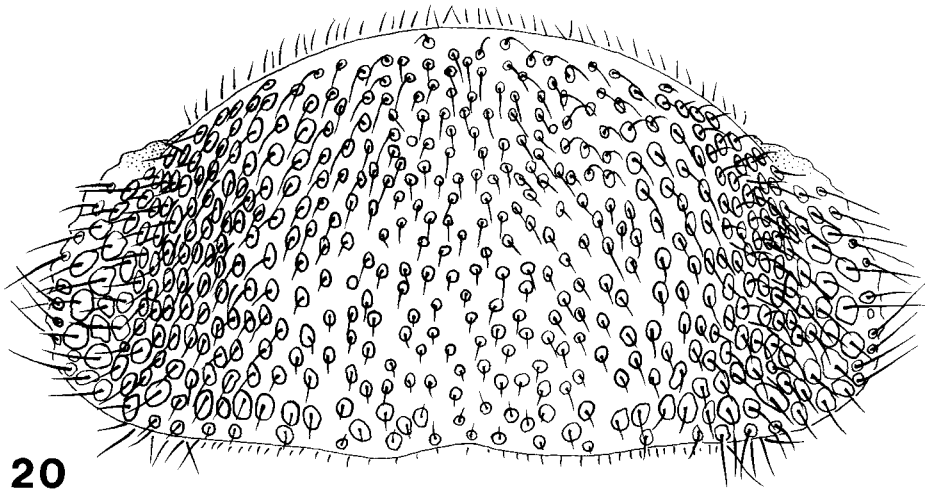
Figs 9–14. *Eurysphindus hirtus*. 9, Left antenna, anterior; 10, Labium, dorsal. 11–13, Left mandible, dorsal; 11, Mandible (note: mandible is damaged between second tooth and prosthecal fringe); 12, Mandibular cavity and tubercle; 13, Mola region; 14, Crown of stout setae, distal end of metatibia.

ex *Fuligo septica*, 1♂, 1♀; Natick, 8.vii.1928 (*Frost*) 1♀; Holliston, 1.viii (*Banks*) 1♂; Framingham (*Frost*): 20.iv.1902, 1♀; 22.iv.1923, 'sifting humus', 1♀; Sherborn (*Frost*): 27.iv.1935, 'sifting', 2♂♂; MICHIGAN, Detroit (*Hubbard & Schwarz*) 1♂; MINNESOTA, Itasca State Park, 15.vii.1960, 'tanglefoot trap', (*Ruske*) 1♂; NEW HAMPSHIRE, Strafford Co.: 4 miles W Durham, 23–25.vii.1982, 'Window trap', (*Reeves*) 1♂; 18–21. vi.1982, 'malaise trap', (*Reeves*) 1♀; 10–12.viii.1982, 'window trap', (*Reeves*) 1♂; 3 miles SW Durham, Spruce Hole, 7–20.viii.1987, 'FIT', (*Chandler*) 1♀; 1 mile SW Durham, 2–9.vii.1987, 'FIT', (*Chandler*) 2♀♀; NEW JERSEY, Hillsdale, Quirsfeld, 15.xi.1931, (*Frost*) 1♂; PENNSYLVANIA, Ulke, 1♀; Philadelphia, 28.vii (*Slevin*) 1♀.

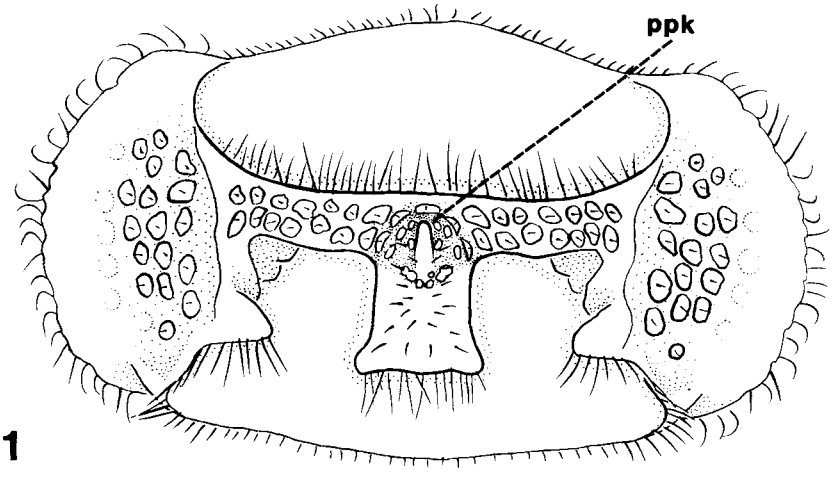
Natural history. This species is apparently a general



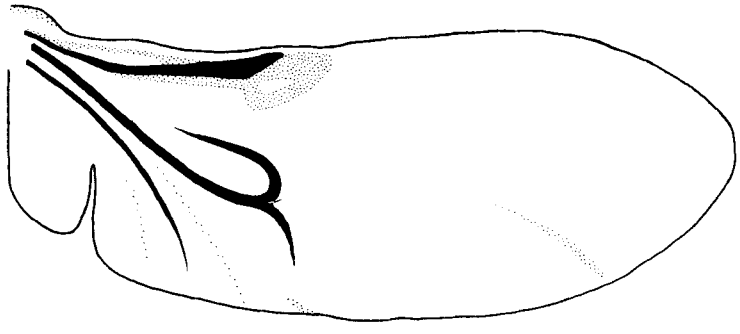
Figs 15–19. *Eurysphindus hirtus*, mouthparts. 15, Right maxilla, dorsal; 16–17, Labrum; 16, dorsal; 17, ventral; 18–19, Labium; 18, ventral; 19, dorsal.



20



21



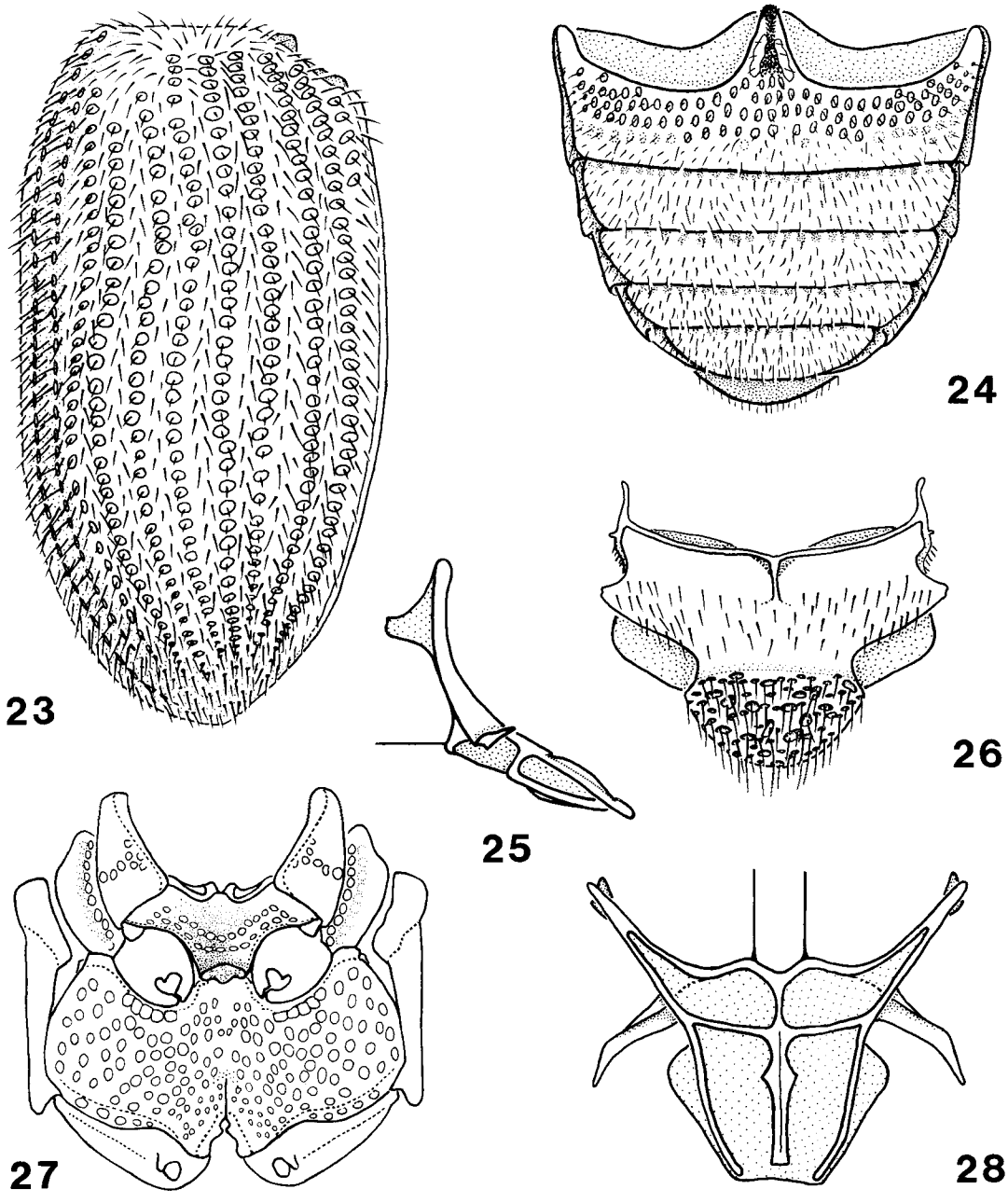
22

Figs 20–22. *Eurysphindus hirtus*. 20–21, Prothorax; 20, Dorsal; 21, Ventral, ppk = prosternal process keel; 22, Right wing, dorsal.

myxomycophage. It has been collected feeding on a diverse assemblage of slime mould species including *Diachea thomasii*, *Stemonitis axifera*, *Fuligo septica* and *Tubifera ferruginosa*.

Distribution. In the East, it is known from Pennsylvania and New Jersey in the South, to Quebec, Canada. At the western edge of its distribution, *E.hirtus* is known from Iowa northwest to Manitoba (Fig. 58).

Remarks. See remarks for *E.comatulus*.



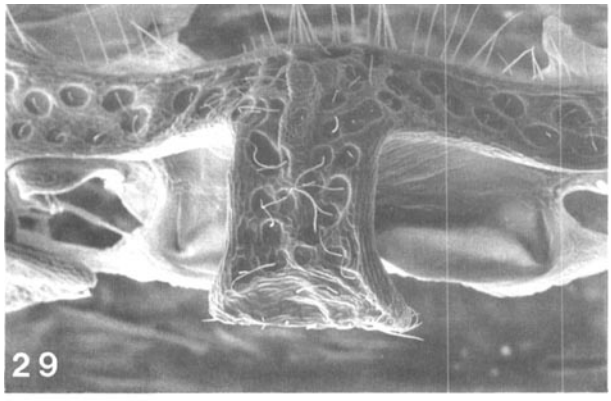
Figs 23–28. *Eurysphindus hirtus*. 23, Left elytron, dorsolateral; 24, Abdomen, ventral; 25, Metendosternite, lateral; 26, *E.comatulus*, Scutellum, dorsal; 27–28, *E.hirtus*; 27, Pterothorax, ventral; 28, Metendosternite, dorsal.

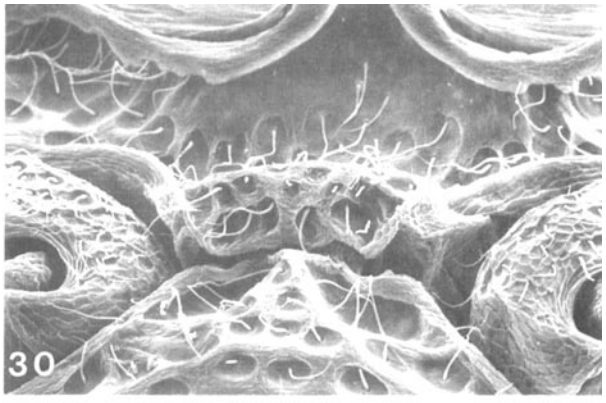
***Eurysphindus infuscus* sp.n.** (Fig. 59)

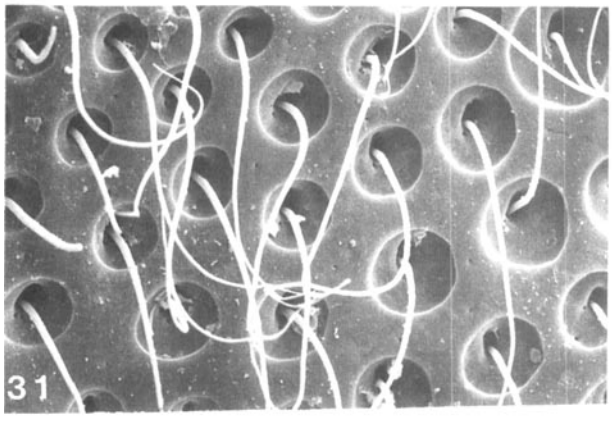
Description. Head and pronotum black, pronotum with margins lighter reddish-black; elytra and sterna dark reddish-brown and legs slightly lighter. Setation short, suberect to erect, weakly curled, golden. Length 1.75.

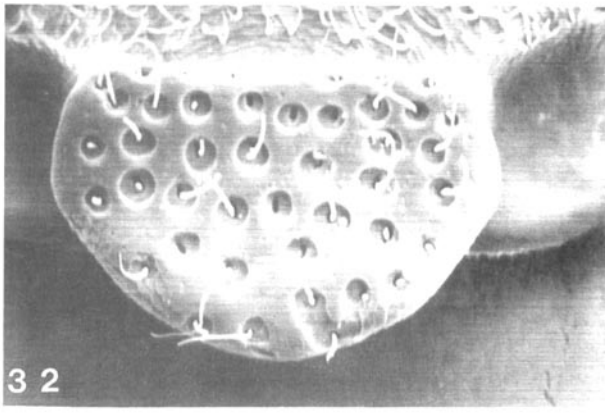
Head with dorsal surface sparsely and feebly punctulate anteriorly, becoming very densely punctate posteriorly; clypeus width 0.21, length 0.18; eyes pale golden; antennomere III about 3 times as long as wide; IV–V slightly elongated; VI submoniliform; VII broader and darker than III–VI; VIII–X enlarged in a relatively small, gradual, compact club; X about length of VIII–IX combined; VIII–IX dark brown, X light brown.

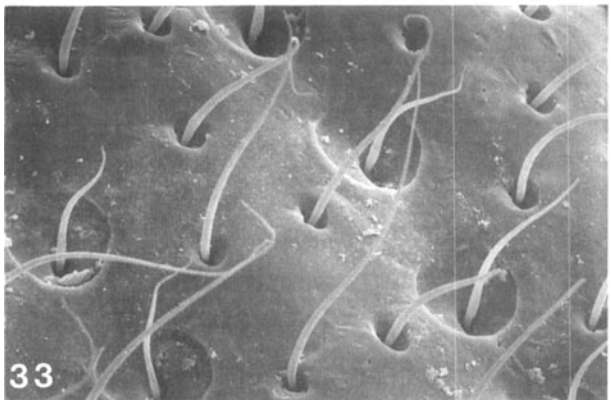
Pronotum with crenulate lateral margin, basal margin sinuate opposite scutellum, disc with pair of lateral depressions and short posterior median longitudinal depression; pronotal width 0.87, length 0.46; dorsal surface with dense punctures becoming larger laterally and in depressions; prosternal process with large anterior keel

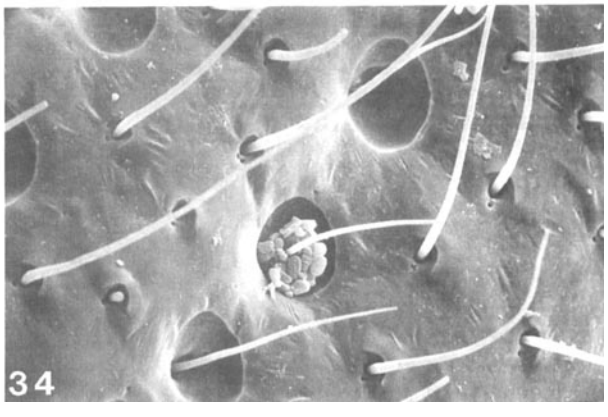












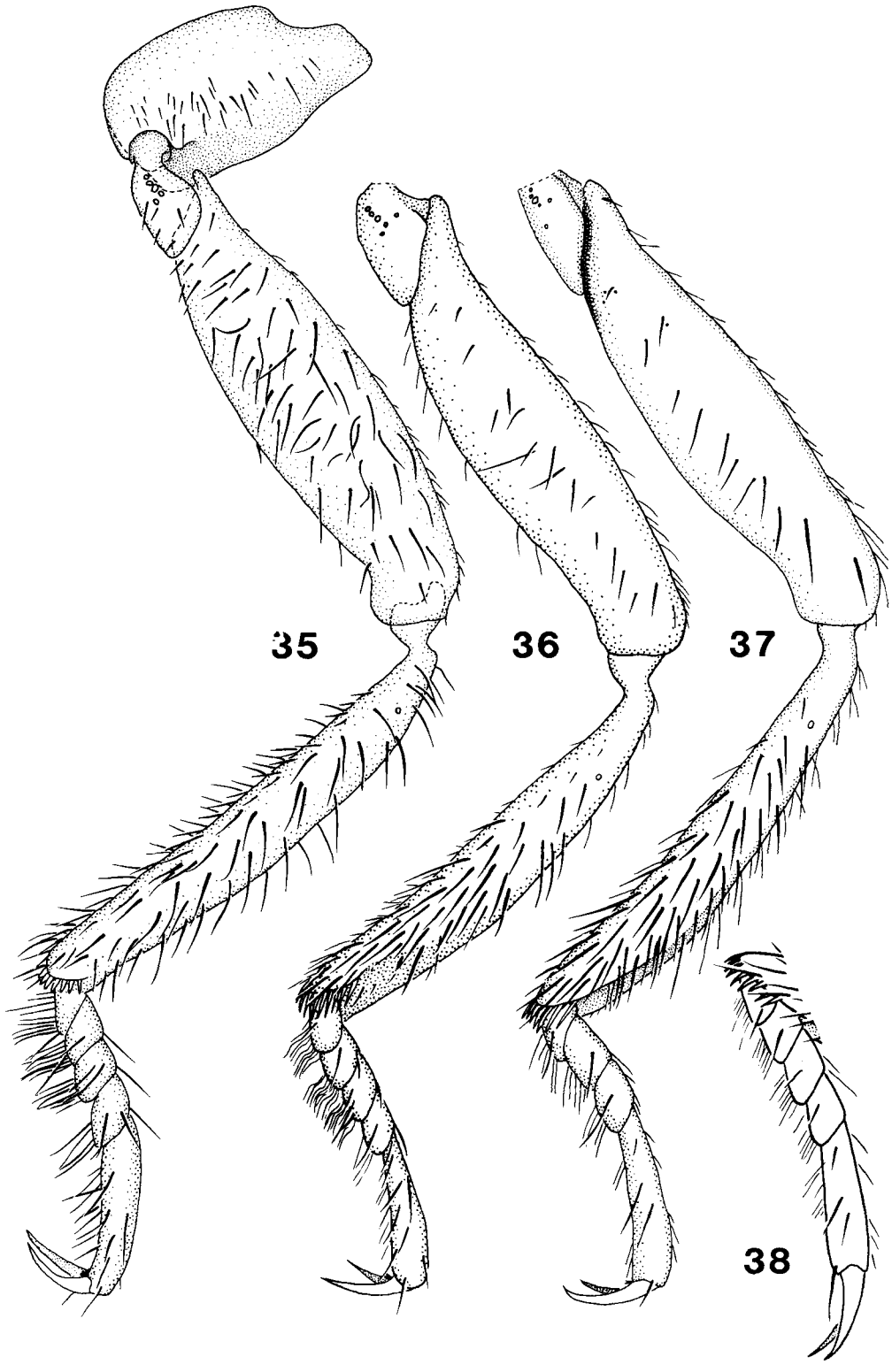
Figs 29–34. *Eurysphindus hirtus*. 29, Prosternal process; 30, Meso-metasternal juncture; 31, Pronotal punctation; 32, Scutellum, 33, Elytral surface, dorsal; 34, Elytral surface, dorsal (note: slime mould spores in central puncture).

(Fig. 53). Scutellum scutelliform with feeble, confused punctation; setation similar to that of pronotum. Elytra with weak subhumeral depression, epipleura rugulose and complete to about basal margin of sternite IV; elytral width 1.07, length 1.17; dorsal surface with strial interspaces shiny and weakly convex anteriorly, flat posteriorly.

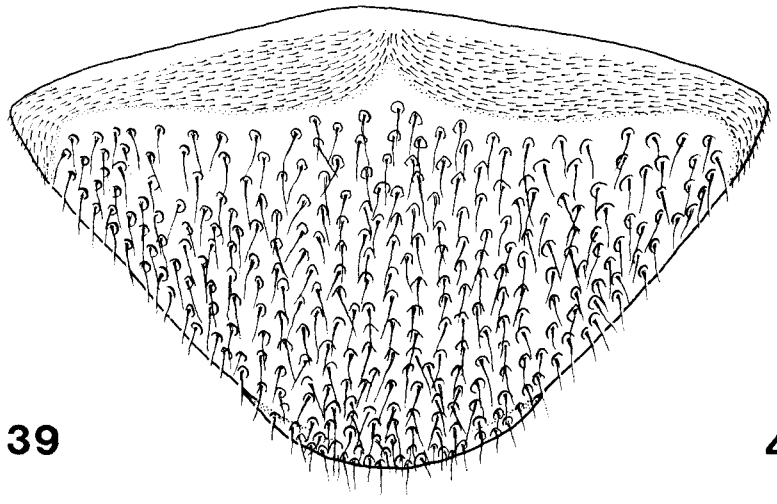
Abdomen with sternite I shallowly punctate, segments 2–5 about equal in length and with basal row of small depressions partially hidden by anterior sternite. Intercoxal process narrow with blunt apex.

Holotype, ♀, MEXICO: TAMAULIPAS, label data: 'MEX: Tamps. 1000 m nr Gomias Farias Rancho del Cielo 6-vi/7-viii 1983 cloud forest S&J. Peck' (ANIC); measurements: TBL 1.82, ELL 1.15, ELW 1.12, PNL 0.46, PNW 0.86, PHW 0.58, CLL 0.18, CLW 0.22.

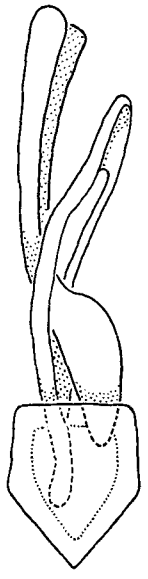
Paratype, with same data as holotype (1♀, CUIC).



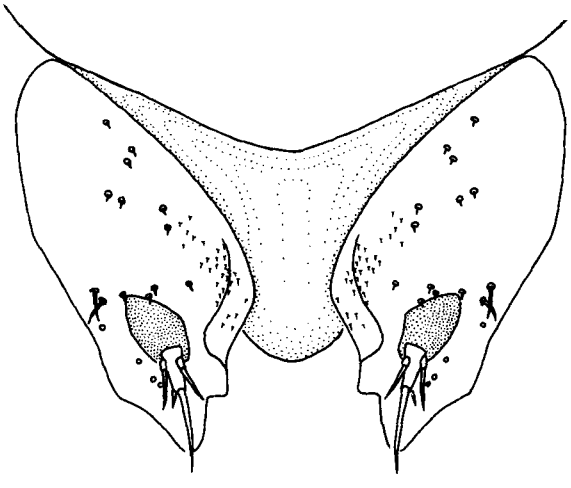
Figs 35–38. *Eurysphindus hirtus*, left legs, anterior. 35, proleg; 36, mesoleg; 37, male metaleg; 38, female metatarsus.



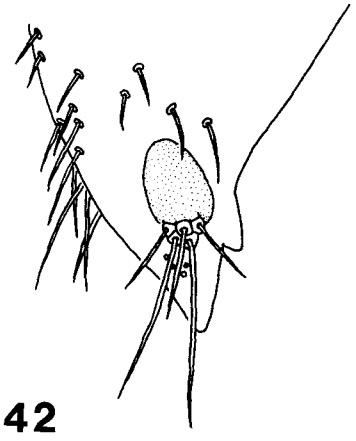
39



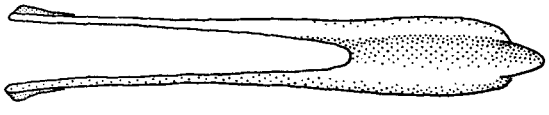
40



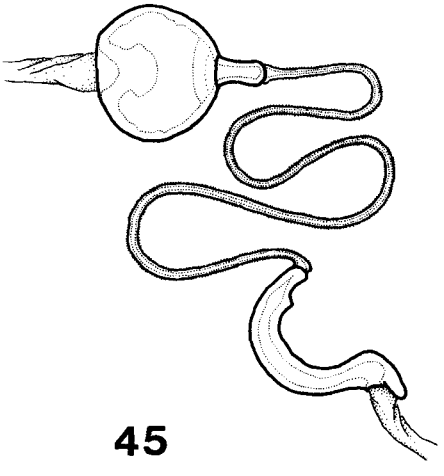
41



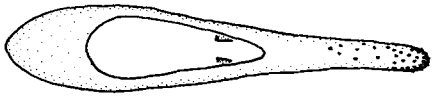
42



43

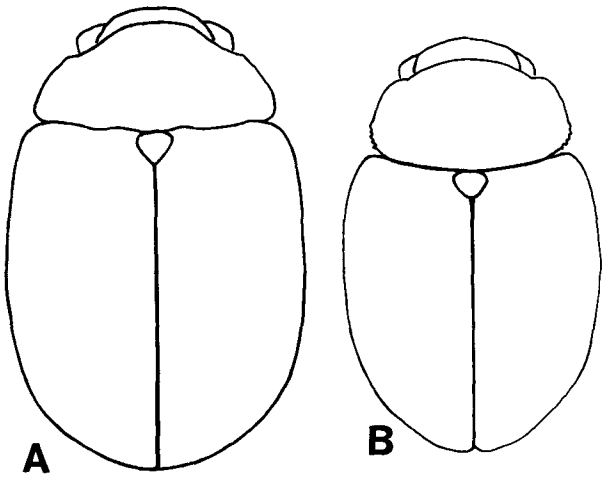


45



44

Figs 39–45. *Eurysphindus* terminalia and genitalia. 39–40, *E.hirtus*. 39, Pygidium dorsal; 40, Aedeagus and terminal abdominal segment, dorsal; 41, *E.comatulus*; Female genitalia apex, ventral; 42–44, *E hirtus*; 42, Right coxite and stylus, ventral view; Male genitalia, 43, Median lobe; 44, Parameres (fused) and basal piece; 45, *E.comatulus*. Spermatheca.



Figs 46A–B. Body forms. 46A, *Eurysphindus brasiliensis*; 46B, *E.hirtus*.

Etymology. Latin, meaning 'dusky, dark brown, blackish' in reference to the coloration of this species.

Distribution. Known only from the type locality.

Remarks. This species is similar to *E.comatulus* in appearance, but differs in that the elytra and scutellum are darker in colour. The pronotum of *E.infuscus* is shorter and more convex than that of *E.comatulus*. *E.grandiclaviger* is also similar in appearance to *E.infuscus* (and was taken at the same locality). However, *E.infuscus* lacks the angled femoral apex and the very large antennomere X. The head of *E.infuscus* is not nearly as strongly deflexed as that of *E.grandiclaviger* and is easily visible in dorsal aspect.

Eurysphindus plaumanni Sen Gupta & Crowson

Eurysphindus plaumanni Sen Gupta & Crowson, 1977: 184.

Description. Body light reddish-brown with slightly darker antennal clubs. Body broad, elytra tapering gradually posteriorly. Length 2.0.

Head depressed opposite frontoclypeal suture; dorsal surface densely and evenly punctulate; clypeus length 0.2, width 0.2; eyes small, dark with golden highlights; antennomere IV slightly elongate, V–VI submoniliform, VII slightly wider than III–VI, segment VIII slightly asymmetrical, IX wider than VIII, IX–X symmetrical, more compact than VIII–IX, X about twice length of either VIII or IX.

Pronotum with moderately crenulate lateral margin, basal margin sinuate; disc with pair of lateral depressions and a median longitudinal depression; pronotal length 0.5, width 1.0; dorsal surface densely and evenly punctulate, punctules enlarged laterally and basolaterally; prosternal process with anterior keel produced as tubercle (Fig. 54). Metasternum depressed opposite mesosternal process. Scutellum large, scutelliform, covered with feeble punctules, moderately setose. Elytra lacking a subhumeral depression, epipleura rugulose and complete to about posterior edge of abdominal sternite 3; elytral length 1.3, width 1.2; dorsal surface with strial interspaces rugulose, feebly convex.

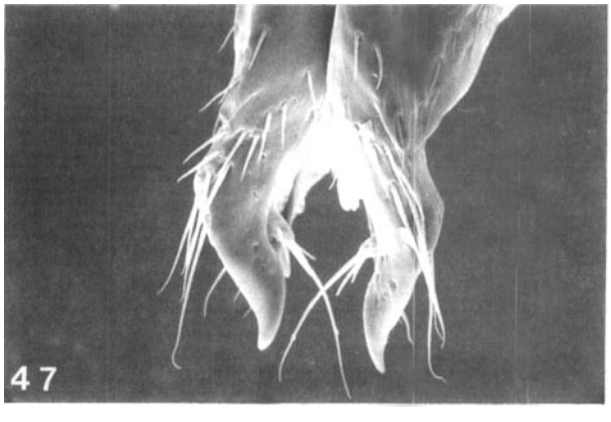
Abdomen with sternite I densely and shallowly punctate, II–V with row of small, basal depressions nearly concealed by anterior sternite. Abdominal intercoxal process broad at base, acute anteriorly.

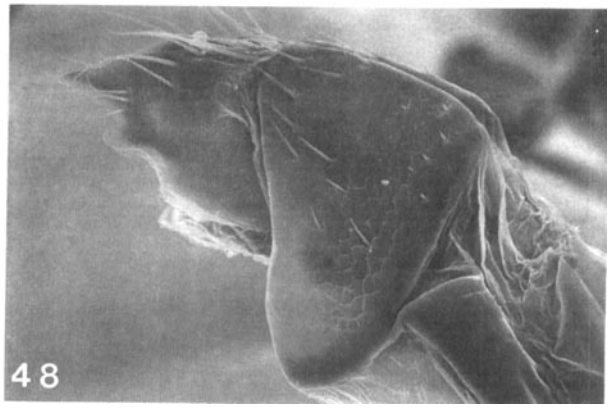
Holotype, ♂, BRASIL: label data: 'Brasilien, Nova Teutonia, 27 11'8. 52 23'1, Fritz Plaumann, VIII.1957, 300–500 M', 'Manchester Museum, Holotype' and 'Eurysphindus plaumanni sp nov, det. R. A. Crowson' (MANM); Measurements: TBL 2.0, ELL 1.3, ELW 1.2, PNL 0.5, PNW 1.0, OHW 0.6, PHW 0.5, CLL 0.2, CLW 0.2.

Paratype, none.

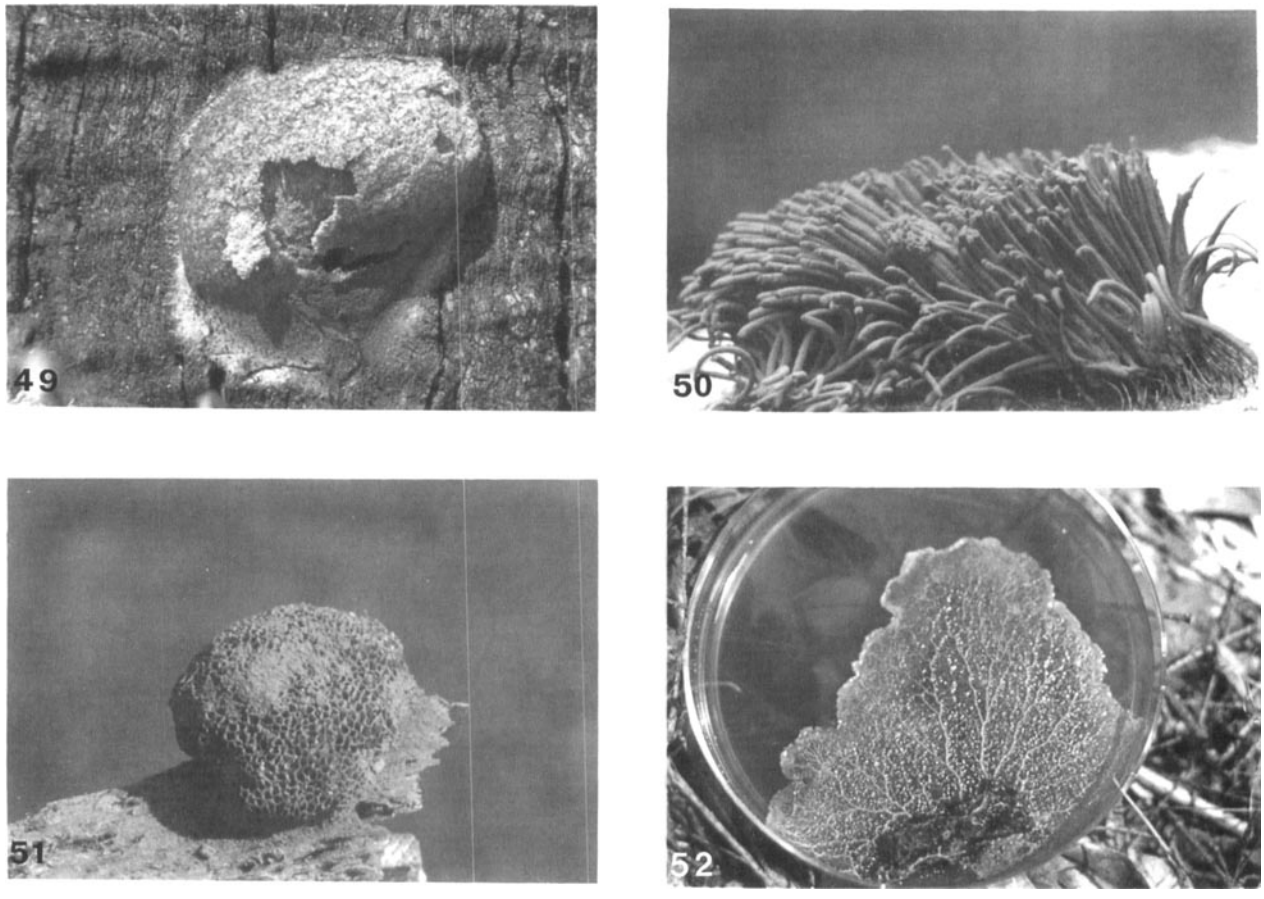
Distribution. Known only from the type locality (Fig. 60).

Remarks. See remarks for *E.brasiliensis*.

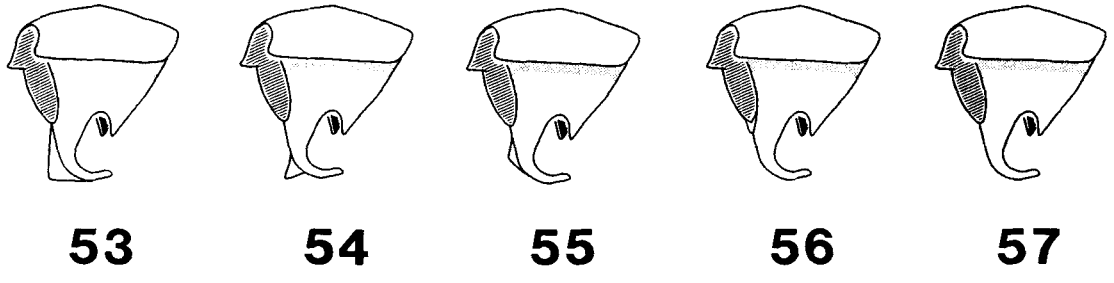




Figs 47–48. *Eurysphindus comatulus*, female genitalia. 47, Ventral; 48, Lateral.



Figs 49–52. Myxomycetes. 49, *Fuligo septica* fruiting body; 50, *Stemonitis* sp. fruiting body; 51, *Tubifera ferruginosa* fruiting body; 52, Myxomycete plasmodium.



Figs 53–57. Prosternal processes, lateral, diagrammatic. 53, *Eurysphindus halli*; 54, *E.brasiliensis*; 55, *E.hirtus*, *E.infuscus*; 56, *Genisphindus latisternus*; 57, *G.laevicollis*, Typical, non-carinate form.

Genisphindus, gen.n.

Type species: *Genisphindus roxanneae* McHugh.

A phylogenetically based justification for erecting this genus is provided in 'Cladogram analysis' section.

Description. Body oval, convex, widest near middle, head partially visible from above (Fig. 61). Colour of body uniformly brown to reddish-brown, shiny. Length 1.4–2.0.

Head with a pair of dorsal antennal grooves extending from between antennal insertions and clypeus to beyond top of eye (Fig. 78), ventrally with three pairs of pits, frontoclypeal suture arcuate (Fig. 78); dorsal surface punctulate with basal row of enlarged punctures (Fig. 78); clypeus large, emarginate laterally, broad distally (Fig. 78); eye black and coarsely facetted (Fig. 61); antenna 10-segmented, with robust and asymmetrical antennomeres I and II, antennomere III elongate, VII slightly wider than III–VI, VIII–X forming densely pubescent,

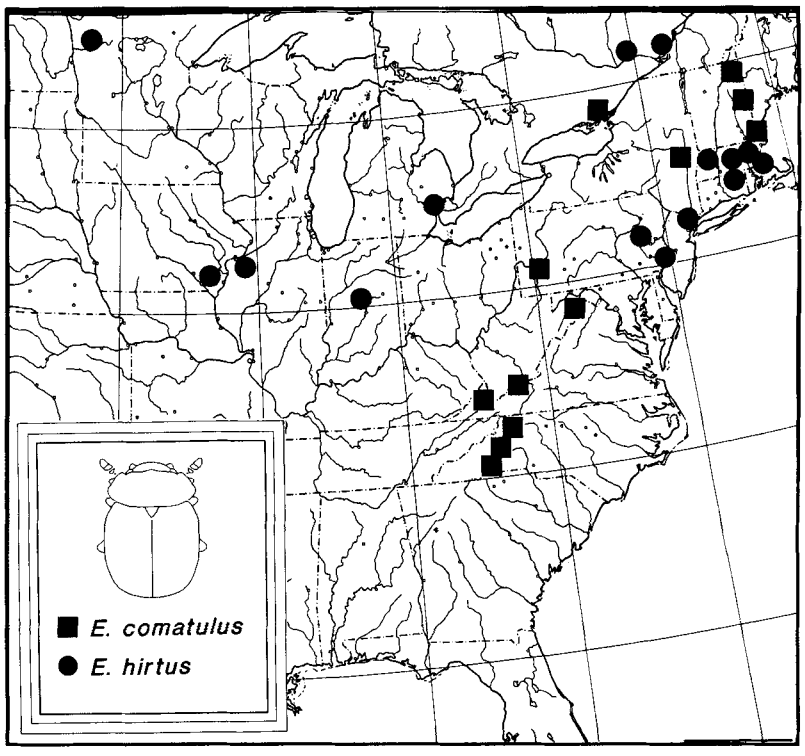


Fig. 58. Distribution of North American *Eurysphindus* spp.

compact club (Fig. 71) IX and sometimes VIII much darker than other antennomeres; labrum nearly completely covered by clypeus, bilobed distally (Fig. 76); mandible robust, flattened apically, bidentate, with tubercle and cavity (Fig. 77).

Pronotum slightly narrowed in front, rounded at sides, flattened laterally, with acute, smooth edges, basal margin sinuate (Figs 61, 83), procoxal cavities widely open (Fig. 83); dorsal surface punctulate with a row of slightly enlarged punctures along basal and lateral margins, punctures often enlarged on anterolateral flanges and in paired depressions when present; prosternal process raised, narrow, not widened as lateral flanges apically (Fig. 83), prosternal process with (Fig. 56) or without (Figs 57, 83) a raised anterior edge forming a 'V' shaped ridge, lateral edges reflexed and irregularly punctate. Mesosternum vertical, concave to receive prosternal process (Figs 65, 73); mesosternal process with two pits separated by a central ridge (Figs 65, 67, 73); trochantins exposed. Metasternum inflated, with large punctures (Fig. 65). Legs long and slender (Figs 80–82). Coxae transverse. Femora with pointed distal ends (Figs 61, 72, 74, 80–82), sparsely to moderately setose, hind femora with a weak posterior flange at about one-third length partially covering tibia when folded (Fig. 82). Tibiae dilated at middle, narrowed basally and ridged, moderately to densely covered with anteriorly directed setae, lacking spurs except for a very short crown distally (Figs 80–82). Tarsi 5-5-5 female, 5-5-4 male, simple to slightly elongate (Figs 80–82). Scutellum scutelliform (Fig. 61) to quadrate, shallowly and irregularly punctate. Elytra broad, covering abdomen, strongly depressed opposite lateral margins of scutellum, with no trace of subhumeral depression (Fig. 61), humeral calli moderately (Fig. 61) to weakly developed, epipleuron rugulose and complete to about middle of abdominal sternite III; dorsal surface with one scutellary and ten long, usually well-marked punctate strial interneurs (Fig. 61), strial interspaces weakly (Fig. 61) to strongly convex with 1–2 rows of setae (Figs 61, 75).

Abdomen with 5 visible sternites, sternite I about 1–2 times length of other sternites and punctate, sternites II–V with a row of large basal depressions and sparsely and irregularly punctulate (Fig. 85), sternites not arranged in same plane giving shingled appearance. Anterior abdominal intercoxal process narrow, acute anteriorly and with central carina (Fig. 85). Pygidium densely and evenly punctulate (Fig. 88).

Etymology. Latin, 'kneed Sphindus', in reference to the characteristic pointed distal ends of the femora.

Natural history. All species presumably feed on myxomycetes.

Distribution. Neotropical.

Remarks. This genus is similar to *Eurysphindus* and *Aspidiphorus* in some respects such as the highly oval body form, concave hypomera, widely externally open procoxal cavities and sinuate pronotal posterior margin. It differs from *Aspidiphorus* and *Eurysphindus* in that the apex of the femur is produced to an acute point and the apex of the mesosternal process is knoblike and characterized by a pair of large lateral pits (see Figs 65–68).

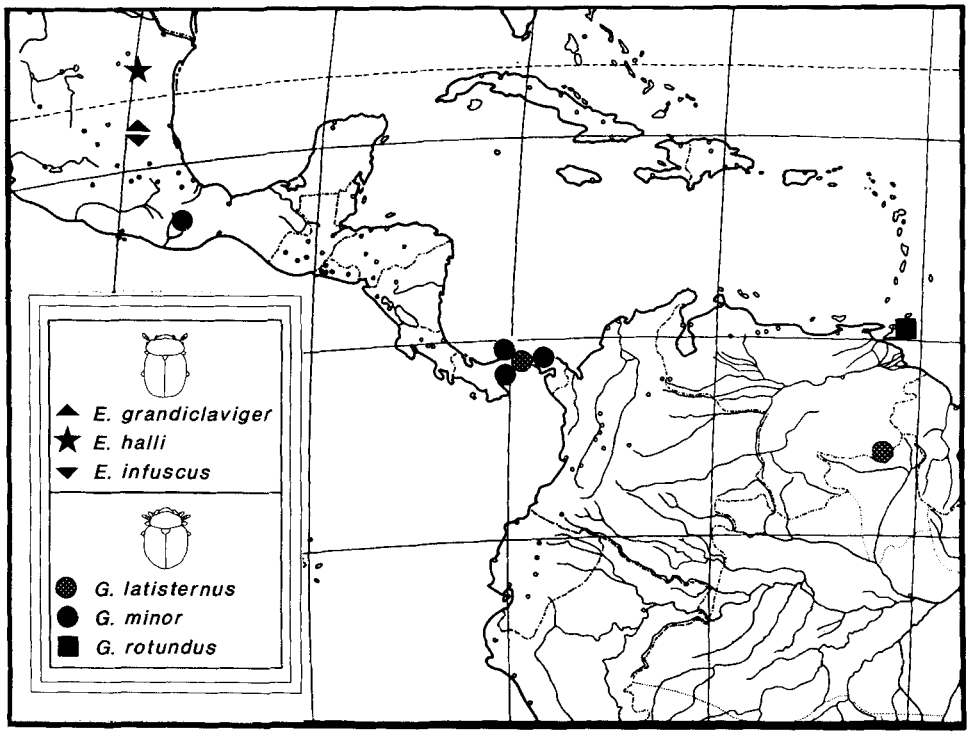


Fig. 59. Distribution of Central American *Eurysphindus* and *Genisphindus* spp.

The pygidial groove and dorsal head grooves seen in *Aspidiphorus* are absent in *Genisphindus*. The pronotal lateral margin is crenulate in *Eurysphindus* and smooth in *Genisphindus*. The head in *Eurysphindus* lacks the impunctate dorsobasal region and the transverse row of greatly enlarged punctures seen in *Genisphindus* (Fig. 78).

Species included: *G.laevicollis* (Sen Gupta & Crowson), comb.n. from *Eurysphindus*, Brasil; *G.latisternus* sp.n., Canal Zone (Panama); *G.minor* sp.n., Panama and Mexico; *G.rotundus* sp.n., Trinidad; *G.roxanneae* sp.n., Peru and Ecuador.

Key to *Genisphindus* species

1 Mesosternal process apex with broad median piece and a pair of small widely separated lateral pits (Fig. 66); prosternum with anterior longitudinal 'V' shaped keel terminating between procoxae (Fig. 56) 4

– Mesosternal process apex with narrow median piece and a pair of large adjacent pits (Figs 65, 67, 68, 73); prosternum lacking keel (Figs 57, 83) 2

2 Scutellum width at base greater than length; body form moderately globose (Fig. 64) to moderately globose with body weakly parallel-sided (Fig. 62); relatively small (<1.75 mm); pronotum and elytra dark brown to reddish-brown (Central and South America) 3

– Scutellum length nearly equal to width at base; body form highly globose (Fig. 63); relatively large (>1.95 mm); pronotum brown and elytra yellowish-brown (Trinidad) ..... *rotundus* sp.n.

3 Body light reddish-brown; blunt posteriorly (Fig. 62) (Ecuador, Peru, Bolivia) ..... *roxanneae* sp.n.

– Body dark reddish-brown to brown; slightly tapered posteriorly (Fig. 64) (Central America) ..... *minor* sp.n.

4 Body form moderately globose (as in Fig. 62), light yellowish-brown (Brasil) ..... *laevicollis*

– Body form highly globose (as in Fig. 63), reddish-brown (Central America) ..... *latisternus* sp.n.

Genisphindus laevicollis (Sen Gupta & Crowson), comb.n. (Figs 56, 60)

Eurysphindus laevicollis Sen Gupta & Crowson, 1977: 184.

Description. Body oval, blunt posteriorly. Colour of elytra and pronotum light brown, head light brown to brown, body weakly shiny. Setation short, suberect. Length 1.7.

Head with 3 pairs of ventral antennal pits, pit III (see Fig. 7) not well-defined; ocular head width 0.6; median head length 0.3; dorsal surface sparsely and irregularly punctulate, with basal row of enlarged punctures; clypeus width 0.2, length 0.2; antennae with segment III about twice as long as wide, IV–VI submoniliform, segment VII wider than III–VI, antennomere X about 3 times length of either VIII or IX, antennal pubescence light brown to white.

Pronotum sinuate posteriorly; pronotal width 0.9,

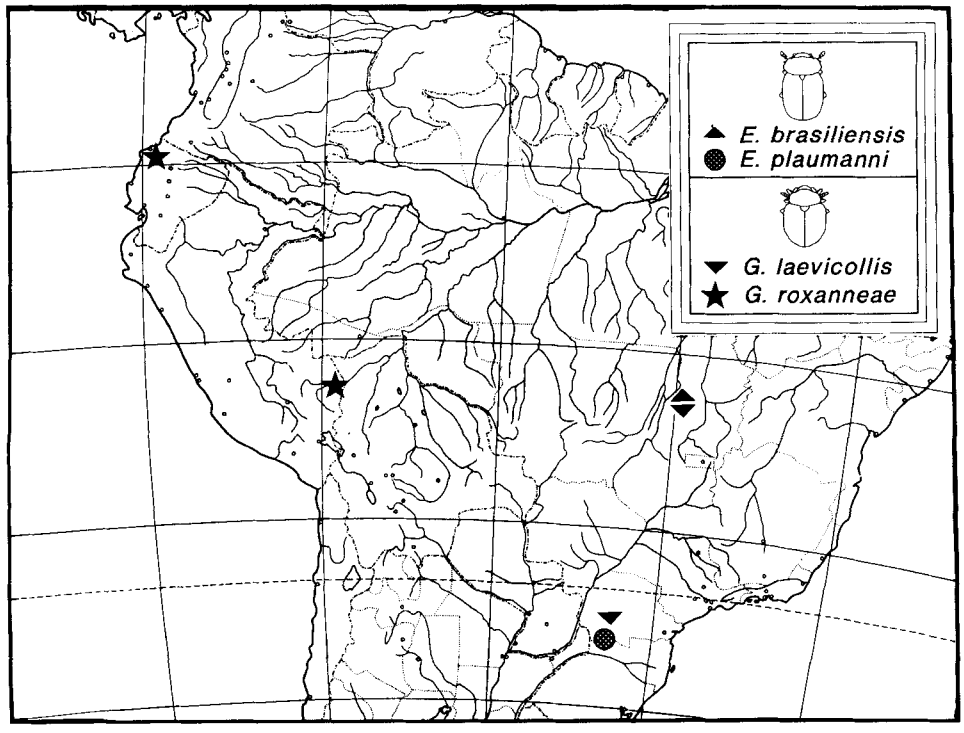


Fig. 60. Distribution of South American *Eurysphindus* and *Genisphindus* spp.

length 0.5; dorsal surface with sparse, shallow, irregular, punctation, punctures enlarged on anterolateral flange and in pronotal depressions; prosternal process with raised anterior edge forming a 'V' shaped ridge (Fig. 56). Mesosternal process with two pits separated by narrow central piece. Tarsomeres simple, apical tarsomere about as long as others combined. Scutellum cordate–quadrate, with shallow, irregular punctures. Elytra lacking subhumeral depression, epipleura rugulose and complete to about basal margin of abdominal sternite IV; elytral width 1.2, length 1.1; dorsal surface with punctures gradually decreasing in size but remaining distinct posteriorly, strial interspaces slightly convex.

Abdomen with sternite I about twice length of other sternites and with large, shallow punctures, sternites II–V with large basal depressions to about one-third length of sternites. Abdominal intercoxal process with central carina.

Holotype, ♀, BRASIL: label data: 'Brasilian, Rondon, 24 38′ B. 54 07′ L, Fritz Plaumann, VIII 1952, 500 m', 'Eurysphindus laevicollis sp.nov., det. R. A. Crowson', 'HOLOTYPE, det. R. A. Crowson' (MCZ); measurements: TBL 1.7, ELL 1.1, ELW 1.1, PNL 0.5, PNW 0.9, MHL 0.3, PHW 0.6, CLL 0.2, CLW 0.2.

Distribution. In addition to the type locality, I have seen one ♂ from Chapada, Brasil (MCZ), with following data: 'Chapada Brasil Acc.No.2966 Nov.' (Fig. 60).

Remarks. G.laevicollis differs from *G.roxanneae* (also South American) in that the prosternum has a raised 'V' shaped anterior ridge (Fig. 56) which is lacking in the latter species (Fig. 57). *G.laevicollis* is light brown in colour and moderately shiny while *G.roxanneae* is reddish-brown and very shiny. The body form of *G.laevicollis* (similar to *G.roxanneae*, see Fig. 62) is more parallel-sided than that of *G.latisternus* (similar to *G.rotundus*, see Fig. 63) which is known from Panama and Venezuela.

Genisphindus latisternus sp.n. (Figs 56, 59, 66)

Description. Body oval, blunt posteriorly. Head, prothorax and elytra reddish-brown, legs and antennae light reddish-brown, body shiny. Setation short, suberect. Length 1.8.

Head with 3 pairs of well-defined ventral antennal pits. Ocular head width 0.7; median head length 0.4; dorsal surface densely and evenly punctulate with impunctate basal band and basal row of enlarged punctures; clypeus width 0.2, length 0.2; antennomere III about twice as long as wide, IV–VI submoniliform, VII slightly wider than III–VI, apical segment about 3–4 times length of either VIII or IX, VIII and IX about same length, X lighter in colour than VIII–IX, pubescence of club white.

Pronotum with no trace of paired dorsal depressions, strongly sinuate posteriorly; pronotal width 1.0, length 0.6; dorsal surface evenly punctulate, with row of enlarged punctures along lateral and basal margin, row absent opposite scutellum; prosternal process with raised anterior edge forming 'V' shaped ridge (Fig. 56). Mesosternal process with two pits widely separated by broad median piece (Fig. 66). Tarsi simple, with apical tarsomere not quite as long as others combined except on male metatarsus.

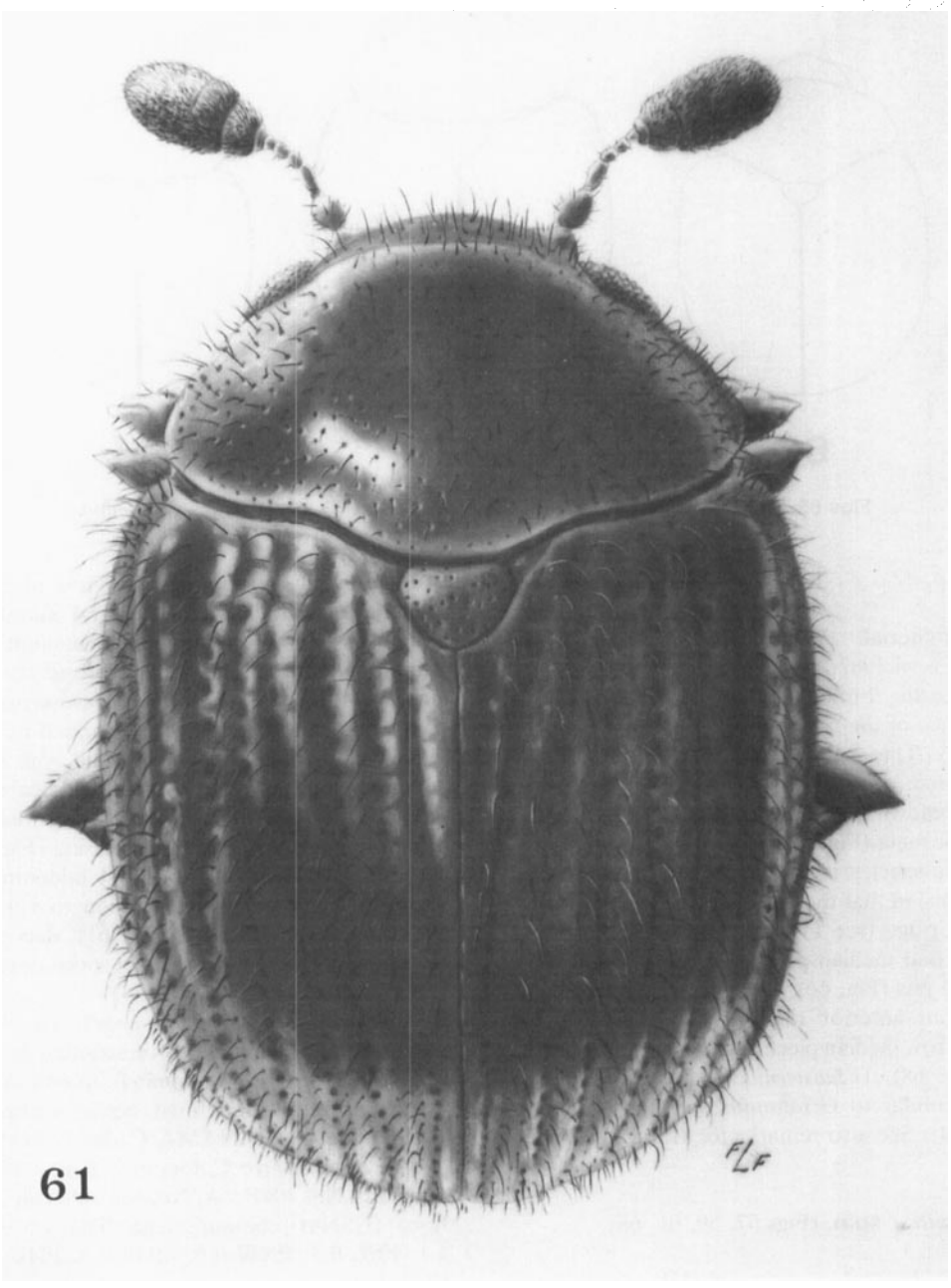


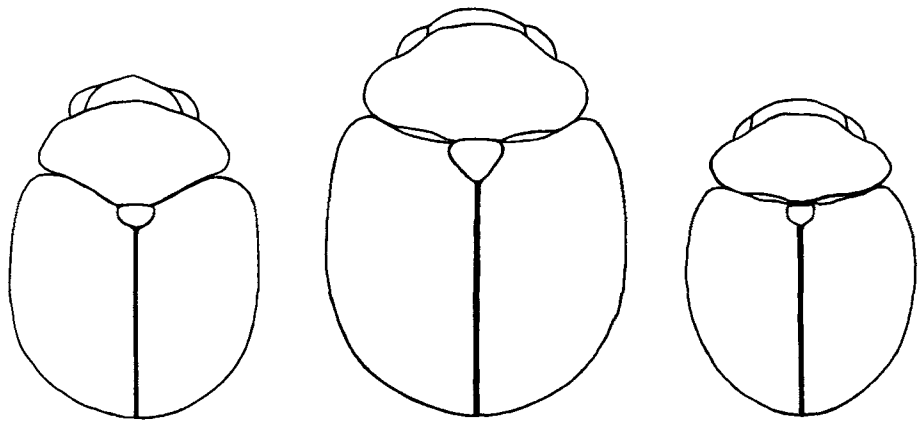
Fig. 61. *Genisphindus minor*, female.

Scutellum quadrate-scutelliform, slightly broader at base than long, shallowly and irregularly punctate. Elytra lacking subhumeral depression, epipleura weakly rugulose and complete to about middle of abdominal sternite III; elytral width 1.3, length 1.3; dorsal surface with punctures darkened, decreasing abruptly in size but remaining distinct posteriorly, strial interspaces convex.

Abdomen with sternite I with shallow irregular punctures and about 1.5 times length of sternites II–V, sternites II–V with basal depressions to about one-third visible length of sternites. Abdominal intercoxal process with rounded apex and well-defined, central carina.

Holotype, ♂, PANAMA CANAL ZONE: label data: 'Canal Zone: Is., Barro Colorado, II/19-III/9–75, Lawrence, Erwin', 'J. F. Lawrence, Lot 3776', 'ex *Stemonitis fusca*', 'GENUS?, Det., J. F. Lawrence' (USNM); measurements: TBL 1.9, ELL 1.1, ELW 1.4, PNL 0.7, PNW 1.2, MHL 0.4, PHW 0.7, CLL 0.2, CLW 0.2.

Paratypes, same data as holotype (1♀, MCZ; 1♂ and 1♀, ANIC; and same date and location data but collected



Figs 62–64. Body forms. 62, *Genisphindus roxanneae*; 63, *G.rotundus*; 64, *G.minor*.

on *Stemonitis* sp. (2 ♂ ♂, 1 ♀ and 1 sex undetermined, MCZ).

Additional material, VENEZUELA: BOLIVAR, Icabarú, 490 M, 6.vii.1987, 'Malaise trap', (*Ivie*) 1 ♂.

Etymology. Latin, 'broad breast' in reference to the wide median piece of the mesosternal process.

Natural history. This species has been collected feeding on *Stemonitis fusca*.

Distribution. Known from type locality and one location in southern Venezuela (Fig. 59).

Remarks. This species is distinct from *G.minor* (also Central American) in that the prosternal process has a 'V' shaped anterior ridge (see Fig. 56) and the mesosternal process has a broad median piece and two small, widely separated lateral pits (Fig. 66). The prosternal process of *G.minor* lacks an anterior ridge and the mesosternal process has a narrow median piece and two large, adjacent, lateral pits (Fig. 68). *G.latisternus* is also more robust in body form (similar to *G.rotundus*, see Fig. 63) than *G.minor* (Fig. 64). See also remarks for *G.laevicollis*.

***Genisphindus minor* sp.n.** (Figs 57, 59, 61, 68)

Description. Body oval, tapering slightly posteriorly. Head, prothorax, elytra dark brown to reddish-brown, legs brown to yellowish-brown, body shiny. Setation short, erect (Fig. 61). Length 1.6.

Head with 3 pairs of well-defined ventral antennal pits; ocular head width 0.6; median head length 0.4; dorsal surface punctulate with impunctate basal band and basal row of enlarged punctures; clypeus width 0.2, length 0.2; antennomere III about twice as long as wide, IV slightly elongate, V–VI submoniliform, antennomere VII slightly wider than III–VI, X about twice as long as either VIII or IX, VIII and IX about same length, X lighter in colour than VIII–IX, club pubescence light brown to white.

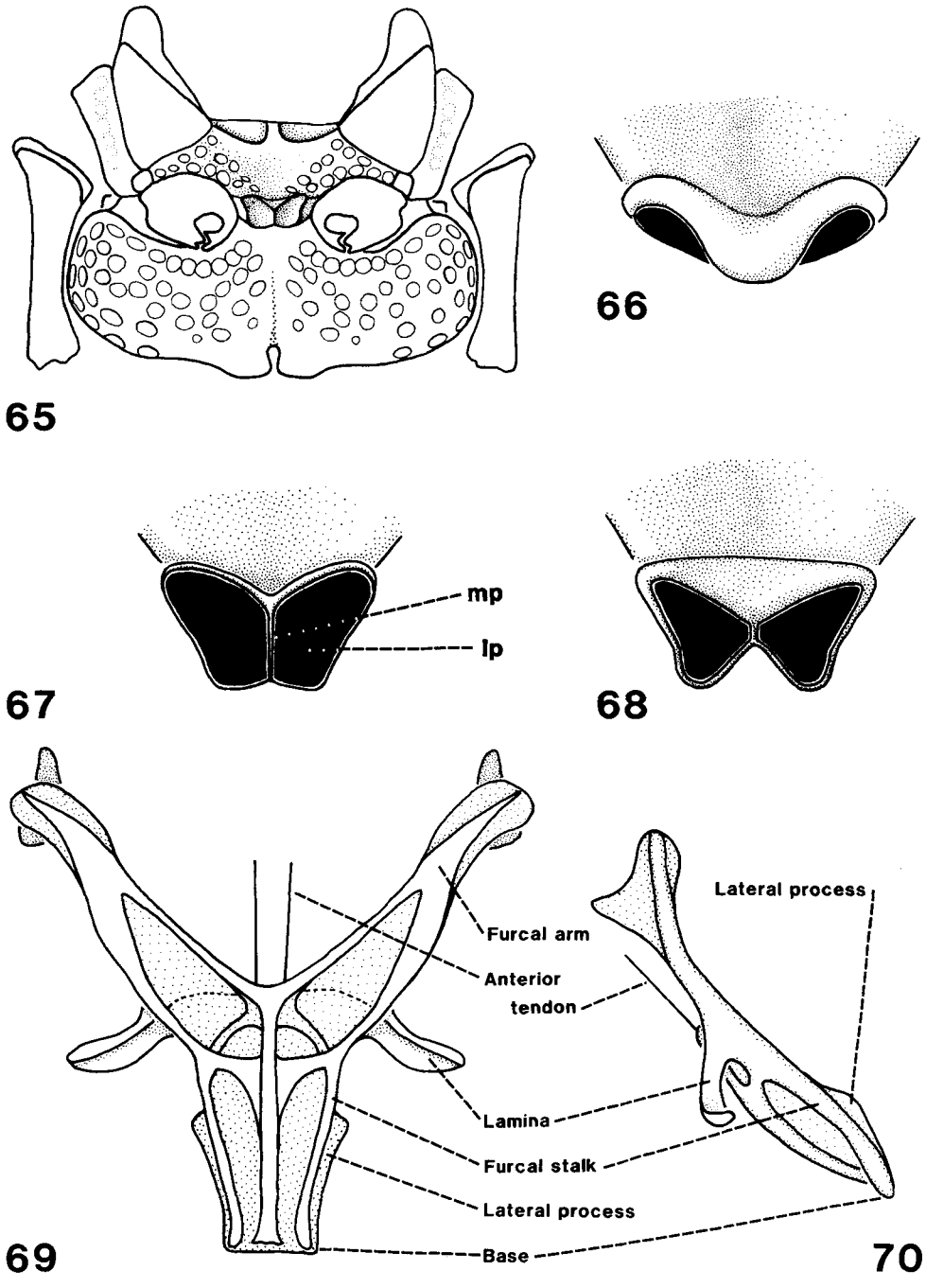
Pronotum with a pair of dorsal depressions, sinuate posteriorly (Fig. 61); pronotal width 0.9, length 0.6; dorsal surface evenly punctulate, with row of slightly enlarged punctures along basal and lateral margins, row nearly complete but absent opposite scutellum, punctures enlarged on anterolateral flanges; prosternal process lacking an anterior ridge (Fig. 57). Mesosternal process with two well-defined lateral pits separated by a short narrow median piece (Fig. 68). Tarsi simple, with apical tarsomere about as long as others combined. Scutellum quadrate-scutelliform (Fig. 61), irregularly and weakly punctulate. Elytra lacking subhumeral depression (Fig. 61), epipleura rugulose and complete to about midpoint of abdominal sternite III; elytral width 1.2, length 1.0; dorsal surface with punctures darkened (Fig. 61), decreasing gradually in size but remaining distinct posteriorly, strial interspaces convex.

Abdomen with sternite I about twice length of other sternites, basal depressions on sternites II–V at least half length of sternite. Abdominal intercoxal process with acute apex and well-defined, central carina.

Holotype, ♂, PANAMA CANAL ZONE: label data: 'Canal Zone: Barro Colorado I. Feb., 1976', 'J. F. Lawrence Lot No. 4091', 'A. Newton collector', 'ex Stemonitis fusca' (USNM); measurements: TBL 1.5, ELL 1.0, ELW 1.1, PNL 0.5, PNW 0.9, MHL 0.3, PHW 0.6, CLL 0.2, CLW 0.2.

Paratypes, same data as holotype (1 ♂ and 1 ♀, MCZ); PANAMA: Cerro Azul, 2000', 22.vi.1976, collected on logs at night (*Newton*) (3 ♂ ♂, MCZ); Capira, Cerro Campana, Q. D. Wheeler lot 7867, 19.viii.78, ex *Stemonitis* sp. (*Wheeler*) (1 ♀, QWHE); PANAMA CANAL ZONE: Barro Colorado Island, J. F. Lawrence Lot 3776, 19.ii–9.iii.1975, ex *Stemonitis fusca* (*Lawrence & Erwin*) (1 ♂ and 1 ♀, ANIC); Barro Colorado Island, ex *Stemonitis* sp. (*Lawrence & Newton*) (1 ♂ and 2 ♀ ♀, ANIC); MEXICO: OAXACA, 6 mi. S. Valle Nacional, 2000', 19.v.1971, 'S.Peck Ber. 203', ex leaf litter (*Peck*) (1 ♀, CNC).

Etymology. Latin meaning 'less, little' in reference to their size.



Figs 65–70. 65, *Genisphindus roxanneae*. Pterothorax, ventral; 66–68, Mesosternal process apices, ventral. 66, *Genisphindus latisternus*; 67, *G.roxanneae*, mp = median piece, lp = lateral pit; 68, *G.minor*; 69–70, *G.roxanneae*. Metendosternite; 69, Dorsal; 70, Lateral.

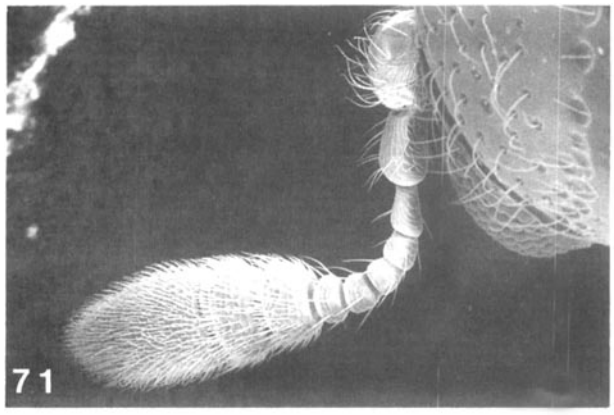
Natural history. This species has been collected on logs at night, in leaf litter and feeding on *Stemonitis fusca* and an unidentified *Stemonitis* species.

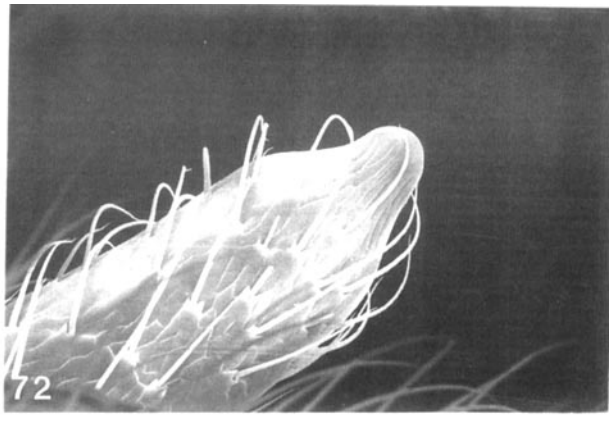
Distribution. Known only from the type localities (Fig. 59).

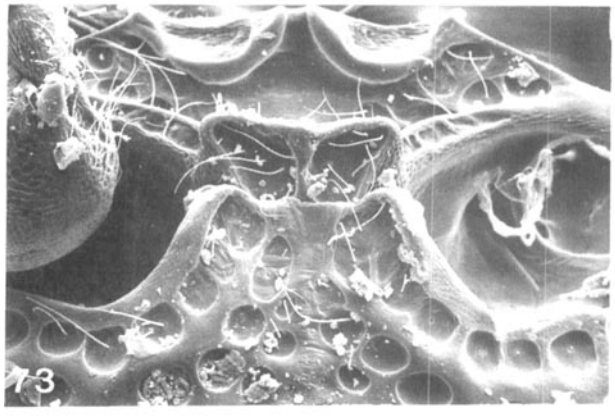
Remarks. See remarks for *G.latisternus*.

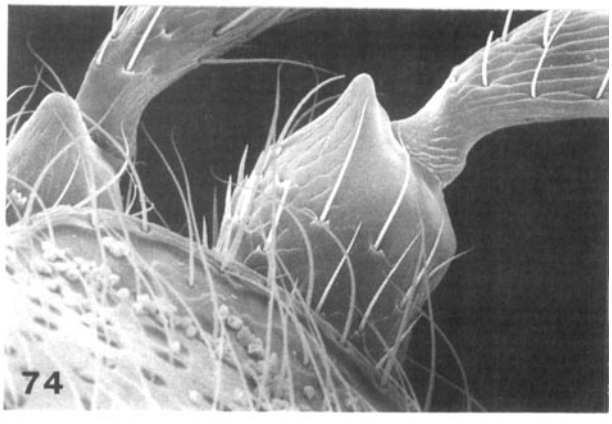
Genisphindus rotundus sp.n. (Figs 57, 59)

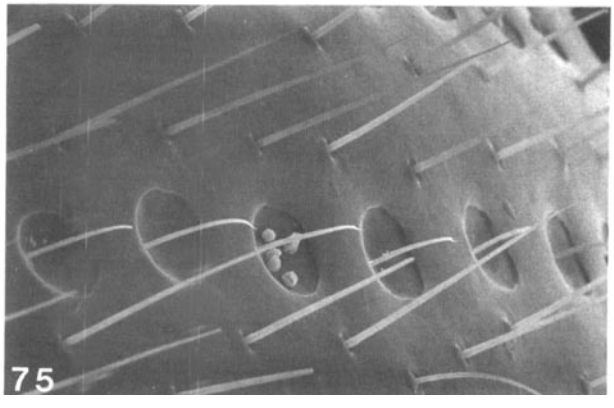
Description. Body very broadly oval, blunt posteriorly, elytra large in relation to head and pronotum. Elytra and legs yellowish-brown, head and pronotum slightly darker brown, body shiny. Setation short, erect. Length 2.0.







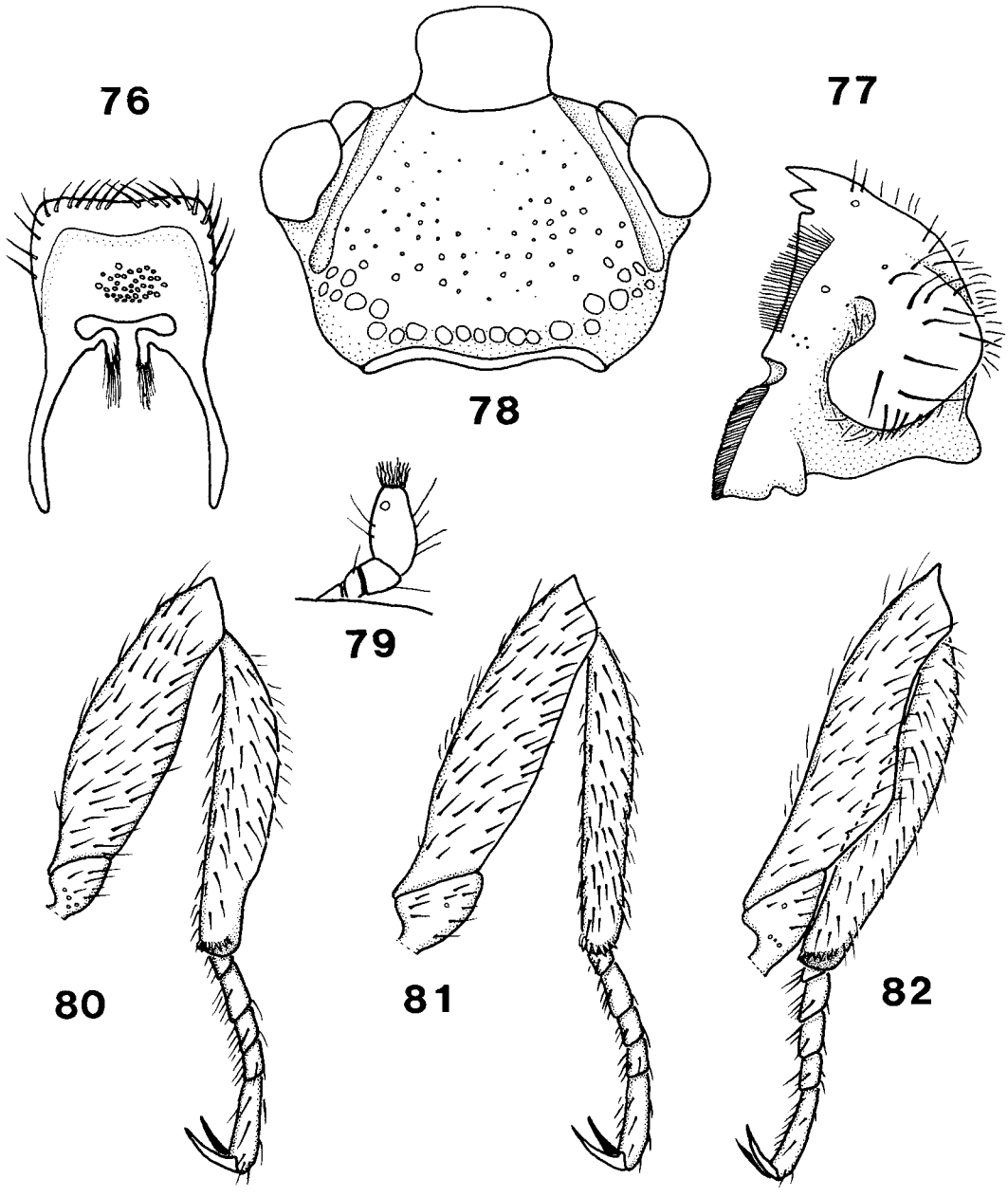




Figs 71–75. *Genisplindus roxanneae*. 71, Left antenna, dorsal; 72, Distal end of profemur; 73, Mesosternal–metasternal juncture; 74, Distal ends of profemur and mesofemur; 75, Elytral surface, dorsal (note: slime mould spores in central puncture).

Head with 3 pairs of well-defined ventral antennal pits; ocular head width 0.7; median head length 0.5; dorsal surface moderately punctulate with basal impunctate band and basal row of enlarged punctures; clypeus width 0.2, length 0.2; antennomere III about twice as long as wide, IV slightly elongate, V–VI submoniliform, antennomere VII slightly wider than III–VI, X at least 3 times length of either VIII or IX, segment VIII slightly longer than IX, club pubescence light brown.

Pronotum with a trace of paired dorsal depressions, basal margin strongly sinuate; pronotal width 1.1, length 0.7; dorsal surface evenly punctulate with basal row of slightly enlarged punctures, row nearly complete except opposite scutellum, punctures enlarged on anterolateral



Figs 76–82. *Genisphindus roxanneae*. 76, Labrum, ventral; 77, Right mandible, dorsal; 78, Head, dorsal; 79, Right labial palpus, dorsal; 80–82, Right legs, anterior; 80, Proleg; 81, Mesoleg; 82, Folded metaleg.

flanges and in depressions; prosternal process lacking anterior ridge (Fig. 57). Mesosternal process with narrow median piece and two large pits with poorly defined anterior and lateral margins. Apical tarsomere about as long as others combined. Scutellum scutelliform with irregular punctation. Elytra very broad, lacking subhumeral depression, with weakly produced humeral calli, epipleura broad, weakly rugulose and complete to about middle of abdominal sternite III; elytral width 1.5, length 1.4; dorsal surface with punctures darkened, becoming abruptly smaller posteriorly.

Abdomen with sternite I about 1.5 times length of sternites II–V and densely punctate, sternites II–V with basal depressions about half length of sternites. Abdominal intercoxal process long, narrow, with well-defined, central carina, apex acute.

Holotype, ♂, TRINIDAD: label data: 'Trin.Maracas, 2–6.XII.1977, W.R.M.Mason' (CNC); measurements: TBL 1.9, ELL 1.3, ELW 1.4, PNL 0.7, PNW 1.0, MHL 0.5, PHW 0.7, CLL 0.2, CLW 0.2.

Paratype, same data as holotype (1♂, CNC).

Etymology. Latin meaning 'circular, round, spherical' in

reference to the robust body.

Distribution. Known only from the type locality (Fig. 59).

Remarks. The large size and robust body form (Fig. 63) of this species easily distinguish it from the other *Genisphindus* species that have a narrow median piece and two large pits on the mesosternal process.

Genisphindus roxanneae sp.n. (Figs 60, 62, 65, 67, 69–90)

Description. Body broadly oval, blunt posteriorly. Head, pronotum and elytra light reddish-brown, body shiny. Setation moderately long, erect. Length 1.7.

Head with 3 pairs of well-defined ventral antennal pits; ocular head width 0.6; median head length 0.4; dorsal surface sparsely punctulate with basal, impunctate band and basal row of enlarged punctures (Fig. 78); clypeal length 0.2, width 0.2; antennae with antennomere III about twice as long as wide, IV slightly elongate, V–VI submoniliform, antennomere VII slightly wider than III–VI, X about 3 times length of either VIII or IX (Fig. 71), VIII and IX darker than other antennomeres, club pubescence light brown–white; mandibles with prosthecal fringe of setae inset from edge apically, close to edge basally (Fig. 77); labium with 4-segmented palp, apical segment longer than others combined, distal end with long sensillae (Fig. 79).

Pronotum with weak trace of paired dorsal depressions, basal margin strongly sinuate; pronotal width 0.9, length 0.5; dorsal surface evenly punctulate with basal row of enlarged punctures nearly complete except opposite scutellum, punctures enlarged on anterolateral flanges; prosternal process lacking a raised anterior ridge (Figs 57, 83). Mesosternal process with narrow median piece separating two large pits (Figs 65, 67, 73). Metendosternite with narrow base, broad apically, anterior tendons moderately separated, furcal arms with enlarged and complex apex, lamina long and narrow with reflexed apex (Figs 69, 70) Apical tarsomere not quite as long as others combined except in male metatarsi (Figs 80–82). Wings with jugal lobe, media, cubitus, medio-cubital crossvein, costa, radius, radial spur and one weakly developed anal vein (Fig. 84). Scutellum scutelliform with irregular, shallow, punctation. Elytra lacking subhumeral depression, with moderately produced humeral calli, epipleura rugulose and complete to about basal margin of abdominal sternite III; elytral width 1.2, length 1.1; dorsal surface with punctures darkened, gradually decreasing in size but distinct posteriorly, strial interspaces weakly convex (Fig. 75).

Abdomen with sternite I about 1.5 times as long as other sternites and densely punctate, basal depressions on sternites II–V about half length of sternites (Fig. 85). Abdominal intercoxal process with central carina and acute apex (Fig. 85).

Male. Aedeagus with parameres nonarticulated and fused into a broad structure (Fig. 87), median lobe with concavity housing fused tip of parameres (Figs 86, 89).

Female. Genitalia with bidentate coxites, with sparse setation, stylus long, narrow, preapical, with two apical setae (Fig. 90).

Holotype, ♀, PERU: label data: 'JM87157', 'Peru: Madre de Dios, Rio Tambopata Res., 18.Jan.1987, J. McHugh, Q.Wheeler', 'ex.pink slime mold, overgrown clearcut area' (CUIC); measurements: TBL 1.6, ELL 1.1, ELW 1.2, PNL 0.5, PNW 0.9, MHL 0.4, PHW 0.6, CLL 0.2, CLW 0.2.

Paratypes, same data as holotype (3♂♂, 2♀♀, CUIC); ECUADOR: Rio Palenque, 47 km S. of Santo Domingo, 700', 22–27.ii.1976, malaise trap (*Howden & Howden*) (1♀, CNC).

Etymology. A patronym for my wife, Roxanne.

Natural history. This species has been collected feeding on a pink myxomycete (*Arcyria* sp.?) on the underside of log in a weedy, clear-cut area.

Distribution. Known only from the type localities (Fig. 60).

Remarks. See remarks for *G.laevicollis*.

Cladistic analysis

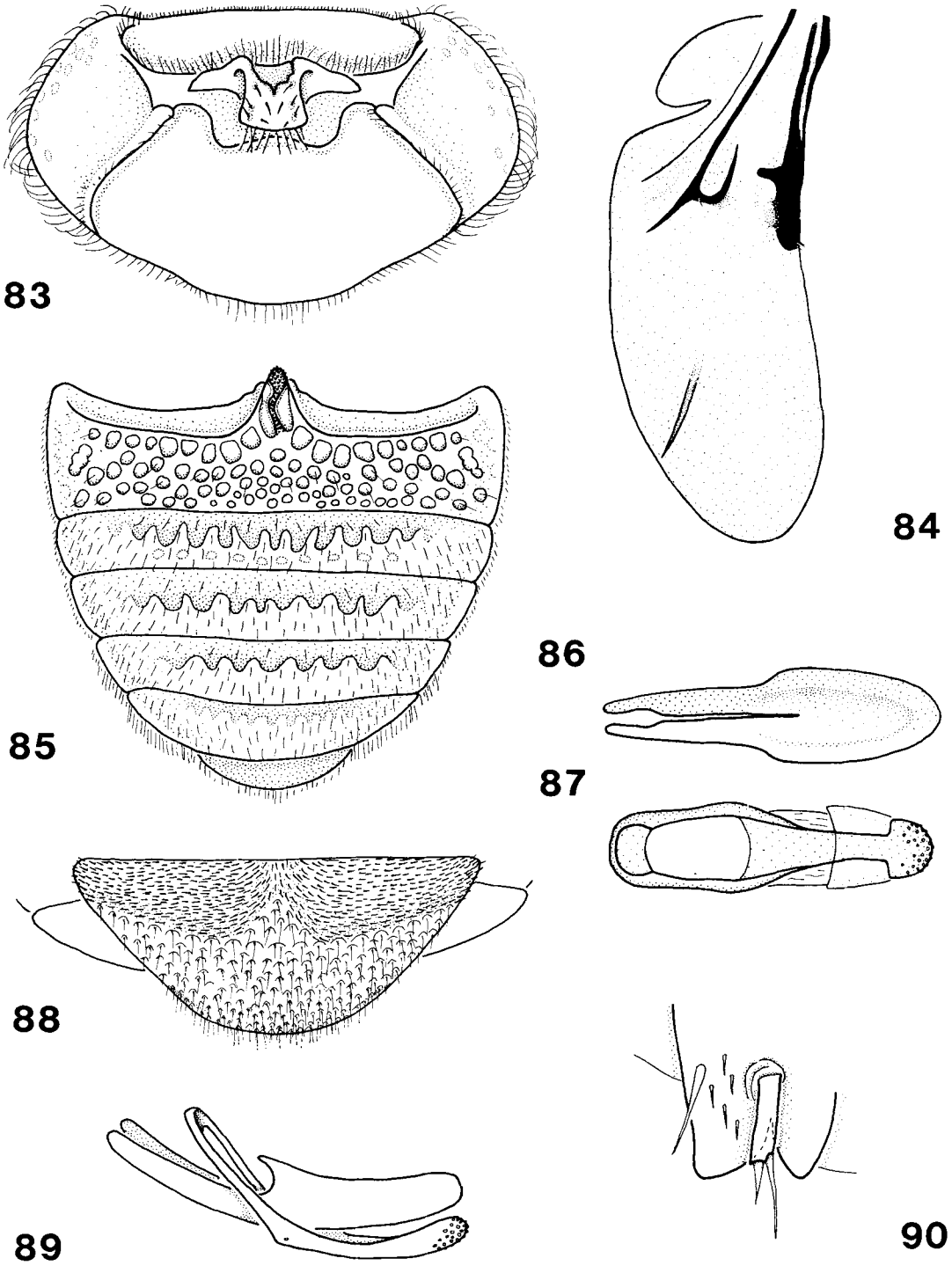
Included in the analysis are all known species of *Carinisphindus*, *Eurysphindus*, *Genisphindus*, *Notosphindus* and *Sphindiphorus*. In addition, a single species of each of the following genera is included: *Aspidiphorus*, *Protosphindus*, *Odontosphindus* and *Sphindus*.

Character analysis

During character analysis, outgroup comparison (Watrous & Wheeler, 1981) was used to polarize the character states in each transformation series. Choice of outgroups was difficult due to the present uncertainty about the phylogenetic relationships of the Cucujoidea. Crowson (1967) notes that *Sphindus* and *Aspidiphorus* have variously been associated with Byrrhidae, Ptinidae, Bostrychidae, Cryptophagidae, Cisidae and Tenebrionidae. Crowson himself considered the Sphindidae most directly related to Protocucujidae, although suggested relationships also with Rhizophagidae or Cryptophagidae. Sen Gupta & Crowson (1977) suggest sphindid affinities with Phloeostichidae–Hymaeinae, primitive Silvanidae and Boganiidae–Boganiinae, in addition to Protocucujidae. Thomas (1984) agrees that at least the first three groups and probably also the fourth form a monophyletic group with Sphindidae, based on mandibular morphology. Nevertheless, it is generally agreed that Sphindidae is a primitive cucujoid family.

The protocucujid, *Ericmodes sylvaticus* (Phil.), was used as an outgroup in the analysis. The similarity of this species to Sphindids is far more striking than that of Silvanidae, Boganiidae or Phloeostichidae and thus facilitated the process of making homology hypotheses.

All autapomorphies were removed from the matrix as they are cumbersome and relatively uninformative cladistically. Below is a list of the hypothesized apomorphic



Figs 83–90. *Genisphindus roxanneae*. 83, Prothorax, ventral; 84, Right wing, dorsal; 85, Abdomen, ventral; 86–87, Male genitalia; 86, Median piece; 87, Parameres (fused); 88, Pygidium, dorsal; 89, Male genitalia, dorsolateral; 90, Female genitalia, apex of right coxite and stylus, ventral.

(A) and plesiomorphic (P) states for the remaining forty-one characters and a brief discussion of each.

1. Head with punctation on dorso-basal region (A) characterized by a very weakly punctate or impunctate region and a more basal single row of enlarged punctures (Fig. 78); (P) not distinctly weak or absent and lacking a row of enlarged punctures (Fig. 8).

2. Head with dorsal punctures (A) elongated and fused, forming a series of longitudinal grooves originating between the base of the antenna and the clypeus on both

sides of the head and extending back at least to the middle of the head; (P) not fused, lacking dorsal grooves.

3. Head with a pair of well-defined, dorsal antennal grooves extending from the base of each antenna to at least the top of the eye and often projecting well beyond it posteriorly (Figs 8, 78) (A) present; (P) absent.

4. Clypeus (A) with at least half length projecting beyond anterior margin of head; (P) deeply embedded in head with one-third length or less projecting beyond anterior margin of head.

5. Clypeus lateral margin (A) emarginate; (P) arcuate.

6. Clypeus with anterior margin (A) with weak lateral notches; (P) lacking notches.

7. Antennae composed of (A) 10 antennomeres, (P) 11 antennomeres.

8. Antennae with dense setose punctures on (A) the three apical antennomeres; (P) the apical half of ultimate antennomere only.

9. Mandible (A) flattened at apex, with all teeth visible in dorsal aspect; (P) broad at apex with one tooth hidden beneath two other teeth in dorsal aspect.

10. Mandible with (A) only one well-developed tooth; (P) at least two well-developed teeth.

11. Galea apex (A) narrow and tapered; (P) broad and truncate.

12. Labial palps at base (A) widely separated; (P) close.

13. Apices of femora (A) produced to an acute point (Figs 61, 72, 74, 80–82); (P) rounded (Figs 3, 35–37) to somewhat angular, but not pointed.

14. Male metafemora (A) with posterior tooth at about one-third length; (P) lacking tooth.

15. Pronotum (A) with a strong, continuous, median, longitudinal carina; (P) smooth or with a depression medially, lacking a carina (Figs 3, 20, 61).

16. Pronotal lateral margin (A) smooth, irregularities absent (Figs 61, 83); (P) denticulate to crenulate (Figs 3, 20, 21).

17. Posterior margin of pronotum (A) sinuate; (P) arcuate.

18. Pronotal hypomera (A) anteriorly concave, capable of receiving antennal clubs; (P) not concave.

19. Tibial spurs (A) present; (P) absent.

20. Procoxal cavities internally (A) opened; (P) closed.

21. Procoxal cavities externally (A) widely opened posteriorly (Figs 21, 83); (P) closed or nearly so.

22. Prosternum (A) narrower than prosternal process at midpoint; (P) broader than prosternal process at midpoint.

23. Prosternal process (A) with an anteriorly projecting protuberance or ridge (Figs 21, 29, 53–56); (P) lacking an anteriorly projecting protuberance or ridge (Fig. 57).

24. Mesosternal process (A) narrow and knob-like (Figs 27, 65); (P) broad and flat.

25. Mesosternal process (A) with a pair of large pits at apex (Figs 65–68, 73); (P) punctate and/or knobby but lacking a well-developed pair of pits (Figs 27, 30).

26. Mesosternum (A) moderately concave anteriorly to strongly concave near midpoint for receiving prosternal process; (P) flat to inflexed.

27. Metasternum (A) with impunctate region around notch receiving intercoxal process; (P) punctate opposite intercoxal process.

28. Mesosternal excavations at anterior margin for receiving procoxae (A) present; (P) absent.

29. Scutellum (A) with strong, median, longitudinal carina; (P) lacking a carina (Figs 3, 26, 32, 61).

30. Wing with anal cell (A) absent (Figs 22, 84); (P) present.

31. Wing venation with anal vein IV (A) absent; (P) present.

32. Wing venation with anal vein III (A) absent; (P) present.

33. Anal vein I (A) absent; (P) present.

34. Elytral colour pattern with distinct black to grey bands alternating with yellowish-brown bands (A) present; (P) absent.

35. Elytra with (A) strongly raised strial interstices, forming sharp ridges; (P) interstices weakly to not at all raised.

36. Elytral striae (A) distinct; (P) confused.

37. Abdominal sternites II–V (A) with a distinct basal row of depressions or with a basally depressed band of fused depressions (Fig. 85); (P) lacking a basal row of depressions or a depressed band.

38. Abdominal sternites with anterolateral depressions (A) absent; (P) present.

39. Apex of intercoxal process (A) broad; (P) narrow.

40. Pygidium (A) with a pair of large setulose impunctate patches; (P) evenly punctate or nearly so.

41. Pygidium (A) with a longitudinal, median depression or groove, (P) lacking a median, longitudinal depression (Figs 39, 88).

Cladogram analysis

Sphindidae is treated as a monophyletic group in current classifications and I have found no reason to believe otherwise. It is difficult in this group, however, to find an unambiguous synapomorphy. Myxomycophagy, at first, might appear to be a synapomorphy. Unfortunately, slime mould feeding has apparently arisen independently at least ten times within the Coleoptera: once within the Caraboidea, in Rhysodidae (Lawrence, 1989); four times within the Staphylinoidea, once in Scaphidiidae and three times in Leiodidae (Wheeler, personal communication); twice in the Elateroidea, in Eucinetidae and Clambidae; and three times in the Cucujoidea, in Lathridiidae and Sphindidae (Lawrence & Newton, 1980), and in Cerylonidae (Ślipiński, 1988; Newton & Stephenson, 1990). Within the primitive Cucujoidea, slime mould feeding might have evolved only in the Sphindidae. Therefore, with an outgroup composed of primitive cucujoid taxa, slime mould feeding would be a synapomorphy for the ingroup, the Sphindidae.

The characteristic cavity and tubercle of sphindid mandibles (Figs 5, 11, 12, 77) seem to be another potential synapomorphy; however, as Sen Gupta & Crowson (1977) and Thomas (1984) point out, a similar mandibular arran-

gement occurs in Phloeostichidae–Hymaeinae, primitive Silvanidae and Boganiidae–Boganiinae. An unambiguous synapomorphy for the family is presently lacking as it is difficult and beyond the scope of this revision to conduct a morphological analysis of the basal cucujoid families.

Figs 91–92 illustrate the two most parsimonious cladograms (fifty-five steps, c.i. = 0.74, r.i. = 0.75) for the forty-one characters given above. The 'Nelsen' function of HENNIG86 was used to produce a strict consensus tree (Fig. 93).

Because the character states observed for *Carinisphindus*, *Eurysphindus* and *Genisphindus* did not vary among congeneric species, the species of each of these genera moved about on the cladogram as a block. For clarity, they are each represented as a single terminal taxon in Figs 91–94.

The two competing cladograms (Figs 91–92) illustrate that the most weakly supported area of the cladogram involves the placement of *Notosphindus*. In Fig. 91, *Notosphindus* is the sister taxon to the clade ((*Aspidiphorus* + (*Eurysphindus* + *Genisphindus*)) + (*Carinisphindus* + *Sphindus*)). In Fig. 92 it is the sister taxon to the (*Carinisphindus* + *Sphindus*) clade.

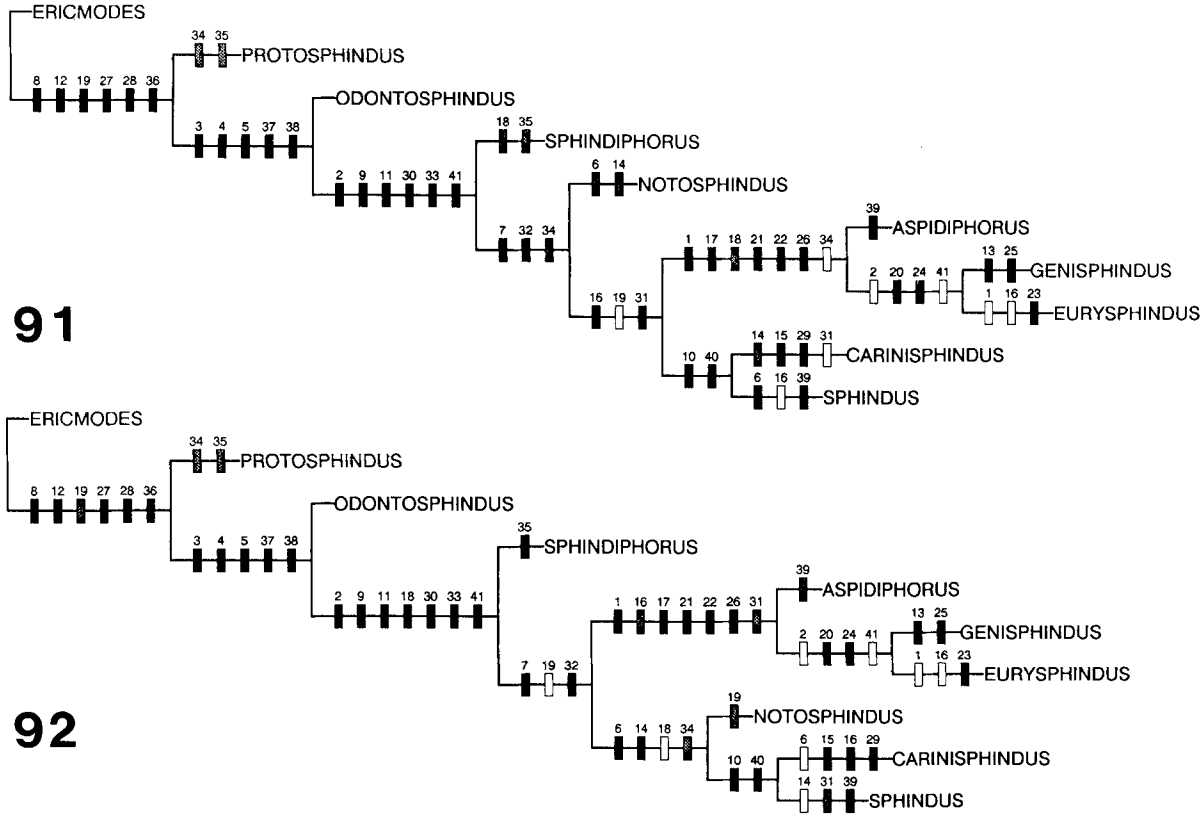
The characters lending support for the phylogenetic hypothesis in Fig. 91 over that illustrated in Fig. 92 (and vice versa) are ones that would be homoplasious in either scenario. In order to be conservative in selecting an hypothesis a strict consensus tree is used for the various interpretations of the results.

Five points should be made about the consensus tree (Fig. 93). First, *Carinisphindus* forms a monophyletic group outside what has been considered Eurysphindinae. *Carinisphindus* has the following autapomorphies (the character numbers are given in parentheses): a strong, median, longitudinal carina on the pronotum (15) and on the scutellum (29).

Second, *Genisphindus* forms a monophyletic group and is the sister group to *Eurysphindus*. The degree of divergence between these two groups warrants generic level recognition. *Genisphindus* has the following autapomorphies: distal end of the femur produced as an acute point (13) and the apex of the mesosternal process with a pair of distinct pits (25).

Third, *Eurysphindus* forms a monophyletic group with a single synapomorphy, prosternum with an anteriorly projecting protuberance (23).

Fourth, the character state distributions summarized in the cladogram support the removal of *Odontosphindus grandis* from *Sphindus* by Sen Gupta & Crowson (1977). Specifically the wing venation (see Crowson, 1967; fig.



Figs 91–92. The two most parsimonius cladograms summarizing the distributions of the characters described in the 'Character Analysis' section and listed in Table 1. Black boxes indicate synapomorphies. Homoplasious characters are optimized as having either reversals (white) or parallelisms (grey).

Table 1. Distribution of character states. '0' indicates the plesiomorphic condition; '1' indicates the apomorphic condition.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
E.sylvaticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P.chilensis	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0
O.denticollis	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0
S.natalensis	0	1	1	1	1	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	1	1	1	0	0	1
N.slateri	0	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	0	1	1	1	0	0	1
C.isthmensis	0	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1
C.platysphinctos	0	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1
C.leptosphinctos	0	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1
C.bicolor	0	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1
S.americanus	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1
A.orbiculatus	1	1	1	1	1	0	1	1	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	0	0	1	1	1	0	1	1	1	1	0	0	1	1	1	1	0	1
G.roxanneae	1	0	1	1	1	0	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0
G.rotundus	1	0	1	1	1	0	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0
G.latisternus	1	0	1	1	1	0	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0
G.minor	1	0	1	1	1	0	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0
E.hirtus	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0
E.brasiliensis	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0
E.plaumanni	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0
E.halli	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0
E.comatulus	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0
E.grandiclaviger	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0
E.infuscus	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0

112) exhibits the plesiomorphic state for characters 30–33. In addition, the eleven-segmented antenna is plesiomorphic (character 7).

Fifth, the cladogram supports strongly the placement by Jacquelin du Val (1859–63) of *Aspidiphorus* in Sphindidae.

Fig. 93 is a comparison of the tentative classification scheme of Sen Gupta & Crowson (1977) with the cladogram of the Sphindid genera. There are several points of agreement and disagreement between the two. Below is a discussion of three incompatibilities.

First, the subfamily Aspidiphorinae *sensu* Sen Gupta & Crowson (1977) includes *Sphindiphorus* and *Aspidiphorus*. These two taxa share no synapomorphies that are not also shared with several other taxa. The longitudinal groove on the pygidium (41) is seen in a modified form in *Notosphindus*, *Carinisphindus* and *Sphindus*. It is apparently lost in *Eurysphindus* and *Genisphindus*.

There are several synapomorphies that place *Aspidiphorus* in a nested set of clades including other genera but excluding *Sphindiphorus*, such as the ten-segmented antenna (7), sinuate posterior margin to the pronotum (17), externally open procoxal cavities (21), narrow prosternum (22), presence of concavity on mesosternum (26) and loss of third anal vein (32). It seems that Aspidiphorinae *sensu* Sen Gupta & Crowson (1977) is a paraphyletic group.

Second, the subfamily Eurysphindinae *sensu* Sen Gupta & Crowson (1977) includes one genus, *Eurysphindus* with five species. Sen Gupta & Crowson (1977) suggest that *C.bicolor* (Fisher) might not belong in *Eurysphindus* but decide not to remove the species. The cladogram indicates that this species, which is removed from *Eurysphindus* by McHugh (1990), does not form a monophyletic group with the remaining *Eurysphindus* species. Eurysphindinae, including *C.bicolor*, is paraphyletic.

Third, the subfamily Sphindinae *sensu* Sen Gupta & Crowson (1977) includes *Odontosphindus* and *Sphindus*. These two genera share no synapomorphies that are not also shared with *Sphindiphorus*, *Notosphindus*, *Carinisphindus*, *Aspidiphorus*, *Eurysphindus* and *Genisphindus*.

There are many synapomorphies that place *Sphindus* in a nested set of clades excluding *Odontosphindus*, including flattened mandibles (9); ten-segmented antenna (7); the reduction to a single well-developed tooth on the mandible (10); narrowed galea apex (11); loss of an anal cell (30) and the first (33); third (32) and fourth (31) anal veins in the wing; and the presence of two large setulose patches on the pygidium (40). Sphindinae *sensu* Sen Gupta & Crowson (1977) appears to be a paraphyletic group.

Classification

While producing a classification compatible with the hypothesized phylogeny, and attempt was made to minimize nomenclatural changes by modifying the basic system of Sen Gupta & Crowson (1977). There are several acceptable solutions. Below are two possibilities worthy of discussion.

(1) The basic system of Sen Gupta & Crowson (1977) could be used with modification to avoid paraphyletic groups. Sphindinae and Aspidiphorinae could each be split into two subfamilies. In this situation, *Carinisphindus* and *Notosphindus* would each also have to be recognized

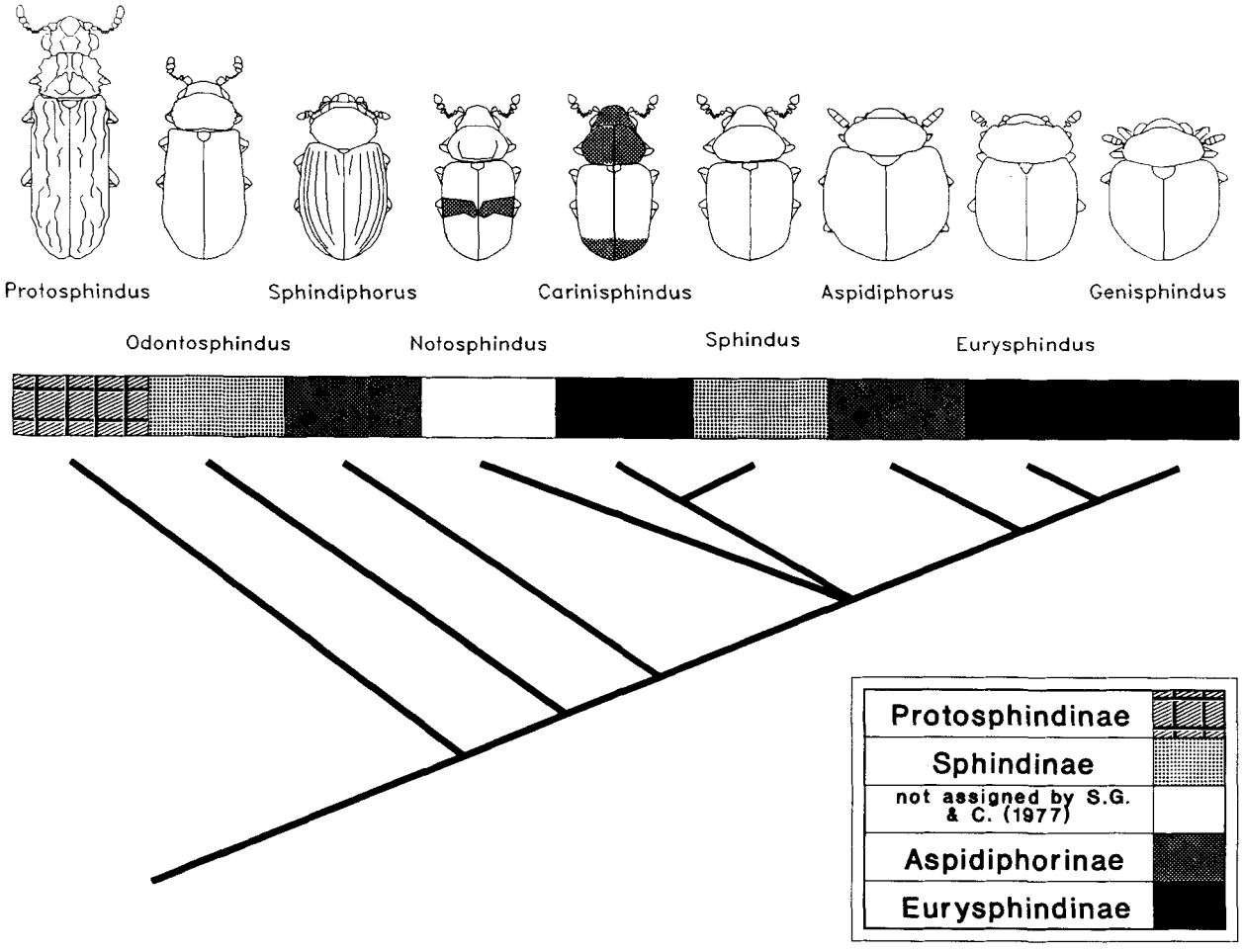


Fig. 93. Strict consensus tree of the two most parsimonius cladograms compared to the classification scheme of Sen Gupta & Crowson (1977).

at the subfamilial level. The resulting classification would have nine genera organized within eight subfamilies.

(2) Another possible approach would be to recognize *Protosphindus*, *Odontosphindus* and *Sphindiphorus* each in a monogeneric subfamily and to recognize the remaining six genera (those with ten-segmented antennae) in a fourth subfamily.

The first option seems unreasonable in that the resulting classification would be redundant at the generic, tribal and subfamilial levels. Very little phylogenetic information would be provided in such a classification. For this reason, the classification proposed here (Table 2) is derived from the cladogram using the second approach.

Table 2. A phylogenetically based classification of the family Sphindidae.

Subfamily:	Protosphindinae Sen Gupta & Crowson, 1977
Genus:	*Protosphindus* Sen Gupta & Crowson, 1977
Subfamily:	Odontosphindinae Sen Gupta & Crowson, 1977
Genus:	*Odontosphindus* LeConte, 1878
Subfamily:	Sphindiphorinae McHugh, **subfam.n.**
Genus:	*Sphindiphorus* Sen Gupta & Crowson, 1977
Subfamily:	Sphindinae Sen Gupta & Crowson, 1977,
Genus:	*Notosphindus* McHugh & Wheeler, 1991
Genus:	*Carinisphindus* McHugh, 1990
Genus:	*Sphindus* Chevrolat, 1833
Genus:	*Aspidiphorus* Latreille, 1829
Genus:	*Eurysphindus* LeConte, 1878
Genus:	*Genisphindus* McHugh **gen.n.**

Biogeography

Biogeographical information for the genera of Sphindidae is summarized using an area cladogram (Fig. 94). The area patterns are not particularly informative in this case. Four main points may be made from this illustration:

First, *Protosphindus* and *Sphindiphorus* have presumably relict distributions in temperate South America (Chile) and South Africa respectively. These areas are rich in relict insect taxa.

Second, *Sphindus* is nearly cosmopolitan, being known from every major geographic region except Australia. This

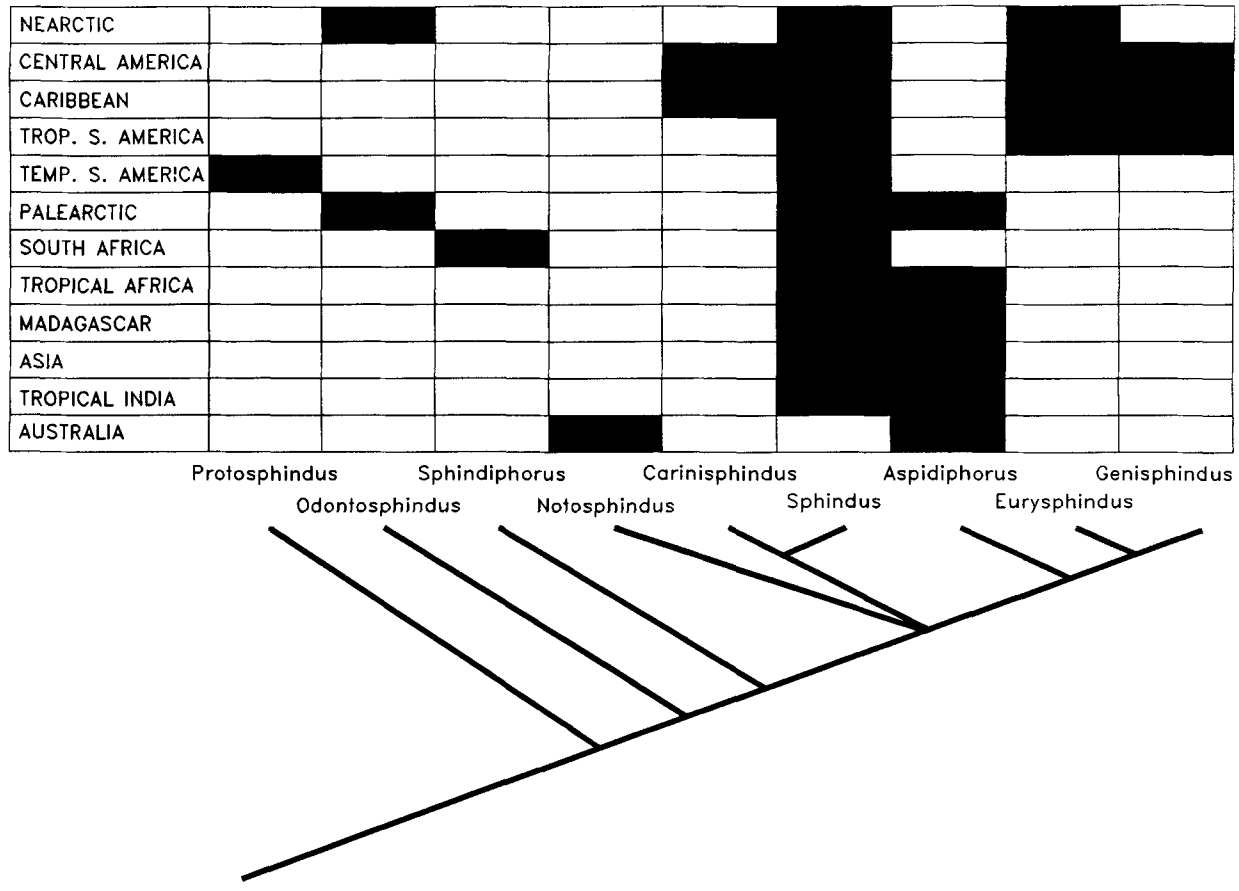


Fig. 94. Area cladogram of sphindid genera (based on strict consensus tree).

suggests that either: (a) these beetles have remarkable dispersal abilities and have managed to reach many of these regions after the formation of ocean barriers, or (b) they are also part of an old group that was present before the formation of barriers between some of these regions. In this case, (b) seems more likely as the family is thought to be one of the most primitive in the Cucujoidea.

Furthermore, there is no known feature of *Sphindus* beetles that would bestow stronger dispersal ability than other sphindids. On a scale of 1–5, with 1 being the worst dispersers and 5 being the best, *Sphindus* and probably all sphindids for that matter fit very poorly but most closely into Crowson's (1981) second dispersal category which includes 'those taxa in which the adults are usually long-lived but rarely fly on more than two or three occasions in their life and in which larvae are not borers in dead timber.' Sphindid beetles seem to fly more often than only two or three times during a lifetime but overall they fit this category better than any other.

It should be noted that *Sphindus* is in need of revision and thus the 'cosmopolitan' distribution should be considered suspect until the monophyly of the species included in the distribution is verified.

Third, *Aspidiphorus*, *Eurysphindus* and *Genisphindus* are each restricted to a broad distribution in either the Old World or the New World. This pattern suggests that they evolved no earlier than the late Eocene, when a North Atlantic dispersal route existed between North America and Eurasia (Sen Gupta & Crowson, 1977; Pielou, 1979).

Fourth, the distribution of *Odontosphindus* is curious, considering its position on the cladogram. It is likely that the known distribution is either an underestimate or is the relictual remains of a once larger distribution.

It should be noted that there is a superficial resemblance between members of *Sphindus* and those of *Odontosphindus* (Fig. 93). The taxonomy of *Sphindus* is in need of revision. Some of the species presently placed in *Sphindus* may actually belong to *Odontosphindus* and the actual distribution of *Odontosphindus* could be greater than the present estimate. This point is illustrated by the fact that until Sen Gupta & Crowson (1977) reassigned *S.grandis* Hampe (a Palearctic species) to *Odontosphindus*, the genus was known only from two Nearctic species. Sen Gupta & Crowson (1977) also suggest that *S.major* Reitter, a Neotropical species, may belong to *Odontosphindus*.

Fossils and amber specimens have yet to be located for this family. Information from these sources may clarify

the biogeographic patterns seen today and help to understand certain character state transformations.

Sphindidae are not usually observed in nature except by individuals who concentrate on finding their slime mould hosts. These beetles appear to be more common and speciose than previously thought, particularly in the tropics. While sampling techniques such as sifting leaf litter and flight intercept traps are relatively effective methods of collecting this group, it is possible that large distributional gaps still exist.

Acknowledgments

This project was done in partial fulfillment of Master's Degree requirements at the University of Connecticut. I thank my M.S. Degree Committee members: J. A. Slater, C. Henry and G. Anderson (all of University of Connecticut) and Q. D. Wheeler (Cornell University) for the support and guidance that they provided during my tenure at Storrs, Connecticut.

I thank the following individuals for initiating loans of material: J. F. Lawrence (ANC), D. Azuma (ANSP), P. M. Hammond (BMNH), D. H. Kavanaugh (CAS), A. Smetana (CNC), J. K. Liebherr (CUIC), A. F. Newton (FMNH), G. G. Kennen (GKEN), J. Pakaluk (JPAK and SEM), J. Parkinson (JPAR), K. Stephan (KSTE), M. A. Ivie (MAIC), C. Johnson (MANM), S. R. Shaw (MCZ), T. L. Schiefer (MEM), I. Löbl (MHNG), L. J. Joly (MIZA), Q. D. Wheeler (QWHE), S. Peck (SPEC), L. Bailey-Segal (UCB), R. O. Schuster (UCD), D. S. Chandler (UNH), G. F. Hevel (USNM).

The carbon-dust habitus illustrations (Figs 3, 61) were composed by F. Fawcett (Ithaca, N. Y.). Q. D. Wheeler provided an opportunity to do fieldwork in the Caribbean and South America from which this project benefitted and for which I am indebted. I thank K. Loeffler (Cornell University) for his skilled photographic work and A. Wachtel (University of Connecticut) for assistance with the scanning electron microscope. The photographs in Figs 50–52 were taken by B. Schwartz (West Tremont, Maine), S. Ristich (Cumberland, Maine) and Q. D. Wheeler respectively. C. N. Duckett and P. Fraissinet (both of Cornell University) tested the dichotomous keys. E. R. Hoebeke (Cornell University), P. Fraissinet, C. H. C. Lyal (BMNH) and an anonymous reviewer read early versions of this paper and provided many valuable comments that greatly improved the final form.

Correspondence with R. A. Crowson (Glasgow University), J. Pakaluk (University of Kansas, Lawrence) and S. A. Ślipiński (Institute of Zoology, Polish Academy of Sciences) was very helpful. I am particularly grateful to J. F. Lawrence (CSIRO, Entomology Division) for his kind assistance and advice.

This study was supported by the following sources: NSF Grant No. BSR-840-7049 (to J. A. Slater), NSF Grant No. BSR-83-15457 (to Q. D. Wheeler), NSF Grant No. BSR-87-17401 (to Q. D. Wheeler) and Hatch Project No. NY(C)-139426 (to Q. D. Wheeler).

References

Alexopoulos, C.J. & Mims, C.W. (1979) *Introductory Mycology*. John Wiley and Sons Inc., New York.

Arnett, R.H., Jr (1963) *The Beetles of the United States*. Catholic University of America Press, Washington, D.C.

Batra, L. (1963) Ecology of ambrosia fungi and their dissemination by beetles. *Transactions of the Kansas Academy of Science*, **66**, 213–236.

Beaver, R.A. (1989) Insect–fungus relationships in the bark and ambrosia beetles. In: *Insect–Fungus Interactions* (ed. by N. Wilding, N. M. Collins, P. M. Hammond and J. F. Webber). Academic Press, London.

Benick, L. (1952) Pilzkäfer und Käferpilze. *Acta Zoologica Fennica*, **70**, 1–250.

Blackwell, M. (1984) Myxomycetes and their arthropod associates. In: *Fungus–Insect Relationships: Perspectives in Ecology and Evolution* (ed. by Q. Wheeler and M. Blackwell), Columbia University Press, New York.

Bradley, J.C. (1939) *The Coleoptera or Beetles, The Dominant Order of Insects. A text for the use of student of taxonomy of insects in Cornell University*. Privately published, Ithaca, New York.

Burakowski, B. & Ślipiński, S.A. (1987) A new species of *Protosphindus* (Coleoptera: Sphindidae) from Chile with notes and descriptions of immature stages of related forms. *Annali del Museo Civico di Storia Naturale, Genova*, **86**, 605–625.

Chevrolat, L.A.A. (1833) Description du genre *Sphindus*. In Silbermann, *Revue Entomologique*, **1**, (8), 145–146.

Crowson R.A. (1967) *The Natural Classification of the Families of Coleoptera*. E. W. Classey Ltd, Middlesex.

Crowson, R.A. (1981) *The Biology of the Coleoptera*. Academic Press, New York.

Dejean, P.F.M.A. (1821) *Catalogue de la Collection de Coléoptéres de M. le baron Dejean* (Deuxième Édition). Crevot, Paris.

Erwin, T.L. (1974) Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part II: a revision of the New World-Australian genus *Pericompsus* LeConte. *Smithsonian Contributions to Zoology*. Washington D.C.

Fisher, W.S. (1936) A new sphindid beetle from Cuba. *Memorias de La Sociedad Cubana de Historia Natural 'Felipe Poey'*, **10**, (4), 201–202.

Hampe, C. (1861) Einige neue Käfer aus Croatien und Siebenbürgen. *Wiener Entomologische Monatschrift*, **5**, 65–69.

International Trust for Zoological Nomenclature (1985) *International Code of Zoological Nomenclature*, 3rd edn. University of California Press, Berkeley.

Jacquelin du Val, P.N.C. (1859–63) *Genera des Coléoptères d'Europe*, Tome III. Chez A. Deyrolle, Naturaliste, Paris.

Latreille, P.A. (1829) *Les crustacés, les arachnides et les insectes, destribués en famille naturelles, ouvrage formant les tomes 4 et 5 de celui de M. le Baron Cuvier sur le Règne animal* (Deuxième Édition), Vol. 1. Paris.

Lawrence, J.F. (1989) Mycophagy in the Coleoptera: feeding strategies and morphological adaptations. In: *Insect–Fungus Interactions* (ed. by N. Wilding, N. M. Collins, P. M. Hammond and J. F. Webber). Academic Press, London.

Lawrence, J.F. (1991) Sphindidae (Cucujoidea): (including Aspidiphoridae). In: *Immature Insects* (ed. by F. W. Stehr), vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Lawrence, J.F. & Newton, A.F. (1980) Coleoptera associated with the fruiting bodies of slime molds (Myxomycetes). *The Coleopterists' Bulletin*, **34**, (2), 129–143.

LeConte, J.L. (1866) New species of North American Coleoptera. *Smithsonian Miscellaneous Collections*, **167**, 87–177.

LeConte, J.L. (1878) Descriptions of new species. In Hubbard, H.G. and Schwarz, E.A. eds., The Coleoptera of Michigan. *Proceedings of the American Philosophical Society*, **17**, 593–626.

Martin, G.W. & Alexopoulos, C.J. (1969) *The Myxomycetes*. University of Iowa Press, Iowa City.

McHugh, J.V. (1990) *Carinisphindus*, a new genus and three new species of Neotropical Sphindidae (Coleoptera: Clavicornia). *The Coleopterists' Bulletin*, **44**, (3), 307–322.

McHugh, J.V. & Wheeler, Q.D. (1991) *Notosphindus slateri* a new genus and species of Australian Sphindidae. *Journal of the New York Entomological Society*, **99**, (3), 527–537.

Merkl, O. (1986) Erotylidae, Mycetophagidae, Endomychidae, Arpidiphoridae and Cisidae of the Kiskunság National Park (Coleoptera). In: *The Fauna of the Kiskunság National Park (ed. by S. Mahunka)*, Vol. I. Akadémiai Kiadó, Budapest.

Newton, A.F., Jr & Stephenson, S.L. (1990) A beetle/slime mold assemblage from northern India (Coleoptera; Myxomycetes). *Oriental Insects*, **24**, 197–217.

Pielou, E.C. (1979) *Biogeography*. John Wiley & Sons, New York.

Russell, L.K. (1979) Beetles associated with slime molds (Mycetozoa) in Oregon and California (Coleoptera: Leiodidae, Sphindidae, Lathridiidae). *The Pan-Pacific Entomologist*, **55**, 1–9.

Sen Gupta, T. & Crowson, R.A. (1977) The coleopteran family Sphindidae. *The Entomologist's Monthly Magazine*, **113**, 177–191.

Sen Gupta, T. & Pal, T.K. (1982) Three new species of Sphindidae (Coleoptera: Clavicornia) from India and Sri Lanka. *Entomologica Basiliensia*, **7**, 387–393.

Ślipiński, S.A. (1988) Revision of the Australian Cerylonidae (Coleoptera: Cucujoidea). *Annales Zoologici*, **42**, (1), 1–74.

Thomas, M.C. (1984) A new species of apterous *Telephanus* (Coleoptra: Silvanidae) with a discussion of phylogenetic relationships of the Silvanidae. *The Coleopterists' Bulletin*, **38**, (1), 43–55.

Watrous, L. & Wheeler, Q.D. (1981) The out-group comparison method of character analysis. *Systematic Zoology*, **30**, 1–11.

Wheeler, Q.D. (1980) Studies on Neotropical slime mold/beetle relationships. Part I. Natural history and description of a new species of *Anisotoma* from Panama (Coleoptera: Leiodidae). *Quaestiones Entomologicae*, **15**, 447–479.

Wheeler, Q.D. (1984) Evolution of slime mold feeding in leiodid beetles. In: *Fungus–Insect Relationships: Perspectives in Ecology and Evolution* (ed. by Q. Wheeler and M. Blackwell). Columbia University Press, New York.

Accepted 24 August 1992