REVISION OF THE
GENERA OF LYMEXYLIDAE
(COLEOPTERA: CUCUJIFORMIA)

QUENTIN D. WHEELER

REVISION OF THE GENERA OF LYMEXYLIDAE (COLEOPTERA: CUCUJIFORMIA)

QUENTIN D. WHEELER

Research Associate, Department of Entomology
American Museum of Natural History
Assistant Professor of Systematic Entomology
Cornell University

This article completes Volume 183.

CONTENTS

FRONTISPIECE.   *Hylecoetus flabellicornis* (Schneider), male: Head-on view (above); lateral view of forebody (below), by J. Nagy.

ABSTRACT

The world genera of Lymexylidae (Coleoptera: Cucujiformia: Lymexyloidea) are revised, including descriptions of two new genera. All described species are given generic assignments. Seven genera are recognized and assigned to three subfamilies: Hylecoetinae Boving and Craighead, 1931, including *Hylecoetus* Latreille; Lymexylinae Boving and Craighead, 1931 (sensu novo), including *Lymexylon* Fabricius and *Atractocerus* Palisot de Beauvois (including *Raractocetus* Kurosawa, new synonym, *Hymaloxylon* Kurosawa, new synonym, *Arractocetus* Kurosawa, new synonym, and *Fusicornis* Philippi); and Melittomminae, new subfamily, including *Australymexylon,* new genus, *Melittomma* Murray, *Melittommopsis* Lane, and *Protomelittomma,* new genus. *Neohylecoetus* Kurosawa is synonymized with *Melittomma* Murray, and *Hylecoetopsis* Lane is excluded from the Lymexylidae (and presumed to belong to the Cleridae). Species of the endemic Australian genus *Australymexylon* are revised and include *A. australe* (Erichson) (transferred from *Lymexylon*) and *A. fuscipennis* (Lea) (*Hylecoetus*). *Hylecoetus linearis* Lea and *Lymexylon adelaidae* Blackburn are synonymized with *Australymexylon australe.* Species level taxonomic changes include the following: *Hylecoetus cossis* Lewis, *H. matsushitai* Kono, and *H. cribricolle* (Fairmaire) are all synonymized with *H. dermestoides* (L.);

Melittomma javanus (Kurosawa) (*Neohylecoetus*), *M. pervagum* (Olliff) (*Hylecoetus*), *M. philippensis* (Kurosawa) (*Neohylecoetus*), and *M. vigilans* (Lea) (*Hylecoetus*) are new combinations (but see Kurosawa, 1985); *Melittommopsis validum* (Schenkling) (*Melittomma*), *M. ruficolle* (Pic) (*Melittomma*), and *M. abdominale* (Pic) (*Melittomma*) are new combinations; and *Protomelittomma insulare* (Fairmaire) (*Melittomma*) is a new combination.

For each genus, the following are given: a habitus drawing; illustrations of important characters; diagnosis; description of a representative species; list of species included; summaries of cladistic relations, geographic distributions, fungus hosts, arboreal hosts and bionomics; and a discussion. The cladistic relations among the genera are discussed, and my hypothesis is summarized as follows: (*Hylecoetus* + ((*Lymexylon* + *Atractocerus*) + (*Australymexylon* + (*Protomelittomma* + (*Melittomma* + *Melittommopsis*)))))). The geographic history of the family is discussed.

A key to and diagnoses of world subfamilies and genera are given, as well as discussions about the constitution of Lymexyloidea, natural history and economic importance of Lymexylidae, a detailed account of the morphology of *Hylecoetus dermestoides,* and a reclassification of supraspecific taxa.

INTRODUCTION

Considering the structural diversity, phylogenetic placement (as a superfamily of Cucujiformia), and mycological habits of the Lymexylidae, it is surprising that few comparative studies of the family have ever been done. The family, including about 50 living species, varies from heavily sclerotized, melandryidlike forms (fig. 249) to soft-bodied, cleroidlike forms (fig. 1) and brachelytrous forms that are scarcely beetlelike at all in general appearance (fig. 123). Lymexylidae has been classified in its own superfamily, Lymexyloidea, for most of the 20th century and its relationship with Cleroidea, Clavicornia,

and Tenebrionoidea in the Cucujiformia remains enigmatic (Crowson, 1955, 1960, 1981; Lawrence and Newton, 1982). Adult lymexylids are short-lived (a few days) while larvae are woodboring and sometimes require two or more years to develop. Lymexylids are "fungus growing" (sensu Wilson, 1971). Larvae of hylecoetines are known to cultivate an ascomycete fungus in their tunnels and those of other genera are suspected of similar habits.

The taxonomic history of Lymexylidae has consisted largely of isolated contributions and no single work has ever examined world gen-

era in a detailed, systematic way. In this paper I present a revision of the genera of lymexylids analyzed cladistically (Hennig, 1966; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wheeler and Blackwell, 1984; Wiley, 1981) and a classification consistent with my cladistic hypotheses. This study neither resolves the placement of Lymexylidae in the higher classification of the Coleoptera, nor taxonomically reviews all its constituent species. It does provide an explicit framework of genera from which both of these goals may be pursued.

Naturhistorisches Museum Wien, Vienna; M. Uhlig, Zoologisches Museum, Humboldt Universität, Berlin.

CONSTITUTION OF LYMEXYLOIDEA

This category [Lymexyloidea] is usually admitted to be an isolated group of debateable ancestry, and its chief component family, Lymexylidae, has suffered nearly as many shifts of position as there have been writers of the classification of beetles.

J. Chester Bradley

The taxonomic controversies surrounding the lymexylid beetles have improved little since the comments Bradley made in 1939. As recently as 1979 the family was suggested to belong in Cleroidea (Bright, 1979) and Arnett (1971) removed one genus (*Atractocerus*) to the Telegeusidae in the Cantharoidea. While I will not directly discuss the relationships of the Lymexyloidea, Crowson's assessment of their relations seems to be the best possible at the present. Crowson has suggested a close relationship of Lymexyloidea, Cleroidea, and Cucujoidea (in the broad sense, including Cucujoidea and Tenebrionoidea of Lawrence, 1982) as an unresolved trichotomy (Crowson, 1955, 1960, 1981). Bright (1979) and Lawrence and Newton (1982) have implied close relationship of lymexyloids with cleroids, but the available evidence is no stronger for this relationship than for one with cucujoids, as suggested by Boving and Craighead (1931) on larval data. It may be asserted that no satisfactory resolution of the higher classification of the Cucujiformia (Lawrence and Newton, 1982) will be possible excluding consideration of Lymexyloidea. Of more interest to this study of the genera of Lymexylidae, are the taxa included within the family and the constitution of the superfamily Lymexyloidea.

Lymexyloidea is here recognized with the single family Lymexylidae, as has been customary since Leng (1920). Crowson has recently (1981) suggested that the Stylopidae be included in Lymexyloidea. I agree with Lawrence and Newton (1982) that there is no compelling evidence to support this. Wing reduction in the two groups is easily viewed as convergent, and the fact that other parasitic taxa (e.g., Ripiphoridae) have apparently arisen from wood-boring ancestors is scarcely reason to justify inclusion of stylopids near lymexylids. Further, if evidence is tilted toward any side of the argument on the relationships of Strepsiptera, it is in favor of their status as a sister group of Coleoptera, which would indicate classification as a separate order (as is done by Boudreaux, 1979; Hennig, 1981; Kinzelbach, 1971; and Kristensen, 1981) or conceivably as a suborder of Coleoptera, but in neither case within or even near Lymexyloidea.

Differences of opinion with regard to the genera included in Lymexylidae have almost exclusively dealt with *Atractocerus*. Several placements have been suggested, including Arnett's placement in Telegeusidae (Arnett, 1971) and King's (1955) assignment of the genus to subordinal status (see also Forbes, 1956; Selander, 1959). Evidence given herein, however, supports Crowson's (1955) inclusion of the genus in Lymexylidae. The genus *Hylecoetopsis,* proposed by Lane in 1955 for *Hylecoetus cylindricus,* is excluded from this analysis. On evidence to be discussed elsewhere by W. F. Barr and me, that genus is removed from the Lymexylidae to the Cleridae. Two genera are herein proposed as new, bringing the total for the family (subtracting new synonymies) to seven.

The genera of Lymexylidae were described at a slow rate. *Lymexylon* was erected by Fabricius in 1775; *Atractocerus* by Palisot de Beauvois in 1801; *Hylecoetus* by Latreille in 1806; *Melittomma* by Murray in 1867; and *Melittommopsis* by Lane in 1955. Some other genera, not recognized here as valid or as lymexylids, were also proposed. *Heteromeroxylon* Pic (1939a) was erroneously catalogued as a lymexylid, but was described as a Rhipiphoridae. *Neohylecoetus* was proposed for specimens from Java and the Philippines by Kurosawa (1956), but close examination of his figures clearly shows this taxon to be synonymous with *Melittomma.*

Lymexylids were known to coleopterists before the publication of Linneaus' (1758) 10th edition of *Systema Naturae* (e.g., Uddman, 1753, as cited by Pfeil, 1859), and Linneaus himself described taxa known today as *Lymexylon navale* (1758) and *Hylecoetus dermestoides* (1761). Most species have been described in isolated publications. An in-

crease in the rate of description of species after about 1820 may be correlated with the great 19th century colonial explorations.

Complete generic synonymies and lists of constituent species accompany discussions of each genus below.

NATURAL HISTORY

Mycophagy is a widespread ecological habit in the Coleoptera (Crowson, 1955, 1981), but most host associations have been with Basidiomycetes (e.g., Benick, 1952) and fewer with Ascomycetes (e.g., Crowson, 1984; Wheeler and Hoebeke, 1984). Further, most mycophagous beetles are free-living, feeding directly on spores, hymenia, or other parts of fungi. Ectosymbioses between beetles and fungi are well known in few taxa. The "ambrosia beetles," here restricted to the Scolytinae and Platypodinae (Curculionidae), are perhaps best known. All beetles that cultivate fungi in wood as a food source (especially for larvae) may be termed "fungus growing," as suggested by Wilson (1971). Although the fungus-growing habits of lymexylids are in some ways less sophisticated than those of the more familiar ambrosia beetles (Francke-Grosmann, 1967; Graham, 1967; Schedl, 1958; Wilson, 1971), it is probable that the lymexylids were among the first Coleoptera to evolve such habits, and as such there is considerable interest in studies of their fungal associations.

The fungus associate and many details of the biology of *Hylecoetus dermestoides* are relatively well documented (Buchner, 1928, 1953; Lyngnes, 1958; Francke-Grosmann, 1967; Egger, 1974), as well as the significance of the "fungus pouches" of the female genitalia. Development of the pouches is difficult to assess without fresh specimens and the ability to make cross sections. However, the membranous nature of the midline of the genitalia in many lymexylids makes the inference that they share similar habits reasonable (Wilson, 1971). This is given further support by the description of another fungus of the same genus, *Ascoidea africana,* by Batra and Francke-Grosmann (1964). The fungus was associated with an unidentified lymexylid larva in *Chlorophora excelsa* (Moraceae) wood imported to Germany from West Africa. The larva can reasonably be inferred to have been either a *Melittomma* or an *Atractocerus,* neither of which have documented mycosymbionts.

Interesting aspects of the *Hylecoetus* symbiosis with an *Ascoidea* species can be extracted from the works by Buchner (1928, 1953), Francke-Grosmann (1967), Lyngnes (1958), and Egger (1974). Females oviposit on wood substrates. Logs over a year old and slightly fermented are apparently preferred over freshly cut ones. Arboreal hosts for the genus *Hylecoetus* include *Pinus* (Batra and Francke-Grosmann, 1961; Batra, 1967), *Liriodendron* (Simmonds, 1956), and a range of softwoods (Peterson, 1961). Egg laying takes place above temperatures of 8°C. Neonatal larvae are morphologically distinct from later instars (Grandi, 1961), possessing stemmata and very long setae, both lost in later instars (a dimorphism true of other taxa as well, including *Atractocerus*). First instar larvae are said to have a characteristic prolonged twisting behavior assuring contact of the larva with siblings and eggs, and resulting in the transfer of fungal spores onto the integument. They bore into wood head-first, pushing debris from the tunnel with the tail-end which is blunt in the first instar larva (elongate in later instars). Later instar larvae face the tunnel entrance and it has been speculated that the sawlike ninth abdominal segment may be partially used for boring. Fungi grow on the tunnel walls during larval development, including the host fungus species *Ascoidea hylecoeti* (Batra and Francke-Grosmann, 1961) and a variety of contaminant species such as *Isaria, Aspergillus,* and *Verticillium.* Pupation takes place within the tunnel. Adult females emerge bearing spores in the special vaginal pouches (Buchner, 1928; Francke-Grosmann, 1967), eventually depositing them in a slimy matrix with eggs. Adults live only a few days.

It is noteworthy that the host fungus is found only in association with *Hylecoetus,* but is capable of growing on a wide variety of wood substrates including many European hardwoods and all softwood species (Francke-Grosmann, 1967). While the fungus is an excellent source of nutrients, an overabundance of fungus growth seems to retard the growth of beetle larvae (Francke-Grosmann, 1953,

1967). Enzymatic activity of the fungus probably makes wood more manageable for larval boring activities (Batra and Francke-Grossmann, 1961). The host fungus belongs to the Ascoidaceae (Ascomycetes: Hemiascomycetidae) as recognized by Alexopoulos and Mims (1979).

The deutonymph of a tyroglyphid mite, *Histiogaster hylecoeti,* is carried under the elytra of *Hylecoetus.* The mite leaves the beetle at the time of oviposition and coinhabits the larval tunnels of *Hylecoetus* along with the symbiotic fungi (Cooreman, 1952).

Lyngnes (1958) suggested that the maxillary palporgan of the male *Hylecoetus* could be used in finding suitable substrata. The obvious problem with this interpretation, and part of the evidence favoring mate location as a function of the palporgan, is its presence in males and absence in females of most lymexylid genera, as discussed by Slifer et al. (1975). Aside from the obvious kinds of experimental physiology studies needed, increased knowledge about the biology of *Atractocerus* (with palporgans in both sexes) and *Australymexylon* (with palporgans lost in both sexes) should be useful in understanding the function and evolutionary significance of these organs.

The biology of other Lymexylidae is less well known. One of the most intensive efforts to acquire such information involved *Protomelittomma insulare* (Fairmaire), new combination, a serious pest of coconut palms in the Seychelles. This beetle breeds in several cultivated coconuts and wild palms (including *Sterensonia, Nephrosperma, Deckenia,* and *Roscheria*) and, in spite of extensive field studies, no fungal host has been positively identified. Larval tunnels were found to have a mixed flora, including gram negative bacteria and yeasts. References on the biology of *Protomelittomma* include Brown (1954), Lepesme (1947), Lever (1969), Nye (1961), Simmonds (1956), and Vessey-Fitzgerald (1941).

Wasmann (1902) suggested that two species of *Atractocerus* in West Africa and Brazil might be associated with nests of termites, but no confirmation of termite associations has been made for any member of the family. Further, Buchner (1953) pointed to the morphological evidence for fungus pouches in the

vagina of *Atractocerus,* suggesting a symbiosis similar to that in hylecoetines. Laporte (1832) linked *Melittomma brasiliense* with a bolete, but no similar relationships have been reported since. *Atractocerus reversus* has been noted in association with "mold and sap" (Roonwal, 1972). Fungi in the larval tunnels of *Atractocerus kreuslerae* in Australia reportedly killed the larvae (Clark, 1925). Other "associations," primarily with arboreal hosts, are noted in the section on taxonomy.

ECONOMIC IMPORTANCE

Considering my jubilation over the collection of adult *Melittomma* and *Atractocerus* during fieldwork in Panama, and a single larva of *Melittomma sericeum* by my wife in Ohio, it is difficult to think of lymexylids, comparatively rare beetles, as economic pests. In fact, few species are. But this may change as the tree species utilized in tropical countries, and our perceptions of their values to us, change. Also, some lymexylids were serious pests in the past but are much less so now.

Lymexylon navale, the true "ship-timber beetle" (a common name sometimes given to the family, e.g., by Arnett, 1971), was a serious pest of wooden ships and structural wood in past centuries in Europe and Scandinavia. Although this is still a widespread species, changes in ship building materials and other factors have eliminated its serious economic importance.

Hylecoetus dermestoides sometimes causes local damage to cut wood in Europe. Dominik (1975; Dominik and Kinelski, 1976) has discussed its economic importance and measures for its control. It is interesting that the North American species, *H. lugubris,* is virtually identical to *dermestoides* in morphology and shares the same fungal host but is of virtually no economic importance.

Melittomma sericeum, the only other member of the family occurring widely in the United States, is another former pest species. During the 19th century this beetle infested as much as 50–90 percent of chestnuts locally and larval borings inflicted serious losses to chestnut lumber (Craighead, 1950). There has also been a report of damage by this species

to structural timbers (Champlain and Knull, 1923). The blight of American chestnuts, however, has rendered this species a collector's item in the United States.

Perhaps the most serious pest in the family during this century has been *Protomelittomma insulare*. Damage to coconut palms in the Seychelles was immense. Between 1953 and 1958, 77 percent (or more than 95,000) of the trees on Praslin Island were infested. After careful removal of infested wood and plugging of damaged areas of the bole with tar, however, infestation had been reduced to about 18 percent by 1961 (Nye, 1961). Production on one plantation fell from 22,000 coconuts per month in 1948 to about 15,000 per month in 1952, largely due to this beetle. The annual loss of mature trees on one estate

of 350 acres was about 150 trees. Currently this species is under control (Nye, 1961).

Clark (1925) reported damage by the "pinhole borer" in Western Australian forests, observing that "Probably no insect does greater damage to the commercial timber growing in Western Australian forests" (than *Atractocerus kreuslerae*). This species bores in a large number of *Eucalyptus* species, and larvae were found by Clark to require at least two years of development time.

Another reported pest is *Atractocerus reversus* in India, where it is "a serious pest of standing trees, felled logs, billets and plancks of the salai, *Boswellia serrata* Roxb., and the jhingan, *Lannea corommandelica* (Hout) Merr. (synonym of *L. grandis* (Dennst.) Engl.), according to Roonwal (1972).

MORPHOLOGY

No lymexylid has ever been described in detail. A representative species, *Hylecoetus dermestoides,* has been chosen here for detailed description to fulfill two needs; one as a basis for comparison within this study of genera, and the other as a point of reference for systematists working on related families of beetles. This taxon was selected for several reasons. First, it is a relatively common European species and there were many specimens available for study. Second, its biology is better known than any other single species in the family, making possible functional interpretations of structures a little less speculative. And finally, it is a fairly "primitive" member of the family, in spite of a series of autapomorphs making it distinctive.

ADULT STRUCTURE

Body Form (fig. 1): Elongate, nearly parallel-sided, moderately dorsoventrally flattened; length about 4.8–16 mm; lightly sclerotized; clothed in fine setae; legs long, thin; elytra long, covering fully developed hindwings and most of abdomen; color variable (see generic discussion under Taxonomic Synopsis below).

Cranium (figs. 2–5): Prognathous, broadly ovate, dorsoventrally compressed; about as wide as long (dorsal view: fig. 2); rounded behind eyes, not narrowed to form a "neck" region; vertex with evident epicranial pit (figs. 2, 30); integument with dense, rough, nearly reticulate punctation and very fine, dense, suberect setae; antennae inserted anterior and mesad to eyes; frontoclypeal suture absent; gula short, narrow (fig. 3); gular sutures nearly parallel, slightly divergent anteriorly and posteriorly; ventral opening of foramen margined by distinct ridge (figs. 4, 5).

Antenna (figs. 12, 18, 22–24, 29): Two antenna morphs are described, termed "typical" and "flabellate" morphs. "Typical" refers to *dermestoides* sensu stricto; "flabellate" to *flabellicornis*. The latter species is conservatively recognized here, but, as discussed later, there is evidence to suspect that it may be conspecific with *dermestoides* to which it is obviously closely related. Typical morph: slender, 11-segmented, not much longer than length of cranium at midline; scape (segment I) elongate, slightly clavate (fig. 12); pedicel (segment II) short, little longer than wide; segment III elongate, clavate; segments IV–X short, transverse, asymmetrically shaped;
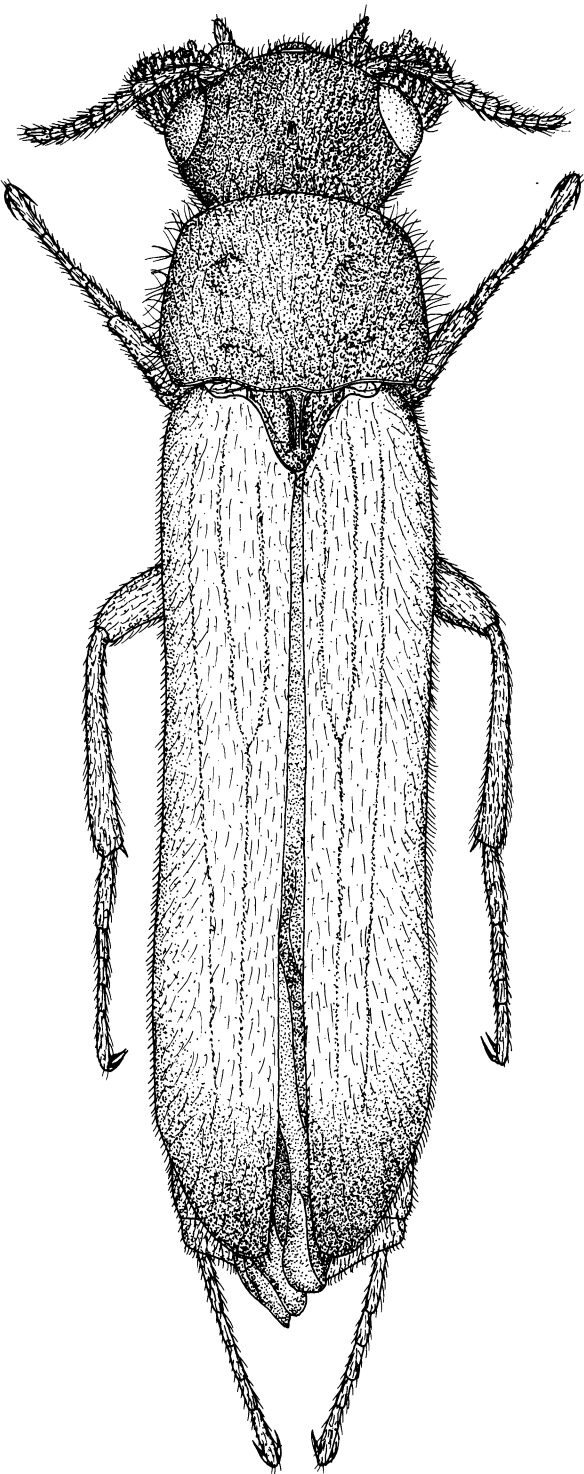
FIG. 1. *Hylecoetus dermestoides* (L.), male, dorsal view.
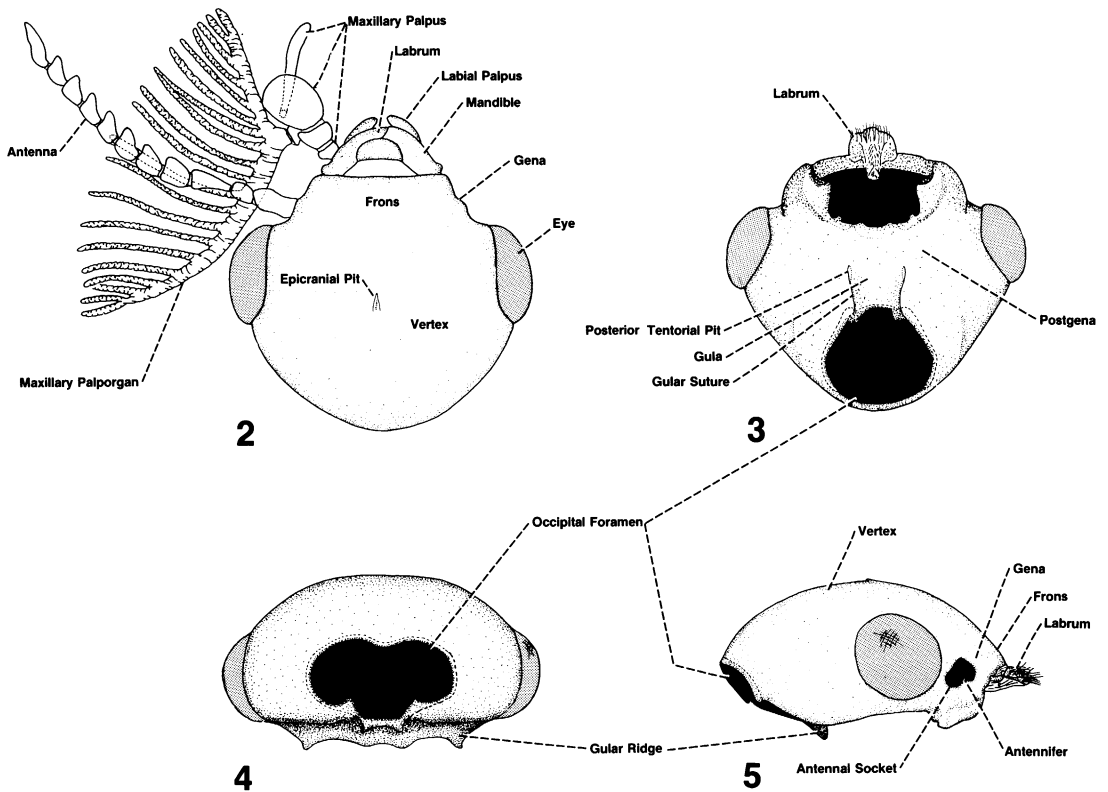
FIGS. 2–5. *Hylecoetus dermestoides,* head. **2.** Dorsal view. **3.** Ventral view. **4.** Posterior view. **5.** Lateral view.

scape with patch of sparse, short, spinose setae near base and with long, stout, fluted setae generally distributed on surface; pedicel similar, but with only a few short, spinose setae near base; apical portion of III and entire surfaces of IV–XI with long, stout setae and short, broad (putatively thin-walled) sensilla (see fig. 29); other setose structures include small cuticular openings surrounded by minute projections (fig. 29), and microtrichiae (fig. 18). The typical morph occurs in all females of both species, and males of all morphs of *dermestoides,* but not of *flabellicornis. Flabellate morph:* strongly flabellate (figs. 22, 23, 24, and frontispiece); surface with long, fluted setae (as in typical morph), broad more or less imbricate scales, and elongate (probably) thin-walled setae (figs. 23, 24). Fluted setae lacking on inner surface of antennal branches; this is similar to the kinds of surface details of the maxillary palporgan, which is highly developed in males of the typical morph but

highly reduced in males of the flabellate morph.

Labrum and Epipharyngeal Region (figs. 10, 11, 16, 17): Labrum broad, flat, small, lobate, separated from clypeus by broad membrane; lightly sclerotized, especially at margin; dorsum with long setae, densely packed at apex, converging medially with similar ventral setae to form a dense "brush"; venter with longitudinal, medial patch of setae, denser apically (figs. 10, 11, 17). Tormae short, expanded ventrally and medially as broad plates; with few fine setae along mesal margins (fig. 11). Epipharyngeal membrane thin, posterior to labrum and between and ventral to tormae; with few fine setae generally distributed, dense mesal patch of microtrichiae, convergent at midline (figs. 11, 16).

Mandibles (fig. 27): Simple, small, stout; prostheca nearly absent, with few setae; left and right mandibles similar; apical incisor
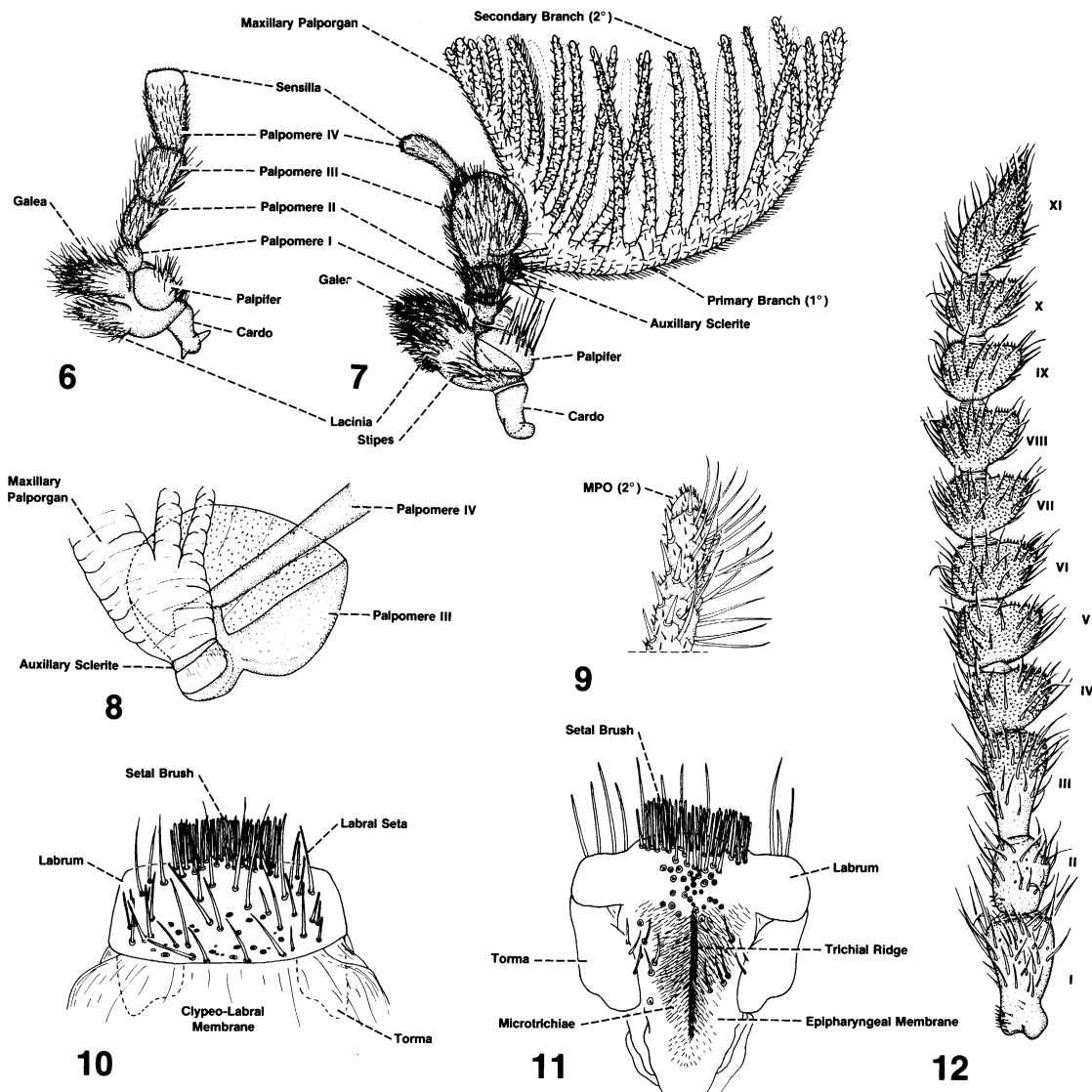
FIGS. 6–12. *Hylecoetus dermestoides.* 6–9. Maxilla. **6.** Female. 7–9. Male. **8.** Palpomere III and bases of palpomere IV and maxillary palporgan. **9.** Apex of secondary branch of palporgan. **10.** Labrum, dorsal. **11.** Labrum and epipharynx, ventral. **12.** Antenna.

lobe with apical dens and poorly defined secondary dens; mola indistinct.

Maxilla and Maxillary Palporgan (figs. 2, 6–9, 13, 14, 19, 25, 26, 28): Sexually dimorphic, male with maxillary palporgan (see below), female with typical cucujiform maxilla. *Female.* Cardo small, narrowed basally (figs. 6, 7); stipes not separated from lacinia and galea by distinct suture (figs. 6, 7); lacinia small, narrowed, membranous, with dense long setae; galea broad, rounded, with dense,

long setae; palpifer broad, ringlike, with several long setae mesally; palpus 4-segmented, covered with dense, long, fine setae (fig. 6); segment I short, II long and slightly expanded apically, III similar to II but nearly parallel-sided, IV elongate, with numerous apical sensilla (figs. 6, 19). *Male.* Similar to female, except palpus; segment I short, as in female, II short, transverse, III greatly enlarged (figs. 7, 8), broadly rounded, with maxillary palporgan arising in apical membrane, and IV
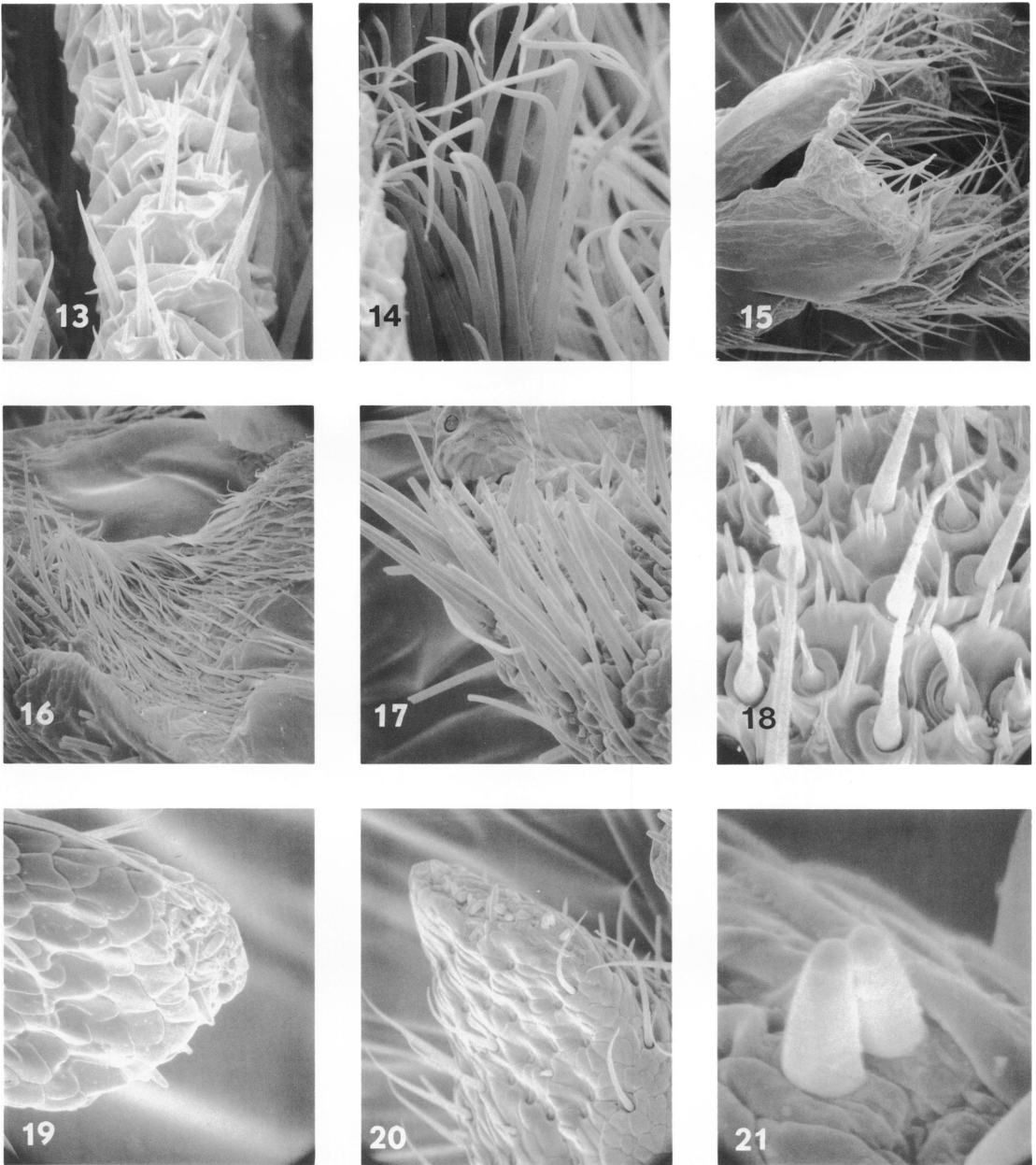
FIGS. 13–21. *Hylecoetus dermestoides.* **13.** Maxillary palporgan, outer surface. **14.** Maxillary palporgan, inner surface. **15.** Hypopharyngeal setae. **16.** Epipharyngeal setae. **17.** Labrum apex, ventral. **18.** Antennomere IV surface detail. **19.** Maxillary palpomere IV apex, male. **20.** Labial palpomere III apex. **21.** "Peg" sensilla, apex labial palpomere III.

long, thin, with typical apical sensilla (fig. 19). Maxillary palporgan arises from cuplike segment III apex, to side and near base; membrane connecting organ to palpus with small elongate sclerite (fig. 8); multibranched, with two primary branches and parallel secondary branches forming basketlike structure, compact and retracted in repose and erect and protruding when under pressure in use; expanded, these organs may surpass dorsal sur-
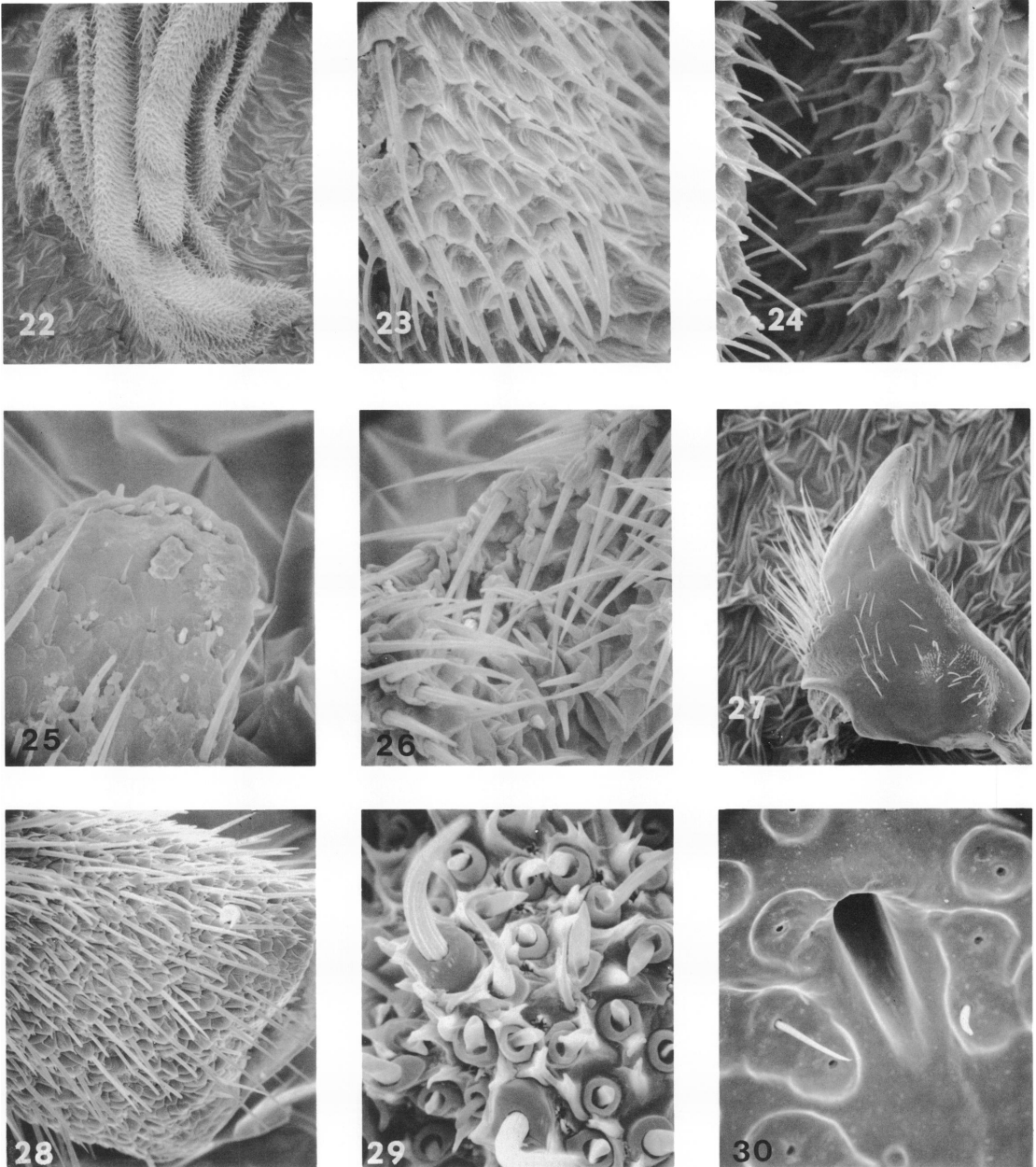
FIGS. 22–30. *Hylecoetus* species. 22–26. *H. flabellicornis.* **22.** Antenna. **23.** Flabellate process of antenna, outer surface. **24.** Flabellate process of antenna, inner surface. **25.** Maxillary palpus apex, male. **26.** Maxillary palporgan surface detail. 27–30. *H. dermestoides.* **27.** Mandible, dorsal. **28.** Maxillary palpomere IV surface, male. **29.** Antennomere VII surface detail. **30.** Epicranial pit.

face area of head; inner surface of each branch with long (supposedly) thin-walled sensilla and outer surface with shorter, thicker, fluted and probably tactile setae (figs. 13, 14, 26; see also, Slifer et al., 1975); surface of each branch characteristically wrinkled in appearance.

Labium and Hypopharyngeal Region (figs. 15, 20, 21, 31, 32): Labium small, lightly sclerotized, with 3-segmented palpus (figs. 31,
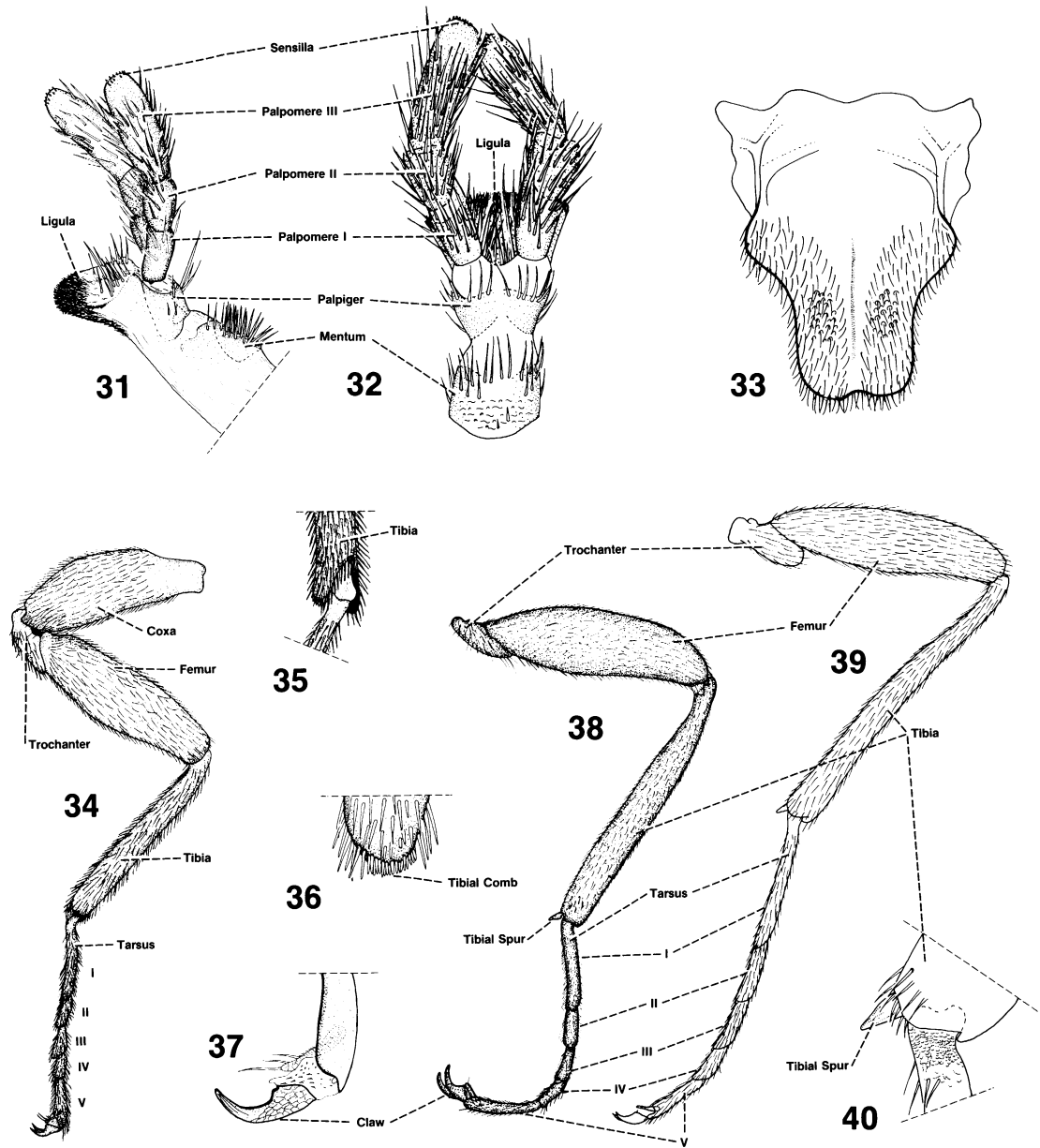
FIGS. 31–40. *Hylecoetus dermestoides*. **31.** Labium, lateral. **32.** Labium, ventral. **33.** Scutellum. **34.** Prothoracic leg. **35.** Protibia apex, posterior margin. **36.** Protibia apex, anterior margin. **37.** Mesothoracic tarsal claw. **38.** Mesothoracic leg. **39.** Metathoracic leg. **40.** Metatibia apex.

32); mentum small, subquadrate, with several long setae; palpigers lightly sclerotized ventrally and proximally, poorly defined, with long setae apically and laterally; palpus segment I elongate, II similar to I, but shorter, III about as long as first two combined in female and 80 percent of their combined lengths in males; apex with several peglike sensilla (figs. 20, 21).

Prothorax (figs. 44–46): Pronotum small, subquadrate (fig. 46); posterior margin slightly sinuate; anterior margin broadly rounded; surface irregular, some areas depressed, others elevated as bumps; with dense, small, fine
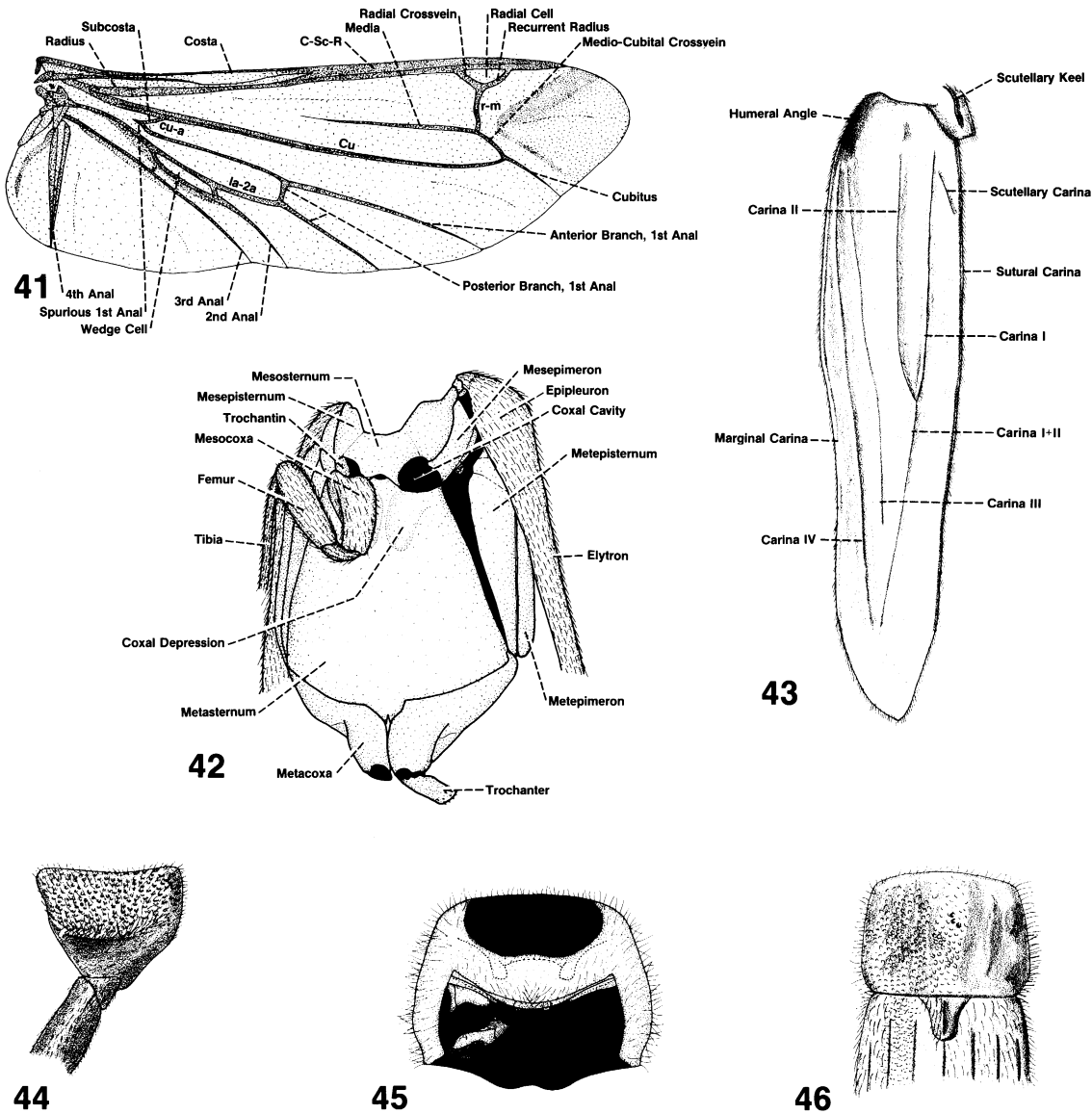
FIGS. 41–46. *Hylecoetus dermestoides*. **41.** Hindwing. **42.** Pterothorax, ventral. **43.** Elytron. **44.** Prothorax, lateral. **45.** Prothorax, ventral. **46.** Pronotum, scutellum, and base of elytra.

setae; lateral margins distinct (fig. 44). Procoxal cavities poorly defined (fig. 45), broadly open behind. Prosternum short, transverse (fig. 45); without intercoxal process. Prothorax connected to cranium by wide cervical membrane, bearing pair of elongate cervical sclerites (see also Baehr, 1976).

Pterothorax, Excluding Wings and Legs (fig. 42): Mesosternum small, subquadrate; mesepisternum small, but slightly larger than mesosternum, weakly separated from mesosternum; mesepimeron narrow, elongate; mesonotum with elongate, broad scutellum with sinuate lateral margins and double, elevated median keel (fig. 33). Metasternum large, subquadrangular, anteriorly with large shallow depressions; metepisternum and metepimeron elongate (fig. 42), separated by groove.

Legs (figs. 34–40): Long, thin, with dense
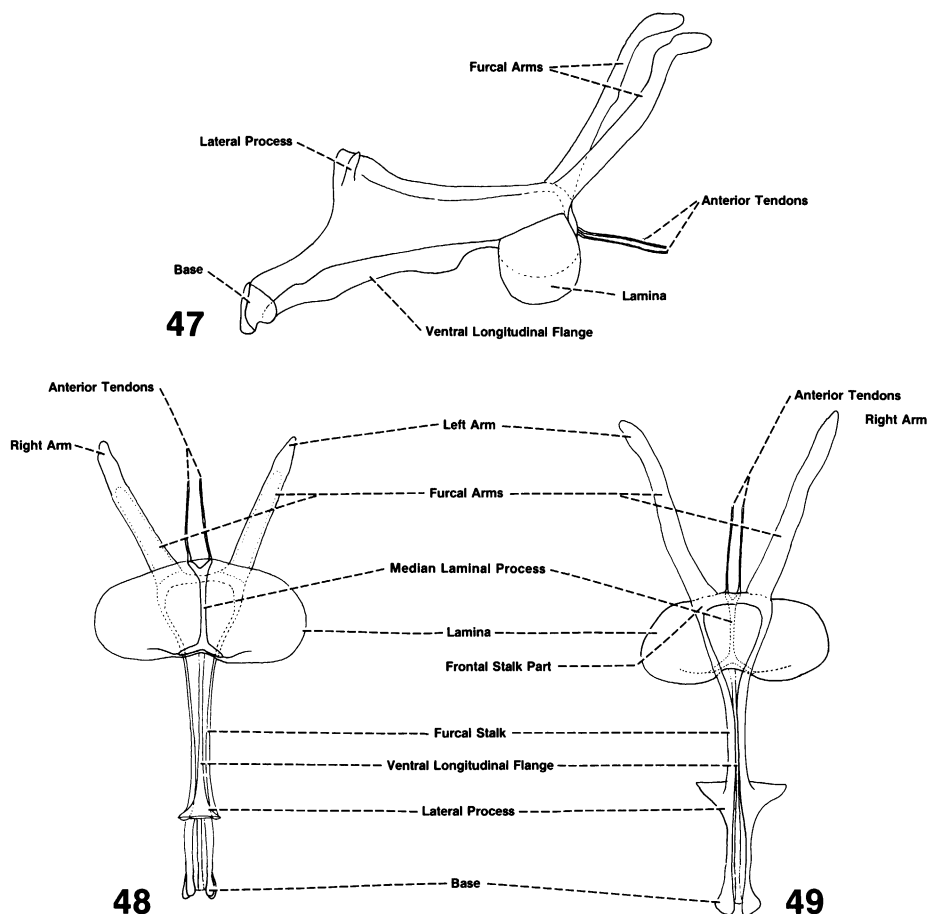
FIGS. 47–49.   *Hylecoetus dermestoides,* metendosternite. **47.** Lateral. **48.** Dorsal. **49.** Ventral.

shallow punctures and long, fine setae; tarsal formula 5-5-5; tibial spur formula 0-1-1 in both sexes; coxae of front and middle legs cylindrical; mesocoxa with base transversely enlarged; metacoxa transverse, part near midline projecting ventrally, lateral part shallowly concave receiving hind femur; trochanter small, "normal" type (Crowson, 1955); femur elongate, about twice as wide as tibia; tibia long, narrow, nearly parallel-sided, apex of protibia with anterior comb of setae (fig. 36) and posterior excised area (fig. 35); tarsus with segment I very long, segments II–IV shorter, V longer than IV.

Elytron (figs. 1, 43): Long, nearly covering abdomen; lightly sclerotized, with dense, shallow punctures and long, fine setae; humeral angle swollen; epipleuron poorly developed, broad anteriorly, narrowed posteriorly, terminating short distance beyond mesosternal-metasternal juncture; basally with tongue-and-groove mechanism, ending before apex; each elytron carinate, with short oblique carina near suture, fused with second carina beyond middle, third carina ending near middle (1 + 2 and 4 extend further posteriorly), and raised lateral rib or marginal carina.

Hindwing (fig. 41): Large, membranous, covered by elytron at rest; venation nearly complete. Anterior margin bordered by costa (C). Subcosta short, fused with C at about middle of wing. Radius (R) fused with C + Sc at about middle. Medial vein (M) arising spuriously, joining radial cell (formed near apex of wing by radial crossvein and "recurrent radius," Rr) by r-m crossvein. An m-cu crossvein connects M and Cubitus (Cu) below radial cell. First anal vein (1A) arises spuriously near wing base. Posterior branch of
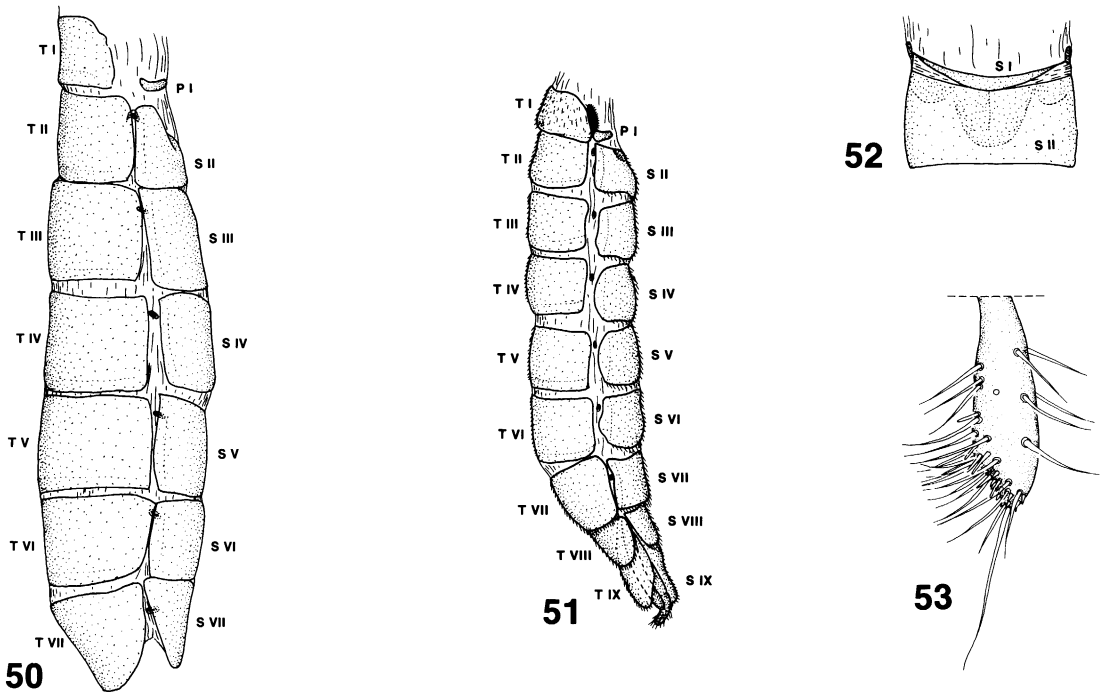
FIGS. 50–53. *Hylecoetus dermestoides.* **50.** Abdomen, female, lateral. **51.** Abdomen, male, lateral. **52.** Abdomen, female, base, ventral. **53.** Female genitalia stylus.

1A (1A₂) arises about middle of wing, resembling a crossvein. Wedge cell between 1a-2a crossvein and second anal (2A). Third and fourth anals (3A, 4A) simple, near wingbase.

Metendosternite (figs. 47–49): Furcal stalk long, parallel sided; pair of lateral processes near base of furcal stalk, and ventral longitudinal flange along its prelaminal length; anteriorly, furcal stalk forks above lamina; narrow, transverse frontal part bears furcal arms that are anterolaterally directed; anterior tendons very thin, arising proximally between bases of furcal arms and apex of median laminal process (on ventral surface of lamina).

*Abdomen (figs. 50–52), Excluding Genitalia: Male.* Elongate, tubular in form, with eighth sternite visible; tergites and sternites wider than long; segments II–VIII similar in form, VIII smaller than VII (fig. 51); IX forms circum-genitalic capsule (see Male Genitalia below); tergite I present, well developed, small pleural floating sclerite present, and small, narrow, transverse ventral sclerite present anterior to sternite II (fig. 52) may represent remnant of sternite I. *Female.* Similar to male, with seventh sternite last visible, eighth internal; VIII with long, narrow spiculum.

Female Genitalia (figs. 53–56): Connected to abdominal segment VIII by large, tubular membrane covered by dense, minute setae; excluding baculi, lightly sclerotized to membranous. Valvifers (figs. 54–56) paired, elongate, poorly defined anteriorly and ventrolateral in position. Anus opening dorsally between and at about posterior limits of valvifers. Valviferal baculi present ventrally (valvifers proximal, but separate ventrally; nearly as long as coxites). Coxites (figs. 54–56) paired, positioned distad to valvifers, with ventral coxital fold separating basal and distal parts; distal parts each with elongate, clavate stylus near apex. Stylus with single, long, apical seta, and several smaller setae on surface (fig. 53), and with apical, small, peglike sensilla. Distal portion of coxites with many long, fine setae set in large, membranous sockets. Basal part of each coxite giving rise to coxital baculus, articulating with valviferal baculus; with many setae on distal half. Fungus-pouch present mesally between basal parts of coxites, extending laterally from midline; consisting of membranous infolds, with median groove and lateral extensions (the "pouches"); see Francke-Grosmann (1967).
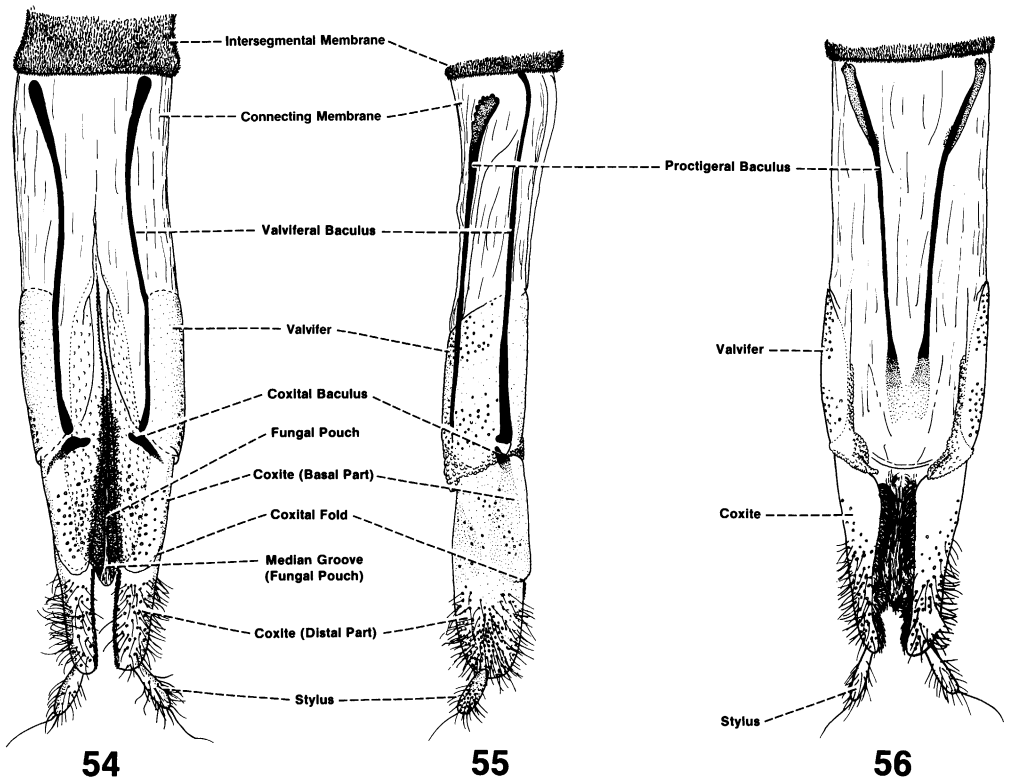
FIGS. 54–56. *Hylecoetus dermestoides,* female genitalia. **54.** Ventral. **55.** Lateral. **56.** Dorsal.

Proctigeral baculi (figs. 55, 56) arise dorso-medially, about same length as valviferal baculi; anterior apices lightly sclerotized, expanded into poorly delimited lobes. Coxital baculus (figs. 54, 55) short, oblique, narrow distad to valviferal baculi (see also Tanner, 1927).

Male Genitalia (figs. 57–59): Asymmetrical, rotated 90°. Median lobe long, narrow, widest at base; apex gradually curved; base recurved; lying in abdomen curved toward right side of beetle; curvature dorsad when extruded from abdomen. Tegmen consisting of broad tegminal plate, poorly defined; paired tegminal struts; and lateral lobes which are paired, proximal, and placed asymmetrically to one side (see also Lyngnes, 1956).

LARVAL STRUCTURE
Figures 60–72

Body elongate; prothorax enlarged, hood-like (fig. 60); meso- and metathoraces smaller, similar to abdominal segments; creamy white in color (preserved). Head moderately sclerotized, oval shaped, dorsal surface with sparse, long setae of several lengths; with short coronal suture; no epicranial sutures evident; five ocelli present in first instar (Grandi, 1961), absent in later instars; antennae (fig. 66) minute, 3-segmented (see Grandi, 1961), sometimes apparently 2-segmented (late instars) (short, broad, ringlike basal segment with digitiform organ and about four smaller sensilla; terminal segment slightly longer than digitiform organ, with about four apical sensilla, two longer than others); labrum elongate, rounded at apex; epipharynx with two pairs large setae (fig. 62), a few intermediate sized setae, and dense, small setae converging medially, and with parallel ridges; mandibles (figs. 70–72) broad, short, heavily sclerotized, with distinct molar area bearing parallel, transverse grooves; maxillae lightly sclerotized, with many setae; cardo small, elongate; stipes narrow basally, expanded distally, not clearly separated from mala by a suture; mala partially divided into lacinia and galea; la-
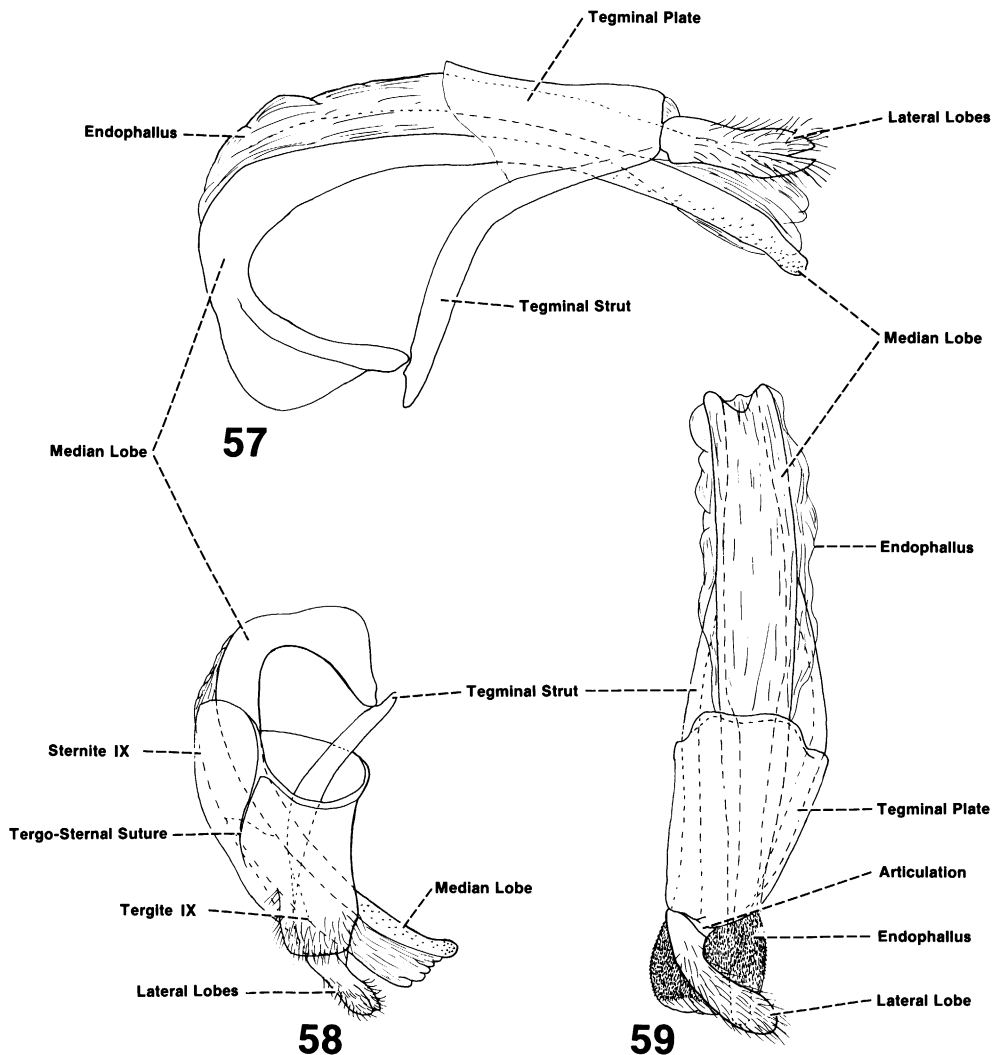
FIGS. 57–59. *Hylecoetus dermestoides,* male genitalia and postabdomen. **57.** Aedeagus, lateral. **58.** Aedeagus within postabdominal capsule, dorsal. **59.** Aedeagus, ventral.

cinia with double row of setae and less sclerotized than dorsal or ventral surface of mala; maxillary palpus 3-segmented; labium small, with 2-segmented palpus and broad, membranous ligula with dense microtrichiae (fig. 61). Hypopharyngeal sclerome present, elongate, narrow. Legs (fig. 65) small, stout; tarsungulus pleurisetose (fig. 64). Prothoracic spiracle large, transverse, oval, located posterior and slightly dorsal to front leg; abdominal spiracles on segments I–VIII small, oval, located on side of each segment, anterior to middle. Abdomen with segment IX heavily

sclerotized, very elongate, and forked apically, bearing teeth along dorsal margins; X small, membranous, inferior; VIII simple, with teeth dorsally (fig. 63).

PUPAL STRUCTURE
Figure 73

Lightly sclerotized, head and pronotum covered by small, dense spines; similar in most structures to adult; sexed by presence/absence of maxillary palporgans (see fig. 73, a male).
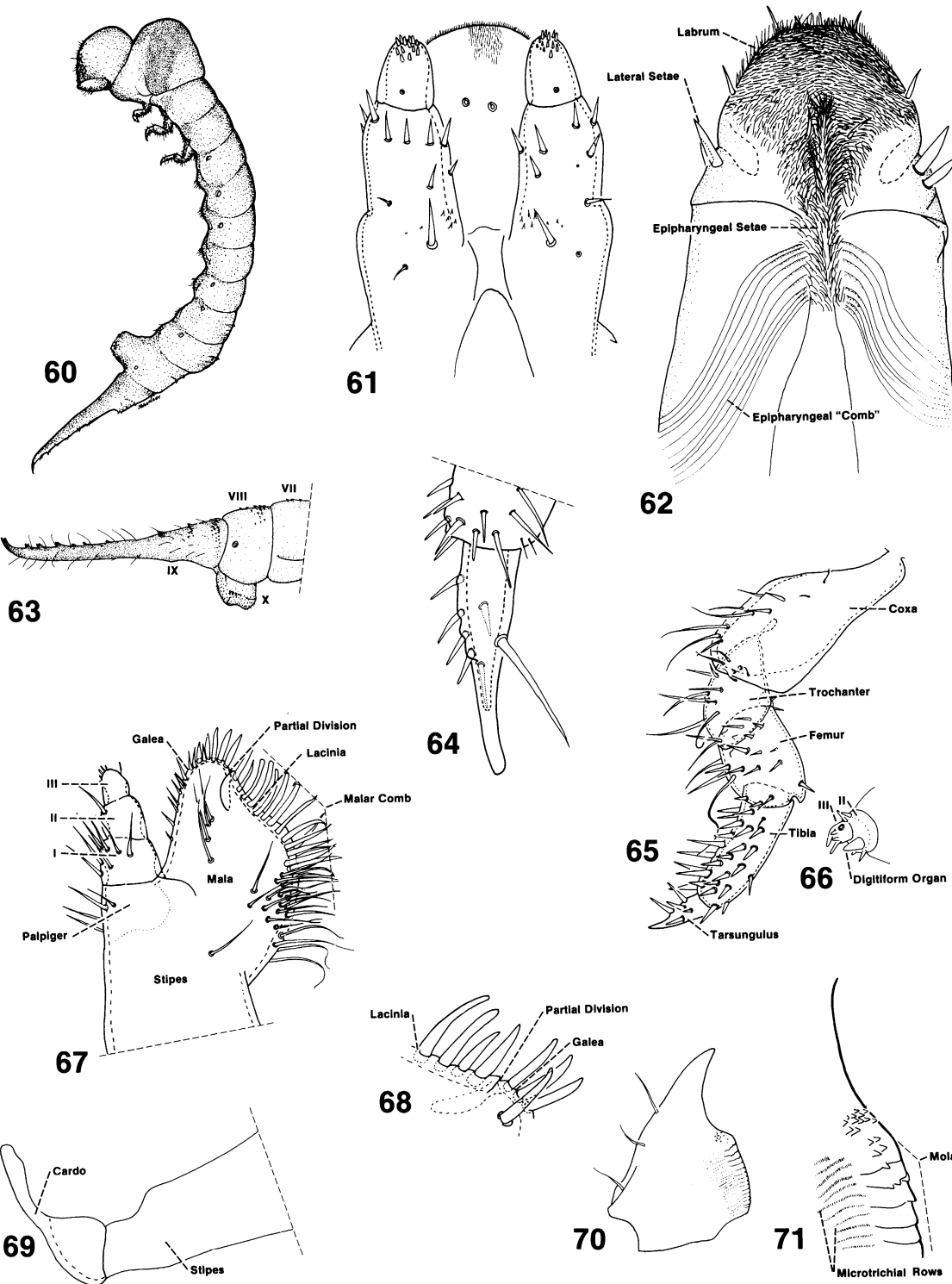
FIGS. 60–71. *Hylecoetus dermestoides,* larva. **60.** Habitus, lateral, by J. Nagy. **61.** Labium, ventral. **62.** Labrum, ventral. **63.** Abdomen apex, lateral. **64.** Tarsungulus. **65.** Proleg. **66.** Antenna. **67.** Maxilla apex. **68.** Mala apex. **69.** Maxilla base. **70.** Mandible, left dorsal. **71.** Mandible, detail of mola region.

TAXONOMIC SYNOPSIS

FAMILY LYMEXYLIDAE FLEMING, 1821[1]

Lymoxylonidae Fleming, 1821, p. 49.
Malacodermi (pars) Gyllenhal, 1808, p. 314.
Xylotrogi (pars) Latreille, 1825, p. 354.
Malacodermata (pars) Perty, 1830–1834, p. 25.
Oedomeridae (pars) Stephens, 1832, p. 52.
Lymexylonitae Laporte, 1836, p. 58.
Atractocerites Laporte, 1840, p. 290.
Teredyles Lacordaire, 1830, p. 251.
Terediles Boheman, 1851, p. 519.
Lymexylones Redtenbacher, 1849, pp. 5, 36.
Ptinidae (pars) Melsheimer, 1853, p. 86.
Lymexylonidae, M. J. Thomson, 1858, p. 82.
Lymexylonides Redtenbacher, 1858, pp. L, CII.
Lyttidae (pars), Walker, 1858, p. 285.
Lymexylidae, LeConte, 1861–1862, pp. XXIV, 198.
Diversipalpes Mulsant and Rey, 1863–1864, p. 13.
Xylophaga (pars) Gerstaecker, 1873, p. 160.
Lymexylini, Heyden, Reitter, and Weise, 1891, p. 228.
Lymexylonidae, Schenkling, 1915, p. 1.
Lymexylidae, Leng, 1920, p. 152.
Lymexylidae, Barber, 1952, p. 163.

DIAGNOSIS: Coleoptera, Cucujiformia, Lymexyloidea (Crowson, 1955, 1981; Lawrence, 1982; Lawrence and Newton, 1982); *Adults*—Procoxae cylindrical, projecting; tarsi 5-5-5; antennae filiform to serrate, rarely flabellate; male usually with maxillary palp-organ arising at apex palpomere III, rarely present in female and rarely absent in both sexes; head typically narrowed behind eyes forming neck; aedeagus trilobed, sometimes highly modified; female genitalia with coxites partially divided (ventrally); elytra usually with very weak carinae, sometimes greatly reduced and often not attaining apex of abdomen; *Larvae*—Head partially retractable into hoodlike pronotum; pronotum distinctly larger than meso- or metanota; legs short, stout; antennae minute; ocelli absent in late instars; abdominal segments usually with distinct lateral folds; abdominal segment IX large, superior to X and highly modified as elongate, sawlike structure (fig. 63), bulbous structure (figs. 119, 178), truncate structure (fig. 266), or rarely smaller structure armed with a pair of hooks (see Britton, 1970); maxilla with mala partially divided, and mesal margin bordered by parallel rows of long setae.

Taxonomic literature on various genera is cited in the sections that follow. Some general works on larvae that include the Lymexylidae are Boving and Craighead (1931), Britton (1974), Peterson (1961), and Rymer-Roberts (1930), and on European adults, Lohse (1979).

KEY TO WORLD SUBFAMILIES AND GENERA OF LYMEXYLIDAE

1. Head with epicranial pit (figs. 2, 30), rounded behind eyes without neck (fig. 2); elytra long, surpassing metacoxae (fig. 1); male abdomen with one more visible sternite than female (figs. 50, 51); lateral lobes of male genitalia asymmetrical (figs. 57–59); eyes round, small, entire (fig. 2); *larva* abdominal segment IX very long, narrow, heavily sclerotized with teeth along dorsal edges (figs. 60, 63); distribution Holarctic. Subfamily Hylecoetinae .... *Hylecoetus*
Head without epicranial pit; head narrowed behind eyes forming distinct neck; elytra long, shortened, or brachelytrous; male and female with same number visible abdominal segments; lateral lobes symmetrical; eyes moderate to large, emarginate anteriorly; *larva* abdominal segment IX bulbous (figs. 119, 178) or cylindrical-truncate (fig. 266) 2
2(1). Elytra shortened (fig. 82) or brachelytrous (fig. 123), tongue-and-groove locking

---

[1] So far as I have been able to determine, this is the first modern attribution of the family name Lymexylidae to Fleming, 1821. Schenkling (1915) and most authors have given credit for the name to "Leach, 1817," supposedly in the fifth edition of the *Encyclopaedia Brittanica*. There is no evident reason for this citation. Leach did contribute entomological information to Brewster's *Edinburgh Encyclopedia* in about 1815 (see also Sherborn, 1937), but did not recognize a suprageneric category for any lymexylid beetle, nor did he accord any such rank in other contemporary works (Leach, 1817). Fleming, 1821, is the earliest suprageneric usage of which I am aware.

The family name Lymexylidae is derivable from Fleming only with certain emendation. First, Fleming misspelled the root, resulting in "Lymoxylonidae" and this must be corrected. Second, the family name should be derived from the root "Lymexyl-" and thus be Lymexylidae rather than the commonly used Lymexylonidae as discussed by Barber (1952). This parallels similar problems in other beetles, such as Cerylidae versus Cerylonidae (see Kuschel, 1979).
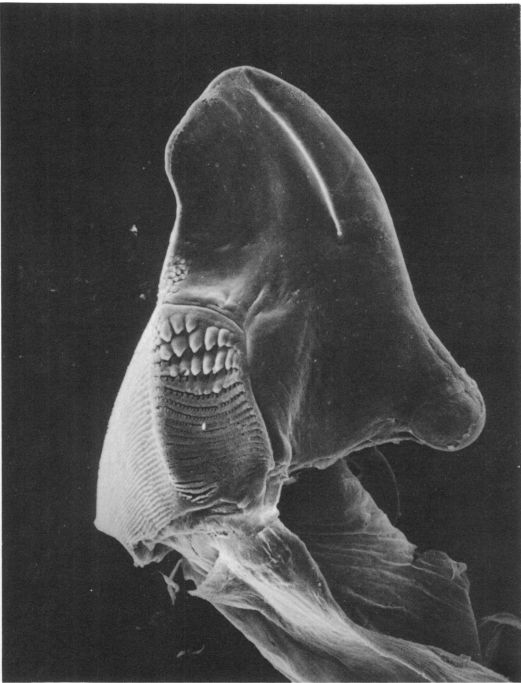
FIG. 72. *Hylecoetus dermestoides.* Mesal surface of left larval mandible. SEM courtesy of J. F. Lawrence.

mechanism present along suture; lateral lobes short and truncate (fig. 111) or very large and broad or elongate (figs. 148–152); *larva* with abdominal segment IX large, membranous and bulbous, often with asperites on apex (figs. 119, 178); distribution Palearctic or Pantropical. Subfamily Lymexylinae 3

Elytra covering abdomen or only slightly shortened (figs. 188, 225, 249), tongue-and-groove mechanism present, but sometimes ending before apex of elytron; lateral lobes large and concave medially (figs. 193–195, 214, 215) or small and lobate (figs. 238, 239, 258), rarely elongate with apical row of teeth (fig. 273); *larva* with abdominal segment IX heavily sclerotized, cylindrical and truncate (fig. 266); distribution Nearctic, Australian, South American, Pantropical, including Madagascar and the Seychelles. Subfamily Melittomminae, new subfamily 4

3(2). Elytra long, surpassing metacoxae (fig. 82); male only with maxillary palporgan (figs. 82, 90); antennae long, filiform (fig. 97); hindwings with crossveins and transverse folding (fig. 99); eyes not unusually large (figs. 83, 84); lateral lobes of male genitalia

short, truncate (fig. 111); female genitalia with spurious baculus joining vaviferal baculus (fig. 103); ovipositor lightly sclerotized; *larva* with a tooth at apex of abdominal segment IX (figs. 118, 119); distribution Palearctic .... *Lymexylon*

Elytra very short, brachelytrous, not reaching metacoxae (fig. 123); male and female with maxillary palporgan, organ smaller in female (figs. 138, 140); antenna short, spindle-shaped (figs. 125, 145); lateral lobes very large and broad (fig. 151) or elongate (fig. 148); hindwing without crossveins, folding only longitudinally (fig. 127); eyes very large (fig. 124); female genitalia heavily sclerotized, without spurious baculus (fig. 158); *larva* with asperites on abdominal segment IX (fig. 178); tarsungulus pleurisetose (fig. 176); distribution Pantropical .... *Atractocerus*

4(2). Eyes moderately large, widely separated (fig. 188); maxilla simple (fig. 192), maxillary palporgan absent in male and female; male abdominal sternite VIII with setose pads (figs. 211–213); lateral lobes of male genitalia large, mesally concave (figs. 194, 214); *larva* with abdominal segment IX heavily sclerotized apically, bearing a few minute teeth around margin (fig. 222); distribution Australian ....
.... *Australymexylon,* new genus

Eyes large, often proximal; maxillary palporgan present in male (figs. 244, 281), absent in female; male abdominal sternite VIII without setose pads; lateral lobes variable, never concave mesally (figs. 239, 258); *larva* with abdominal segment IX heavily sclerotized, apex variable, usually nearly smooth or heavily toothed or notched; distribution primarily Pantropical, but present in North America. *Melittomma* complex 5

5(4). Adults usually lightly to moderately sclerotized (fig. 225), rarely heavily sclerotized (figs. 249, 250); male abdominal segment IX with paratergites appendiculate (figs. 240, 257); lateral lobes of male genitalia small, lobate, setose (figs. 238, 258); female maxilla with segment IV narrow apically; mesosternum simple anteriorly, or elevated and "A"-shaped; *larva* with apex of abdominal segment IX distinctly, often deeply, notched at margin (figs. 245, 266); distribution Pantropical, North American
.... *Melittomma*

Adults heavily sclerotized (fig. 268); male abdominal segment IX without appendiculate paratergites; lateral lobes of male
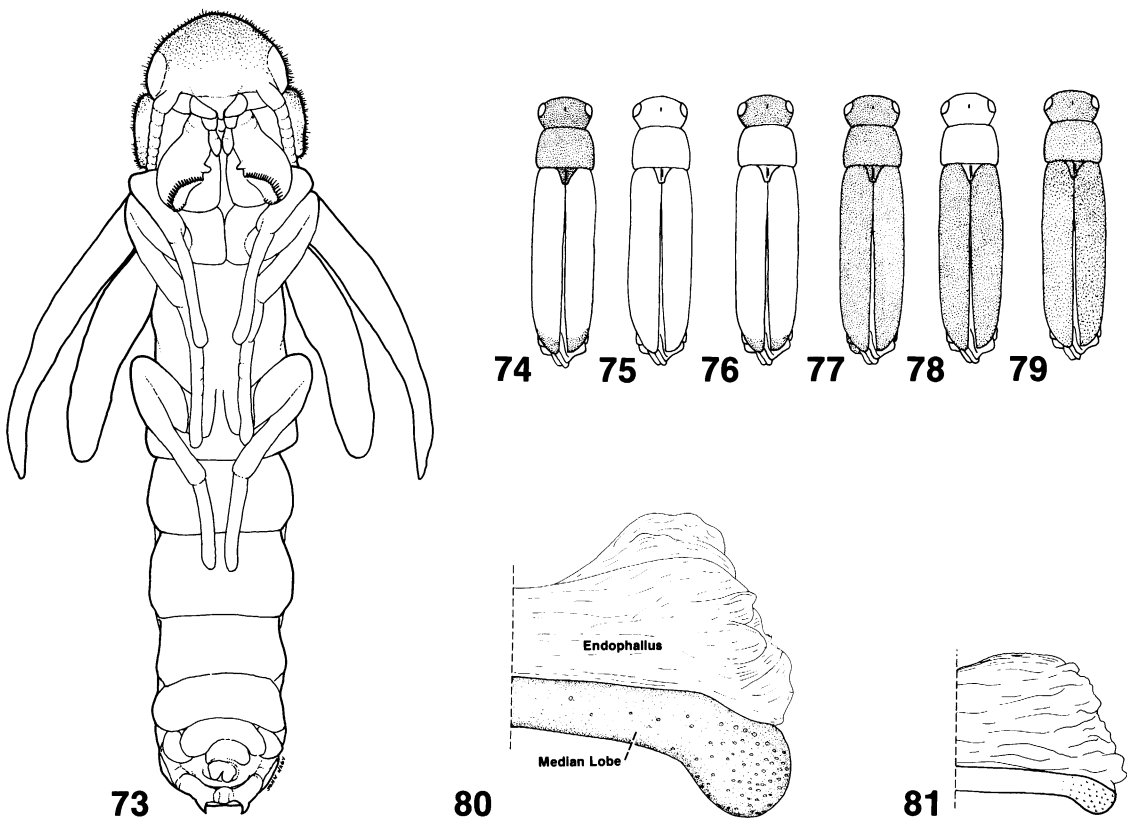
FIGS. 73–81. *Hylecoetus* spp. **73.** *H. dermestoides* pupa, ventral, by J. Nagy. 74–79. Semidiagrammatic habitus drawings showing color patterns of species and morphs. **74.** *H. dermestoides* typical morph, male. **75.** *H. dermestoides* typical morph, female. **76.** *H. dermestoides* "cossis" morph, female. **77.** *H. dermestoides* "morio" morph, male. **78.** *H. lugubris* male. **79.** *H. lugubris* female. 80, 81. Apex of median lobe of aedeagus. **80.** *H. dermestoides*. **81.** *H. lugubris*.

genitalia large, with apical row of teeth (fig. 273), or of normal size (fig. 297); female maxilla with apex of palpus segment IV narrow or securiform; *larva* with apex of abdominal segment IX nearly smooth, with few minute spines (fig. 286), in known larvae 6

6(5). Female maxilla with palpus segment IV securiform (fig. 291); mesosternum with anterior area elevated, elongate, and very narrow (fig. 289); basal half of stylus of female genitalia sclerotized, apical half membranous (fig. 293), coxite membranous, with narrow basal sclerotized area (fig. 294); male abdominal segment VIII with enlarged paratergites; paratergites of IX enlarged with spines, but not appendiculate (fig. 295); *larva* unknown; distribution: South America .... *Melittommopsis*
Female maxilla with palpus segment IV nar-

row apically (fig. 282); mesosternum with anterior elevated "A"-shaped area; proctigeral baculus of female genitalia fused for much of length (fig. 276); stylus and coxite more uniformly sclerotized; lateral lobes of male genitalia large, elongate, with rows of teeth (figs. 269, 273); *larva* with apex of abdominal segment IX nearly smooth around edge, with a few simple spines (fig. 286); distribution: Madagascar, Seychelles ....
.... *Protomelittomma*, new genus

SUBFAMILY HYLECOETINAE

Hylecoetinae Boving and Craighead, 1931, p. 68.

TYPE GENUS: *Hylecoetus* Latreille.
DIAGNOSIS: See *Hylecoetus* (below).

TABLE 1
List of Species of Genus *Hylecoetus* Latreille

Species	Citation	Distribution
H. dermestoides	Linnaeus, 1761, p. 201	Eurasia
H. flabellicornis	Schneider, 1791, p. 109	Europe
H. orientalis incertae sedis	Foursow, 1935, p. 92	East Siberia
H. formosanus	Miwa, 1935, p. 456	Taiwan
H. lugubris	Say, 1835, p. 166	USA, Canada

CLADISTIC RELATIONS: See *Hylecoetus* (below).

GENERA INCLUDED: The single genus *Hylecoetus* Latreille.

Genus *Hylecoetus* Latreille

Hylecoetus Latreille, 1806, p. 266; Jaquelin du Val, 1863, p. 206.
Elateroides Schaeffer, 1766, p. 139; 1777, table cxxxix.
Hylecerus Jacquelin du Val, 1863, p. 206.
Hyloceotus Melsheimer, 1853, p. 86.
Hyloecotus Lacordaire, 1857, pp. 500, 502.
Hyloecotus Chenu, 1860, p. 223.
Xylecoethus Gyllenhal, 1827, p. 234.

TYPE SPECIES: *Cantharis dermestoides* Linnaeus, 1761, p. 201.

DIAGNOSIS: Body elongate, nearly parallel sided, dorsoventrally flattened, lightly sclerotized (fig. 1); elytra long, surpassing metacoxae and costate (fig. 43); scutellum with double median carina (fig. 33); tibial spur formula 0-1-1/0-1-1 (male/female); eyes small, round, entire (figs. 2–5); head not narrowed behind eyes to form a neck (fig. 2); procoxae slotted at apex; hypomeron of prothorax not slotted; male genitalia with lateral lobes asymmetrically placed, articulated (figs. 57–59); metendosternite with large furcal arms, large laminal plates, and anterior tendons proximal (figs. 47–49); larva with pleurisetose tarsungulus (fig. 64) and abdominal segment IX very long, heavily sclerotized, and serrate (fig. 63).

DESCRIPTION: See Morphology section (above).

DISTRIBUTION: Species of temperate forests of North America (north of Mexico), Europe, U.S.S.R., China, and Japan.

FUNGUS HOST: *Ascoidea hylecoeti* (Ascomycetes), see Batra and Francke-Grosmann (1961).

ARBOREAL HOSTS AND BIONOMICS: Many hardwoods, and most softwoods, especially *Pinus* and *Liriodendron* (Batra, 1967; Batra and Francke-Grosmann, 1961; Collart, 1952; Dominik and Kinelski, 1976; Richter, 1933; Rummukainen, 1947, 1949; Schneider-Orelli, 1920; Simmonds, 1956; Strohmeyer, 1907; Thomsen, 1950; Vrydagh, 1952; see also Natural History, above).

SPECIES INCLUDED: There are five nominal species included in *Hylecoetus,* including one of incertae sedis (table 1).

DISCUSSION: Study of intraspecific variation within *Hylecoetus dermestoides* is badly needed (see Pfeil, 1859). This widely distributed species embraces so much variation that a number of species names have been proposed for it. *H. orientalis* (Foursow, 1935) and *H. formosanus* Miwa are probably synonyms of *dermestoides,* but the types were not seen. *H. flabellicornis* is recognized here, but there is some doubt about its validity as a distinct species. Females associated with *flabellicornis* males are indistinguishable from those of *H. dermestoides,* and males are sympatric, at least in part, with those of *dermestoides.* The development of the extraordinary flabellate antennae in *flabellicornis* is correlated with a poor development of the maxillary palporgan. The underlying developmental and genetic mechanisms associated with this antennal-palporgan relationship need to be investigated, and it seems likely that *flabellicornis* is in actuality a remarkable variation within *dermestoides.* The North American species, *lugubris,* differs relatively little from the Palearctic populations of *dermestoides,* even sharing the same ascomycete fungus host. Constant differences in color and

the median lobe, and allopatric distributions, however, support its recognition as a separate species. These three species may be separated with the following key:

1. Maxillary palporgan present (male) 2
   Maxillary palporgan absent (female) 4
2. Apex of median lobe bulbous (fig. 80); elytral color black, head and pronotum pale; antennae filiform, maxillary palporgan large (fig. 7); distributed in eastern North America ..
   .... *H. lugubris*
   Apex of median lobe narrow (fig. 81); antenna filiform, or antenna flabellate and maxillary palporgan small (frontispiece); color black, or testaceous and black; Eurasia 3
3. Antennae flabellate, maxillary palporgan small; color black .... *H. flabellicornis*
   Antennae filiform, maxillary palporgan well developed, large; color variable ....
   .... *H. dermestoides*
4. Color nearly uniformly testaceous (fig. 75), sometimes testaceous with black head and elytral apices (fig. 76); Eurasia ....
   ..... *H. dermestoides* and *H. flabellicornis*
   Color uniformly dark reddish-brown to black (fig. 79); North America ..... *H. lugubris*

Color variation within *dermestoides* is striking. Females have been seen from China and Japan with black head and elytral apices. This color morph was named *cossis* by Lewis (1896), and is here designated a junior synonym of *dermestoides*. Females with only the head dark and others with only the elytral apices dark also exist in Japan. The "typical" female color morph is nearly uniformly testaceous, with the elytral apices more or less darkened. The "typical" male color morph is testaceous with black head, scutellum, pronotum, and elytral apices (fig. 74), although entirely black males do occur (fig. 77), formerly named *morio* (Fabricius, 1787).

Two additional new synonymies are proposed for *dermestoides*. One is *Hylecoetus cribricolle* Fairmaire (1889), of which the type specimen is a large female with black elytral apices (seen, Museum National d'Histoire Naturelle, Paris). The other is *Hylecoetus matsushitai* Kono (1938). This species was based on a typically colored female specimen (pale, with darkened elytral apices), mistakenly identified as a male. Kurosawa (1985, p. 118) considered this species a synonym of *flabellicornis*. Insofar as *flabellicornis* itself is likely to eventually be synonymized with *der-*
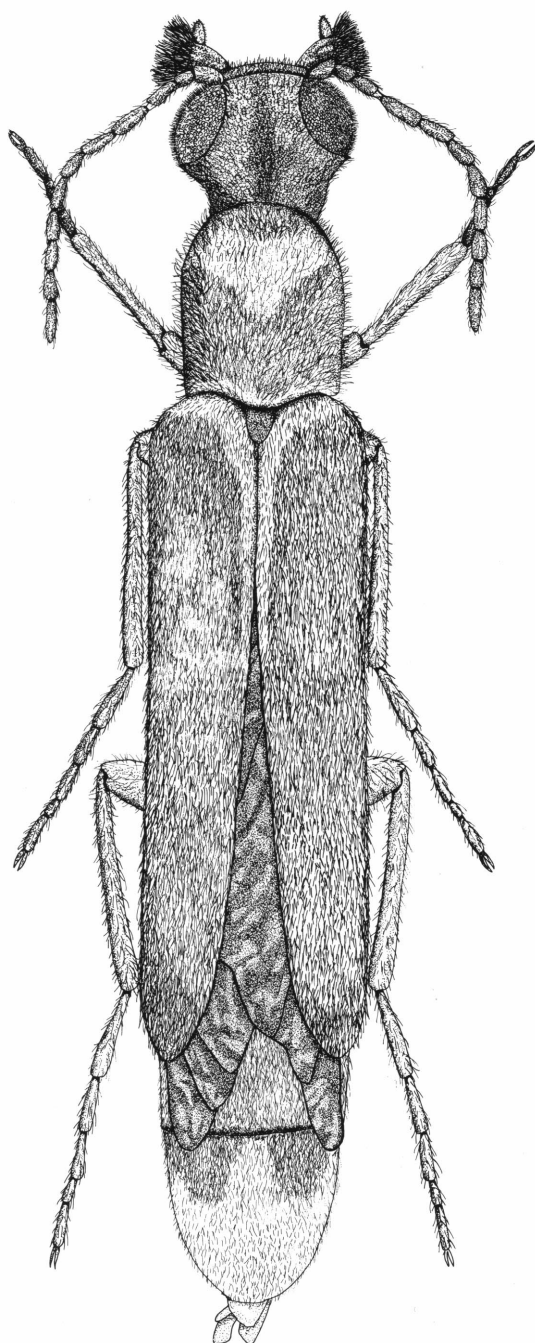

FIG. 82. *Lymexylon navale* (L.) male, by J. Nagy.

mestoides this is a defensible position. However, for the time being there is no reason to make such a synonymy since female *flabellicornis* are morphologically indistinguish-

able from those of *dermestoides*. Further, Kurosawa synonymizes a species omitted from my list, *Hylecoetus formosanus* Miwa with *flabellicornis*; his paper (Kurosawa, 1985, p. 118) can be consulted for details.

Synonymies are given below for *H. dermestoides* and *H. lugubris*:

Hylecoetus dermestoides (Linnaeus)

Cantharis dermestoides Linnaeus, 1761, p. 201 [type not examined; presumed lost].
Meloe marci Linnaeus, 1766, p. 681.
Lymexylon probiscideum Fabricius, 1781, p. 256 [lectotype male, here designated, no label, in Kiel collection, Copenhagen; 2 paralectotypes, one identified as *flabellicornis*].
Mordella barbatus Schaller, 1783, p. 322 [type, Zoologsiches Museum, Berlin; examined].
Lytta francofurthanus Herbst, 1784, p. 145 [2 syntypes, female, Zoologisches Museum, Berlin; examined].
Lymexylon morio Fabricius, 1787, p. 165.
Hylecoetus aestivalis Gistel, 1857, p. 14.
Hylecoetus nycturgus Gistel, 1857, p. 25.
Hylecoetus cossis Lewis, 1896, p. 65. NEW SYNONYMY [type, female, British Museum (Natural History); examined].
Hylecoetus julvipennis Reitter, 1911, p. 299.
Hylecoetus matsushitai Kono, 1938, p. 199. NEW SYNONYMY [type female, mistaken for male by Kono, Hakkaido University, Sapporo, Japan, examined, with following label: "Saghalien, H. Kono, Hagu, Shimizu"].
Hylecoetus cribricolle (Fairmaire), 1889, p. 45. NEW SYNONYMY [type female, Museum National d'Histoire Naturelle, Paris, examined, with following labels: "Hylecoetus cribricollis Fairm."/"Melittomma cribricollis Fairm."/ "TYPE"/"Museum Paris, Mou-Pin, A. David 1870"].

Hylecoetus lugubris Say

Hylecoetus lugubris Say, 1835, p. 166 [type not examined, presumed lost].
Hylecoetus americanus Harris, 1841, p. 52; Leng, 1920, p. 152.

Hylecoetus flabellicornis (Schneider)

Lymexylon flabellicornis Schneider, 1791, p. 109 [lectotype, male, here designated, no label data, with my label, Zoologische Museum, Berlin; also six paralectotypes].

SUBFAMILY LYMEXYLINAE, SENSU NOVO

Lymexylinae Boving and Craighead, 1931, p. 68.

TYPE GENUS: *Lymexylon* Fabricius.
DIAGNOSIS: Maxillary palporgan with tertiary branches: pronotum without sharp, lateral margins; tongue-and-groove elytral locking mechanism absent; crossvein 1a-2a of hindwing incomplete; larval abdominal segment IX large, bulbous, with asperites (see also key), rarely smaller with paired hooks.
CLADISTIC RELATIONS: Lymexylinae is sister group of the subfamily Melittomminae. See Cladistic Analysis (below).
GENERA INCLUDED: *Lymexylon* Fabricius and *Atractocerus* Palisot de Beauvois.

Genus Lymexylon Fabricius
Figures 82–122

Lymexylon Fabricius, 1775, pp. 3, 204.
Calolymus Thunberg, 1791, p. 26.
Cantharis (in part) Linnaeus, 1758, p. 403.
Pterophorus Herbst, 1784, p. 47.

TYPE SPECIES: *Lymexylon navale* Linnaeus, 1758, p. 403.
DIAGNOSIS: Body elongate, narrow, parallel sided and dorsoventrally flattened (fig. 82); head abruptly narrowed behind eyes forming neck (figs. 83, 84); eyes large, emarginate anteriorly (fig. 84); metendosternite with anterior tendons arising near middle of lamina, but distinctly separate (figs. 92–94); male with large maxillary palporgan, with tertiary branching pattern and long, dense sensilla on inner surface of each branch (figs. 88, 90); median lobe of aedeagus elongate, curved, narrowed at apex, about as long as distance from base of tegminal struts to apex of lateral lobes (figs. 107, 108); lateral lobes short, wide, separated by distinct gap (fig. 111); hindwing with nearly complete venation (fig. 99); elytron shortened, exposing one or two tergites and sometimes part of third; hypomeron of elytron short, narrow, terminating at about metacoxa; apical portion of elytron narrowed, lying over abdomen (fig. 82); larva with abdominal segment IX large, membranous, posteriorly directed (figs. 119, 120), trochanter of each leg enlarged, lobate (fig. 121), tarsungulus bisetose (fig. 122).
DESCRIPTION, *LYMEXYLON NAVALE* (L.): Body elongate, parallel sided, dorsoventrally

compressed (fig. 82). Pronotum narrower at base than combined width of elytral bases (figs. 82, 109, 110). Length about 4.8–16.5 mm, males usually not exceeding about 13 mm. Color sexually dimorphic. Males with head black, pronotum dark reddish-brown to nearly black with more or less defined V-shaped lighter reddish transverse band in front of middle; elytron testaceous at base including humeral angles, pale area narrowing apically along suture, extending $7/10$ length of elytron; humeral angles, lateral aspects, and apex of elytron dark reddish-brown to nearly black; abdominal terga dark reddish-brown, except tergum VII, testaceous; antenna, palpus, mandible dark, other mouthparts and legs yellowish; thoracic sterna dark, abdominal sterna pale. Female with antenna less dark and all mouthparts, except apex of mandible, pale. Pronotum paler, lacking V-shaped mark. Elytron predominantly yellowish, dark color confined to lateral area beginning behind humeral angle, widening until entire apical area is dark; dark color ventrally confined to metasternum, metepisternum, and metepimeron.

Body lightly sclerotized. Elytron sometimes with irregular bumps. Head with heavier sclerotization than body; with dense, deep, coarse punctures, sometimes confluent on neck region producing rugose pattern. Pronotum with dense, small, shallow punctation. Elytral punctation similar to that of pronotum, less defined. Punctation of abdominal sterna dense, shallow, poorly defined. Integument with dense, fine, short setae.

Head small relative to body (fig. 82); broad in form (figs. 83, 84), widest at eyes; narrowed behind eyes, forming neck; with prominent supraantennal ridge. Frontoclypeal suture absent, but transverse impression present. Gula incomplete; gular sutures short, subparallel, slightly convergent anteriorly. Integument near eyes ventrally wrinkled in appearance. Eyes large, prominent, widely separated dorsally and ventrally (figs. 83, 84); facets fine, with long, erect setae between. Labrum small, transverse; dorsal surface with long setae; epipharynx with irregularly distributed microtrichiae. Mandible short, broad; prostheca with dense setae near middle of mesal margin (fig. 89); outer margin with sparse, long setae; basal transverse rows

of microtrichiae may be remnants of mola. Maxillae sexually dimorphic. *Female* of generalized form; lacinia long, narrow, with long setae and basal microtrichiae; galea short, broad, rounded apically, divided by membranous area into basigalea and distigalea; stipes with microtrichiae, cardo elongate; palpifer large. Palpus 4-segmented: I short, little longer than wide; II much longer, clavate; III short, transverse; IV broad, expanded apically, with dense, long, blunt sensilla. *Male* with galea and lacinia distinct, but small. Palpomere I short; II abruptly larger, apically widened; III small, ringlike; IV short, with dense area of sensilla; maxillary palporgan arising near apex of palpomere III, with primary-secondary branching pattern, and few tertiary branches (fig. 90); surfaces of branches with short, bristlelike setae externally and long, dense, setae internally (fig. 88). Labium small, lightly sclerotized. Palpigers separate, palpus with 3 segments: I very short; II elongate, parallel sided, with several setae; III elongate, with long apical sensilla; ligula membranous, with sparse microtrichiae, bordered by sparse, long setae. Antenna (fig. 97) similar in males and females, inserted anterior and ventral to eyes under small, prominent frontal ridge; long, narrow, filiform; I elongate, constricted basally; II short, broad; III–X elongate, slightly apically expanded; XI wider basally, narrowed in apical half.

Pronotum broad; male width about 0.8 length at midline; anterior margin broadly rounded; posterior margin sinuate, posterior angles produced. Male pronotum shorter than female pronotum (figs. 109, 110). Prosternum simple, quadrate, less than 0.5 length of pronotum. Prothorax without distinct lateral margin; without coxal slot; intercoxal process absent. Mesosternum small, subtriangular; mesepisternum nearly equal in size to mesosternum, simple; mesepimeron rectangular, smaller than mesepisternum, digitiform. Metasternum elongate, nearly quadrangular with anterior depressions receiving mesocoxae; metepisternum narrowed posteriorly, separated from metepimeron by very deep suture. Procoxae elongate, cylindrical, not slotted. Tibial spur formula 2-2-2 in both sexes. Hind coxae oblique, with deep transverse femoral grooves.

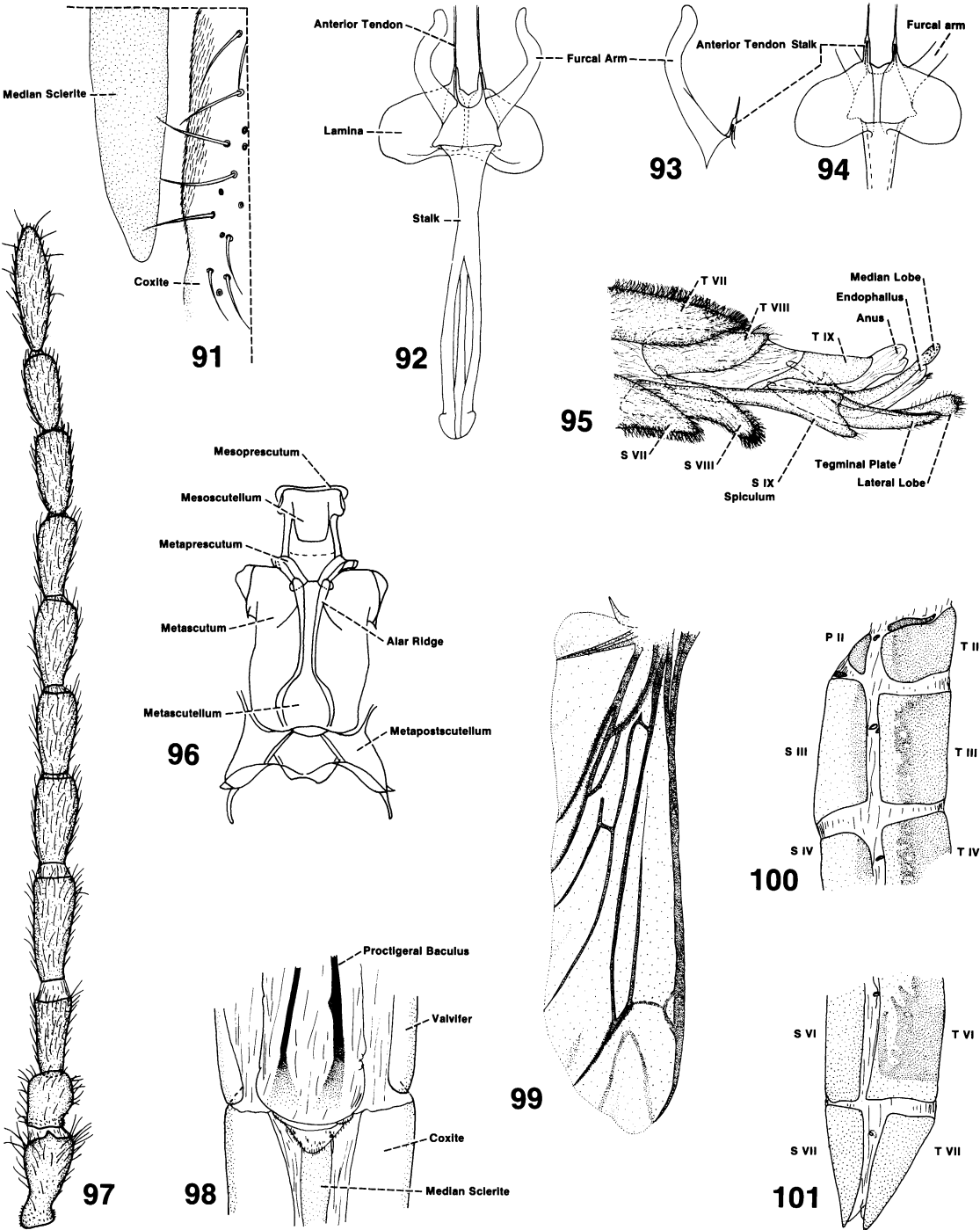Metendosternite (figs. 92–94) with lateral
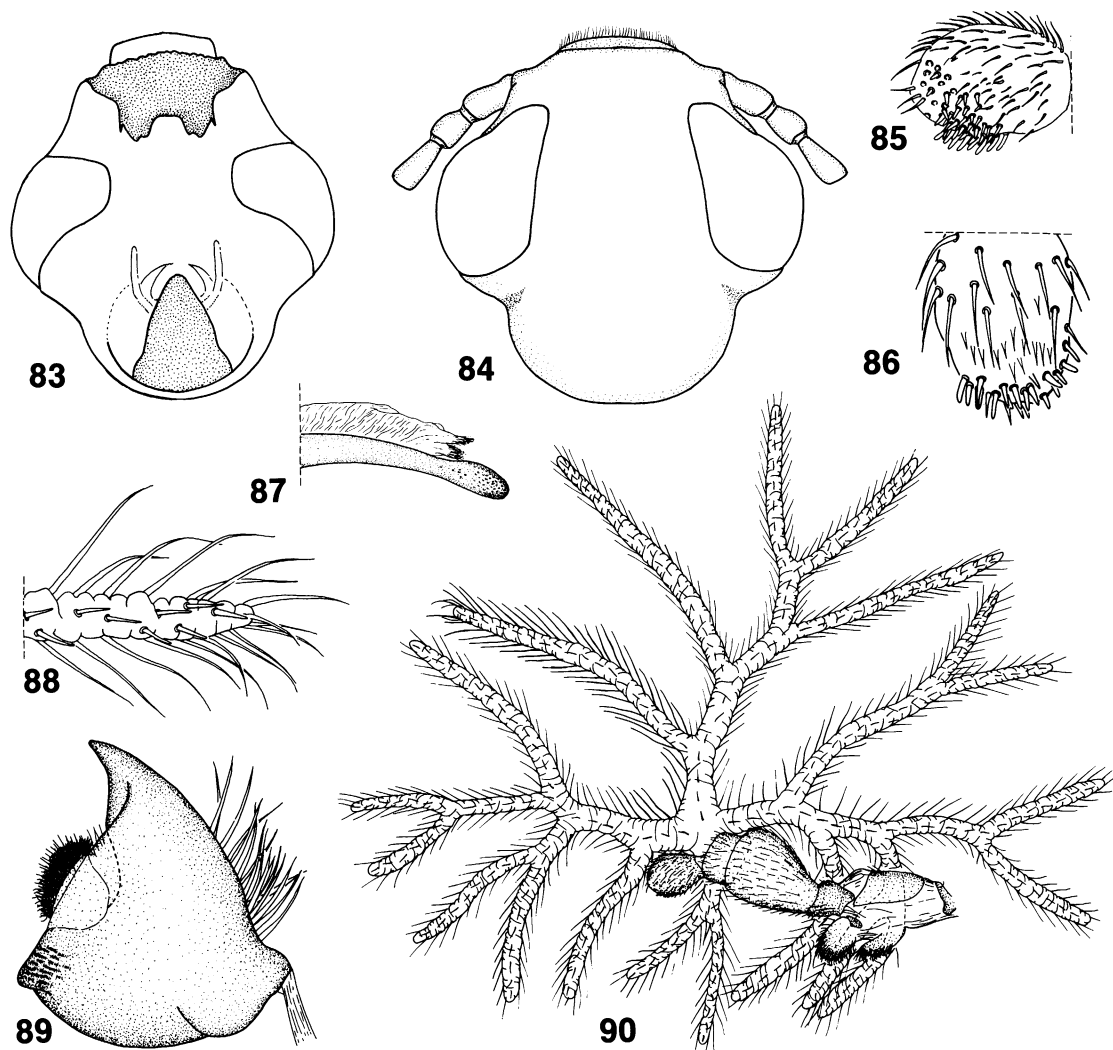
FIGS. 83–90. *Lymexylon navale.* **83.** Head, ventral. **84.** Head, dorsal. **85.** Labial palpus, male apex. **86.** Maxillary palpomere IV, male. **87.** Aedeagus, apex median lobe. **88.** Maxillary palporgan, apex of secondary branch. **89.** Mandible, right dorsal. **90.** Maxilla, male.

parts of furcal stalk fused dorsally in distal half; heavily sclerotized portion of stalk truncate, widening into lightly sclerotized plate with small, triangular protruding basal angles giving rise to furcal arms. Arms long, curved. Anterior tendons more widely separated than in *Hylecoetus,* arising from anterior tendon stalks of lamina. Furcal stalk without a lateral process.

Scutellum simple, apically rounded lobe; unexposed portion with small, pointed pos-

terior corners. Punctures and setae as on elytron.

Elytron long, narrow. Tongue-and-groove locking mechanism absent. Epipleural fold received in concave space between metepisternum and metepimeron; widest basally, gradually narrowed posteriorly, ending at about metacoxae with apices of elytra lying over abdomen and not touching mesally. Shortened, exposing 1.5 to 3 tergites in males, 0.5 to 2.5 tergites in females.

FIGS. 91–101. *Lymexylon navale.* **91.** Female genitalia, dorsal details. **92–94.** Metendosternite. **92.** Dorsal. **93.** Furcal arm base. **94.** Laminal region, ventral. **95.** Male abdomen, lateral apex. **96.** Notum of pterothorax. **97.** Antenna, male. **98.** Female genitalia, dorsal apex. **99.** Hindwing. **100.** Abdomen, basal segments, lateral. **101.** Abdomen, apical segments, lateral.
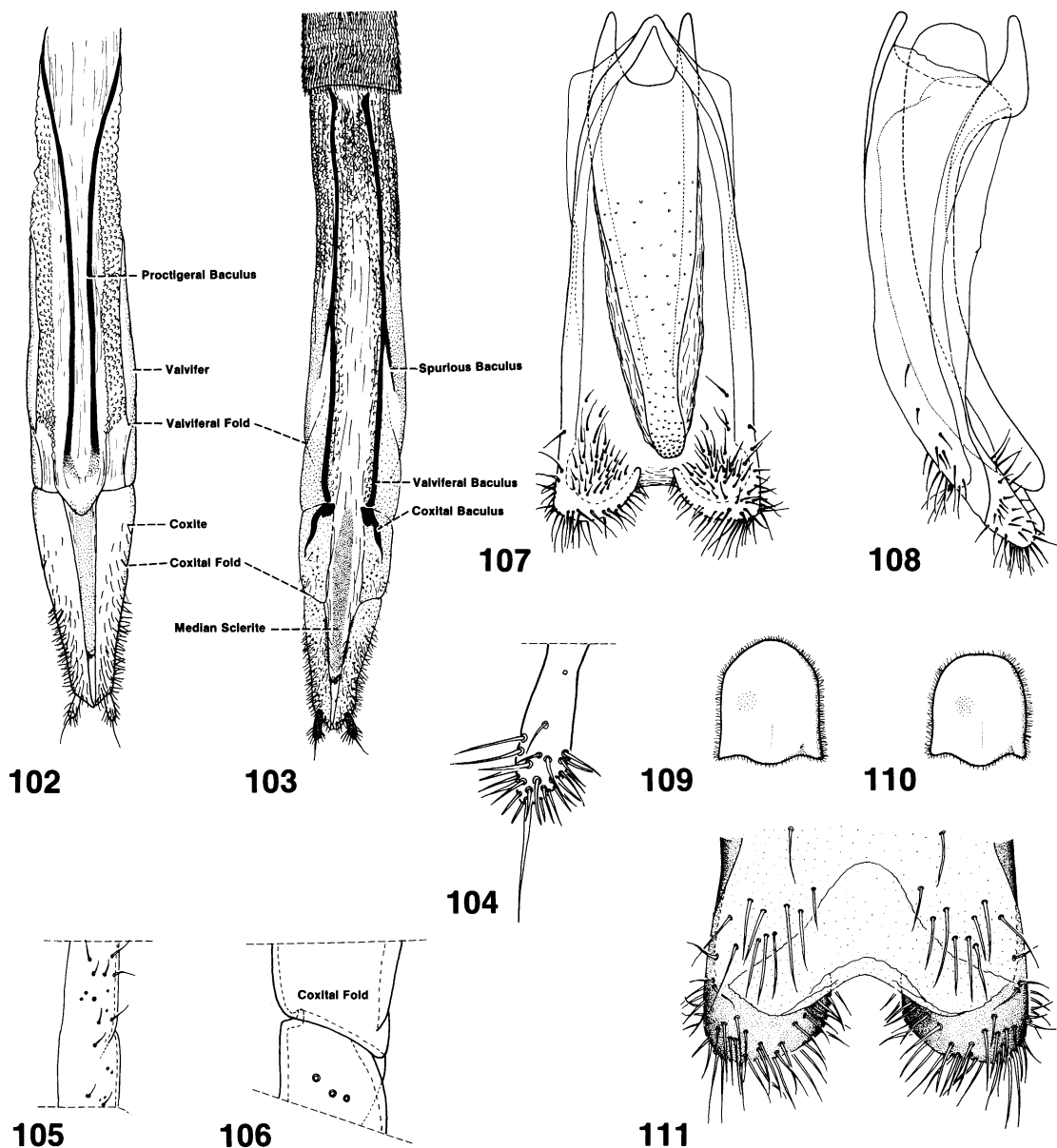
FIGS. 102–111. *Lymexylon navale.* 102–106. Female genitalia. **102.** Dorsal. **103.** Ventral. **104.** Stylus. **105.** Coxital fold, dorsal. **106.** Coxital fold, ventral. **107.** Aedeagus, dorsal. **108.** Aedeagus, lateral. **109.** Pronotum, female. **110.** Pronotum, male. **111.** Aedeagus, lateral lobes, ventral.

Hindwing venation (fig. 99) relatively complete; 1a-2a crossvein incomplete between 1A2 and Wedge cell; venation sexually dimorphic, male with extra 1a1-1a2 crossvein, forming minute cell distad of Wedge cell; brachial cell poorly defined; M spurious.

Abdomen elongate, dorsoventrally compressed (figs. 100, 101) with sterna wider than terga, pleurally curved, resembling paratergites in dorsal view; spiracles in membrane separating terga and sterna; Males and females with sterna III–VII visible; terga II–VII well developed. Evident remnants of sternum II and tergum I visible, and pleural elements of II in membrane.

Male postabdomen (fig. 95) with abdom-
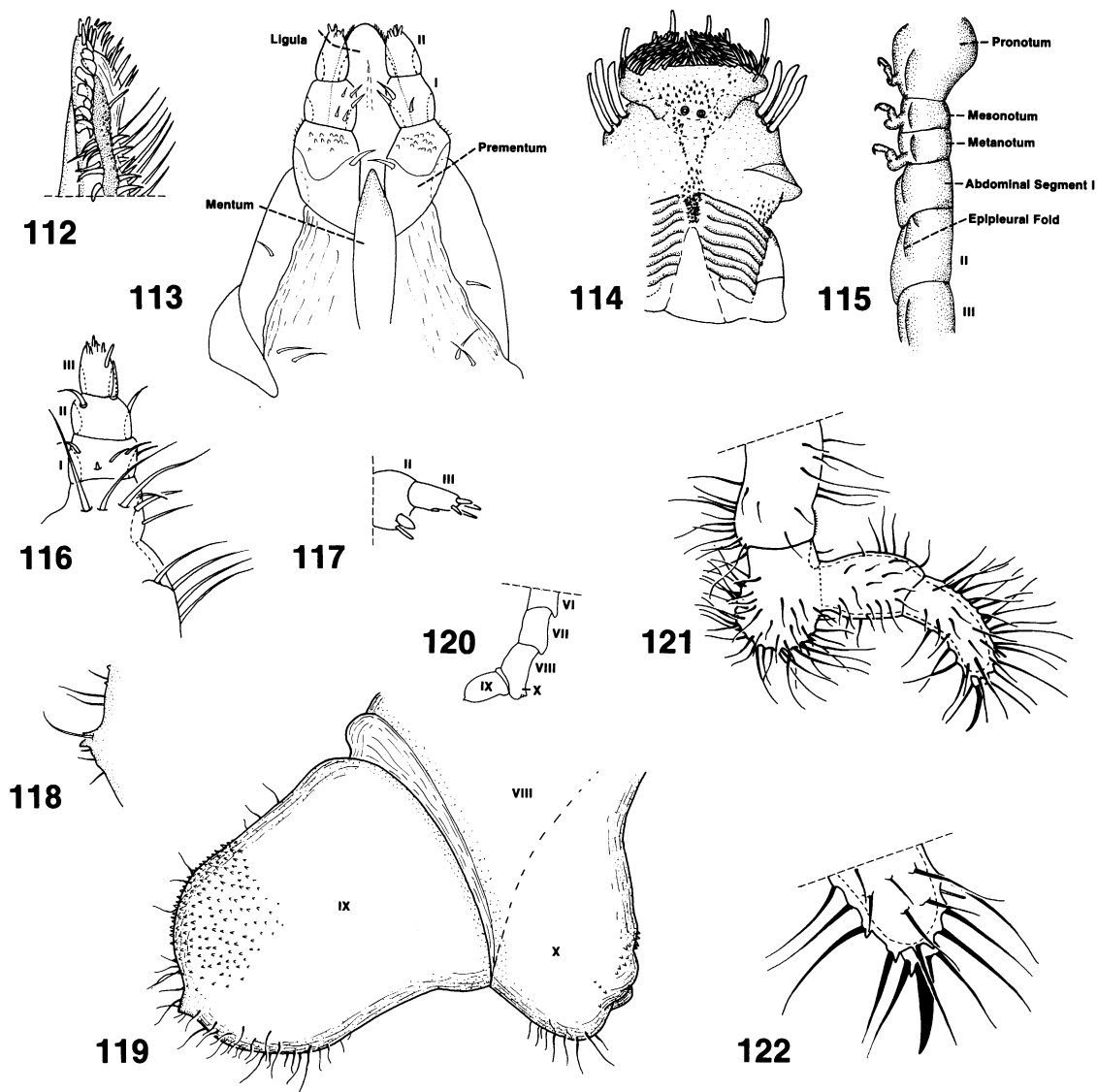
FIGS. 112–122. *Lymexylon navale,* larva. **112.** Mala, apex, mesal surface. **113.** Labium, ventral. **114.** Labrum, ventral. **115.** Thorax and base of abdomen, lateral. **116.** Maxillary palpus. **117.** Antenna. **118.** Abdominal segment IX, apex. **119.** Abdominal apex (segments VIII–X). **120.** Abdominal apex (semi-diagrammatic of segments VII–X and portion of VI). **121.** Mesothoracic leg. **122.** Tarsungulus and apex mesotibia.

inal segment VIII simple; tergum and sternum small; telescoped into segment VII. Segment IX forms small genital capsule; dorsal plate and ventral plate with pair of struts, fused apically. Male genitalia (figs. 107, 108, 111) with median lobe broad at base, gradually narrowed; length about equal to tegminal struts and lateral lobes combined; heavily sclerotized dorsally, lightly sclero-

tized ventrally. Tegminal plate large, semi-membranous. Tegminal struts wide, partially indistinguishably fused to tegminal plate. Lateral lobes short, broad, truncate, with many long setae; widely separated medially. Tegminal struts fused on ventral side of median lobe near base.

Female abdomen with segment VIII simple, partially membranous, with long spicu-

TABLE 2
Nominal Species of Genus *Lymexylon* Fabricius

Species	Reference	Distribution
L. navale (Linnaeus)	Linnaeus, 1758, p. 403 (Cantharis)	Europe, Asia
L. ruficolle Kurosawa	Kurosawa, 1949, p. 27	Japan
L. amianum Kurosawa	Kurosawa, 1985, p. 116	Japan, Formosa
L. persicus Foursow	Foursow, 1935, p. 92	USSR: Caucasus

lum gastrale ventrally. Female genitalia (figs. 102–106) with distal part of coxites longer than basal part; coxital fold strongly impressed ventrally, slightly visible dorsally (figs. 105, 106); apical area on distal part with dense minute setae, remaining coxital surfaces with sparse setae. Styli short, clavate, with many setae, including single long apical seta (fig. 104); valviferal baculus with short spurious baculus arising from sclerite about 0.5 distance from base of valviferal baculus to apex (fig. 103). Proctigeral baculi and valviferal baculi separate entire lengths. Median sclerite broad, elongate (fig. 103).

Larva (figs. 112–122) elongate, narrow in form. Color creamy yellowish to light brown. Head broad (length/width about 0.75), ovate. Labrum simple, lobate; epipharynx with microtrichiae, few sensilla except dense patch near apex (fig. 114). Mandible short, stout with single apical dens, fine parallel ridges on mola, no prostheca. Maxillary mala with mesal membranous area bordered by setae, some taeniaform (fig. 112); palpus with palpomeres short (fig. 116). Labium with lobate ligula and simple palps; prementum poorly defined, mentum narrow (fig. 113). Pronotum large, hoodlike (fig. 115). Legs small, with trochanter enlarged (fig. 121), tarsungulus bisetose (fig. 122). Abdominal segment IX large, membranous, bustlelike (figs. 119, 120), with pointed apical process (fig. 118). Thoracic terga and apex of IX tuberculate. Large, conspicuous epipleural fold on each abdominal segment, and each segment ventrally overlapping segment posterior to it. Antenna very small, 3-segmented, I short, transverse, II stout, little longer than wide, with large pointed sensillum, few setae, III elongate, narrow single large seta, a few smaller setae, and two long, blunt sensilla (fig. 117).

DISTRIBUTION: *Lymexylon* is Palearctic in distribution, occurring widely in Europe and Asia.

FUNGUS HOSTS: Unknown.

ARBOREAL HOSTS AND BIONOMICS: Hardwoods, including oak and chestnut (Donisthorpe, 1939; Simmonds, 1956).

SPECIES INCLUDED: Four nominal species are included in *Lymexylon,* but from published descriptions it seems probable that some or all of them are synonymous with *L. navale.* Type specimens were not examined for *ruficole, amianum,* or *persicus.* See table 2.

CLADISTIC RELATIONS: Sister group of *Atractocerus.*

DISCUSSION: *Lymexylon* includes the true "ship-timber beetle," *L. navale,* a common name sometimes given to the family as a whole (e.g., Arnett, 1971). This species was formerly a serious pest of timber and wooden ocean vessels, but is today of no serious economic concern. There are three other nominal species, all of which are probable synonyms of *navale* (table 2). Two of these were described from Japan (Kurosawa, 1949, 1985) and one from the U.S.S.R. (Foursow, 1935). Larvae were discussed by Dominik (1957).

Genus *Atractocerus* Palisot de Beauvois
Figures 123–187

Atractocerus Palisot de Beauvois, 1801, p. 6.
Atractourus Palisot de Beauvois, 1801, text (*lapsus calami*).
Necydalis (part) Linnaeus, 1766, p. 643.
Fusicornis Philippi, 1866, p. 115.
Raractocetus Kurosawa, 1985, p. 111. NEW SYNONYMY.
Hymaloxylon Kurosawa, 1985, p. 112. NEW SYNONYMY.
Arractocetus Kurosawa, 1985, p. 112. NEW SYNONYMY.

TYPE SPECIES: *Necydalis brevicornis* Linnaeus, 1766, p. 643.

DIAGNOSIS: Body very long, narrow (fig. 123); eyes large, emarginate; head narrowed behind eyes, forming neck; elytron very short, exposing most abdominal terga; hindwing venation reduced, hindwing folding longitudinally only in fanlike fashion (fig. 127); pronotum without lateral margin; antenna short, compact, usually narrowed apically and spindlelike (fig. 145); maxillary palporgan present in males and females, but much larger in male; procoxa not slotted; prohypomeron not slotted; scutellum with lateral grooves, receiving bases of elytra; tibial spur formula reduced (0-0-0 male/0-0-0 or 0-1-1 female); lateral lobes of male genitalia very large relative to median lobe; metendosternite simple; female genitalia heavily sclerotized in part and leathery; larva with abdominal segment IX large, membranous, bulbous with apical asperites or rarely smaller with paired sclerotized hooks; tarsungulus pleurisetose.

DESCRIPTION, *ATRACTOCERUS BREVICORNIS* (L.): Body very long, narrow, nearly parallel-sided in form (fig. 123); length variable, from about 15.0–60.0 mm. Color varies from pale yellowish to very dark reddish-brown; all individuals with pale yellowish stripe extending along midline of vertex of head, pronotum, and scutellum (fig. 123). Entire body leathery in texture, moderately sclerotized. Most surfaces covered by small, poorly defined, setose punctures; setae short, fine, suberect. Dorsal surface of head, between and posterior to eyes, covered by transverse "wrinkles."

Head broadly oval, strongly flattened dorsoventrally (figs. 124, 125). Eyes large, ovate, conspicuous, occupying much of both dorsal and ventral surfaces of head; at widest point ratio of eye width/head width about 0.62; facets of eyes moderate-sized, hexagonal, appearing fine under low to moderate magnifications. Gular sutures short, nearly parallel (slightly convergent anteriorly). Antenna inserted under lateral, broad, conspicuous supra-antennal ridge; antenna little longer than head. Frontoclypeal suture absent; labrum fused to head. Epipharynx small, simple, reduced, consisting of row of small setae along midline of ventral surface of labrum. Posterior foramen large. Vertex widest between eyes
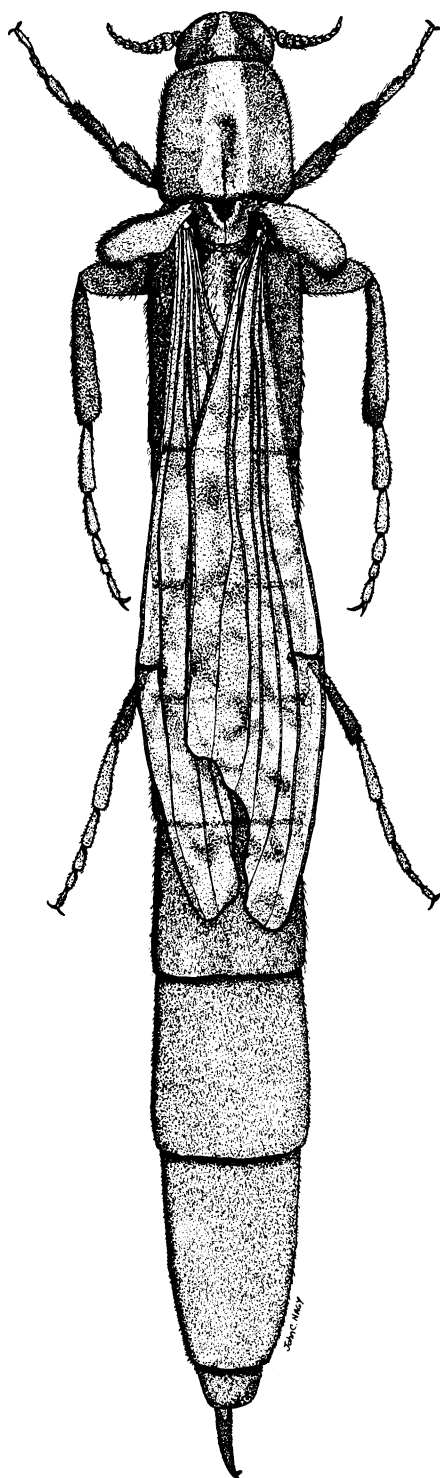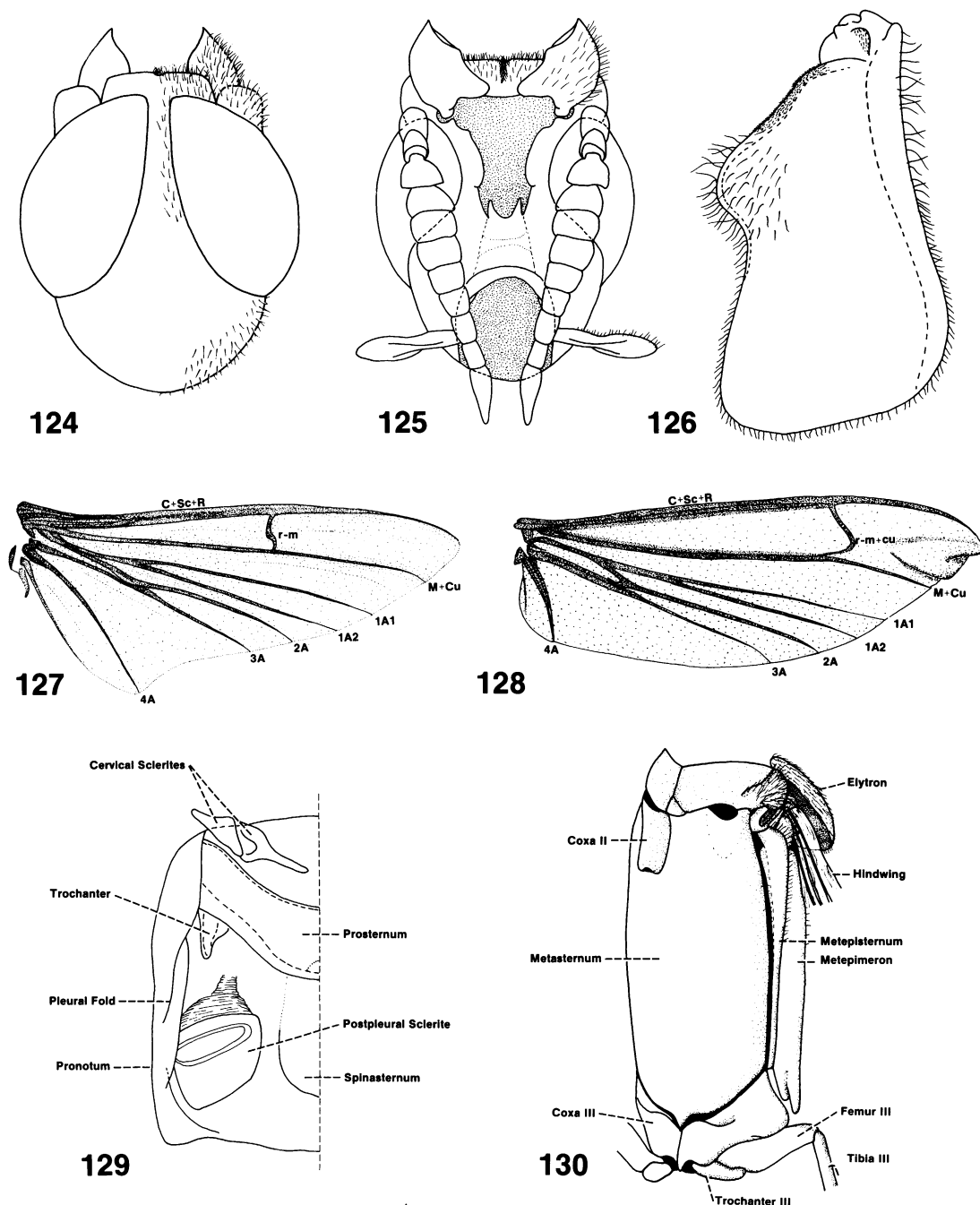

FIG. 123. *Atractocerus brevicornis* (L.), female, by J. Nagy.

FIGS. 124–130.   *Atractocerus* spp. **124.** *A. brevicornis,* female head (dorsal). **125.** *A. brevicornis,* female head (ventral). **126.** *A. brevicornis,* right elytron (dorsal). **127.** *A. brasiliensis,* hindwing. **128.** *A. procerus,* hindwing. **129.** *A. brevicornis,* right half prothorax, ventral. **130.** *A. brevicornis,* pterothorax, ventrolateral.

posteriorly, narrowed anteriorly. Mandibles small, broad; apex bidentate; no evidence of mola or prostheca; much of surface with long, dense setae. Antenna similar in both sexes (fig. 145), short, spindle-shaped; antenno-mere I elongate, clavate; II much shorter,
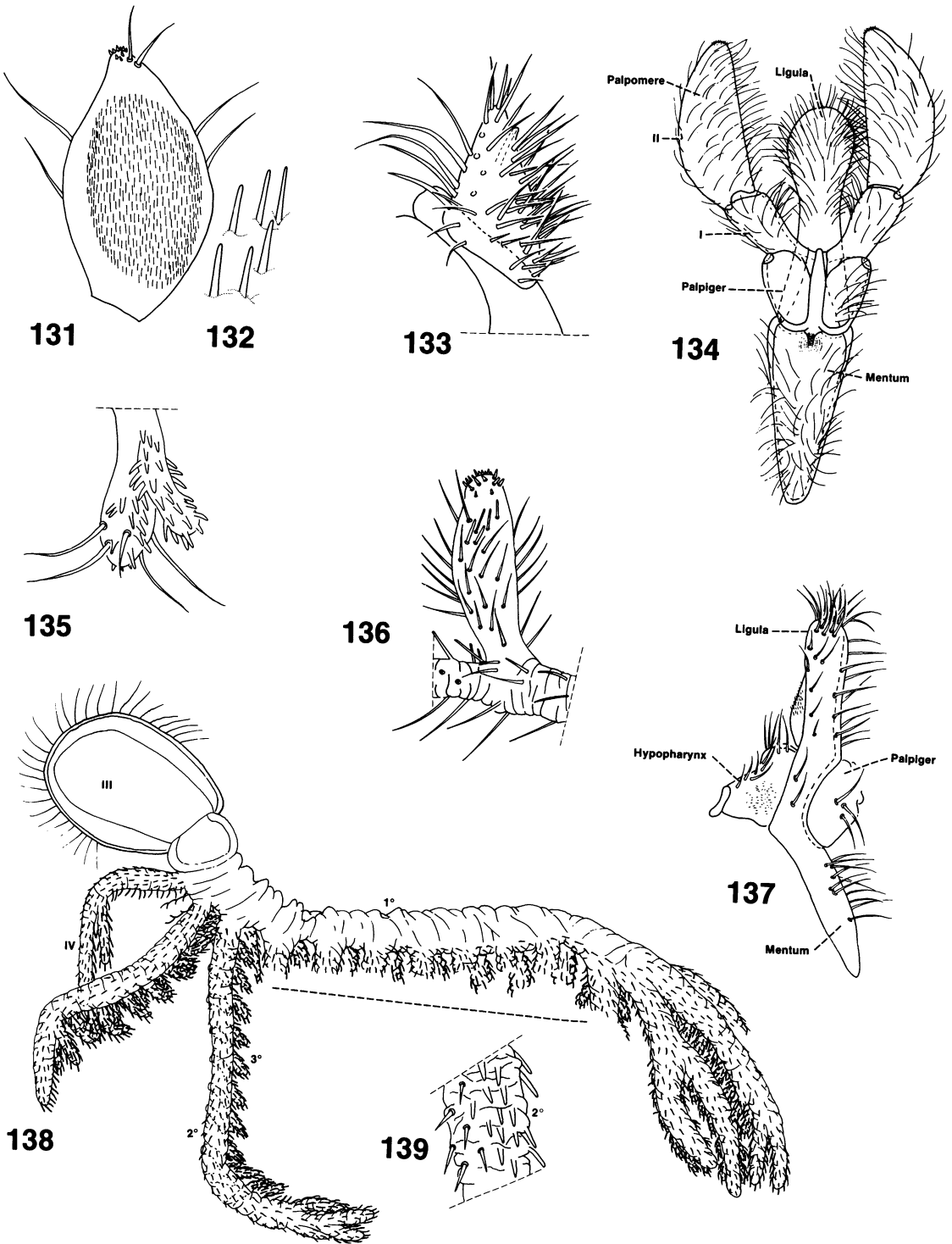
FIGS. 131–139. *Atractocerus* spp. **131.** *A. brevicornis,* apical segment of labial palpus, female. **132.** *A. brevicornis,* recumbent sensilla on surface labial palpomere III, female. **133.** *A. brevicornis* mala, female. **134.** *A. brevicornis* female labium, ventral. **135.** *A. brevicornis,* apex maxillary palpomere IV, male. **136.** *A. procerus,* maxillary palpomere IV, female. **137.** *A. brevicornis* labium, female, lateral. **138.** *A. brevicornis,* maxillary palporgan and palpomeres III and IV, male. **139.** *A. brevicornis,* secondary maxillary palporgan branch, surface detail.
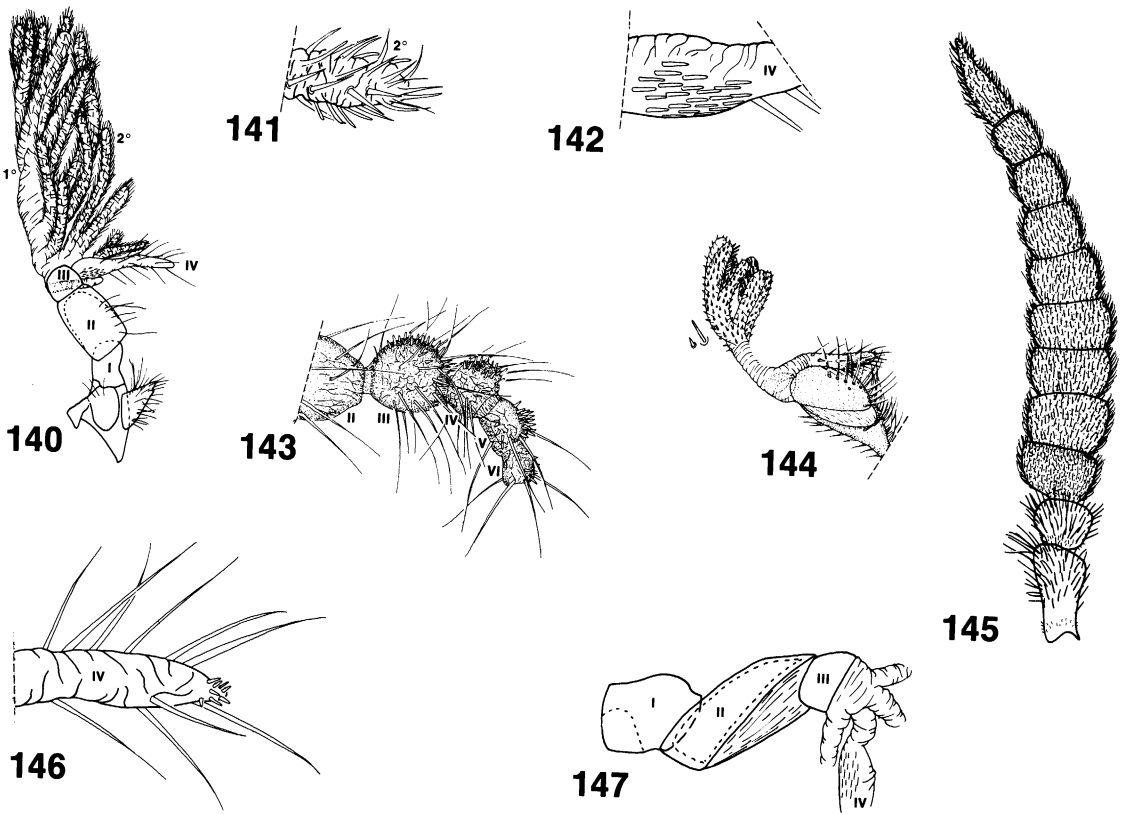
FIGS. 140–147. *Atractocerus* spp. 140–142. *A. brevicornis* female. 140. Maxilla. 141. Secondary branch of palporgan, apex. 142. Maxillary palpomere IV, base. 143, 144. *A. tasmaniensis* male. 143. Antennal segments II–VI. 144. Maxillary palporgan and palpomeres II, III, and IV. 145–147. *A. brevicornis* female. 145. Antenna. 146. Maxillary palpomere IV, apex. 147. Palporgan base in relation to palpomeres.

wider than long; III–VIII broader than long (V–VI widest), IX about as long as wide; X slightly shorter than IX, XI elongate, apically pointed; surface of I–II finely reticulate, with sparse, short setae near base and dense, long, fine setae over much of surface; III–XI covered by dense setae, shorter than setae of I–II; entire surface with dense, minute, peglike sensilla (cf. fig. 172). Maxilla sexually dimorphic, with palporgan present in both male and female; female maxilla (figs. 140–142, 146, 147) with mala undivided, pointed apically with single lateral tooth and dense setal cover; palpifer small, ovate; palpus with four palpomeres: I short, II short, very broad, and strongly oblique with membranous apex (fig. 147), III short, ringlike, giving rise to IV and palporgan; membrane connecting III to both IV and palporgan with wrinkled texture, setae, and sensilla as on palporgan; IV appears

to be part of palporgan, recognizable only by setae and sensilla typical of palpomere (figs. 142, 146); palporgan with primary and secondary branches; male maxilla (figs. 135, 138, 139) as female, except much larger and with primary-tertiary branching pattern (fig. 138); palpomere IV further removed from III by membrane that is itself branched; primary branches with few setae, secondary with tactile outer setae and long, blunt sensilla on inner surfaces, tertiary digitiform, organized in two parallel rows and covered entirely by blunt sensilla. Labium (figs. 134, 137) reduced; mentum elongate, narrowed; palpigers are pair of large plates; palpi with two palpomeres: I elongate, subparallel, II robust, much larger; ligula very large, leathery, about as long as mentum, narrow, expanded apically; hypopharynx small, membranous, with dense microtrichiae, sparse long setae; outer

surface of II with large patch recumbent sensilla.

Pronotum short, subquadrate; anterior margin broadly rounded; without sharp lateral margins; broader in female. Prosternum (fig. 129) very short, broad. Prothoracic spiracle on large postpleural sclerite. Spinasternum small, distinct. Coxal cavities broadly open behind, procoxae cylindrical, not apically slotted. Hypomeron not slotted. Mesocoxae large, cylindrical, posteriorly directly; mesosternum small, subtriangular; mesepisterna large, contiguous medially, broadest near midline of body, narrowed laterally, not anteriorly elevated; mesepimeron narrow, obliquely positioned, enlarged near base of elytron, not grooved to receive elytron (fig. 130). Metasternum very long, narrow, with shallow anterior depressions receiving mesocoxae; metepisternum and metepimeron long, narrow, broadest anteriorly and narrowed posteriorly. Elytron (fig. 126) very short; mesal margin with broad lobe near base. Hindwing lacking transverse folds (figs. 127, 128). Tibial spur formula 0-0-0 (male), 0-0-0 or 0-1-1 (female). Metendosternite simple (figs. 164, 167); furcal arms not widely divergent, long, narrow; laminae fused ventrally, forming long thin flange; ventral flange of furcal stalk very short, basad to modified laminae; anterior tendonal attachment sites not observed. Mesoscutellum broad, carinate; grooved to receive elytra (fig. 163).

Abdominal segments II–VII visible in both sexes, VIII small, telescoped inside VII. Abdomen long, somewhat flattened dorsoventrally; tergites and sternites subquadrate; minute, transverse carina near posterior angle of each sternite; lateral fold on each tergite forming nearly vertical, narrow margin; spiracles large, oval, located on pleural folds that are lightly sclerotized and setose except small perispiracular glabrous area. Female with segment VIII simple, bearing long spiculum (fig. 165).

Male segment VIII simple, apex of sternite narrowed (fig. 168); IX with nearly complete tergite, paired, lateral, anteriorly directed struts fused apically with paired ventral struts; sternite IX narrowed apically, divided into pair of long struts, fused anteriorly with dorsal struts (fig. 166).

Male genitalia small, compact, broad (fig. 151); median lobe small, broad at base, and gradually narrowed apically; tegminal plate large, apically bilobed, extending from base of median lobe to apex of medial process of lateral lobes; lateral lobes very large, complex, with truncate and deeply emarginate median process, two pairs of lateral denticuli, and large, paired cuplike lateral processes; tegminal struts short, broad, fused ventrobasally.

Female genitalia (figs. 158, 161) long, narrow; in part membranous, in part heavily sclerotized. Valviferal baculus long, subparallel, narrow, heavily sclerotized; laterally expanded, fused with basal sclerotization of valvifer, distally reaching coxital baculi. Coxital baculi paired, each elongate, lying along longitudinal axis of basal part of coxite, bent sharply near apex and for short distance oriented transversely toward midline. Median baculi paired; each delicate, located mesad to valviferal baculus, extending to about half length of coxital baculus, narrow, over convoluted and membranous internal area. Valvifers indistinguishably sclerotized; pair of distinct, long plates, fused for short distance with valviferal baculi and second, more distal and shorter pair of plates basad of junction with coxites. Coxites elongate, narrowed apically; divided into short basal part and longer distal part; distal part covered by dense, long setae; basal part with sparse, shorter setae; parts separated by ventral coxital fold. Median sclerite distinct on ventral surface, extending from about midpoint of distal part of coxite to point slightly beyond apex of coxital baculi. Styli very long, thin, tubular, heavily sclerotized; with sparse setae near apex, apex with fold in membranous area. Proctigeral baculi paired, separate, long; divergent anteriorly and posteriorly; thickened basally, very narrow apically.

Larva (figs. 175–187) body form elongate, slightly dorsoventrally compressed with distinct lateral folds on each segment of thorax and abdomen. Pronotum very large, hoodlike (fig. 177). Posterior end of abdomen in form of large, membranous lobe (fig. 178) with dense asperites on surface. Color entirely creamy white-yellow (in preserved specimens). Head (fig. 186) oval, heavily sclerotized; epicranial suture short, straight; with small, dark W-shaped area on frons; stem-
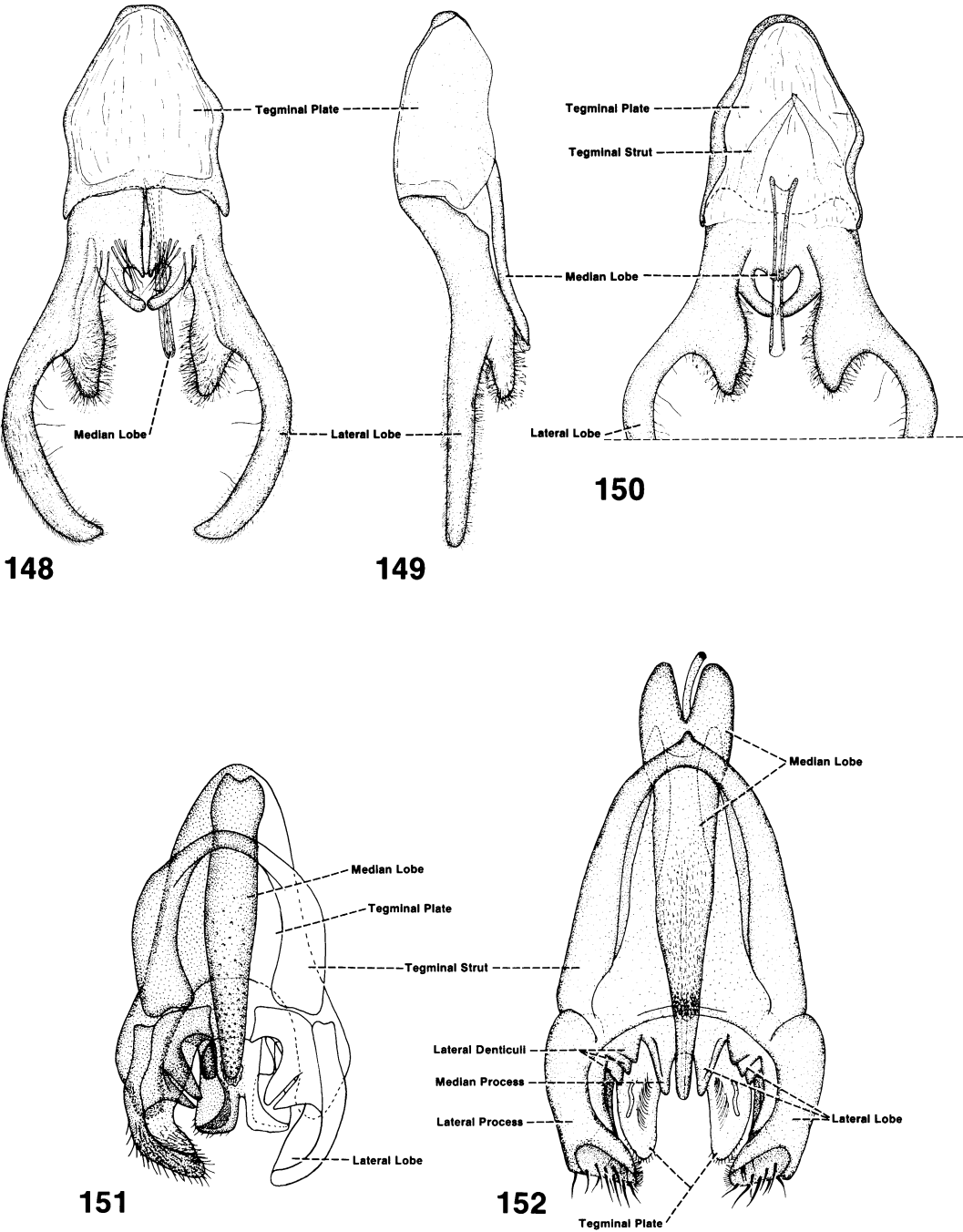
FIGS. 148–152. *Atractocerus* spp. aedeagi. 148–150. *A. procerus.* **148.** Dorsal. **149.** Lateral. **150.** Ventral. **151.** *A. brevicornis,* ventral. **152.** *Atractocerus emarginatus,* ventral.

mata absent; large H-shaped, yellow pattern extending from posterior margin to points above mandibular bases. Labrum small, with

dense, large setae at margin; epipharyngeal region (fig. 182) with small area of fine, long setae and a few short sensilla apicoventrally;
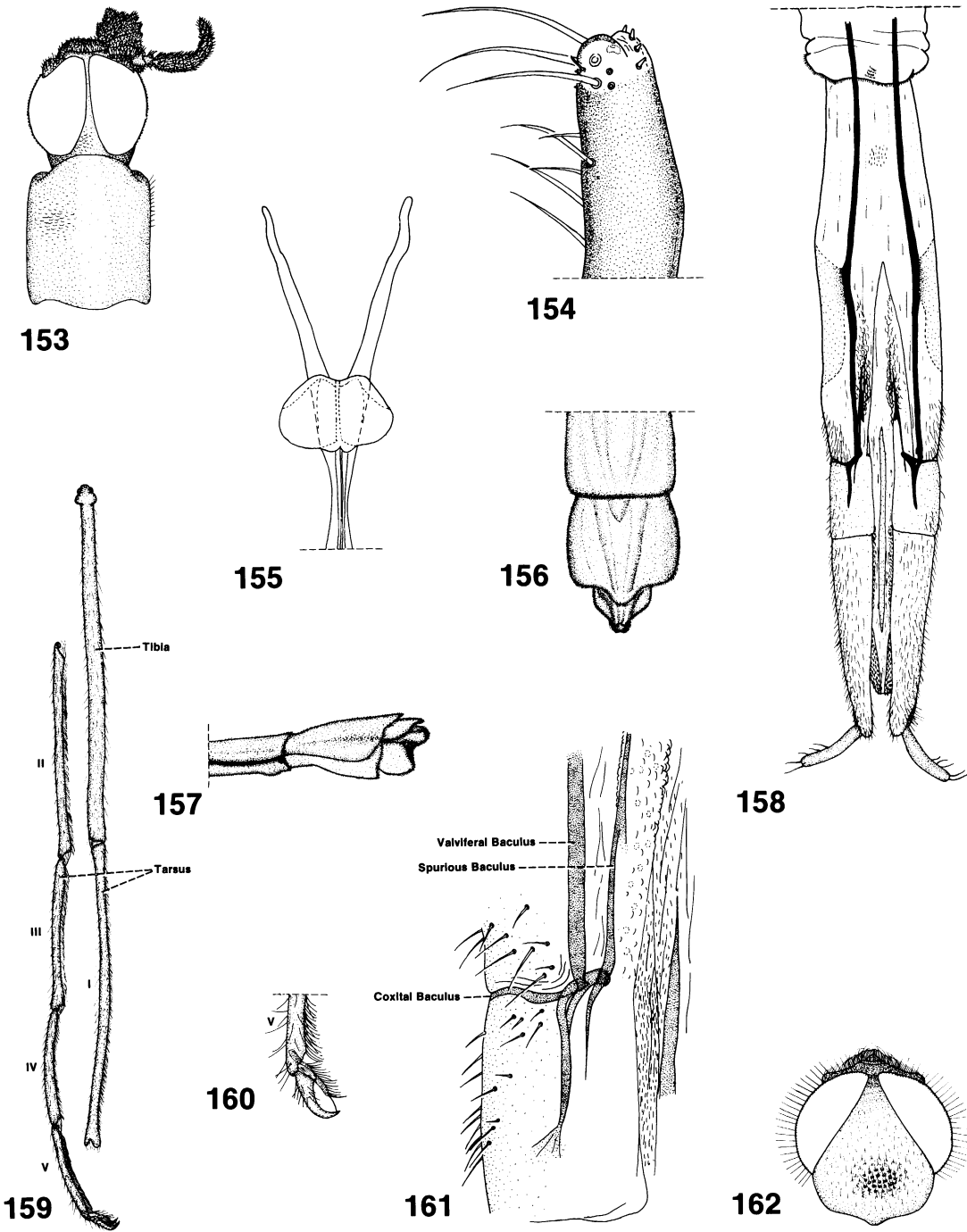
FIGS. 153–162. *Atractocerus* spp. 153, 154. *A. brevicornis*. **153.** Head and pronotum. **154.** Stylus of female genitalia, apex. **155.** *A. procerus* metendosternite. 156, 157. *A. brasiliensis* male abdomen, apex. **156.** Dorsal. **157.** Lateral. **158.** *A. brevicornis* female genitalia, ventral. 159, 160. *A. tasmaniensis* metathoracic leg. **159.** Tibia and tarsus. **160.** Apex tarsomere V and claw. **161.** *A. brevicornis* female genitalia. **162.** *A. tasmaniensis* head, male dorsal.
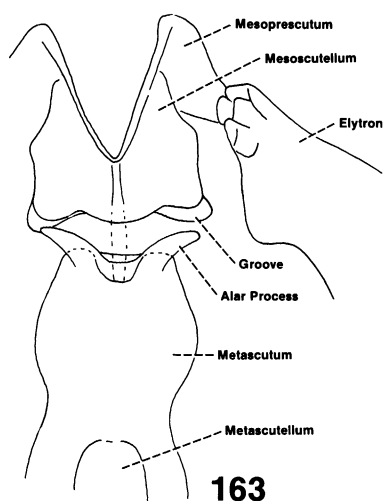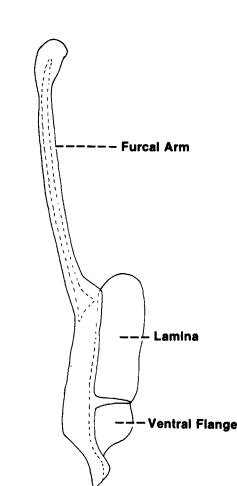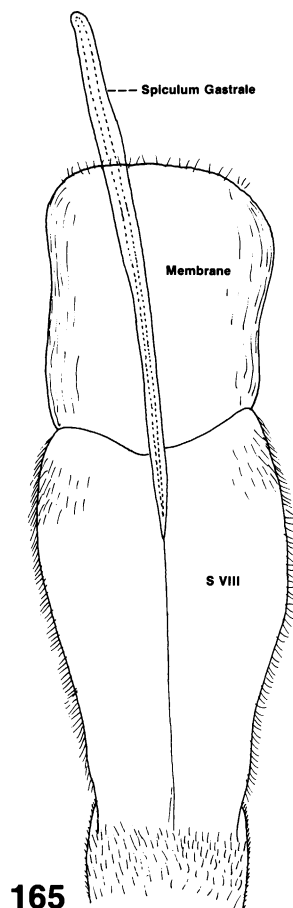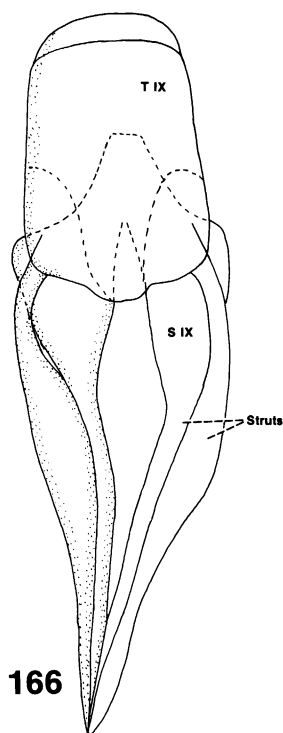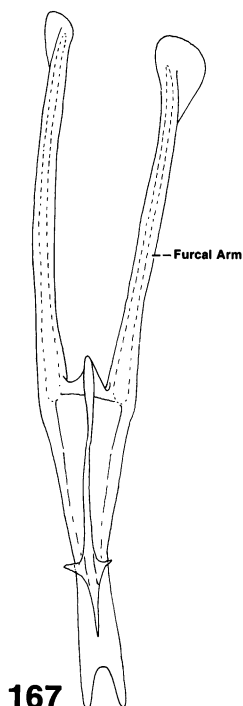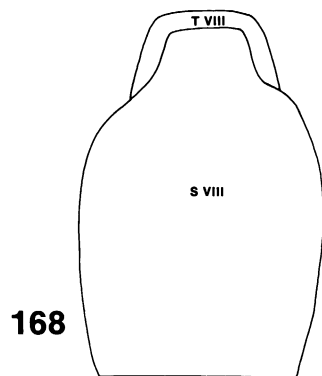
FIGS. 163–168. *Atractocerus brevicornis.* **163.** Pterothoracic nota and bases of elytra. **164.** Metendosternite, lateral. **165.** Abdominal segment VIII, female ventral. **166.** Abdominal segment IX, male ventral. **167.** Metendosternite, ventral. **168.** Abdominal segment VIII, ventral.

with narrow median line of similar setae, and paired, lateral comblike structures; fimbriate patch of very long, fine setae to each side of apex. Mandible short, broad, with single api-
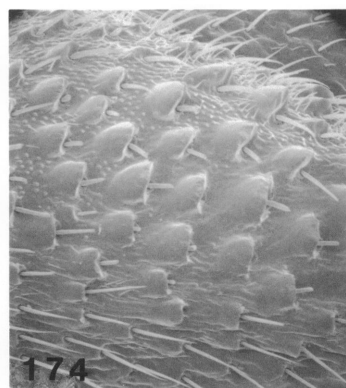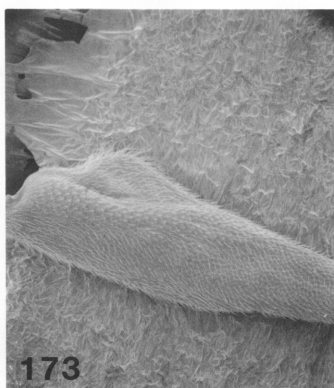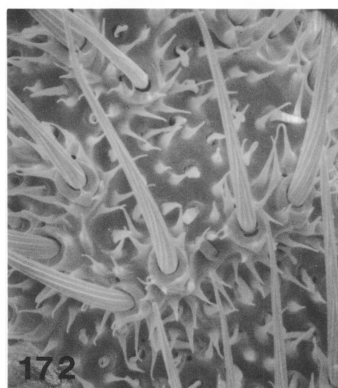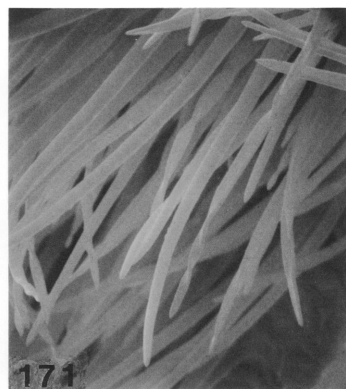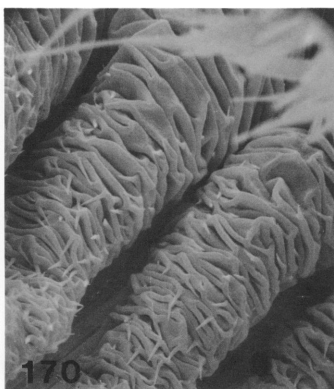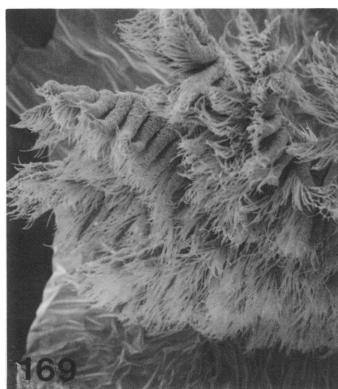
FIGS. 169–174. *Atractocerus procerus* male. **169.** Maxillary palporgan. **170.** Secondary branch of palporgan, outer surface. **171.** Sensilla of inner surface, secondary branch of palporgan. **172.** Antenna, surface detail. **173.** Elytron. **174.** "Tubercles," base of elytron.

cal dens; molar area with parallel rows of minute teeth, perpendicular to longitudinal axis of mandible. Maxilla (figs. 185, 187) compact, moderately sclerotized; with long, stout setae and dense shorter setae; cardo small, broad; stipes broad basally, apically wider; mala partially divided into lacinia and galea; lacinial lobe with elongate patch of very dense setae near palpus; mesal surface of galeal lobe flattened, with broad, elongate, membranous region bearing dense setae. Labium (figs. 179–181, 184) with broad, subtriangular mentum; palpigers separate, poorly defined; palpi with two palpomeres; palpomere I broad, with several setae; II much smaller than I, with several small, peglike sensilla apically; ligula wide, truncate, with single pair short, broad sensilla (fig. 180) and heavily sclerotized and slightly emarginate at apex; hypopharynx with dense lateral and medial setae, large V-shaped sclerite (fig. 181), and covered in part with minute lobes, posteriorly by dense, broad, truncate setae. Antennae minute (fig. 183). Leg (fig. 175) with trochanter slightly produced as lobe beyond femoral base; coxa, femur, and tibia elongate, setose; tarsungulus (fig. 176) with several setae. Abdominal segment X small, inferior to large, bustlelike segment IX (fig. 178).

DISTRIBUTION: *Atractocerus* is a Pantropical genus with species occurring in most major tropical land areas in the Old and New Worlds.

FUNGUS HOSTS: Unknown.

ARBOREAL HOSTS AND BIONOMICS: *Atractocerus brasiliensis* has been reported from the wood of *Mangifera indica* ("mango"), *Mora excelsa*, *Prioria copaifera*, and *Albizzia lebbeck* (Swabey, 1935; Simmonds, 1956) in Trinidad, Costa Rica, and Barbados. *A. al-*
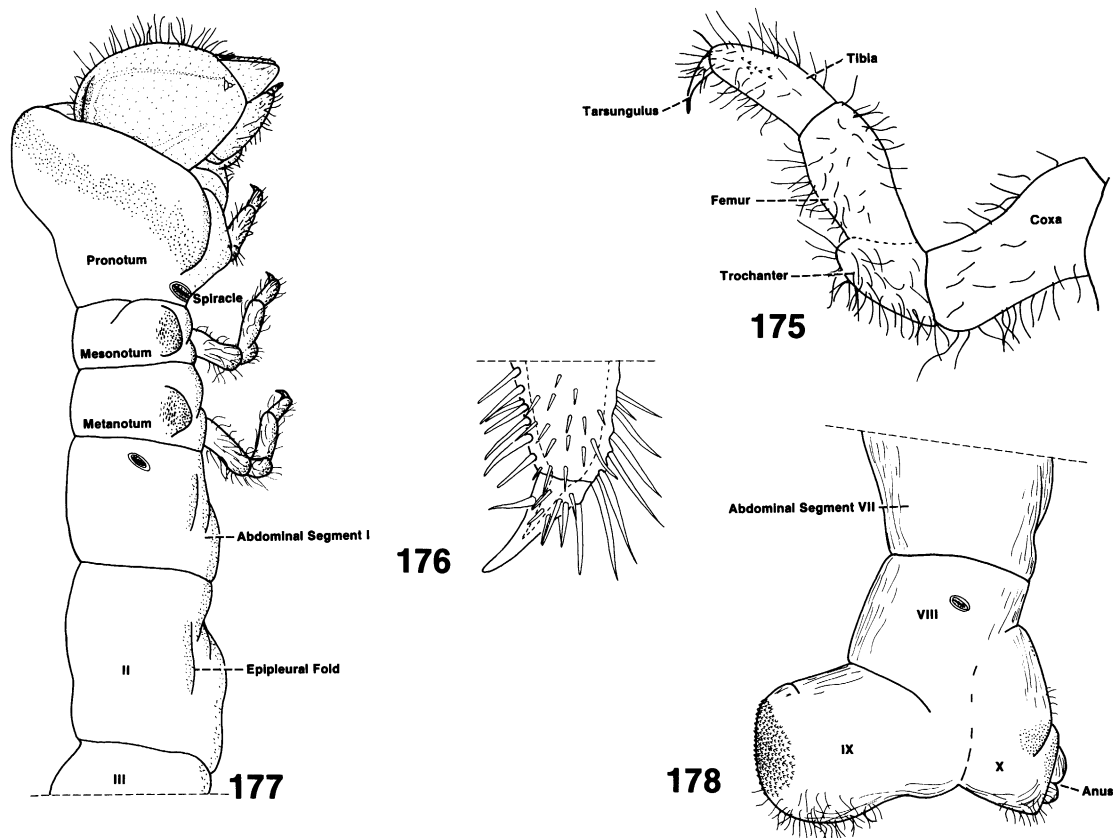
FIGS. 175–178. *Atractocerus brevicornis* larva. **175.** Hind leg. **176.** Tarsungulus, hind leg. **177.** Head, thorax, base of abdomen. **178.** Abdominal apex.

bitarsis was reported by Blair (1936) from *Bombax malabaricum* and *A. quercus* from *Quercus dilitata* by Gardner (1935) in India. *A. brevicornis* was noted by Simmonds (1956) from the following kinds of African woods: "Nkoba" log (Uganda), mahogany log (Gold Coast), Limba log (Belgian Congo), *Ekebergia ruppeliana* "heartwood" (Tanganyika), *Midbraediodendron excelsum*, teak, *Tectona grandis*, *Ricinodendron africanum*, *Triplochiton scleroxylon*, cashew nut, *Anacardium occidentale* (Kenya), and *Swietenia mahogani*. *A. niger* has been associated with *Dipterocarpus indicus* in India (Madras, see Simmonds, 1956). Clark (1925) reported the Australian *A. krueslerae* from "Blackbutt" (*Eucalyptus patens*), "Tuart" (*E. gomphocephala*), "Wandoo" (*E. redunca* var. *elata*), "Flooded Gum" (*E. rudis*), and "Marri" (*E. calophylla*). Clark also noted that a fungus infesting *krueslerae* larval tunnels seemed

correlated with larval mortality. The Indian species *A. reversus* has been reported from "mould and sap," and with the following tree species: *Boswellia serrata* (the "Sallai"), *Lannea coromandelica* ("Jhingan"), and *Lannea grandis* (Beeson, 1961; Roonwal, 1972; Gardner, 1936, 1944) in India and Sri Lanka. Simmonds (1956) noted *A. blairi* in association with the tree *Terminalia myriocarpa* in Assam. Gardner (1936) reported *A. emarginatus* from the following trees in India, Malaya, and Sri Lanka: *Buchanania latifolia*, *Hevea brasiliensis* (rubber tree), and *Dipterocarpus zeylanica*. Wasmann (1902) noted an *Atractocerus termiticola* near the nest of *Cornitermes similis* in Brazil, and *A. brevicornis* associated with termites in West Africa; no associations with termites, however, have since been noted for any species of the genus. An early paper by Gorham (1886) suggested that Central and South American species of
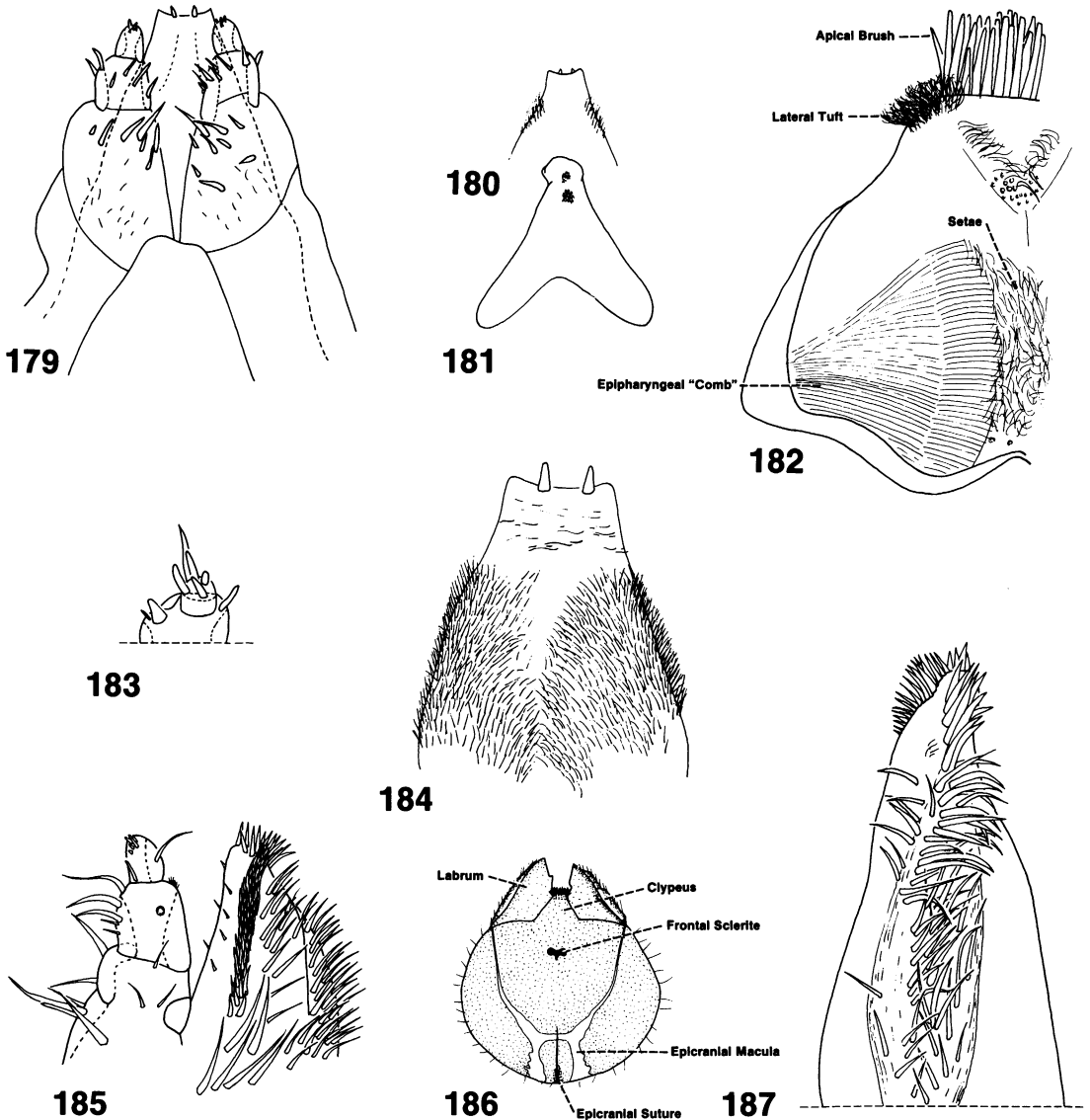
Figs. 179–187. *Atractocerus brevicornis* larva. **179.** Labium. **180.** Apex of ligula. **181.** V-shaped sclerite of hypopharynx. **182.** Labrum, ventral. **183.** Antenna. **184.** Hypopharynx. **185.** Maxilla, dorsal. **186.** Head, dorsal. **187.** Mala, mesal.

Atractocerus might be predators of nocturnal beetles, such as lampyrids; this claim is unsubstantiated. It is of further interest that these beetles, which have extremely high hindwing beat frequencies, were suggested to be arboreal as adults by Clark (1925). Clark's observation could help explain the apparent rarity of many species.

SPECIES INCLUDED: Twenty-three nominal species are included in *Atractocerus,* but sev-

eral synonymies seem intuitively to be needed.

1. *Atractocerus ater* Kraatz, 1895, p. 163. Africa, including Congo, Ivory Coast, and Cameroon (see Villiers, 1969a, 1969b, 1969c). This species was considered synonymous with *brevicornis,* but has been recognized as a valid species by Villiers who provided several diagnostic characters, including those of the male genitalia. I have seen the type specimen

(Deutsches Entomologisches Museum, Berlin), bearing the following labels: "Togo Conradt"/"Coll. Kraatz"/female symbol/"Atractoc. ater Kraatz"/"Schenkling det."/"A. brevicornis L."/"Dtsch. Entomol. Institut Berlin"/"Dtsch. Entomol. Institut Eberswalde"/"HoloType"/"Atractocerus ater Kraatz, A. Villiers 1968." As noted by Villiers, the apex of the male type's abdomen is missing.

2. *Atractocerus bicolor* Strohmeyer, 1910, p. 6. New Guinea (Schenkling, 1915).

3. *Atractocerus bifasciatus* Gestro, 1874, p. 544. New Guinea (Schenkling, 1915). Simmonds (1956, p. 693) stated that the type and other N. Guinea specimens were in Paris (Museum National d'Histoire Naturelle), however I could only locate two series of specimens, all female, that are dated later than the year of published description: (series 1 labels:) "Museum Paris, Nouv.-Guinee, Dorey, Raffray and Maindron, 1878"/red-purple small square label/"Atractocerus bifasciatus Gestro"; (series 2 labels:) "Museum Paris, Nouv.-Guinee, Baie de Mumboldi et Dorey, J. D. Pasteur, O.K. Pasteur 1906."

4. *Atractocerus blairi* Gardner, 1936, p. 181. India (Simmonds, 1956).

5. *Atractocerus brasiliensis* Lepeletier and Audinet-Serville 1825, p. 309. Central and South America, widely from Mexico to Brazil, and in West Indies (Barber, 1952; Blackwelder, 1957; Gorham, 1881; Guérin-Méneville, 1844; Sleeper, 1964; Spilman, 1971; Vaurie, 1957; Vitrac, 1913).

6. *Atractocerus brevicornis* (Linnaeus), 1766, p. 643 (*Necydalis*). Africa and Madagascar, widespread in west Africa (Boheman, 1851; Chenu, 1860; Gardner, 1935; Simmonds, 1956; Villiers, 1969a, 1969b, 1969c; Schenkling, 1915). The larva is described by Gardner (1934).

7. *Atractocerus bruijni* Gestro, 1874, p. 545. Philippines, Celebes, Perak, Hong Kong (Schenkling, 1915; Simmonds, 1956). I have seen 16 specimens, all female, in Paris (Museum National d'Histoire Naturelle), all dark in color (including hindwings), with the head and pronotum yellowish (head varying to very dark).

8. *Atractocerus crassicornis* Clark, 1931, p. 120. This species occurs in north-western Australia.

9. *Atractocerus emarginatus* Laporte, 1836, p. 59. This species occurs in India, Sumatra, Sri Lanka, Java, the Celebes, Burma, Siam, Sarawac, and the Philippines (Fairmaire, 1882, 1885; Fulmek, 1931; Gardner, 1935, 1936; Kalshoven, 1964; Karny, 1922; Simmonds, 1956).

10. *Atractocerus gracilicornis* Schenkling, 1914, p. 320. I have seen the type specimen (Museum National d'Histoire Naturelle), a female with the following labels: "364 51"/ "gen. nov."/"Museum Paris CALIFORNIE Lorquin 1851"/"TYPE"/"Atractocerus gracilicornis Typus! Schkg." It appears that *gracilicornis* may be a synonym of the South American species *valdivianus*, although neither morphological nor geographic characteristics of either are well known. Also, from the label data it is not clear that "California" refers necessarily to either California (United States) or Baja California (Mexico).

11. *Atractocerus kreuslerae* Pascoe, 1864, p. 46. This species occurs in New South Wales and Western Australia, where it has at times been a serious pest (Clark, 1925; Simmonds, 1956).

12. *Atractocerus mirabilis* Miwa, 1935, p. 457. Described from Taiwan.

13. *Atractocerus morio* Pascoe, 1860, p. 117. This species occurs in New Guinea, the Moluccas, Philippines, and Celebes (Schenkling, 1915; Simmonds, 1956).

14. *Atractocerus niger* Strohmeyer, 1910, p. 6. This species occurs in India (Simmonds, 1956).

15. *Atractocerus procerus* Schenkling, 1914, p. 319. This species occurs in Central and South America (Brazil, Surinam, Panama) (Simmonds, 1956) [lectotype, female, designated here: Deutsches Entomolgisches Institut, labeled "Brasil, Corumba, Alto Paraguay, H. Richter"; examined].

16. *Atractocerus quercus* Gardner, 1935, p. 69. This species is known only from India (Gardner, 1936; Simmonds, 1956).

17. *Atractocerus reversus* Walker, 1858, p. 285. This species is reported from India and Sumatra (Bourgeois, 1905, 1909; Gardner, 1935, 1936; Karny, 1922; Roonwal, 1972).

18. *Atractocerus siebersi* Karny, 1922, p. 12. Known only from Sumatra.

19. *Atractocerus tasmaniensis* Lea, 1917, p. 143. This species is mentioned by Clark

(1931, p. 122), and is a very distinctive, small-sized *Atractocerus* with inordinately long legs and large sensilla on the antennae (see text).

20. *Atractocerus termiticola* Wasmann, 1902, p. 104. Known from Brazil.

21. *Atractocerus tonkineus* Pic, 1948, p. 13; from "Tonkin," now North Viet Nam.

22. *Atractocerus valdivianus* (Philippi), 1866, p. 113 (*Fusicornis*). This species is described from Chile (Schenkling, 1915; Simmonds, 1956).

23. *Atractocerus victoriensis* Blackburn, 1891, p. 306. This species is mentioned by Clark (1931, p. 122).

24. *Atractocerus nipponicus* Nakane, 1985, p. 596. This species is said by Kurosawa (1985, p. 113) to be closely related to *morio* Pascoe; it is described from the Moluccas.

25. *Atractocerus monticola* (Kurosawa), 1985, p. 114. This species was described in *Arractocetus* from Formosa.

CLADISTIC RELATIONS: *Atractocerus* is the sister group of the Palearctic genus *Lymexylon* (see Cladistic Analysis below).

DISCUSSION: *Atractocerus* is large and variable, and division of the genus into two or more genera could be defended. Nonetheless, all the species here included form a monophyletic lineage, sister to *Lymexylon,* and there are few reasons commending such splitting at this point. In cranial structure alone there are species with flattened faces and cylindrical crania that are quite distinct from those with dorsoventrally flattened and ovate crania (cf. figs. 153, 162). Male genitalia vary considerably, but follow a recognizable plan. The lateral lobes are invariably more conspicuous than the median lobe, but may be in the form of elongate, antlerlike structures (e.g., *A. procerus,* figs. 148–150) or may be shorter and broader (e.g., fig. 152). The Australian species *tasmaniensis* has extremely long, thin legs (figs. 159, 160), stout setae on eyes (fig. 162), and reduced maxillary palp-organs (fig. 144) that seem correlated with antennomeres bearing dense sensilla (fig. 143). Hindwing structure is recognizable in all species (e.g., figs. 127, 128). The maxillary palporgan structure is also somewhat variable, usually with remarkably numerous sensilla (e.g., fig. 169), and following the pattern for the family with tactile external setae and thin-walled internal sensilla (figs. 170, 171).

Numerous sources of characters exist for use within the genus as here conceived, such as serrate cuticular structures on the elytra (figs. 173, 174) of *procerus* and the peculiar rudderlike form of the apex of the abdomen in forms like *brasiliensis* (figs. 156, 157). Revision of the species of *Atractocerus* will be rewarded by a wealth of variable characters from which phylogenetic affinities may be estimated.

Several larvae from Victoria and New South Wales identified as Lymexylidae in the collections of the Commonwealth Scientific and Industrial Research Organization (Canberra City) and the British Museum (Natural History) represent *Atractocerus crassicornis,* illustrated by Britton (1970, p. 580). In general body form they are extraordinarily long and vermiform (see Britton's fig. 30.66B), and the apex of the abdomen has a pair of sclerotized hooks. Were these hooks to be homologous with urogomphi, they would indicate that the bulbous condition of the ninth abdominal segment in *Lymexylon* and *Atractocerus* is not synapomorphous, but independently derived. This must also be seriously considered in light of the *crassicornis* larva. Provisionally regarded as a modification of the bulbous condition, this character poses no problem; it is also possible, of course, that this condition is closer to an ancestral *Atractocerus* one and that the bulbous state in others has evolved independently of *Lymexylon.*

While this paper was in press, Kurosawa (1985) proposed division of *Atractocerus* into five genera: *Atractocerus* s.s., *Fusicornis* Philippi (1866), and three new genera, *Raractocetus* (based on *emarginatus*), *Hymaloxylon* (based on *quercus*), and *Arractocetus* (including *niger, nipponicus* Nakane, *morio,* and *monticola,* a species described as new). I herein regard all these genera as junior synonyms of *Atractocerus* for the following reasons. As currently defined, *Atractocerus* is easily recognized, includes a modest number of species, and is highly supported by more than 20 apomorphic features. While (as I have stated above) the genus could be subdivided, it should be along valid cladistic lines. Kurosawa's five genera add no clarity to the cladistic relationships among species, make identification more difficult, and are inadequately supported. They are premature at best
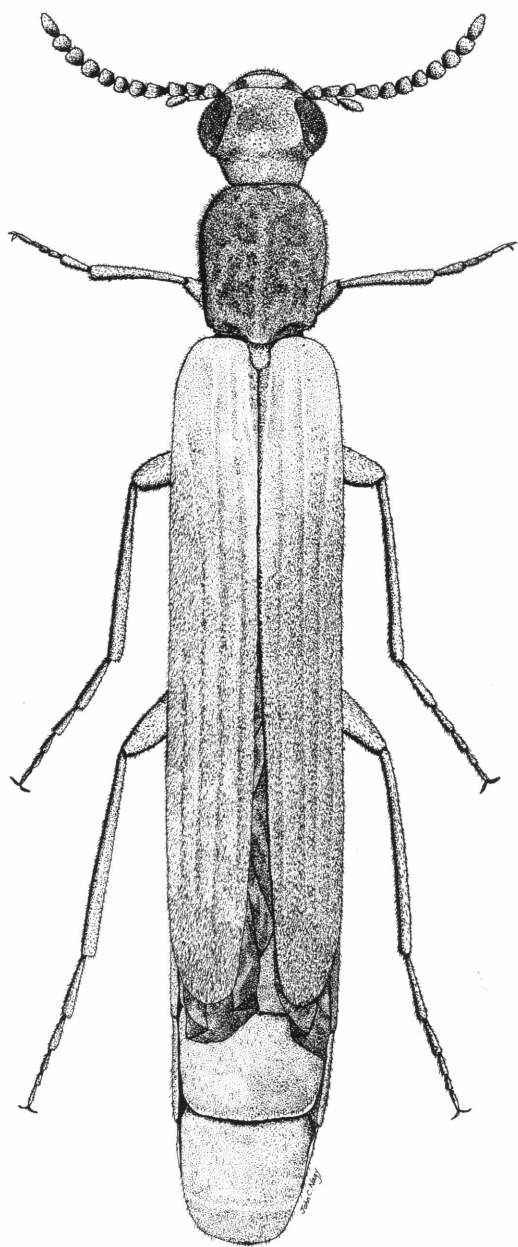
FIG. 188. *Australymexylon fuscipennis* (Lea), male, by J. Nagy.

(should one or more eventually be grounded on credible evidence) and completely arbitrary at worst. I suggest that the single, demonstrably monophyletic genus *Atractocerus* be recognized until all the constituent species

are revised in detail and a cladistic analysis completed.

MELITTOMMINAE, NEW SUBFAMILY

I here propose a new subfamily, Melittomminae, for *Melittomma* and the related genera *Australymexylon* Wheeler, new genus, *Melittommopsis* Lane, and *Protomelittomma* Wheeler, new genus. *Australymexylon* is discussed below, followed by treatment of the other genera termed collectively the nomenclaturally informal "*Melittomma* Complex."

TYPE GENUS: *Melittomma* Murray, here designated.

DIAGNOSIS: Antenna serrate; prohypomeron with supracoxal slot; procoxa with slot; anterior part of mesepisternum elevated (ventrally produced); mesepimeron with depressed lateral area; larval abdominal segment IX heavily sclerotized, cylindrical, and truncate.

CLADISTIC RELATIONS: Melittomminae is the sister group of the subfamily Lymexylinae, sensu novo (see above).

GENERA INCLUDED: *Melittomma* Murray, *Melittommopsis* Lane, *Australymexylon* Wheeler, new genus, and *Protomelittomma* Wheeler, new genus.

Australymexylon Wheeler, new genus
Figures 188–224

TYPE SPECIES: *Lymexylon australis* Erichson, 1842, p. 147.

DIAGNOSIS: Body elongate, parallel sided, dorsoventrally flattened (fig. 188). Eyes large, emarginate. Head constricted behind eyes forming neck. Maxilla of both sexes without palporgans (fig. 192). Antenna slightly to strongly serrate (figs. 189, 190, 203, 204). Elytron shortened, one to two apical terga exposed; apices narrowed, lying flat over abdomen; epipleural fold short; tongue-and-groove locking mechanism ends well before elytral apices. Procoxa slotted (fig. 202). Hypomeron of prothorax slotted (fig. 198). Mesepisternum elevated anteromedially, concave laterally (fig. 196). Mesepimeron with sharp carina, concave lateral groove receiving epipleuron of elytron. Pronotum with sharp lateral margin (fig. 198). Metepisternum and metepimeron form deep groove, re-
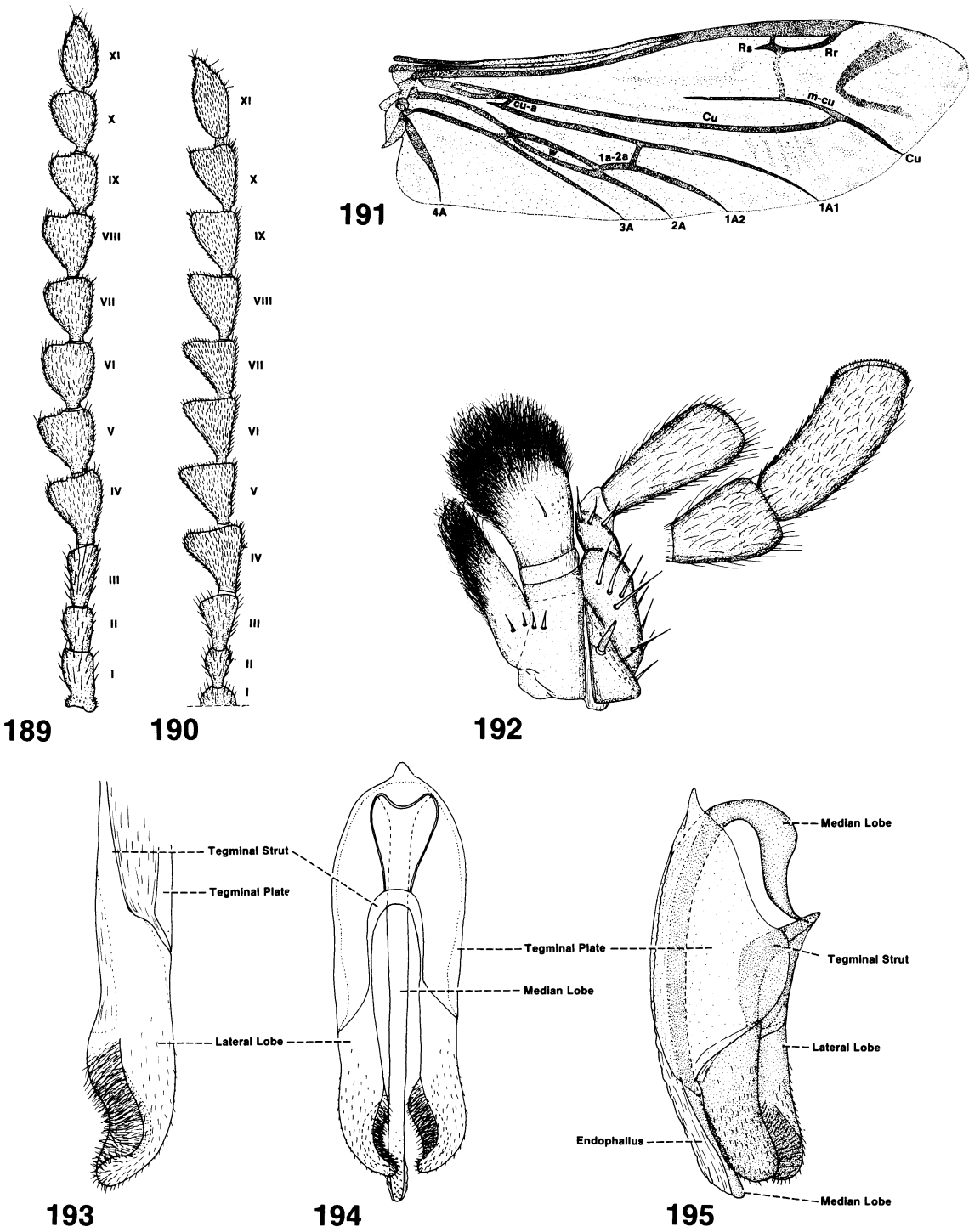
FIGS. 189–195. *Australymexylon australe.* **189.** Antenna, female. **190.** Antenna, male. **191.** Hindwing. **192.** Maxilla, male. **193–195.** Aedeagus. **193.** Lateral lobe, ventromesal. **194.** Ventral. **195.** Lateral.

ceiving part of elytral epipleuron. Abdominal segments III–VII visible (fig. 208). Anterior tendons of metendosternite arising on furcal arms (figs. 209, 210). Female genitalia (fig. 220) with distal part of coxite much longer than basal part; coxital baculus sometimes (*A. fuscipennis*) straight, extending beyond base of distal part of coxite. Male abdominal sternite VIII with pads of dense setae (figs. 211, 213) that are large and circular or very large and oval in form, sometimes curving around sides and occupying much of dorsal surface (in *A. australe*). Lateral lobes of male genitalia large, cuplike (figs. 193, 214); median lobe either very long, or very short. Larva with posterior segments of abdomen similar to *Melittomma* and related forms; IX cylindrical, blunt (fig. 222); tarsungulus bisetose (fig. 219), but with numerous small spines.

KEY TO SPECIES OF *AUSTRALYMEXYLON*

1. Male antenna strongly serrate (fig. 203); female antenna serrate (fig. 204); lateral lobes of male genitalia very large relative to median lobe (figs. 214, 215); abdominal segment VIII of male with large, round, ventral setose pads (fig. 213); color (usually) includes evident pale spot at base of each elytron (fig. 188) . . . . *A. fuscipennis*, new combination
   Male antenna serrate (fig. 190); female antenna scarcely serrate (fig. 189); lateral lobes small relative to median lobe (figs. 193–195); abdominal segment VIII of male with very large setose pads, covering most of sternite and part of tergite (figs. 211, 212); color (usually) uniformly dark, reddish-brown to nearly black . . . . . . *A. australe*, new combination

Australymexylon australe (Erichson), new combination
Figures 189–202, 205, 206, 209–212, 216–224

Lymexylon australis Erichson, 1842, p. 147 [type, female, examined, Zoologsiches Museum, Berlin].
Hylecoetus australe (Erichson), Schenkling, 1915, p. 5; Lea, 1912, p. 467.
Hylecoetus linearis Lea, 1894, p. 603; Schenkling, 1915, p. 8. NEW SYNONYMY [type examined, South Australian Museum].
Lymexylon adelaidae Blackburn, 1898, p. 34;

Schenkling, 1915, p. 10. NEW SYNONYMY. [type examined, South Australian Museum].

DIAGNOSIS: Color uniform, reddish-brown to nearly black; male antenna moderately serrate (fig. 190), female antenna very slightly serrate (fig. 189); male abdominal segment VIII with very large, oval setose pads (figs. 211, 212); median lobe of aedeagus very long relative to lateral lobes (figs. 193–195).

DESCRIPTION: Body very long, parallel-sided, dorsoventrally flattened (fig. 188). Length about 6.8–13.5 mm. Color uniform, varying from reddish-brown to nearly black; head and pronotum usually a little darker than elytron and ventral surface; most individuals seen were paler in color, possibly teneral to some degree. Integument moderately sclerotized. Much of surface covered by short, fine, yellow, suberect setae.

Head about as long at midline as broad; widest at eyes; strongly narrowed behind eyes, forming neck region; head convex. Eyes large, conspicuous, narrowed toward midline ventrally, emarginate anteriorly; widely separated dorsally and ventrally; facets moderately coarse, round. Frontoclypeal suture absent, but with depressed line. Labrum (fig. 201) broad, small, with anterior margin slightly sinuate and with about 10 pairs dorsal setae. Epipharynx membranous; with microtrichiae and dense patch long setae apically. Mandible broad, stout, with apical and subapical dens; without distinct mola. Maxilla (fig. 192) with galea broad, lacinia narrower, each with dense setae; palpus 4-segmented, I small, II elongate, III shorter than II, IV very long, nearly parallel-sided and truncate; maxillary palporgan absent. Labium (fig. 199) with 3-segmented palpus, I small, II elongate, widened apically, III elongate, subtruncate; hypopharynx (fig. 200) broad, membranous with microtrichiae and long setae along apical margin. Gular sutures slightly convergent anteriorly, extending little further anteriorly than "neck." Surface with dense, round, relatively deep punctures, becoming transversely confluent on neck. Antenna (figs. 189, 190) slender, long, extending beyond pronotal base when head deflexed; arising under frontal ridge at anterior excision of eye; antennomere I stout, elongate; II shorter, elongate; III longer than II, slightly expanded apically; IV–X

slightly produced to one side in female, more so in male where distinctly serrate; I–III with moderately dense, long setae only (base of I with some small erect setae); XI elongate, narrowed apically; IV–XI with dense, short setae.

Pronotum (fig. 198) quadrate, dorsoventrally flattened, length/width = 1.25; anterior margin broadly rounded; posterior margin sinuate, with lateral angles strongly posteriorly produced; with sharp lateral margins. Prosternum short, transverse, with small, median, intercoxal carina. Procoxal cavities broadly open behind. Pronotum with sharply defined lateral margins. Hypomeron with coxal slots, and short tergosternal suture from hypomeral slot to anterior orifice. Prosternum with slight depressions in front of coxae. Procoxae elongate, cylindrical, apically slotted (fig. 202). Mesosternum small, triangular (fig. 197). Mesepisternum larger than mesosternum, laterally concave, anteromedially elevated (fig. 196). Mesepimeron smaller, divided by carina into medial, flat area and lateral, strongly concave area receiving elytral epipleuron. Metasternum large, elongate, narrowed anteriorly; area beneath mesocoxae lightly sclerotized, depressed; with narrow, elongate incision at midline of heavily sclerotized part of metasternum. Metepisternum simple, broader anteriorly. Metepimeron broad anteriorly, abruptly narrowed for posterior 0.75 length. Both metepisternum and metepimeron with sharp carinae, steeply elevated areas combining to form groove for elytral epipleuron. Tibial spur formula 2-2-2 (both sexes). Metendosternite (figs. 209, 210) with anterior tendons inserted on furcal arms near its base; laminae simple; furcal stalk with sides folded and fused for short ventral distance; furcal arms not long. Scutellum simple, rounded apically, flat; without carinae.

Elytron with four longitudinal costae plus short scutellary costa. Each elongate, with epipleuron at base fitting into grooves of mesepimeron, metepimeron, and metepisternum. Epipleural fold narrowed along length of first visible abdominal sternite, fold absent beyond its posterior apex. Tongue-and-groove locking mechanism along midline ending well before apex, apices of elytron narrowed, lying flat over abdomen, separated. Elytron shortened, exposing one to two terga. Surface of elytron with dense, small punctures and dense, short, fine setae. Hindwing (fig. 191) narrow in shape, venation rather complete. A spurious Rs vein present (basal to brachial cell). The r-m crossvein (below brachial cell) indistinct.

Abdomen (figs. 207, 208) elongate, cylindrical; male and female with sterna III–VII visible externally; terga II–VII comparably developed. Small pleural sclerite and small sclerite anterior to sternite III may be remnants of segment II. VIII held within VII at rest, simple in female with long spiculum; larger in male, sternite with large setose pads; pads elongate, oval, occupying most of ventral surface of VIII and much of dorsum.

Male genitalia (figs. 193–195): Lateral lobes broad, concave on median face, with dense lining of long, fine setae. Median lobe long relative to lateral lobes, narrow. Recurved basal portion fused with short tegminal struts that are indistinguishably fused with lateral lobes. Tegminal plate very large, poorly defined, lightly sclerotized.

Female genitalia (figs. 217, 220): Elongate, lightly sclerotized, in part membranous. Valviferal plates poorly defined, omitted from figure 220. Styli small, slightly clavate, with dense setae. Coxites exceptionally long, narrow (fig. 217); coxital fold divides short basal part from very long distal part. Proctigeral and valviferal baculi long, simple, separate entire lengths.

Larva[2] (figs. 216, 218, 219, 221–223): Body elongate, rounded dorsally, slightly flattened ventrally; with distinct lateral folds. Color white; yellowish-brown areas dorsolaterally on cranium, dorsally on pronotum, and (as

---

[2] Larval description is based on a series of 4 larvae associated with four adult females, some mistakenly identified as males, from the Division of Entomology, CSIRO, Canberra City, with the following labels: "Little Boys Camp Area," "25-1-40, Adult Lymexylid and larvae—Both sexes," "Melittomma pervagus O11. E. R. Britton det. 195," and my determination label. A second vial, also from CSIRO, contains 2 adult female *australe* and a single pupa. There is a handwritten label, similar to that of the first vial, as follows: "North Cascade Camp. Fire-scared E. regnans," "adult Lymexylonid 25-1-40—Both sexes." The second series, collected the same date, is important because of the limited distribution of *Eucalyptus regnans,* placing these larvae within the known range for *Australymexylon australe.*
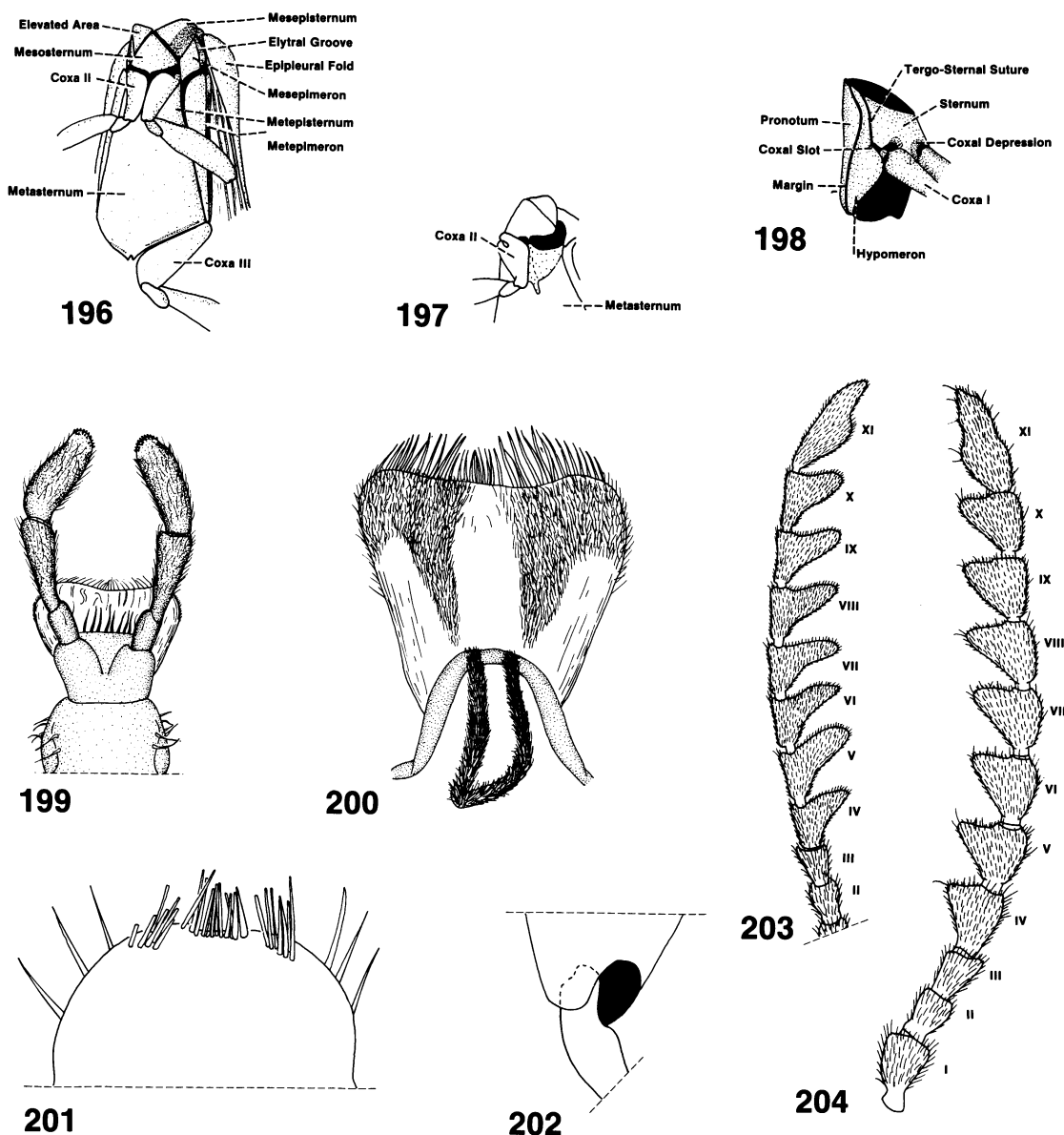
FIGS. 196–204. *Australymexylon* spp. 196–202. *A. australe.* 196. Mesosternum, metasternum, and associated structures. 197. Anterior portion of metasternum with mesocoxa removed. 198. Prothorax, ventrolateral. 199. Labium, ventral. 200. Hypopharynx. 201. Labrum, ventral, epipharyngeal setae omitted. 202. Procoxa apex. 203, 204. *A. fuscipennis* antennae. 203. Male. 204. Female.

spots) on meso- and metanota; with yellowish-brown asperites anterior and posterior to anus on segment X, darkly pigmented arcuate band and asperites posterior to it on tergum VIII; apex of segment IX cylindrical and truncate with sparse, small spines around perimeter and few dark spines dorsally, anterior to apex. Apical third of segment IX heavily sclerotized, darkly pigmented, transition

gradual. Head broadly oval. Hypopharyngeal sclerome present, small, lanceolate. Labrum small, ovate. Epipharynx not observed in detail. Mandible robust, with subapical notch. Antenna minute, 2-segmented (fig. 221). Maxilla with mala undivided, margin of mala with many stout setae. Labium small, ligula a simple membranous lobe (fig. 223). Pronotum much larger than other nota, but less
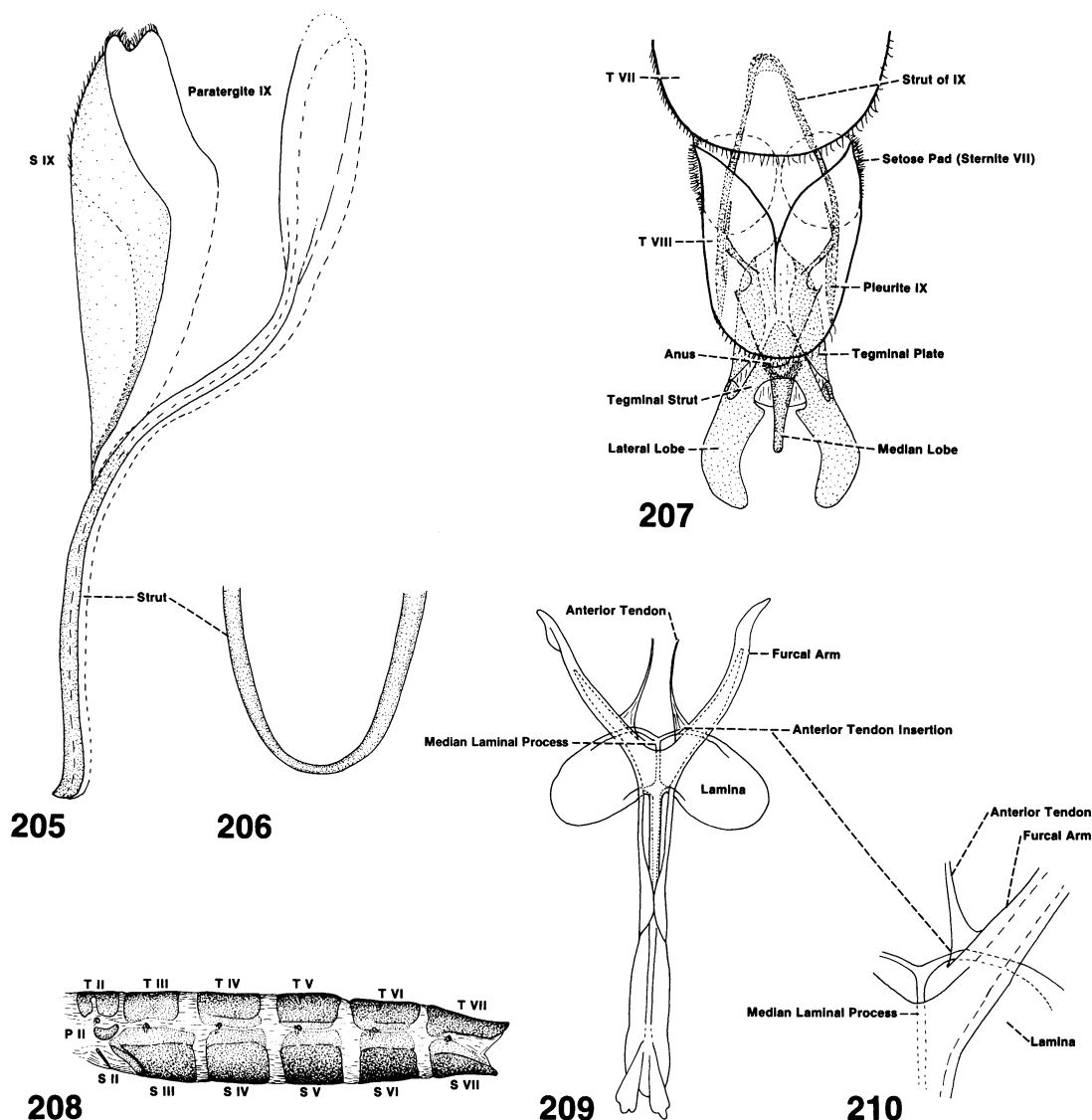
FIGS. 205–210. *Australymexylon* spp. 205, 206. *A. australe.* **205.** Abdominal segment IX, male lateral. **206.** Paratergal struts, male abdominal segment IX, ventral. 207, 208. *A. fuscipennis.* **207.** Postabdomen, male (dorsal). **208.** Abdomen, female (lateral). 209, 210. *A. australe* metendosternite. **209.** Ventral. **210.** Base of furcal arm and anterior tendon insertion, ventral.

hoodlike than in other melittommines. Spiracles small, circular, placed laterally anterior to middle. Legs short, stout (fig. 218), tarsungulus bisetose, but with many small spines (fig. 219). Posterior end of abdomen with X small, inferior, IX large, cylindrical, and truncate (fig. 222), rim of apex with only a few minute teeth. Largest larva of series (ca. 14.0 mm; others ca. 10.1–11.7 mm) with X noticeably less protruding ventrally than smaller larvae.
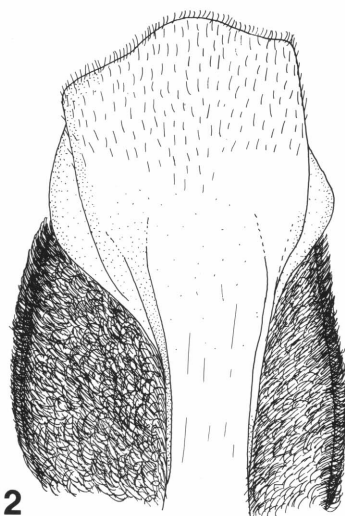
Australymexylon fuscipennis (Lea),
new combination
Figures 188, 203, 204, 207–210,
213–215, 224

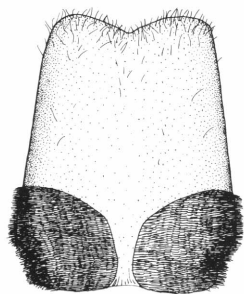*Hylecoetus fuscipennis* Lea, 1912, p. 466 [type, female, South Australian Museum, Adelaide, examined].

DIAGNOSIS: Elytron with pale spot at base (fig. 188). Male antenna strongly serrate (fig. 203), female antenna moderately serrate (fig.
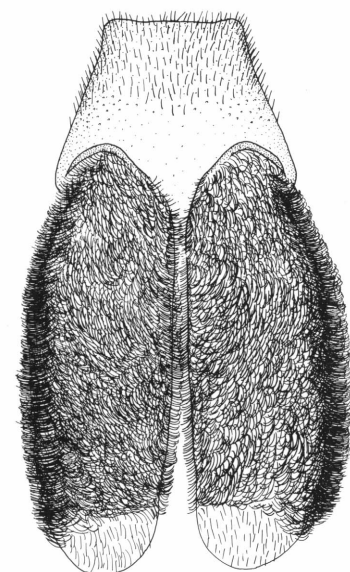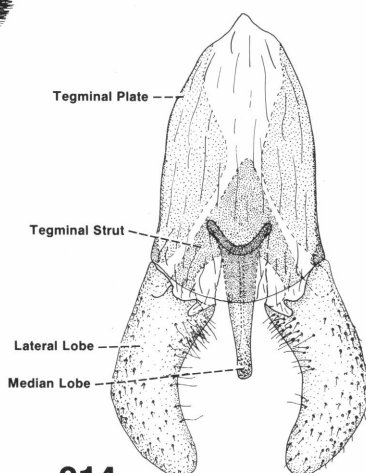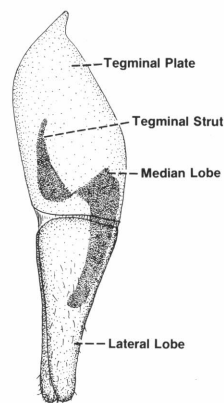
FIGS. 211–215. *Australymexylon* spp. 211, 212. *A. australe,* abdominal segment VIII of male. **211.** Ventral. **212.** Dorsal. 213–215. *A. fuscipennis.* **213.** Abdominal segment VIII, ventral. **214.** Aedeagus, dorsal. **215.** Aedeagus, lateral.

204); male setal pads of abdominal sternite VIII large, round, much less extensive than in *australe* (fig. 213). Median lobe small relative to lateral lobe (figs. 214, 215), tegminal struts fused into small, ventral V-shaped sclerite.

DESCRIPTION: As in *australe,* except key characters and as follows. Male abdominal sternite VIII with paired, large, circular, basolateral setose pads with very dense, long,

erect setae (fig. 213); tergite VIII bifurcate at base, lightly sclerotized at middle, with dense microtrichiae, apex rounded at middle and with dense, long setae. Aedeagus short and broad in form (figs. 214, 215); lateral lobes elongate, wide, rounded apically, with sparse setae over lateral surface, setae dense in concave mesal area; lateral lobe about as long as tegminal plates, much longer than median lobe; median lobe bifurcate basally, rounded
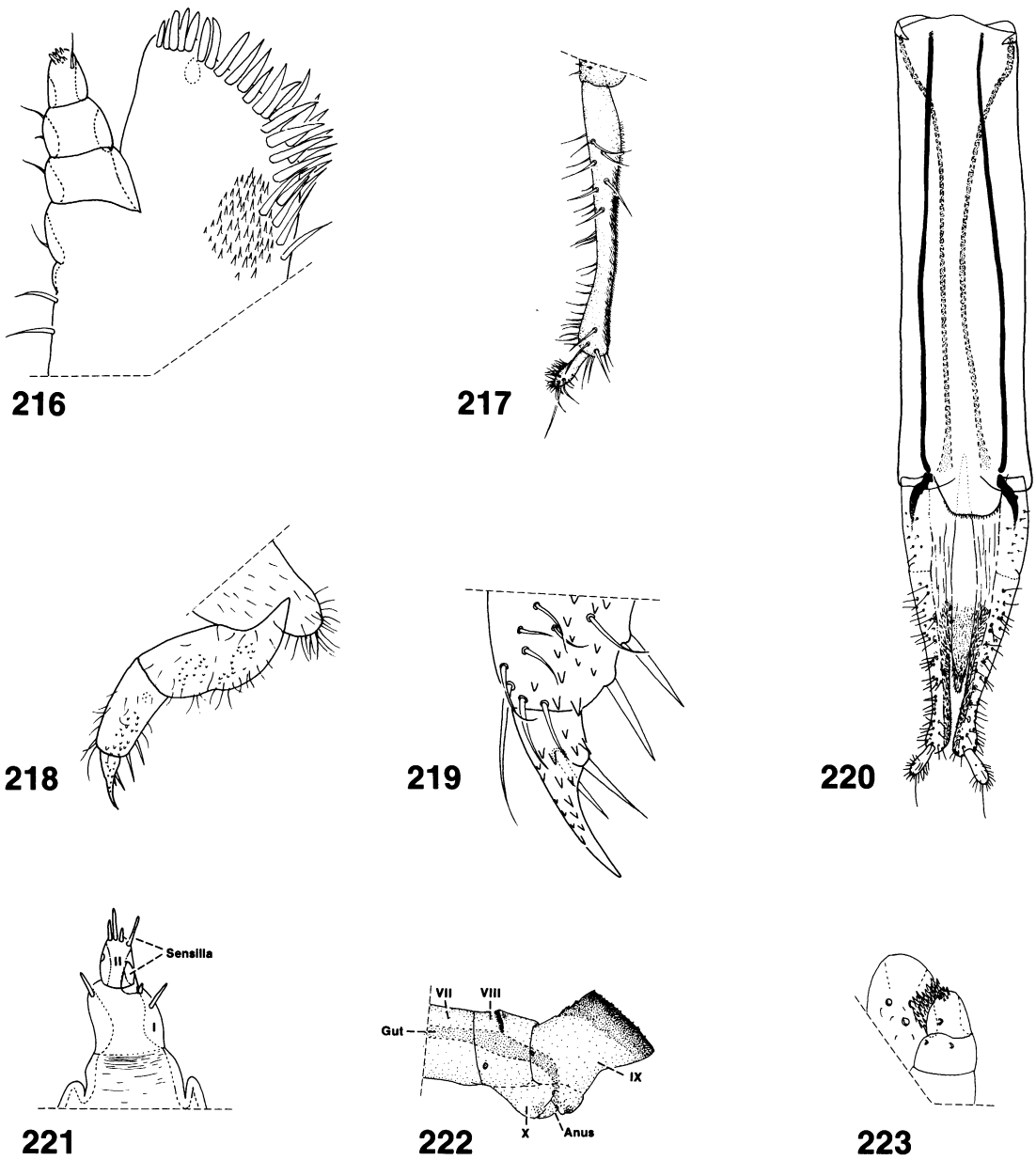
FIGS. 216–223. *Australymexylon australe*. **216.** Apex, larval maxilla. **217.** Coxite and stylus of female genitalia. **218.** Hind leg, larva. **219.** Tarsungulus. **220.** Female genitalia, ventral. **221.** Antenna, larva. **222.** Abdominal apex, larval, lateral. **223.** Larval labium, left half, ventral.

at apex; tegminal plate large, lightly sclerotized, ventral; tegminal struts reduced, flattened, forming a V-shaped sclerite on ventral surface near base of median lobe.

The color of *fuscipennis* is highly variable, at least in part due to relative teneralness of some specimens examined. The following de-

scription of color is based on what is interpreted as a fully mature individual: head dark reddish-brown; antennomeres IV–XI nearly black, basal antennomeres reddish-brown; pronotum dark reddish-brown anteriorly and medially, nearly black laterally and posteriorly; legs dark reddish-brown; exposed ter-
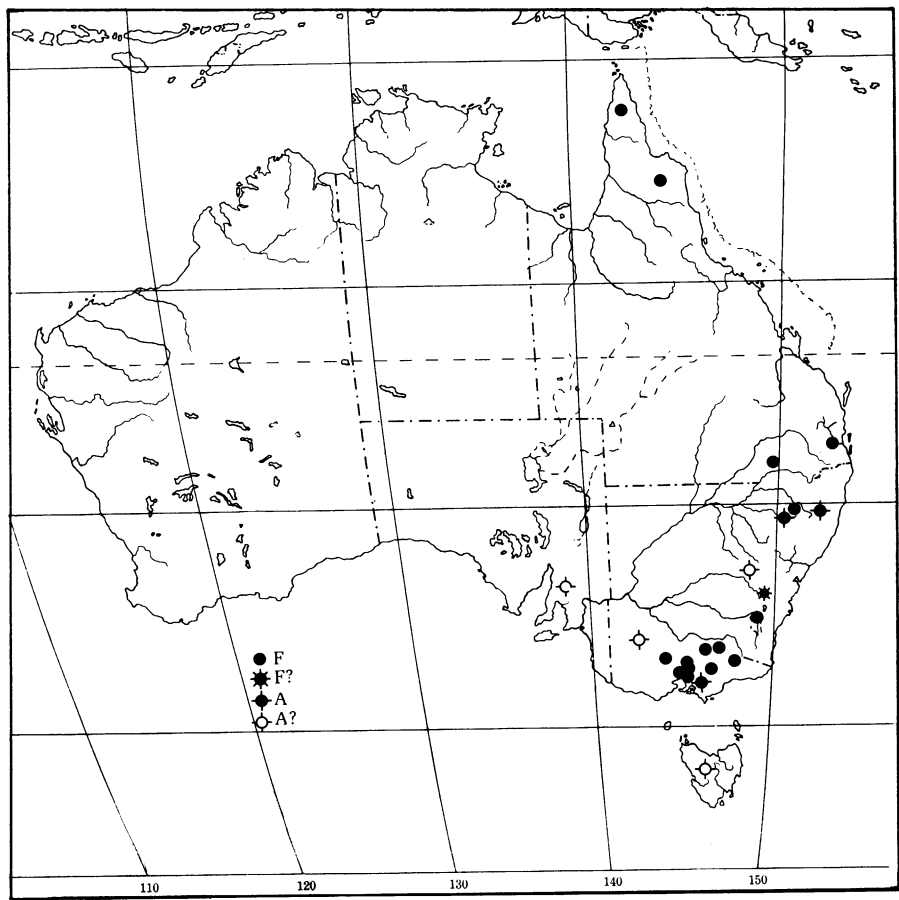
FIG. 224.   Distribution of *Australymexylon* species. F = *A. fuscipennis*; A = *A. australe*; ? = province record only.

ga dark reddish-brown; venter reddish-brown (variable darkness); body covered by yellow setae.

DISTRIBUTION (fig. 224): Eastern Australia, more or less following the Great Dividing Range.

FUNGUS HOSTS: Unknown.

ARBOREAL HOSTS AND BIONOMICS: *Eucalyptus* species.

SPECIES INCLUDED: *Australymexylon australe*, new combination and *A. fuscipennis*, new combiantion. (See taxonomy above, including new synonymies and combinations.)

CLADISTIC RELATIONS: *Australymexylon* is the sister group of other genera of the subfamily Melittomminae (see Cladistic Analysis below).

DISCUSSION: *Australymexylon* is proposed as a new genus to include two valid Austra-

lian species, and it receives four nominal species formerly assigned to *Hylecoetus* and *Lymexylon*. Britton (1970, p. 579) and J. F. Lawrence (in litt.) have previously indicated that these species do not belong to either of the latter north temperate genera. These species are the only Lymexylidae that lack maxillary palporgans in both sexes. Both species occur in eastern Australia, including localities in Queensland, New South Wales, Victoria, South Australia, and Tasmania, apparently (in part) following the Great Dividing Range, although both geographic and ecological information is sparse.

One of the most fascinating things about *Australymexylon* is the presence of large setose pads on the eighth abdominal segment of the male. No comparable structure occurs in females, and it may not be coincidental

that this bizarre structure occurs in the same taxa that lack the equally bizarre maxillary palporgans.

Of all the similarities between these beetles and *Melittomma* and its relatives, it is the appearance of the larva that is perhaps most phenetically impressive. Synapomorphs supporting their placement are discussed in the section on cladistic analysis.

The *Melittomma* Complex of Genera

Three closely related genera of Melittomminae are here referred to as the taxonomically informal "*Melittomma* Complex." This lineage includes *Melittomma* Murray, *Melittommopsis* Lane, and a new genus, *Protomelittomma*, based on *Melittomma insulare* Fairmaire. All these taxa could have been lumped under a broad concept of *Melittomma*, but this would have detracted from a clearly cohesive monophyletic line here delimited by that generic name. I regard the appendiculate paratergites of male abdominal segment IX a strong synapomorph for *Melittomma*. This structure is absent in *Protomelittomma*, which I regard in this and general body form to be primitive (resembling *Melittomma sericeum*, perhaps the most primitive-appearing member of *Melittomma* sensu stricto). Males of the South American genus *Melittommopsis* have structures I interpret as enlarged ninth paratergites, but they are not fully appendiculate as in species of *Melittomma*. There are further male postabdominal modifications (of segment VIII) autapomorphic for *Melittommopsis* and distinguishing this genus from *Melittomma*. Whether *Melittommopsis* is ultimately viewed as a genus distinct from *Melittomma* or not, it remains advisable to remove *insulare* from *Melittomma* to a new genus (*Protomelittomma*) since it does not share any such male postabdominal modifications.

Genus *Melittomma* Murray
Figures 225–267

Melittomma Murray, 1867.
Neohylecoetus Kurosawa, 1956, see synonymy by Kurosawa, 1985, p. 117.

TYPE SPECIES: *Hylecoetus brasiliensis* Laporte, 1832, p. 398 (type not seen).

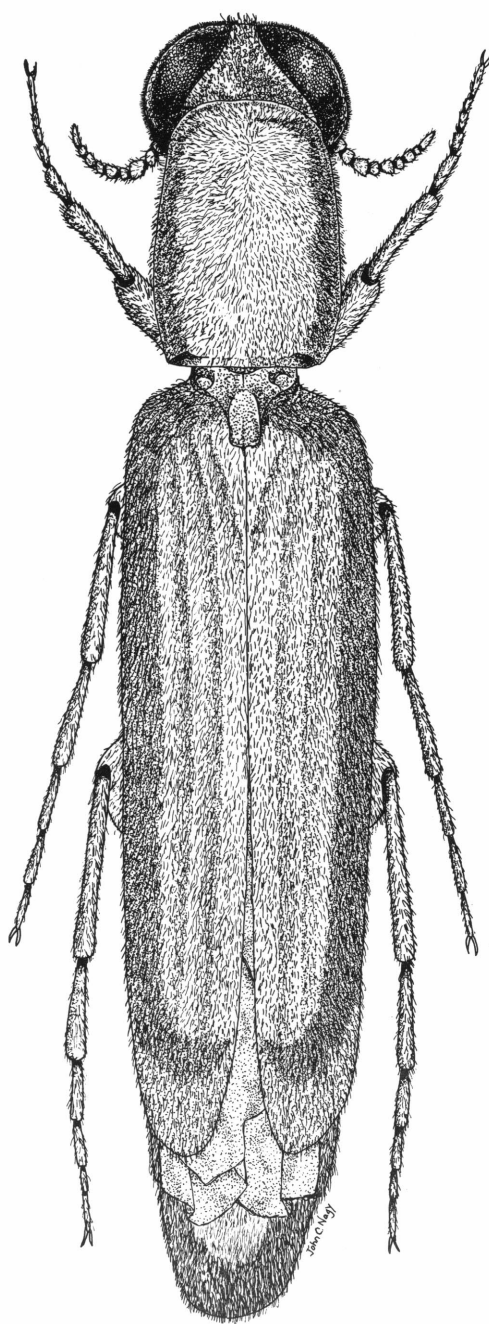DIAGNOSIS: Body elongate, parallel-sided

FIG. 225. *Melittomma brasiliense* (Laporte) male. By J. Nagy.

(fig. 225), moderately sclerotized, only rarely heavily sclerotized; color variable, usually more or less pale, sometimes with dark makings, rarely nearly black; female maxillary

palpus with apical segment narrow; paratergites of ninth male abdominal segment appendiculate (figs. 240, 257); aedeagus with small, setose lateral lobes (figs. 238, 258); larval abdominal segment IX truncate, rimmed by teeth (figs. 245, 266).

DESCRIPTION, ADULT *MELITTOMMA BRASILIENSE* (LAPORTE), AND NOTES ON ITS LARVAL STRUCTURE: Body elongate, parallel-sided, cylindrical (fig. 225); length of male about 4.6–12.0 mm, of female ca. 6.3–25.6 mm. Color testaceous to reddish-yellow in female, often with slight darkened area at humeral angle of elytron and along lateral edge of pronotum; variable in male, with more or less extensive black markings along edge of pronotum and elytron. Integument moderately sclerotized, surface with dense, small punctures bearing small fine setae.

Male with small, triangular vertex between and posterior to very large eyes (fig. 229); eyes widely separated ventrally, nearly confluent dorsally. Female with eyes distinctly separate dorsally (fig. 231). Head narrowed behind eyes, forming constricted neck. Gular sutures nearly parallel, slightly divergent posteriorly. Eye facets large, coarse, hexagonal. Antenna sexually dimorphic; asymmetrically produced to form slightly serrate antenna in male (fig. 234), and biramous (antennomeres III–X) segmented antenna in female (fig. 248); inserted under small ridge set in anterior emargination of eye. Frontoclypeal suture absent, but deep fine impression present. Labrum small, subquadrate, with dense dorsal setae; ventral surface with dense, long anterior setae; epipharynx simple, with very dense microtrichiae meeting along midline. Mandible short, broad, outer margin with long setae, mola with patch of microtrichiae, prostheca absent, with single apical and single subapical dens. Maxilla sexually dimorphic, palporgan present in male, absent in female. Male (fig. 244) with small basigalea separated from large distigalea, covered by dense setae; basistipes small, triangular, separate from larger ovate dististipes; palpifer narrow, ringlike; palpus with four segments; palpomere I short, small, broad; II abruptly larger, transverse; III much larger than II, transverse and broadly oval; IV very long, narrow, widened apically, apex with several long blunt sensilla, surface of base with wrinkles as on palporgan,

but apical portion only with hexagonal impressions; palporgan large, base of primary branch with small, heavily sclerotized area, organ with primary-quintinary branching pattern, outer surface of branches with stout tactile setae, inner surface with long, thin-walled sensilla (figs. 241, 243, 244). Female maxilla as in male except palpomere II long, narrow at base, and wider apically, III shorter than II and gradually widened apically, IV longer than III and gradually widened apically with membranous apex bearing many minute sensilla. Labium simple, marginal setae not forked; hypopharynx with simple setae, ligula not notched (figs. 246, 247).

Pronotum (figs. 227, 230) elongate in male, rounded anteriorly with slightly produced, sharp posterior angles; widest anteriorly; with transverse groove along posterior margin; lateral margins sharply defined; hypomeron without slot; length/width about 1.5. Similar in female, but length/width about 1.3. Mesosternum small, triangular, rounded posteriorly. Mesepisternum elevated anteriorly. Mesepimeron with deep groove. Metasternum very long. Procoxae apically slotted. Tibial spur formula 0-2-2 (male), 1-2-2 (female). Metendosternite with narrow laminae (fig. 242), slightly posteriorly directed; furcal arms narrow. Scutellum simple, narrowed posteriorly (fig. 225). Elytron long, narrow, nearly covering abdomen, exposing half of apical tergite of male and up to two terga of female (figs. 225, 232); tongue-and-groove mechanism present, ending before apex; surface of each elytron with four costae and short sutural costa (fig. 232). Hindwing with relatively complete venation (fig. 226).

Abdomen with five sternites visible in both sexes (segments III–VII); abdomen robust, subcylindrical.

Male abdominal segment VIII small, poorly defined with long pair ventral struts, broad and fused anteriorly. Ninth segment with large, appendiculate paratergites bearing dense, short spines (figs. 237, 240). Aedeagus with small, transverse tegminal plate (fig. 238), small lateral lobes covered by fine setae (figs. 236, 238) and immoveably fused to tegminal plate, median lobe enlarged basally, narrowed apically, curving forward at base (figs. 236, 238, 239), tegminal struts long, wide.

Female abdominal segment VIII small,
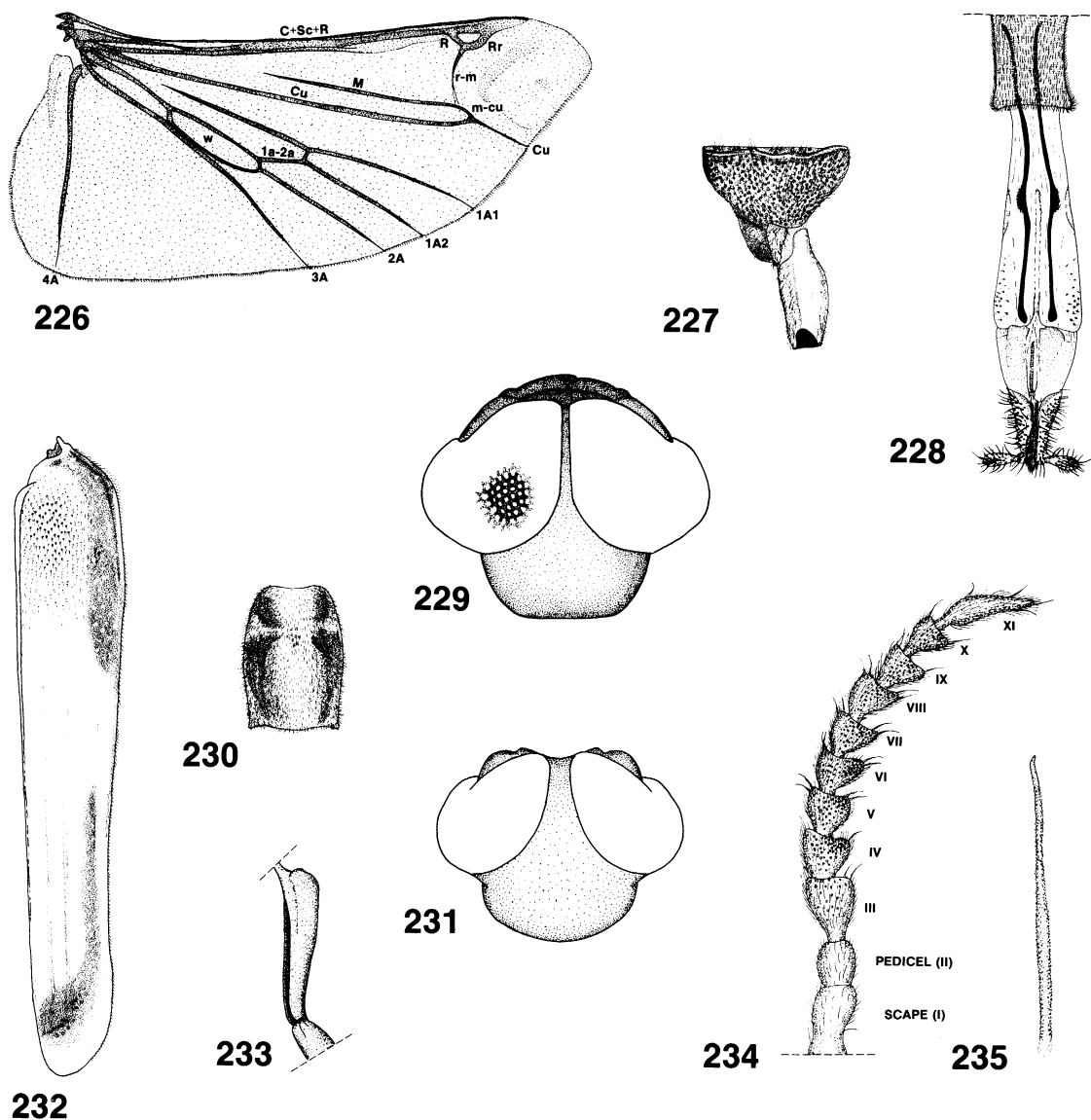
FIGS. 226–235. *Melittomma brasiliense.* **226.** Hindwing. **227.** Prothorax, lateral. **228.** Female genitalia. **229.** Head, male. **230.** Pronotum. **231.** Head, female. **232.** Elytron. **233.** Metepimeron and base of metacoxa. **234.** Antenna. **235.** Sclerotized process between basal parts of coxites of female genitalia.

lightly sclerotized, poorly defined, with long spiculum and long connecting membrane to genitalia. Genitalia (fig. 228) with distal part of coxites differentiated, more heavily sclerotized and setose than basal part; proctigeral baculi fused for most of length, narrowly divergent apically, more divergent basally.

Larval abdominal segment IX elongate, heavily sclerotized, cylindrical, and bearing deeply notched teeth around perimeter (fig. 245).
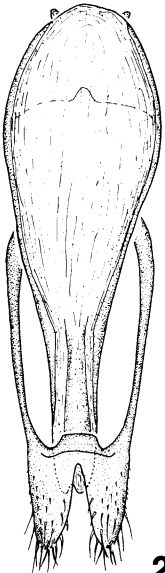
NOTES ON ADULT STRUCTURE AND DESCRIPTION OF LARVA, *MELITTOMMA SERICEUM* HARRIS: This North American species is noteworthy because of its generally plesiomorphic features, including its heavily sclerotized integument (figs. 249, 250), similar to *Protomelittomma* and *Melittommopsis,* and
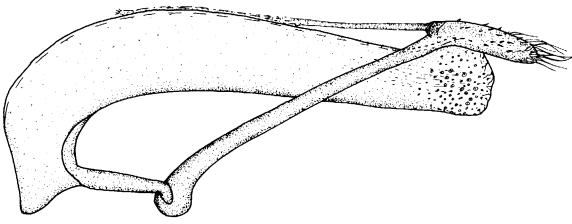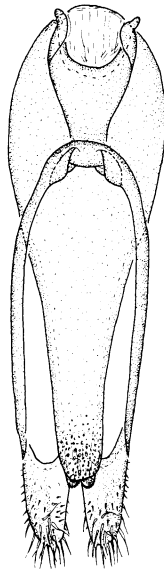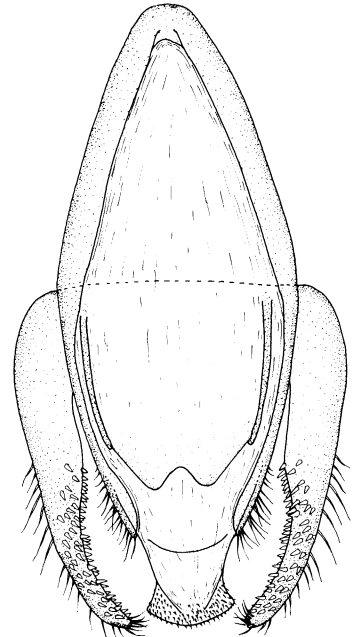
236   **237**

238   **239**   **240**

FIGS. 236–240. *Melittomma brasiliense* male genitalia and postabdomen. **236.** Aedeagus, lateral. **237.** Apex, appendiculate ninth paratergite. **238.** Aedeagus, dorsal. **239.** Aedeagus, ventral. **240.** Abdominal segments VIII and IX nested, ventral (note appendiculate paratergites of IX).

relatively short paratergites of abdominal segment IX of male (fig. 257). The maxillary palporgan, too, is less complex than in *brasiliense* (fig. 252). The apical setae of the labium are fringed (figs. 261, 264), and the distal part of the coxites of the female genitalia are heavily sclerotized and highly differentiated (fig. 265).

Late instar larva, length about 26.1 mm; body elongate, cylindrical. Color yellowish-brown, apex of abdominal segment IX very dark reddish-brown. Pronotum large, hood-like. Head broadly oval in shape. Labrum elongate, narrowed apically; epipharynx not examined in detail. Mandible robust; subapical notch present; mesal margin slightly

crenulate; molar region slightly enlarged, without armature. Maxilla with mala partially divided, mesal margin with long setae. Labium with broad ligula (fig. 261), apex with plumose setae (fig. 264), palpi as in figure 261. Leg with numerous spines and setae; tarsungulus bisetose (figs. 260, 262).

DISTRIBUTION: *Melittomma* is Pantropical in distribution, with species present in the Neotropics, Old World tropics, Australia, Malaysia, Indian subcontinent, Africa, and Madagascar (see also Simmonds, 1956). A single temperate species occurs in North America (*M. sericeum*).

FUNGUS HOSTS: Unknown.

ARBOREAL HOSTS AND BIONOMICS: *Melit-*
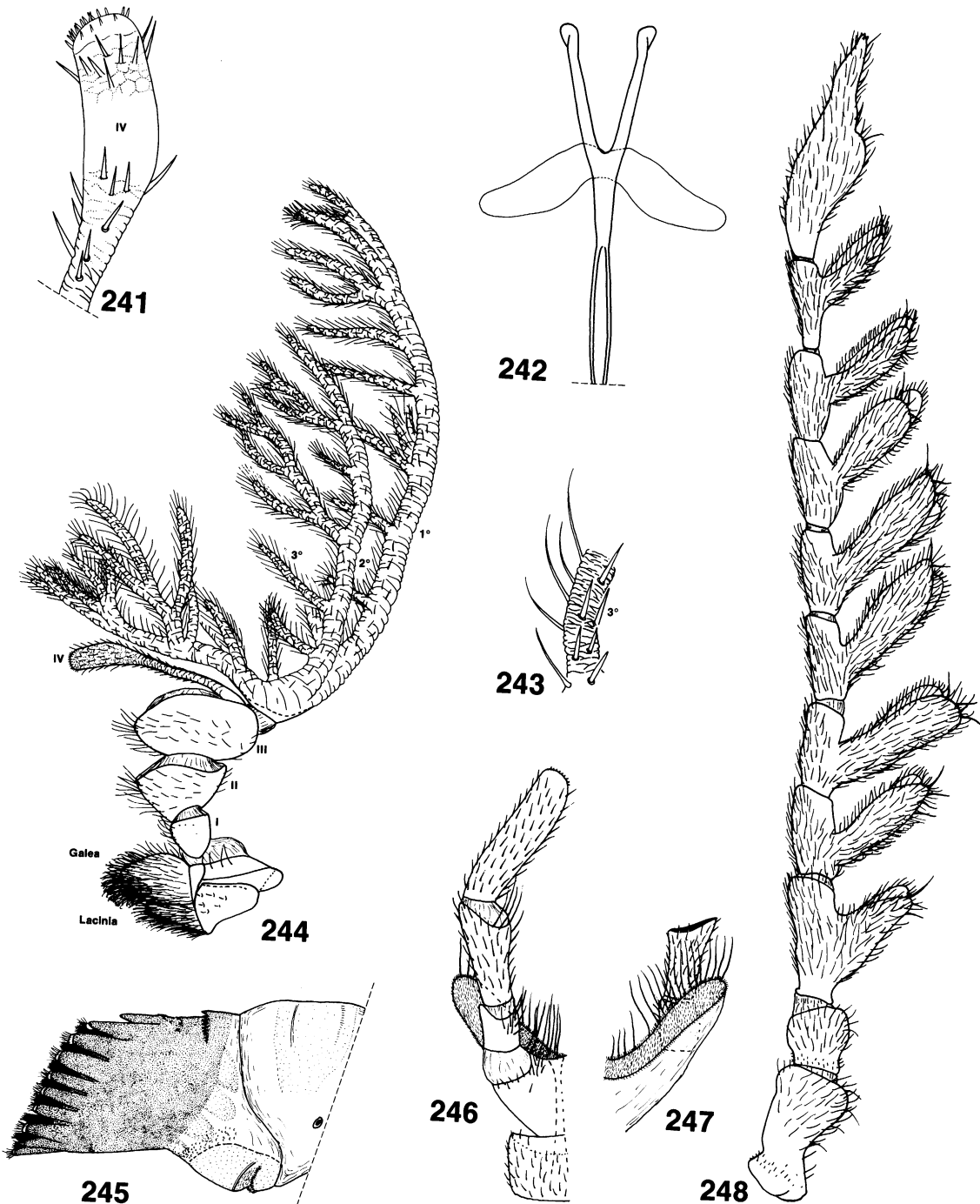
Figs. 241–248. *Melittomma brasiliense.* **241.** Apex palpomere IV of male (representative setae, sensilla and integumental detail only). **242.** Metendosternite apex. **243.** Portion of tertiary branch of palporgan. **244.** Maxilla, male. **245.** Abdominal apex of larva, lateral. **246.** Labium, ventral. **247.** Labium, dorsal. **248.** Antenna, female.

tomma sericeum has been reported from oak, chestnut, and elm (Blatchley, 1910; Sander-

son and Glenn, 1963; Peterson, 1961), and my wife has collected a larva from soft de-
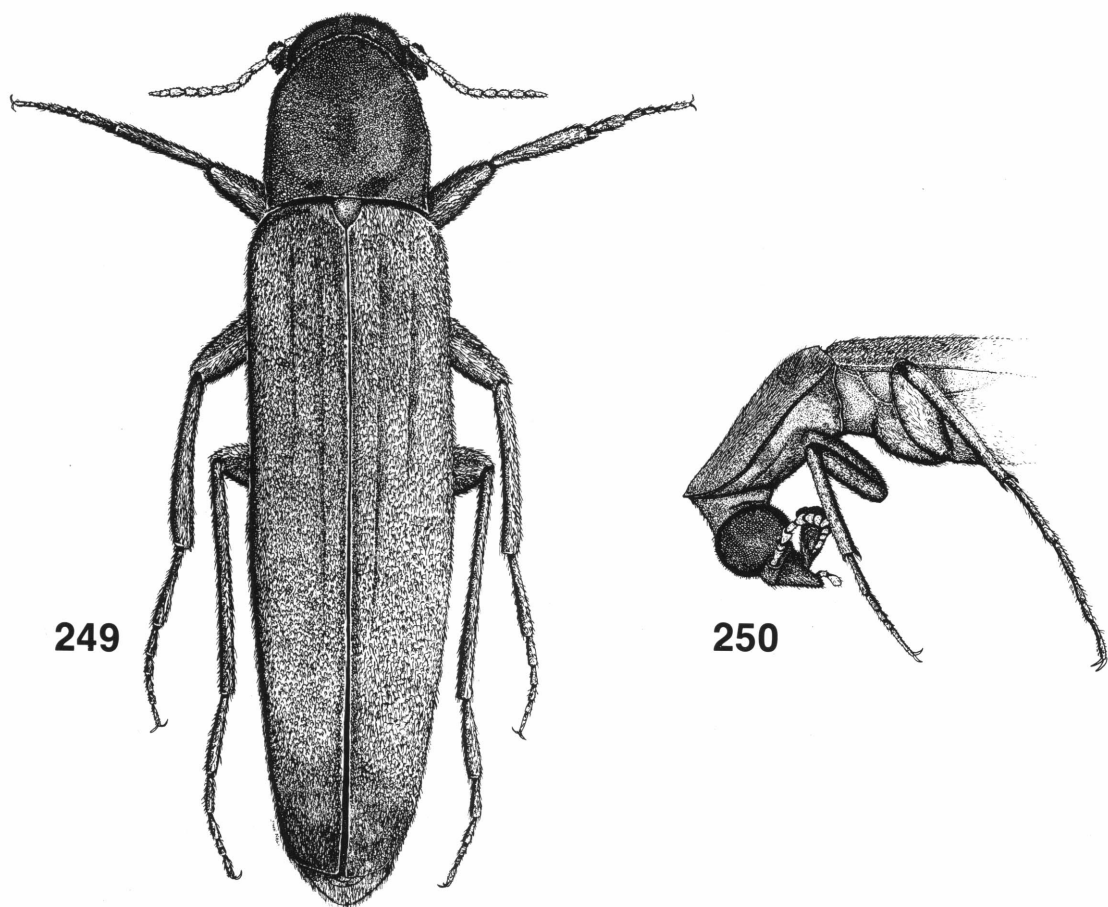
FIGS. 249, 250. *Melittomma sericeum* (Harris), male. By J. Nagy. **249.** Dorsal. **250.** Forebody, lateral.

cayed material along the top of an aged oak log lying on the ground in southeastern Ohio. Laporte (1832) reported the Central and South American species *M. brasiliense* from a bolete fungus, but no similar associations have been corroborated since and this record is no doubt incidental. Simmonds (1956) reported that a *Melittomma* species in West Africa was associated with the following trees: *Ficus exasperata, Funtumia africanum, Triplochiton scleroxylon,* and *Terminalia superba.* As noted under Economic Importance (above), *M. sericeum* was formerly a serious pest of the American chestnut, before its demise by blight in the early 20th century (see also Hopkins, 1894).

SPECIES INCLUDED: Seventeen species are included in *Melittomma,* in its new, restricted sense. *Melittomma curtipenne* Pic and *M. insulare* Fairmaire are removed to a new ge-

nus *Protomelittomma* (see below), and the former synonymized with the latter. *Melittomma ruficolle* Pic, *M. abdominalis* Pic, and *M. validum* Schenkling are removed to *Melittommopsis* Lane (see below).

1. *M. africanum* (Thomson), 1858, p. 82; Villiers, 1969a, p. 78 (Africa).

2. *M. albitarsis* Blair, 1936, p. 154 (India) [two male cotypes examined, British Museum (Natural History), London]. The larva was described by Gardner (1937).

3. *M. auberti* Fairmaire, 1891, p. 246; Villiers, 1969a, p. 81 (Africa) [type, female, examined, Museum National d'Histoire Naturelle, Paris].

4. *M. benitonum* (Fairmaire), 1901, p. 181; Villiers, 1969a, p. 80, 1969b, p. 78; Pic, 1949, p. 309 (as *costatum*), 1955, p. 133 (Africa) [type, female, examined, Museum National d'Histoire Naturelle, Paris].
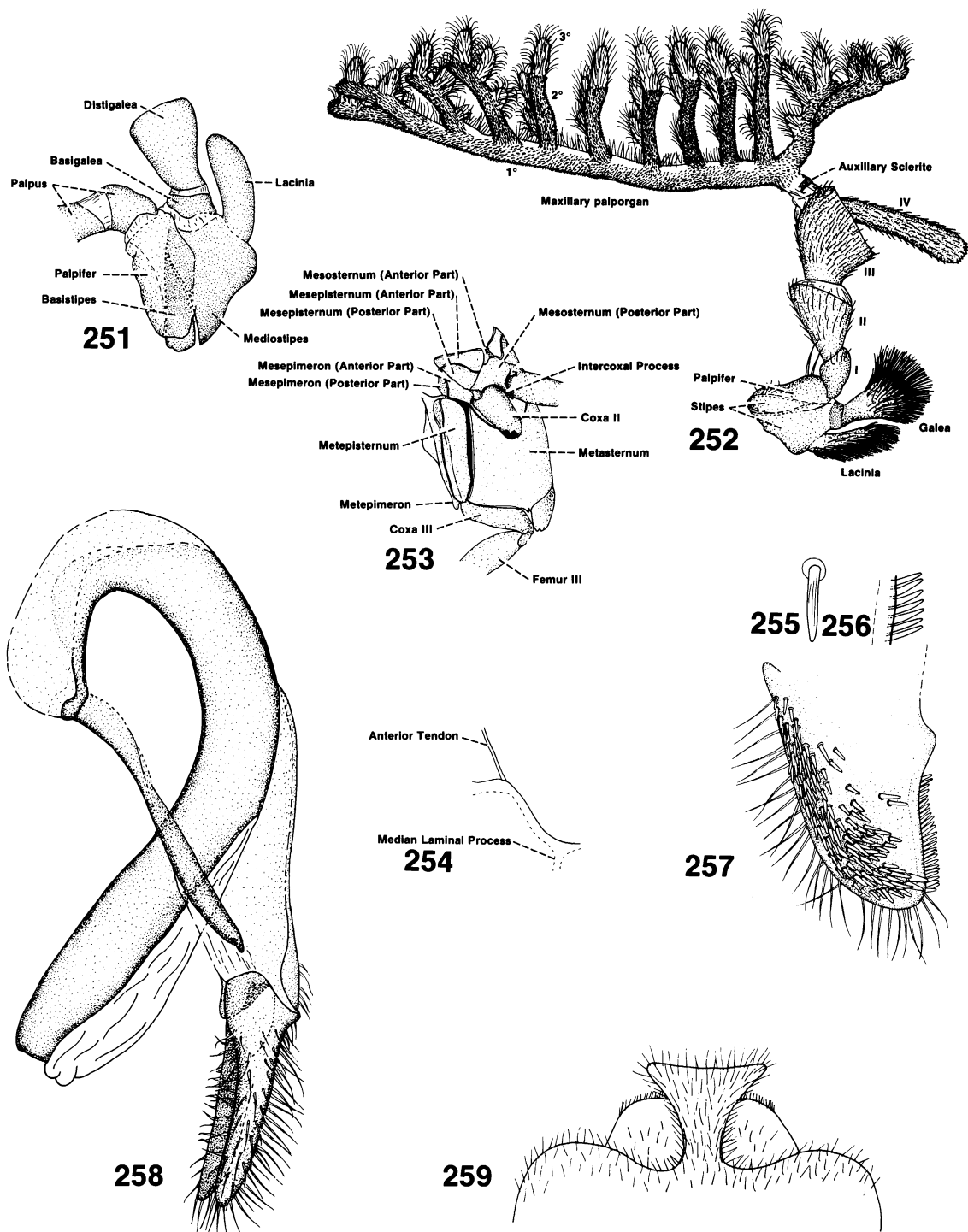
FIGS. 251–259. *Melittomma sericeum*. **251.** Maxilla base, male. **252.** Maxilla, male. **253.** Mesosternum, metasternum, and associated sclerites (ventrolateral). **254.** Anterior tendon insertion on metendosternite. **255.** Spine on surface of ninth paratergite of male. **256.** Marginal spines on ninth paratergite of male. **257.** Ninth paratergite, male (ventral). **258.** Aedeagus, lateral. **259.** Abdominal sternite VIII apex, male.
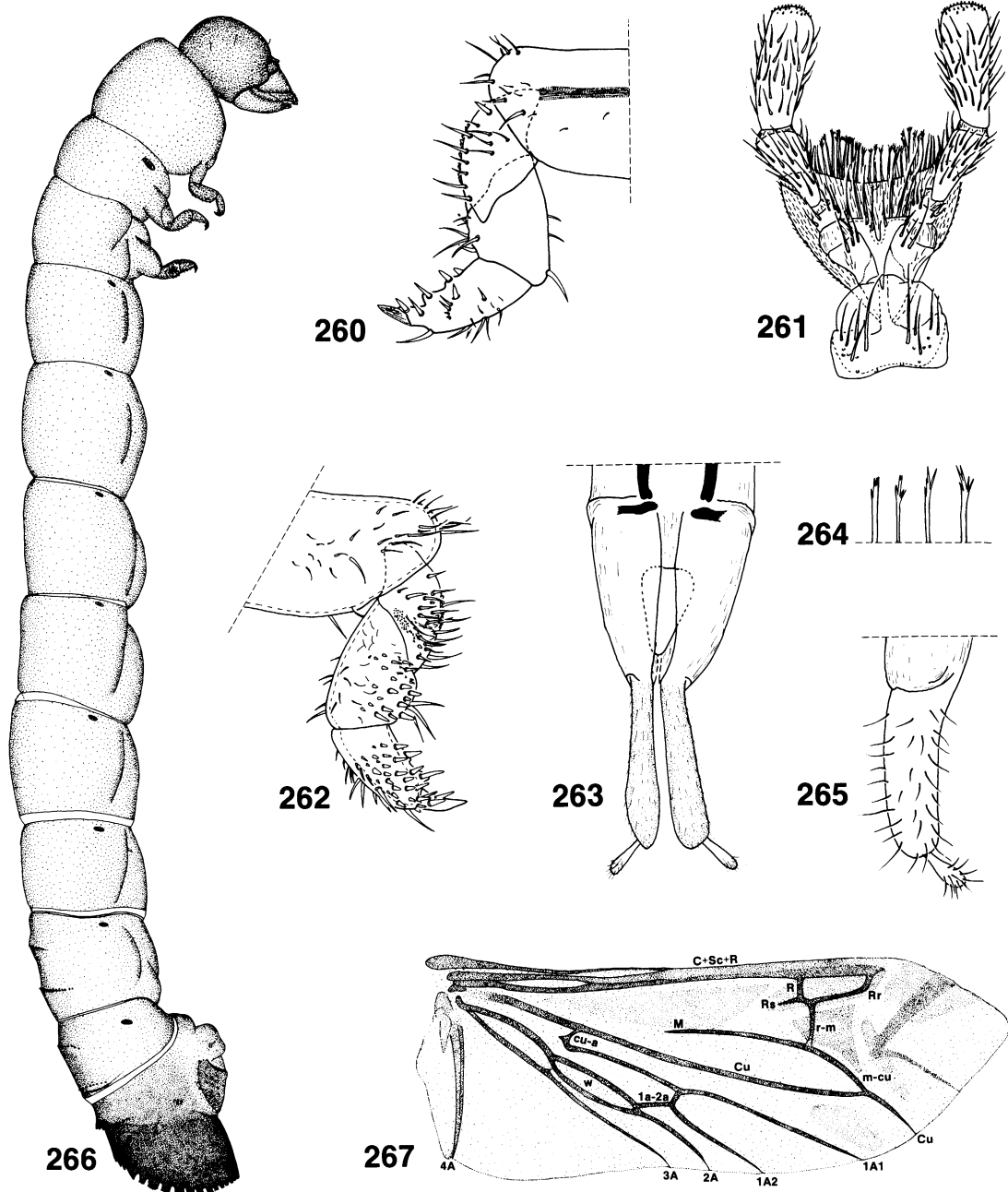
FIGS. 260–267. *Melittomma sericeum.* **260.** Front leg, mesal. **261.** Labium, ventral. **262.** Front leg, lateral. **263.** Female genitalia, ventral view of apex. **264.** Marginal setae of hypopharynx. **265.** Stylus and distal portion of coxite of female genitalia, ventral. **266.** Larva, lateral. **267.** Hindwing.

5. *M. brasiliense* (Laporte), 1832, p. 398; Lane, 1955 (Mexico, Central and South America) [type not seen; not found in Paris].

6. *M. coomani* Pic, 1945, p. 1 ("Tonkin": North Viet Nam) [type, female, examined,

Museum National d'Histoire Naturelle, Paris].

7. *M. javanicum* (Chevrolat), 1844, p. 57 [Java, Sumatra, New Guinea; including *javanum* (Kurosawa)].

8. *M. lateritium* (Fairmaire), 1887, p. 156; Lane, 1955, p. 150 (Surinam) [type not located in Paris; type of var. *ruficolle* Pic examined, similar to typical females of *brasiliense*; type of var. *binotatum* Pic examined, a female with dark spots on elytral apices].

9. *M. marginellum* (Schenkling), 1914, p. 320; Lane, 1955, p. 150 (Ecuador) [type, male, examined, Museum National d'Histoire Naturelle, Paris].

10. *M. oculare* (Nakane), 1963, p. 221 (see Kurosawa, 1985).

11. *M. perrieri* Fairmaire, 1901, p. 181 (Madagascar) [type examained, MNHN, Paris].

12. *M. pervagum* (Olliff), 1889, p. 87, transferred from *Hylecoetus*.

13. *M. philippensis* (Kurosawa), 1956, p. 82, new combination (Philippines). This species was included in *Neohylecoetus* by Kurosawa, here regarded as a junior synonym of *Melittomma*.

14. *M. pubicolle* Pic, 1944, p. 1 (Brazil) [type, male, examined, MNHN, Paris].

15. *M. sericeum* (Harris), 1841, p. 52 (North America).

16. *M. sicardi* Pic, 1939b, p. 32 (Madagascar) [type not located at MNHN, Paris].

17. *M. vigilans* (Lea), 1912, p. 467, transferred from *Hylecoetus* (Australia) [type, female, South Australian Museum, Adelaide, examined].

CLADISTIC RELATIONS: *Melittomma* is the sister group of *Melittommopsis* (see Cladistic Analysis below).

DISCUSSION: Not all the species included in *Melittomma* seem equally likely to withstand the test of time as valid ones, but most probably will. In particular, the variable and widespread South American species *brasiliense* is apparently represented by more than one name, as is a widespread Australasian one. Nonetheless, this is a relatively diverse genus, Pantropical in its distribution, and highly derived by comparison with the closely related taxa *Protomelittomma* and *Melittommopsis*. If the cleroidlike soft bodiedness in this and other taxa (especially hylecoetines) is convergent in the sense discussed by Crowson (1964) for short-lived, chemically active adult beetles, this derived nature of *Melittomma* may be important evidence of such a trend from heavily sclerotized, longer-lived adults to lightly sclerotized, shorter-lived ones.

Bionomic studies of *Melittomma* and related taxa should add important information relevant to such questions.

My restricted definition of *Melittomma* provides a tightly knit, monophyletic group within which species-level studies can progress. Special attention need be paid, however, to the primitive *sericeum* in North America and to the related taxa.

Melittomma brasiliense adults were chosen for the morphology description because the species is the type of the genus and it is common enough so that dissections could readily be made. Larval characters are exemplified by *M. sericeum*, however, because specimens were available for study that were credibly identified. Larvae were also discussed for *Melittomma* by Boving and Craighead (1931) and Peterson (1961).

Protomelittomma Wheeler, new genus
Figures 268–287

TYPE SPECIES: *Melittomma insulare* Fairmaire, 1893, p. 323. *Melittomma curtipenne* Pic (1939b, p. 32) is here synonymized with *insulare* [holotype, female, Museum National d'Histoire Naturelle, Paris, "Madagascar," examined].

DIAGNOSIS: Body elongate, parallel-sided, not dorsoventrally flattened; heavily sclerotized (fig. 268); color nearly black. Anterior part of mesosternum deeply emarginate; aedeagus with lateral lobes very large, elongate, with apicomedial spines (figs. 269, 270, 273). Distal portion of coxite of female genitalia membranous with basal sclerotized band (fig. 275); stylus with apical half membranous and setose, basal half sclerotized and glabrous (fig. 274). Larva with apex of abdominal segment IX crenulate; segment IX cylindrical, truncate, heavily sclerotized (fig. 286).

DESCRIPTION, *PROTOMELITTOMMA INSULARE* (FAIRMAIRE), NEW COMBINATION: Body elongate, robust; combined elytra wider than pronotum, broad, sinuate posteriorly; integument heavily sclerotized, rugose (fig. 268); with dense, shallow punctures and short, fine, golden recumbent setae. Color uniformly dark reddish-brown to nearly black. Length about 6–12 mm (males); 8–20 mm (females).

Head small, widest at eyes and sharply constricted behind eyes, forming distinct neck (fig. 280); eyes large, anteriorly emarginate;
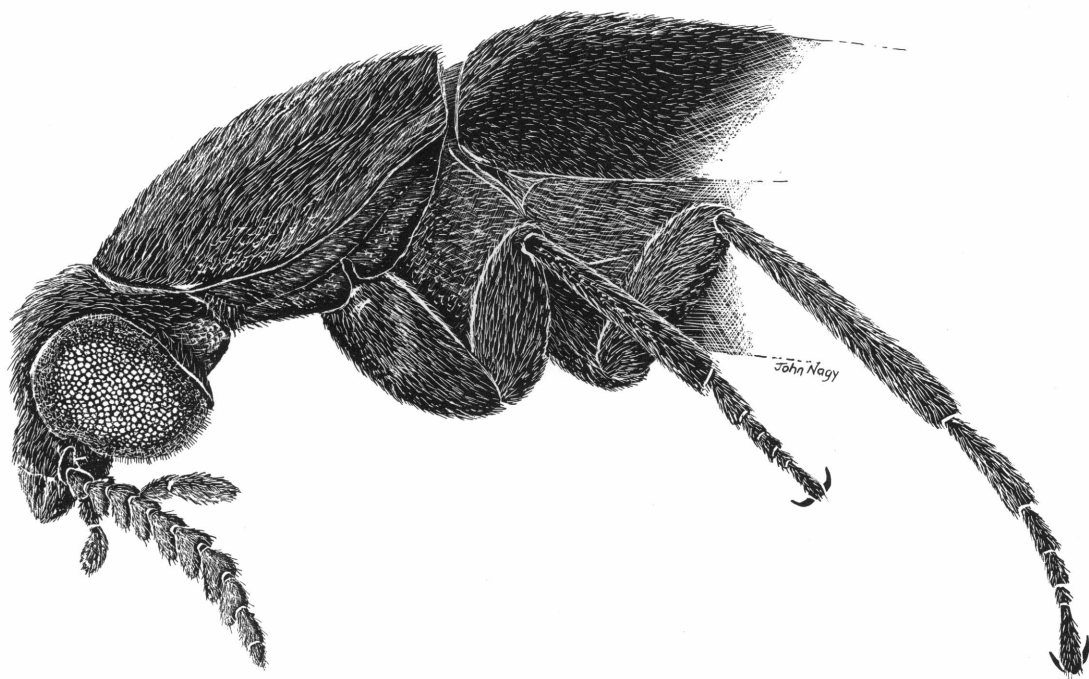
FIG. 268. *Protomelittomma insulare* (Fairmaire). Habitus of forebody by J. Nagy.

nearly contacting dorsally, contacting ventrally; gular sutures short, confined to "neck" region, slightly convergent anteriorly; facets coarse with erect setae between. Antenna (fig. 287) long, narrow, arising under frontal ridge; I large, narrowed basally; II smaller than I; III elongate, widened apically; IV–X serrate, asymmetrically produced mesally; XI long, narrowed apically; I–III with long, fine setae only; IV–XI with both long fine setae and short sensilla. Frontoclypeal suture absent. Labrum small, rounded, separated from clypeal region by wide membrane; epipharynx simple. Mandible (figs. 277, 278) short, broad, apex with apical dens and subapical dens; prostheca a dense patch of long setae; mola marked by short, fine subparallel rows of setae; small patch of setae present near base mesally. Maxilla (figs. 281, 282) with long, narrow, setose lacinia, broad, densely setose galea. Male palpus with small, relatively simple palporgan (fig. 281) and four palpomeres: I small, little longer than wide; II larger than I, broad; III larger than II, broadly rounded; IV elongate, nearly parallel-sided, with minute apical sensilla; palporgan with primary-secondary branching pattern. Female

maxilla similar, except palpomeres II and III more elongate and palporgan absent. Labium similar to that of *Melittomma brasiliense*.

Pronotum wide, rounded anteriorly, with posterior angles slightly produced; lateral margin sharply defined; hypomeron wide, with supracoxal slot; tergosternal suture deeply impressed. Prosternum long, with short, pointed intercoxal process. Procoxae slotted apically (fig. 272). Tibial spur formula 2-2-2 (male), 2-2-2 (female) (fig. 279). Mesosternum broad, triangular, with small anterior triangular area more heavily sclerotized. Mesepisternum with anterior area raised, set off from posterior part by sharp carina. Mesepimeron with lateral groove, set off by carina. Metasternum elongate. Scutellum simple, rounded apically, without carina. Elytron broad, nearly covering abdomen; tongue-and-groove mechanism present, complete to apex; with four longitudinal costae, and short, oblique sutural costa; epipleuron narrow, separated by carina. Hindwing similar to *Melittomma* species, venation relatively complete (cf. *M. sericeum*). Metendosternite (fig. 285) with lateral parts of furcal stalk fused in distal half; laminae short, transverse; an-
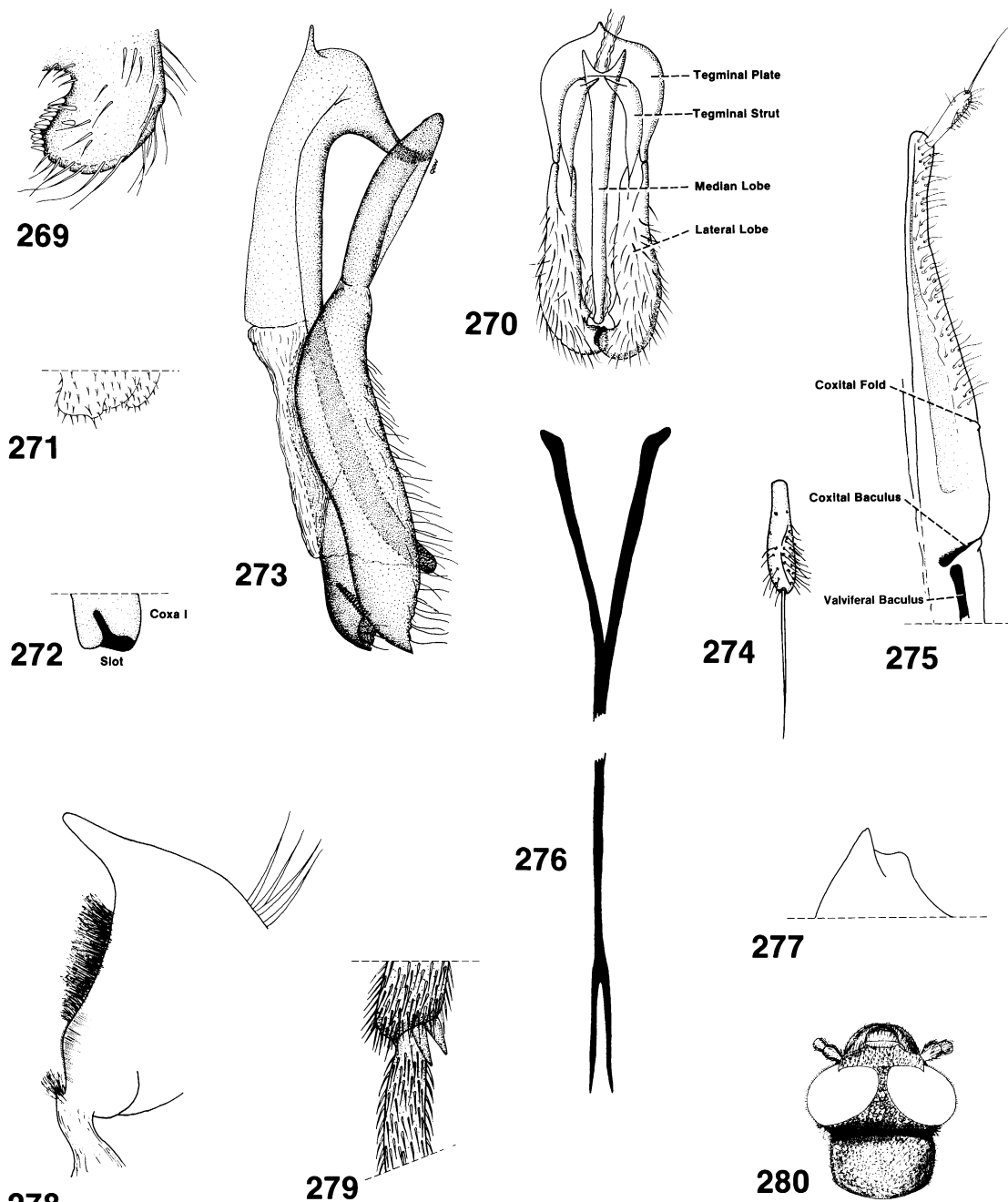
FIGS. 269–280. *Protomelittomma insulare.* **269.** Lateral lobe of aedeagus, apex (ventral). **270.** Aedeagus, ventral. **271.** Endophallus apex. **272.** Procoxa apex. **273.** Aedeagus, lateral. **274.** Stylus of female genitalia. **275.** Female genitalia, apical half (ventral). **276.** Proctigeral baculus of female genitalia, dorsal. **277.** Apex of mandible. **278.** Mandible, dorsal. **279.** Protibial spurs. **280.** Head, female (dorsal).

terior tendons inserted on short stalks on lamina near middle; furcal arms long, twisted, anteriorly directed.

Abdomen of male and female with sternites III–VII visible; abdomen broad, short relative to body length, cylindrical. Apex of
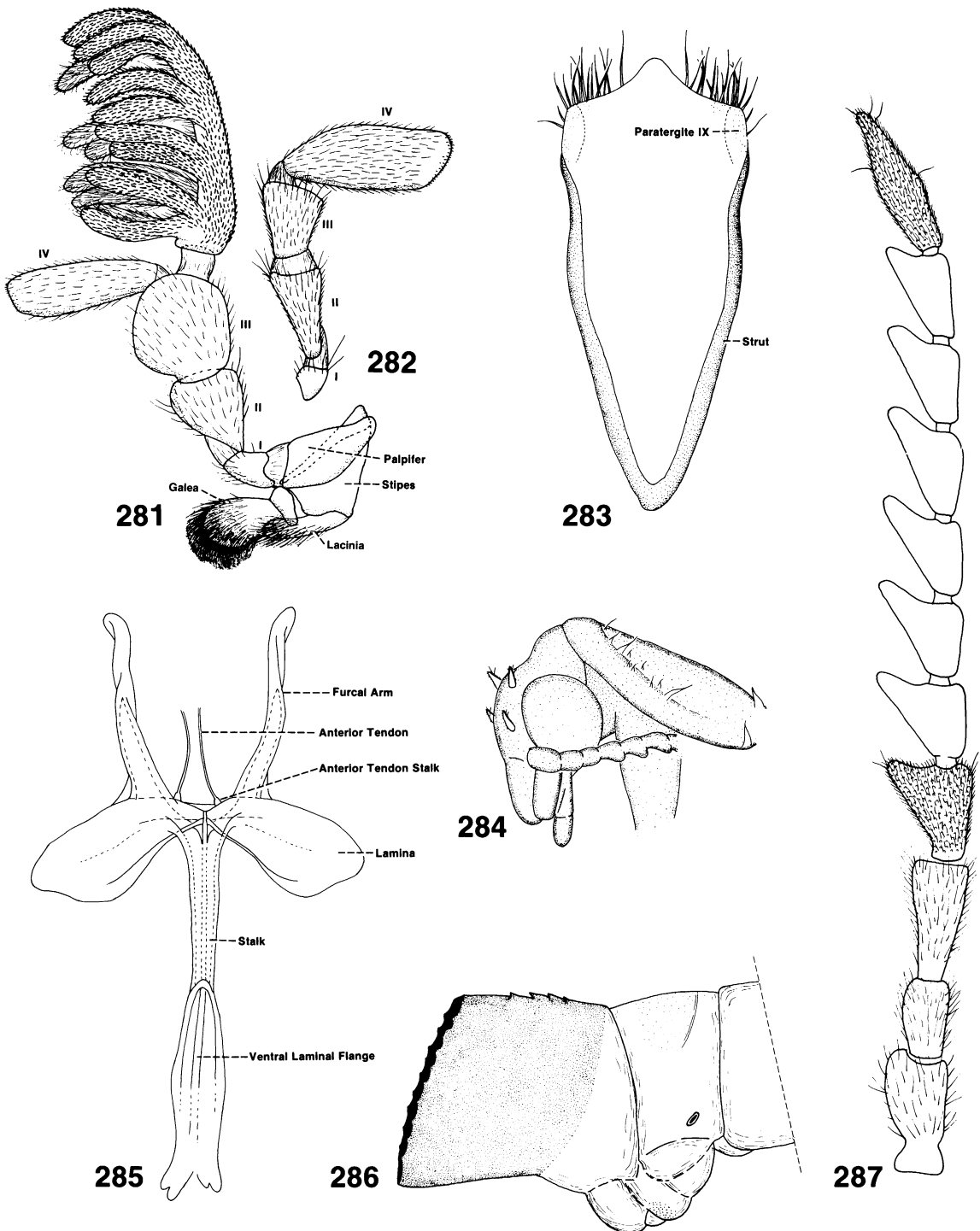
FIGS. 281–287. *Protomelittomma insulare.* **281.** Maxilla, male. **282.** Maxillary palpus, female. **283.** Abdominal segment IX, male. **284.** Pupal head and pronotum. **285.** Metendosternite. **286.** Larval abdomen, apex. **287.** Antenna, male.

tergite VII visible, remaining terga covered by elytra.

Male abdominal segment VIII lightly sclerotized, telescoped within VII; sternite emarginate medially; IX reduced, paired struts fused apically (fig. 283). Genitalia with large, elongate lateral lobes (figs. 270, 273), apically curved mesally and bearing row of broad spines (fig. 269), surface covered by long, fine setae. Median lobe long, narrow (fig. 270). Tegminal struts short, broad. Tegminal plate small, transverse, basal. Endophallus with minute microtrichiae (fig. 271).

Female with abdominal segment VIII simple, lightly sclerotized, narrowed posteriorly. Genitalia long, narrow, lightly sclerotized (fig. 275). Proctigeral baculi narrow, moderately sclerotized, nearly parallel apically, proximal at middle, widely divergent basally. Valviferal baculi widely separated, nearly parallel, heavily sclerotized. Coxital baculi narrow, oblique. Basal part of coxite short, wide; distal part long, narrow, apically attenuate, membranous, covered by long setae; mesal margin on dorsal surface heavily sclerotized. Styli long, narrow, membranous; apical half covered by dense setae, bearing single, long apical seta (fig. 274).

Larva (late instar, about 25.3 mm long) elongate, somewhat flattened ventrally, with prominent lateral folds; color (in ethanol) greyish-white, with yellowish-brown areas on pronotum and lateral folds, yellowish asperites anterior to anus on venter of X, and yellowish grading to chestnut brown on segment IX. Labrum small, simple, lobate. Epipharynx with dense, fine sensilla, apex with very dense sensilla and three stout setae on each side. Mandible short, robust; single apical dens; mola narrow with parallel microridges. Maxilla resembling *Lymexylon*; mala membranous, with rows of mesal setae; palpus with apical segment small. Labium with simple lobate ligula covered with dense, fine setae. Hypopharynx membranous with microtrichiae and fine setae apically; hypopharyngeal sclerome present, short with lateral extensions. Antenna minute with apical two segments sclerotized. Leg with tarsungulus sharply pointed, bisetose. Abdominal segment IX heavily sclerotized, cylindrical, truncate; with apical margin crenulate (fig.

286). See discussion of larvae by Gahan (1908) and Brown (1954).

Pupa with fimbriate spines on head, large spines near base of pronotum (fig. 284).

SPECIES INCLUDED: A single described species is assigned to the genus, *P. insulare,* which occurs in the Seychelles and in Madagascar. I have seen a single female specimen from Sumatra that has biramous antennae, similar to those of *Melittomma brasiliense* (Zoologisches Museum, Berlin), that is provisionally assigned to *Melittomma,* but which could belong to *Protomelittomma.* Also, *Melittomma curtipenne* Pic is here considered synonymous with *P. insulare.*

CLADISTIC RELATIONS: *Protomelittomma* is the hypothesized sister group of *Melittommopsis + Melittomma.*

DISTRIBUTION: It is possible that *insulare* is native to Madagascar, and introduced by humans into the Seychelles where it has had massive economic impact on the coconut industry (Brown, 1954; Simmonds, 1956).

FUNGUS HOSTS: No mycosymbionts are known. Research on the mycoflora of the larval tunnels of *insulare* failed to make such an association, and a diverse flora of fungi, yeast, and bacteria was reported (Brown, 1954).

ARBOREAL HOSTS AND BIONOMICS: All known associations are with palms, including both cultivated and wild species. Recorded hosts are in the genera *Sterensonia, Nephrosperma, Deckenia,* and *Roscheria* (Vessey-Fitzgerald, 1941; Brown, 1954; Simmonds, 1956).

DISCUSSION: *Protomelittomma* resembles *Melittomma sericeum* and *Melittommopsis* species in being heavily sclerotized, cylindrical in body form, and darkly pigmented—suggesting that this was the groundplan for the *Melittomma* Complex, if not for the family (see Cladistic Analysis).
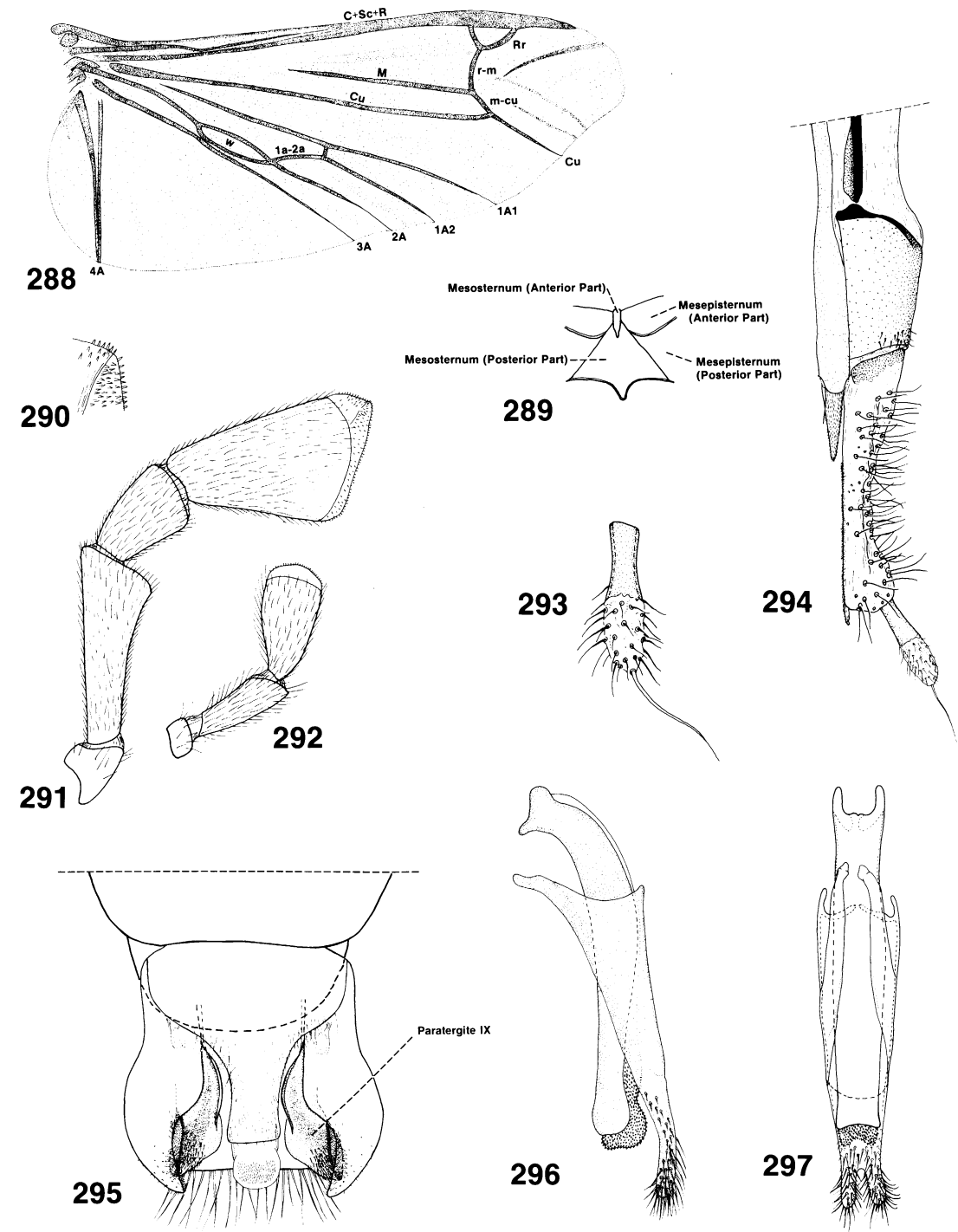
Genus *Melittommopsis* Lane
Figures 288–298

Melittommopsis Lane, 1955, p. 152.

TYPE SPECIES: *Melittommopsis juquiensis* Lane, 1955, p. 152.

DIAGNOSIS: With characters of Melittomminae, *Melittomma* Complex (see key and

FIGS. 288–297. *Melittommopsis* species (Brazil). 288–294. Female. **288.** Hindwing. **289.** Mesosternum and associated sclerites. **290.** Maxillary palpomere IV, apex. **291.** Maxillary palpus. **292.** Labial palpus. **293.** Stylus. **294.** Female genitalia, apical half. 295–297. Male. **295.** Abdominal segments VIII and IX, ventral. **296.** Aedeagus, lateral. **297.** Aedeagus, ventral.

Cladistic Analysis); male maxillary palporgan present, with primary trunk and secondary branches ending in short "thumb" and elbowed process (fig. 298); male postabdomen with enlarged ninth paratergites and enlarged, modified eighth paratergites (fig. 295); aedeagus similar to *Melittomma*, with cylindrical lateral lobes (figs. 296, 297); apical maxillary and labial palpomeres of female securiform (figs. 291, 292); anterior part of mesosternum long and narrow; distal part of coxite membranous, narrow, basal band sclerotized, apical half of stylus membranous and setose, basal half sclerotized and glabrous (figs. 293, 294).

DESCRIPTION, *MELITTOMMOPSIS* SPECIES[3]: Body elongate, robust, more or less cylindrical in form; color (female specimen) very dark, nearly black; integument heavily sclerotized, minutely ruguose, with numerous shallow punctures and fine yellowish recumbent setae. Eyes large with fine facets, widely separated dorsally and separate ventrally. Gular sutures short, slightly divergent posteriorly. Antenna inserted under frontal ridge; antenna short [segments IV–X slightly asymmetrically produced, particularly in second male (Geneva: see footnote)], subserrate in female. Frontoclypeal suture absent. Labrum small, transverse, narrowed anteriorly; dense patch of apical setae on epipharynx. Mandible not seen in detail, similar to *Protomelittomma*, with two apical dens, prostheca present but reduced to patch of microtrichiae. Maxilla (female) with broad lacinia, and very broad galea; palpus long (fig. 291); I short, elongate in shape; II long, broader apically; III much shorter than II; IV large, securiform, apex

membranous, covered by short, pointed sensilla (fig. 290). Labium with ligula lacking medial notch; hypopharynx simple, with very long, dense setae; apical palpomere (III) securiform (fig. 292).

Pronotum elongate, slightly narrower than combined width of elytra; slightly sinuate posteriorly; posteromedial area raised ("humped"); with sharp margin, extending entirely around pronotum. Hypomeron with supracoxal slot; tergosternal suture obscure. Prosternum long anterior to procoxae, with short intercoxal process. Mesosternum with broad, triangular posterior part; small, elongate, posteriorly pointed anterior part; and elevated anterior area (fig. 289). Mesepisternum with raised anterior area, separated by sharp carina (fig. 289). Mesepimeron with depressed lateral area receiving elytral epipleuron, not set off by carina. Metasternum without medial emargination posterior to mesocoxal depressions; mesocoxal depressions separated from metasternum by carinae. Procoxa slotted. Tibial spur formula 1-2-2 male/1-2-2 female. Scutellum simple. Elytron similar to *Protomelittomma*, but third carina and sutural carina not evident.

Male (about 11.6 mm from posterior end to anterior margin of pronotum) nearly black, with pronotum and procoxae paler yellowish-brown. Maxilla with lacinia slightly smaller than galea; each with numerous setae, more apically; I small, subquadrate; II large, wide; III large, wider than II; IV long, parallel-sided, blunt; palporgan similar in branching pattern to *Hylecoetus* with primary trunk (including short primary segment with about 4 pair secondary branches and longer primary segment with about 13 pair secondary branches) and secondary branches; each secondary branch with apex elbowed and with short "thumb" more nearly in line with plane of basal part of branch (fig. 298). Hindwing as in figure 288. Metendosternite not examined. Abdomen with five visible sternites in male and female; abdomen robust, broad, cylindrical.

Male postabdomen (fig. 295) with sternum VIII elongate, narrowed and truncate apically; tergite VIII broad, relatively short; VIII with large subappendiculate paratergites with spines on apicomesal surfaces. Tergite IX small, truncate; sternite not evident; parater-
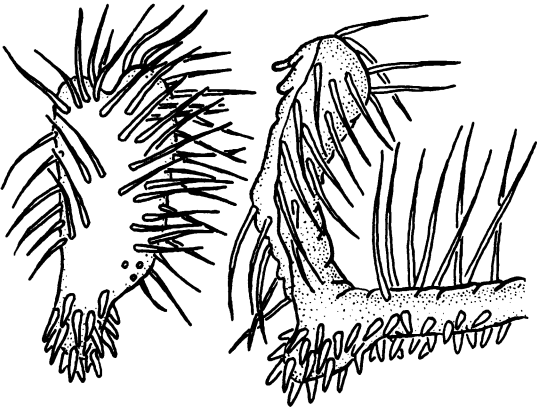
FIG. 298.   *Melittommopsis* species (Brazil), two views of apex of secondary branch of maxillary palporgan of male.

gites lobate, setose, and spinose, not appendiculate; lateral sclerotizations parallel to paratergite VIII might correspond to sternite IX [second male (Geneva) with paratergite VIII sharply hooked apically]. Aedeagus (figs. 296, 297) similar to *Melittomma,* with lateral lobes cylindrical.

Female genitalia (figs. 293, 294) long, narrow, lightly sclerotized; proctigeral baculi long, narrow anteriorly, broader posteriorly (distally), separate and more or less parallel. Valviferal baculi long, parallel, slightly divergent near middle. Coxital baculi transverse, oblique laterally. Basal part of coxite short, broad, sclerotized with few short setae near apex; coxital fold wide; narrow area at base of distal part of coxite sclerotized, but most of long distal part membranous, unpigmented, and setose. Styli long, slightly clavate, basal half sclerotized, without setae, apical half membranous, setose, with single long seta at apex.

Larva unknown.

DISTRIBUTION: All known *Melittommopsis* are South American; areas include Bolivia, Brazil, and Peru.

FUNGUS HOSTS: Unknown.

ARBOREAL HOSTS AND BIONOMICS: Unknown.

SPECIES INCLUDED: Five species are included in this genus.

1. *Melittommopsis juquiensis* Lane, 1955, p. 152 (Brazil).

2. *Melittommopsis nigra* Lane, 1955, p.

156 (Brazil) [paratype, female, British Museum (Natural History), London, examined].

3. *Melittommopsis validum* (Schenkling), 1914, p. 321, new combination (Brazil). I have not seen the type specimen of *validum.* However, three male specimens in the Museum National d'Histoire Naturelle, Paris, identified as *validum* by A. Villiers are *Melittommopsis* of quite large size. One specimen is labeled from the collection of L. Fairmaire (dated 1906, from "Brasilia"; one is from the Oberthur collection (from "Musaeo Mniszech," labeled "Rio J."); and the third is labeled "Brasil" (and "ex Musaeo Mniszech"), and is also in the Oberthur collection.

4. *Melittommopsis abdominale* (Pic), 1936, p. 3, new combination (Peru, Bolivia?). I have examined the type female specimen of this species in the Museum National d'Histoire Naturelle (Paris) with the following labels: "Marcapata, Peru"/"Hylecoetus sp."/ "mihi"/"TYPE"/"abdominale n.sp." This is a typical *Melittommopsis,* except that the basal two abdominal sternites are black, and the apical three are yellowish-orange. Also, there is a second specimen, not a type, in Paris with identical coloration and the following labels: "Bolivie Farinas"/"Museum Paris ex coll. R. Oberthur."

5. *Melittommopsis ruficolle* (Pic), 1936, p. 2, new combination. The type specimen appears to be a female and is in the Museum National d'Histoire Naturelle (Paris), with the following labels: "Te 402 H. n."/"ryne"/ "TYPE"/"Museum Paris ex coll. R. Oberthur"/"Melittomma ruficolle." This species has a pale yellowish-orangish colored pronotum, but is otherwise a typical *Melittommopsis.*

CLADISTIC RELATIONS: *Melittommopsis* is the sister group of the Pantropical genus *Melittomma.*

DISCUSSION: The genus *Melittommopsis* is least well defined and least understood of all Lymexylidae genera. No species are yet known from large series of specimens, only two males are known, and no larvae have been associated with adults. Because of the paucity of material, no complete disarticulations were made.

In general appearance, *Melittommopsis* species closely resemble *Melittomma seri-*

ceum and *Protomelittomma insulare,* but the resemblance is based on what I perceive as a plesiomorphic body form. Enlargement of the ninth paratergite supports a relationship close to *Melittomma,* but the male postabdomen is highly autapomorphic in its structure and when additional males are available for dissection more careful studies should be done to work out homologies of these structures.

CLADISTIC ANALYSIS

Cladistic analysis provides a method of estimating the relative recency of common ancestry shared among taxa (Hennig, 1966). The following scheme represents a general statement about the interrelationships of world genera of Lymexylidae, and is not to be read as or confused with a phylogenetic tree. The cladogram does, of course, represent the best possible approximation of phylogenetic "knowledge" and limits the possible phylogenies to those consistent with it. The analytical method has been discussed by Eldredge (1979), Eldredge and Cracraft (1980), Nelson and Platnick (1981), Platnick (1979), and Wheeler and Blackwell (1984).

My presentation of the cladistic analysis consists of two sections: (1) character analysis, and (2) monophyletic groups. The analysis of characters was done primarily by outgroup comparison, initially with taxa listed in Appendix A and later by functional outgroup comparisons within the family (Watrous and Wheeler, 1981; Wheeler, 1981). Characters were also checked by applying this same polarity information in the form of a hypothetical ancestor bearing all plesiomorphies and by the Lundberg rooting method using David Swofford's PAUP (Phylogenetic Analysis Using Parsimony) computer program at Cornell University.

The initial analysis of monophyletic groupings was done by hand (Wheeler and Blackwell, 1984). The PAUP program, using the two rooting methods mentioned above, also generated isomorphic cladograms and provided some additional information that is incorporated into the discussion that follows. While it is not theoretically necessary to know most closely related taxa as an outgroup in order to polarize characters (Watrous and Wheeler, 1981), our knowledge of the Cucujiformia in general is so poor as to make selection of representative taxa of Cleroidea, Tenebrionoidea, and especially Clavicornia difficult. Aspects of the analysis of characters that follow are therefore compromises under the circumstances; what some hypotheses lack in relative objectivity is mediated by explicit statements of assumed polarities.

Some conventions followed below should be mentioned for clarity. First, numbers in parentheses refer to characters listed in table 3 and also in the cladogram. "Character" is here used in reference to a novel attribute and all of its subsequent modifications, i.e., an apomorph (Platnick, 1979). When reference is made to the plesiomorphic analogue of a character, a number in brackets [ ] refers to the column of plesiomorphic states in the table of apomorphs (characters). Some characters that were not used in the analysis but which seem to show a trend of change within the family are mentioned; many of these are likely to be of value to species-level studies within individual genera. The section on monophyletic groups uses the same character number codes to summarize both autapomorphs and synapomorphs.

CHARACTER ANALYSIS

BODY FORM: A general elongation of the body form is evident within the genus *Melittomma,* in *Atractocerus,* and to a lesser extent in *Lymexylon* and *Australymexylon.* The ancestral form is putatively shorter and more or less cylindrical, as in *Melittomma sericeum* or *Protomelittomma insulare.* Dorsoventral flattening of the body also seems to have occurred within the family, notable in *Hylecoetus, Lymexylon,* and *Australymexylon,* with the plesiomorphic analogue apparent in the taxa cited above.

SCLEROTIZATION: Soft-bodiedness (1), as

TABLE 3
Hypothesized Apomorphs and Plesiomorphic States

No.	Apomorph	Plesiomorphic State
1	Lightly sclerotized	Heavily sclerotized
2	Head narrowed behind eyes, forming "neck" (fig. 229)	Head broadly rounded behind eyes, not forming "neck" (figs. 2, 124)
3	Eyes large, separated by less than single eye width (figs. 153, 229)	Eyes small, separated by at least single eye width (figs. 2, 82, 188)
4	Eyes emarginate anteriorly (figs. 229, 280)	Eyes entire (fig. 2)
5	Epicranial pit present (figs. 2, 30)	Epicranial pit absent
6	Antenna serrate (figs. 189, 190, 203, 204)	Antenna filiform (fig. 97)
7	Antenna short, spindlelike (fig. 145)	Antenna elongate, narrow
8	Palporgan present in male (fig. 7)	Palporgan absent in male
9	Palporgan present in female (fig. 140)	Palporgan absent in female
10	Palporgan (male) with tertiary branches (figs. 90, 138)	Palporgan with secondary branches only (fig. 7)
11	Palporgan with tertiary branches arranged in paired, parallel rows (fig. 138)	MPO without tertiaries paired in parallel rows
12	Pronotum without sharp, lateral margin	Pronotum with sharp, lateral margin
13	Hypomeron of prothorax with slot (fig. 198)	Hypomeron without slot
14	Procoxa with apical slot (fig. 272)	Procoxa simple
15	Tibial spur formula 0-1-1/0-1-1	TSF 2-2-2/2-2-2
16	TSF 0-0-0/0-0-0 or 0-1-1	TSF 2-2-2/2-2-2
17	TSF 0-2-2/1-2-2	TSF 2-2-2/2-2-2
18	Mesosternum elevated anteriorly	Mesosternum simple (fig. 42)
19	Elevated anterior part of mesosternum deeply emarginate posteriorly	Elevated area with shallow emargination posteriorly
20	Elevated anterior part of mesosternum long, narrow, pointed posteriorly (fig. 289)	Elevated area broad
21	Anterior part of mesepisternum elevated (fig. 196)	Mesepisternum not anteriorly elevated
22	Elevated anterior part of mesepisternum separated from posterior part by carina	Carina absent
23	Mesepimeron with depressed lateral area receiving elytral epimeron	Mesepimeron without depression
24	Mesepimeral depression separated by carina	Carina absent
25	Scutellum with median keel (fig. 33)	Scutellum simple, or with lateral areas raised
26	Scutellum with lateral grooves receiving elytra	Scutellum simple
27	Alar ridge modified into elevated process (fig. 163)	Alar ridge simple (fig. 96)
28	Elytron not extending to metacoxa ("brachelytrous")	Elytron long or slightly shortened only
29	Tongue-and-groove mechanism absent along elytral suture	Tongue-and-groove present, but may end before apex
30	Brachial cell absent (fig. 127)	Brachial cell present (fig. 41)
31	Wedge cell absent (fig. 127)	Wedge cell present (fig. 41)
32	Spurious base of M absent (fig. 127)	Spurious base of M present (fig. 41)
33	1a-2a crossvein incomplete (figs. 99, 127)	1a-2a crossvein complete (fig. 41)
34	1A fused with 2A (fig. 127)	1A separate from 2A, arising spuriously
35	Spurious Rs absent	Spurious Rs present
36	cu-1a crossvein absent	cu-1a crossvein present
37	Extra 1A1-1A2 crossvein present (fig. 99)	Single 1A1-1A2 crossvein present
38	1a-2a crossvein absent (fig. 127)	1a-2a crossvein present
39	Wing folded longitudinally only (fanlike)	Wing folded transversely and longitudinally
40	Furcal arms of metendosternite anteriorly directed (figs. 155, 164, 167)	Furcal arms anterolaterally directed (figs. 47–49)
41	Anterior tendons separated (figs. 92, 285)	Anterior tendons proximal (figs. 48, 49)
42	Anterior tendons arise on furcal arms (fig. 210)	Anterior tendons arise between arms (fig. 285)
43	Laminae short and wide (figs. 242, 285)	Laminae longer, narrower (figs. 48, 210)
44	Abdominal segment VIII telescoped within VII	VIII exposed
45	Abdominal segment II absent (or nearly so)	II present

<div align="center">TABLE 3—(Continued)</div>

No.	Apomorph	Plesiomorphic State
46	Male with one more exposed abdominal segment	Male and female with same number exposed
47	Coxital fold present; coxite divided into basal and distal parts on ventral surface (figs. 54–56)	Coxital fold absent
48	Spurious baculus present (fig. 161)	Spurious baculus absent
49	Coxite distally thickened, leathery	Coxite membranous
50	Proctigeral baculi proximal, at least near middle	Proctigeral baculi separate and parallel
51	Proctigeral baculi fused along part of length (fig. 276)	Proctigeral baculi separate
52	Lateral lobes asymmetrical (fig. 59)	Lateral lobes symmetrical (fig. 238)
53	Abdominal segment IX of male asymmetrical (fig. 58)	IX symmetrical
54	Abdominal sternite VIII of male with large setose pads (figs. 211, 213)	VIII simple
55	Paratergites of male abdominal segment IX long, appendicule (figs. 240, 257)	Paratergites of IX small, not appendiculate
56	Lateral lobes greatly enlarged (figs. 148, 151)	Lateral lobes smaller
57	Median lobe small relative to lateral lobes (fig. 214)	Median lobe relatively large (fig. 194)
58	Tegminal struts reduced (figs. 150, 214)	Tegminal struts long (figs. 57, 236)
59	Tegminal plate bifid (fig. 152)	Tegminal plate simple
60	Tegminal plate small (fig. 238)	Tegminal plate large (fig. 57)
61	Lateral lobes long, stout with apicomesal row of spines (fig. 273)	Lateral lobes smaller, simple, lobate
62	Mesal margin of larval mala membranous and bordered by long setae (fig. 187)	Mala not membranous with long setae
63	Ocelli absent in late instar	Ocelli present in late instar
64	Tarsungulus pleurisetose (figs. 64, 176)	Tarsungulus bisetose (fig. 262)
65	Tarsungulus covered by short spines (fig. 219)	Tarsungulus without spines
66	Abdominal segment IX of larva long, narrow, heavily sclerotized with dorsal teeth (fig. 63)	IX shorter, broad
67	Abdominal segment IX of larva large, bulbous, semi-membranous (figs. 119, 178)	IX truncate
68	Apex of larval segment IX with asperites (fig. 178)	IX without asperites
69	Apex of larval segment IX cylindrical, truncate, and heavily sclerotized apically (fig. 286)	IX truncate, but shorter and less sclerotized
70	Rim of IX with teeth (fig. 245)	Rim of IX without teeth (fig. 286)
71	Lateral lobes short, broad, truncate and widely separated (fig. 111)	Lateral lobes rounded, proximal
72	Apex of IX with toothlike process (figs. 118, 119)	Apex of IX without process
73	Labrum with 3 lateral setae (fig. 114)	Labrum with 2 setae (fig. 62)
74	Lateral lobes with 2 or 3 large "teeth" mesally (fig. 151)	Lateral lobes without large teeth
75	Palporgan lost	Palporgan present
76	Apical maxillary palpomere of female securiform (fig. 291)	Apical palpomere parallel or nearly so
77	Apical segment of labial palpus securiform (fig. 292)	Apical segment parallel-sided or nearly so
78	Anterior area of mesosternum long, narrow (fig. 289)	Anterior area broad
79	Distal portion of coxite membranous, except narrow sclerotized basal area (fig. 294)	Distal portion uniformly sclerotized (sometimes entirely semimembranous)
80	Apical half of stylus membranous, setose; basal half sclerotized, glabrous (fig. 293)	Stylus of uniform texture
81	Distal part of coxite very heavily sclerotized, distinctly separate from basal part (figs. 263, 265)	Distal part of coxite less distinctly separate from basal part; not heavily sclerotized
82	Apex of male abdominal segment VIII produced	Apex simple, rounded
83	Apex of larval abdominal IX crenulate (fig. 286)	IX apex not crenulate
84	Lateral lobe with internal receptacle (fig. 258)	Lateral lobe simple
85	Paratergite IX of male enlarged, may or may not be appendiculate	Paratergite IX not enlarged
86	Paratergite VIII of male large, nearly appendiculate (fig. 295, laterad of paratergite IX)	Paratergite VIII small
87	Tibial spur formula 1-2-2/1-2-2	Tibial spur formula 2-2-2/2-2-2

seen in *Hylecoetus, Lymexylon, Australymexylon,* and many *Melittomma* and *Atractocerus,* is hypothesized to be apomorphic. Both primitive Cleroidea and Clavicornia were more heavily sclerotized and the similarity in this regard between lymexylids and higher cleroids is parallel at best and more likely, simply convergent. This weak sclerotization is correlated with the dense cover of fine setae on the integument, as is the case in many "Malacoderm" beetles (Crowson, 1964, p. 277), and adults of such taxa are typically both short-lived and chemically active (Crowson, 1964; Slifer et al., 1975); lymexylids seem to meet all these specifications. I regard the heavy sclerotization of primitive melittommines as representative of the plesiomorphic condition in the family.

HEAD: The cranium is sometimes narrowed behind the eyes forming a distinct "neck" region (2); this condition occurs in most lymexylids, with the exception of a few species of *Atractocerus* and the genus *Hylecoetus,* but is not characteristic of many primitive cucujoids and cleroids, nor of the basal lineage (Hylecoetinae) within the family. The eye size has also increased within the Lymexylidae (3), and the anterior margin of the eye has become emarginate in some forms (4). Eyes are both small and entire in the hylecoetines. The Hylecoetinae have a unique epicranial pit (5) located on the center of the head and of unknown function. Crowson's (1955) suggestion that it might serve to disperse spores seems unlikely considering the complex spore pouches of the female genitalia (Buchner, 1928; Francke-Grosmann, 1967).

Filiform antennae [6, 7] occur in *Lymexylon,* but some structural modification is found in most lymexylid taxa. In the genus *Atractocerus* the antennae are reduced in size and are spindle-shaped (7); slight to strong serration (6) occurs in Hylecoetinae and most Melittomminae. No characters were found on the mandibles, but their relatively simple structure is probably correlated with little or no feeding by adult forms; the prostheca is represented by a few setae at the most, two apical dens are sometimes reduced to one, and the mola is little, if at all, developed.

The presence of maxillary palporgans (8) is a benchmark for the family (Germer, 1912;

Germer and Steche, 1912; Slifer et al., 1975) and nothing directly comparable occurs elsewhere in the Coleoptera (superficial resemblances, such as in Telegeusidae, are never correspondent in morphological detail, including form of these structures, development, or point of insertion). Maxillary palporgans occur in males of all taxa, except in *Australymexylon* where they are absent in both sexes (75). They also occur in females of the genus *Atractocerus* (9), but in females of no other members of the family. The structure of the palporgan in Hylecoetinae involves a simple, basketlike arrangement with a primary trunk and two rows of secondary branches (see External Morphology of *Hylecoetus* above). A similarly simple form occurs in *Protomelittomma* and *Melittommopsis.* A few tertiary branches (10) occur on the palporgan of *Lymexylon;* in *Atractocerus* there is a regular and elaborate branching pattern, including parallel rows of tertiaries (11), each covered by thin-walled sensilla (see Morphology). The branching pattern in *Melittomma sericeum* is similar to that in *Atractocerus,* but other forms, like *M. brasiliense,* have an even more complex pattern with quaternary and quintinary branches. In such cases, all the branches have the inner and outer surfaces differentiated by presence of thin-walled sensilla and tactile setae, respectively. It has long been reported that *Atractocerus* has only three maxillary palpomeres (e.g., King, 1955), compared to the ancestral number which is four. Close examination of the palpi, however, reveal the presence of four palpomeres. Segment IV, however, is removed from the third by expansion of the intervening membrane (that also supports the maxillary palporgan) such that it is visually associated with the palporgan (fig. 138). The integument of the base of the segment looks like the surface of the palporgan (fig. 135), but the apex has the typical setae and sensilla of palpomere IV (fig. 136). Labial palpomere IV with several recumbent sensilla (figs. 131, 132). The ligula of the labium is typically small, but is quite large and elongate in *Atractocerus* (figs. 134, 137).

Slifer et al. (1975) mentioned female lymexylids with palporgans and corresponding males lacking them. To my knowledge, this is never the case. As I have said, they are

present in both sexes in *Atractocerus,* in neither sex in *Australymexylon,* but in all other members of Lymexylidae they are present in males but not females. These authors raise some other points that should be clarified. They questioned whether the thin-walled chemoreceptors on the antennae of *Hylecoetus flabellicornis* were similar to those on the palpi of *Hylecoetus dermestoides.* While no fine-structure studies have been done, examination of these structures with a scanning electron microscope (cf. figs. 13, 14 and 23, 24) show them to be different. Tactile setae are present on the outer surface of the *flabellicornis* antennae as are scales and short, thin-walled processes; the inner surface has only these processes, and lacks the typical, long chemoreceptors of *dermestoides* maxillary palporgans. They may function analogously, but are apparently nonhomologous. Slifer et al. also stated that there were no cases when both the antennae and maxillary palporgan were modified in a single form. This is technically not true. In *flabellicornis* the palporgan is present, but in a greatly reduced form (fig. 26). And the Australian species *Atractocerus tasmaniensis* has small, rudimentary maxillary palporgans and very large, apparently thin-walled sensilla on the antennae (see figs. 143, 144).

PROTHORAX: The shape of the pronotum varies widely within the family: among genera, among species, and between sexes of a single species. The shape is short and quadrate in Hylecoetinae, and quite elongate and narrow in some Melittomminae. A sharply defined lateral margin (12) of the pronotum occurs in Hylecoetinae and Melittomminae, a feature absent in Lymexylinae. The hypomeron of the pronotum is slotted (13) in *Australymexylon, Protomelittomma,* and some species of *Melittomma* (the presence in forms like *sericeum* is plesiomorphic, and its loss in forms like *brasiliense* secondary). *Melittommopsis* has a supracoxal emargination that is less evident than the slots of other taxa, but may correspond to a reduced form of them.

LEGS: The apex of the procoxa in Melittomminae has a narrow, elongate slot (14), as in figure 272; its apex is simple in all other family members.

The general form of legs is long and narrow,

as described for *Hylecoetus* in the morphology section. They are greatly elongated in some *Atractocerus* (e.g., fig. 159). Tarsi are always 5-5-5 segmented, but the number of spurs at the apex of the tibiae vary. These can be expressed as tibial spur formulas. The ancestral condition is interpreted as 2-2-2 (observed in primitive cleroids and clavicorns). Modifications found within the family include the following: 0-1-1 (male)/0-1-1 (female) in Hylecoetinae (15); 0-0-0 (male)/ 0-0-0 or 0-1-1 (female) in *Atractocerus* (16); 0-2-2 (male)/1-2-2 (female) in some *Melittomma* species (e.g., *brasiliense*) (17); and 1-2-2 (male)/1-2-2 (female) in *Melittommopsis* (87).

Mesosternum and associated sclerites. The mesosternum is ancestrally quadrate, narrowed anteriorly. In *Australymexylon* and the *Melittomma*-complex genera a small, anterior area is elevated (ventrally produced) (18), but in some forms (e.g., *brasiliense*) this elevated area is missing. The elevated portion is sometimes broadly triangular (e.g., *Melittomma sericeum*), deeply emarginate posteriorly (*Protomelittomma*), or very long and narrow (*Melittommopsis*) (19 and 20, respectively). The mesepisternum sometimes has the anterior part elevated (21), as in *Australymexylon* and the *Melittomma*-complex (with exception, as *brasiliense*). This area may also be separated from the posterior part of the mesepisternum by a sharp carina (22). The lateral portion of the mesepimeron is sometimes depressed (ultimately deeply grooved) to receive the elytral epipleuron (23). This depressed region may be separated from the remaining part of the mesepimeron by a sharp carina (24).

THORACIC TERGA: Ancestrally, the terga include simple alar ridges (fig. 96), and a simple mesoscutellum, except in Hylecoetinae which has a median scutellar keel (25). The scutellum of *Atractocerus* has lateral grooves (26), receiving the mesal margin of the elytra (fig. 163), and the alar ridge is modified into an elevated process (27) fitting under the elytra (fig. 163).

ELYTRON: The elytron has been shortened on more than one occasion in the family, and is shortened to some degree in *Hylecoetus, Lymexylon, Australymexylon,* and some *Melittomma.* The most extreme example, of

course, is the brachelytry of the genus *Atractocerus* (figs. 123, 126), in which the elytron never surpasses the metacoxa and rarely even approaches this length (28).

The paired elytra are ancestrally joined along the suture by a tongue-and-groove locking mechanism. While present in most Lymexylidae, this mechanism ends before the apex of the elytron in forms like *Hylecoetus* and some *Melittomma,* and the mechanism is lost in Lymexylinae (29).

HINDWING: The terms applied to wing-veins of the hindwing were chosen for convenience and may not be anatomically correct. I have tried to follow the usage, as far as possible, of Doyen (1966), Crowson (1955), and Forbes (1922), with modifications. The terms used may be surmised from figure 41.

The brachial cell is usually present (fig. 41), but is absent in *Atractocerus* (30). Similarly, the wedge cell is lost in *Atractocerus* (31).

The medial vein is usually present, arising spuriously at about half the distance of the wing (fig. 41); the M vein is lost in *Atractocerus* (32). A 1a-2a crossvein (arising distad of the wedge cell) is incomplete (33) in Lymexylinae; it is present, but broken in *Lymexylon* and entirely lost in *Atractocerus* (38). Vein 1A, acestrally a spurious vein, is fused with 2A in *Atractocerus* (34). A spurious Rs is retained in *Australymexylon* and at least *Melittomma sericeum* in the *Melittomma* complex; it is lost in *Hylecoetus, Lymexylon,* and *Atractocerus* (35). Crossvein Cu-1A is sometimes lost (36) in *Atractocerus* and some *Melittomma*-complex taxa (present in *Melittomma sericeum*). Male *Lymexylon* have an extra crossvein connecting 1A1 and 1A2 (37; fig. 99). In *Atractocerus* 1a-2a is lost (38), and the wings are folded longitudinally only in a fanlike fashion (39).

METENDOSTERNITE: Detailed comparative studies of the metendosternite in Coleoptera were done by Crowson (1938, 1944, 1955; see also, Balfour-Brown, 1961). While he did not explicitly polarize character states, a number of such assignments can be interpreted from his important studies.

My interpretations of these apomorphs and plesiomorphs are summarized below, and form a basis for analyzing the metendosternite in Lymexylidae. Briefly, the ancestral

metendosternite has the following description. The "hylecoetoid" type of metendosternite is plesiomorphic for character states denoted by (*) and apomorphic for those denoted (**). Stalk narrow (*); anterior tendons nearly contiguous (*), narrowly separated (*); median projection present, bearing anterior tendons (= median laminal process in my figs. 48, 49) (*); no posterior sclerotization (**); furcal arms pointed laterally (*). My terminology departs from Crowson's and can be surmised by reference to figures 47–49.

The furcal arms are laterally to anterolaterally oriented in the Lymexylidae, and clearly anteriorly oriented in *Atractocerus* (40). The anterior tendons are proximal in Hylecoetinae and more widely separated in other genera (41). *Australymexylon* has the anterior tendons arising on the furcal arms (42), rather than between them. The laminae of the *Melittomma* complex are very short (anterior-posterior) and wide (mesad-laterad) (43), in contrast to the longer and narrower forms in *Australymexylon, Lymexylon, Hylecoetus,* and *Atractocerus.*

ABDOMEN: The following remarks refer to the externally visible parts of the abdomen; apical segments, normally telescoped within the abdomen, are discussed with genitalia below. Hylecoetinae is most unusual in abdominal structure. Males have seven visible sternites (II–VIII), segment IX forming a genital capsule; females have six visible sternites (II–VII: see figs. 50, 51). All other genera have segment VII apical (44); and in many forms (e.g., *Australymexylon* and most *Melittomma*-complex taxa, excluding *Melittomma pervagus*) sternite II is greatly reduced or completely lost (45), making the abdomen appear 5-segmented. It appears 6-segmented in *Atractocerus, Melittomma pervagus,* etc. Sexual dimorphism in this regard is restricted to the Hylecoetinae (46) (see also Jeannel and Paulian, 1944).

FEMALE GENITALIA AND POSTABDOMEN: The coxital fold (47) divides each coxite into a basal and distal part and is hypothesized to be autapomorphic for Lymexylidae. The fungus pouch (figs. 54–56) is certainly a derived feature, but its distribution and modification throughout the family has been difficult to assess without histological studies. I suspect,

however, that it is present in all members of the family in some form. *Atractocerus* has a spurious baculus on the female genitalia, parallel to the valviferal baculus (48); at least the distal part of the coxite is thickened and leathery (49), although the overall shape varies. The proctigeral baculi are sometimes proximal (50) or even fused in the *Melittomma* complex; they are proximal, at least near the middle, in *Protomelittomma* and *Melittomma* spp., and fused (51) in some *Melittomma*.

MALE GENITALIA AND POSTABDOMEN: The unusual asymmetrical structure of the lateral lobes (52) and abdominal segment IX (53) in Hylecoetinae were discussed under Morphology above. *Australymexylon* has large, setose pads on the sternite of abdominal segment VIII in males (54), which are nonpareil in the Coleoptera. Close examination with compound microscopy failed to find any clear remnants of secretory cells (at magnifications up to 450×), but I was able to prepare a very limited number of specimens. Either secretory or sensory function could be implied by these bizarre structures. It is interesting, and probably not unrelated, that this is the only genus in which the maxillary palporgans are lost in males.

Species of *Melittomma,* sensu stricto, have paratergites of abdominal segment IX appendiculate (55). These appendages range from short, broad structures in *sericeum* (fig. 257) to the more common and apomorphic long, narrow forms as in *brasiliense* (figs. 237, 240). It is interesting that the lateral lobes of some *Atractocerus* resemble these paratergites in relative size and shape (cf. figs. 148–150). Enlarged ninth paratergites also occur in *Melittommopsis* (85). *Melittommopsis* also has subappendiculate paratergites of the eighth abdominal segment (86), an autapomorphy without parallel in the family.

Lateral lobes of the aedeagus are very small in Hylecoetinae and most genera of the family, but are enlarged in *Atractocerus* (56). The median lobe is greatly reduced in *Australymexylon fuscipennis* (57), making lateral lobes appear relatively larger than in its sister species *australe*. Ancestrally, the tegminal struts are elongate and connect the tegminal plate to the base of the median lobe. The

struts are, however, greatly reduced in *Australymexylon* and more so in certain *Atractocerus* (e.g., *procerus,* fig. 148). Although apomorphic, reduced struts (58) in these two lineages are viewed as independently evolved. The tegminal plate is typically simple, sometimes being rather membranous and poorly delimited. In some *Atractocerus* it is strongly bifid and resembles a pair of lateral lobes (59; see fig. 152). The plate is usually relatively large, but it is reduced in size (60) in the *Melittomma* complex (fig. 233). The elongate, large lateral lobes of *Protomelittomma* (61), bearing a row of stout spines near the apex of their inner margins, is autapomorphic for this genus (see also Lindroth, 1957; Lyngnes, 1956; Sharp and Muir, 1912).

LARVA: The membranous mesal margin of the larval (maxillary) mala, bordered by long setae, may be an apomorph for the Lymexylidae (62). The partial division of the mala, described as plesiomorphic by Crowson (1955), is lost in some lymexylids. Stemmata ("ocelli") occur in neonatal larvae, as reported for *Hylecoetus* by Grandi (1961) and observed in *Atractocerus brasiliensis* by me, but are lost in later instars (63). The tarsungulus of the larval leg in Coleoptera is ancestrally bisetose (Crowson, 1955, 1964). The presence of many setae on the tarsungulus in *Hylecoetus* and *Atractocerus* (64) is apomorphic. The tarsungulus of larval *Australymexylon* are bisetose, but are covered by many short spines (65). Epipleural folds on the abdominal (and usually thoracic) segments are characteristic of lymexylid larvae. The most striking characters of the larvae, however, involve the form of the abdominal apex. Segment X is always small and inferior, as in other wood-borers like Tenebrionidae, Eleteridae, etc. Segment IX, however, is dorsoterminal, large, and conspicuous. Hylecoetinae have IX modified into a long, heavily sclerotized, toothed, swordlike structure (66) in late instars; in most Lymexylinae it is membranous, bulbous, and "bustlelike" in form (67), and in most *Atractocerus* there are conspicuous dorsal asperites on its surface (68); in the *Melittomma* complex and *Australymexylon* it is truncate, and very heavily sclerotized (69). The border of this structure has deeply excised teeth (70) in *Melittomma,*
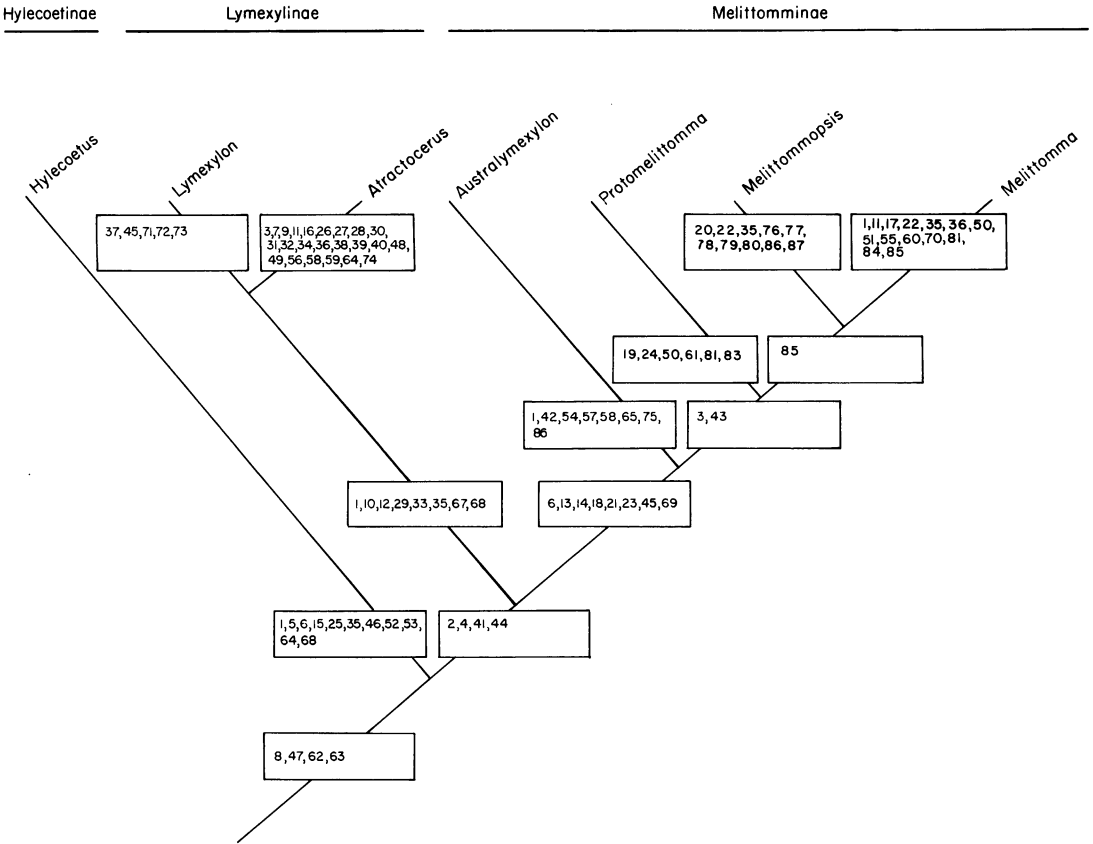
FIG. 299. Cladogram showing hypothesized relationships among the genera of Lymexylidae. Numbers refer to characters in table 3 and discussion of character analysis.

sensu stricto, and *Protomelittomma*; these are absent in *Australymexylon*. The ancestral lymexylid no doubt had an enlarged ninth abdominal segment, but it is not impossible that this structure, used in the tunneling work by these beetles, has been specialized from a less complex ancestral form in all three subfamilies.

Britton (1970, p. 580) illustrated the larva of *Atractocerus crassicornis* (see Discussion under *Atractocerus*). This larva has the ninth abdominal segment less enlarged than most lymexylids and has a pair of sclerotized hooks which Britton (1974, p. 73 et seq.) did not interpret as urogomphi. Accepting his interpretation, these hooks may be de novo structures of this or a limited number of *Atractocerus* species, and the groundplan for the lymexylines would remain an enlarged, bul-

bous ninth segment. A search for the larval abdominal groundplan in the family as a whole is further complicated by ontogenetic evidence in the hylecoetines. The ninth segment is short and truncate in neonatal *Hylecoetus* (see Grandi, 1961) but elongate and autapomorphically modified in later instars. Since only one of these states occurs elsewhere in the lymexylids (the truncate melittommine forms) it is reasonably inferred to be more general, i.e., plesiomorphic, and the "sword" of later instars apomorphic. An implication of this, of course, is an ancestral truncate condition. But this would be questionable in light of the bulbous condition of most lymexylines and the hooks of *Atractocerus crassicornis*. Perhaps, for the time being, a truncate form is best envisioned as basic to lymexylids with the swordlike hylecoetine

condition, bulbous lymexyline condition, and heavy sclerotization and elongate condition of melittommine all apomorphic. Discovery of the larvae of other lymexylids may help with the interpretation of these forms, particularly additional larval *Atractocerus*. Mostly, however, it is a matter of accumulating enough larvae to permit more detailed dissections and studies.

MONOPHYLETIC GROUPS

In this section I briefly discuss the support for each taxon in the study, including autapomorphs for individual genera and synapomorphs for sister genera and higher taxa. Both apomorphs and monophyletic groups can be gleaned from the cladogram in figure 299.

Genus *Hylecoetus*. The autapomorphs of this genus include reduced sclerotization (1), serrate antennae (6), reduced (0-1-1 male/0-1-1 female) tibial spur formula (15), epicranial pit (5), sharp, median keel on scutellum (25), male with one more visible abdominal sternum than female (46), lateral lobes of aedeagus asymmetrical (52), abdominal segment IX of male asymmetrical (53), tarsungulus of larva pleurisetose (64), larval abdominal segment IX very long, narrow, heavily sclerotized (66).

Genus *Lymexylon*. Autapomorphs supporting *Lymexylon* include the presence of an extra (1a1-1a2) crossvein in the hindwing (37), reduced sclerotization (1), maxillary palporgan of male with at least a few tertiary branches (10), lateral lobes of aedeagus short, broad, truncate, with wide separation (71), apex of abdominal segment IX with toothlike process (72), ventral surface of labrum (larva) with three lateral setae (73).

Genus *Atractocerus*. This genus has many autapomorphs, in part explaining its historical removal from other lymexylids. These autapomorphs include reduction in sclerotization (1), large and emarginate eyes (3, 4), short, spindlelike antennae (7), presence of maxillary palporgan in female (9), male palporgan with tertiary branches (10), tertiaries arranged in paired, parallel rows (11), tibial spur formula 0-0-0 male/0-0-0 or 0-1-1 female (16), scutellum with lateral grooves re-

ceiving elytra (26), alar ridge modified into elevated process (27), brachelytry (28), absence of brachial cell (30), absence of wedge cell (31), 1A fused with 2A (34), absence of 1a-2a crossvein (38), wings folding only longitudinally (39), furcal arms of metendosternite strongly anteriorly oriented (40), spurious baculus present near coxital baculus (48), coxite leathery, at least distally (49), lateral lobes greatly enlarged (56), tegminal plate bifid (59), tarsungulus of larva pleurisetose (64), lateral lobes with two or three teeth on mesal surface (74).

Genus *Australymexylon*. Autapomorphs for this genus include the presence of neck (2), emargination of the eyes (4), serration of antennae (6), loss of maxillary palporgan in male (75), presence of large setose pads on male abdominal segment VIII (54), median lobe reduced in size (in one species) (57), tegminal struts reduced in size (58), tarsungulus bisetose, but with many small spines (65), anterior tendons of metendosternite arising on the furcal arms (42).

Genus *Melittomma*. Autapomorphs include appendiculate paratergites on male abdominal segment IX (55), short, small tegminal plate (60), and toothed rim of abdominal segment IX of the larva (70).

Genus *Melittommopsis*. Autapomorphs include securiform apical maxillary palpomere in female (76), securiform apical labial palpomere in female (77), anterior area of mesosternum long and narrow (78), distal part of coxite membranous and narrow, basal band sclerotized (79), apical half of stylus membranous and setose, basal half sclerotized and glabrous (80), male postabdomen with large paratergites on abdominal segment VIII (86), bearing spines and setae, and tibial spur formula 1-2-2 (male)/1-2-2 (female) (87).

Genus *Protomelittomma*. Autapomorphs supporting this genus include the deeply emarginate anterior part of the mesosternum (19), large lateral lobes with mesal row of spines (61), crenulate apex of abdominal segment IX (83), and highly differentiated distal part of female genitalia (81).

Subfamily Hylecoetinae. This subfamily is monotypic, and characters listed for *Hylecoetus* define it.

Subfamily Lymexylinae, Sensu Stricto (*Ly-*
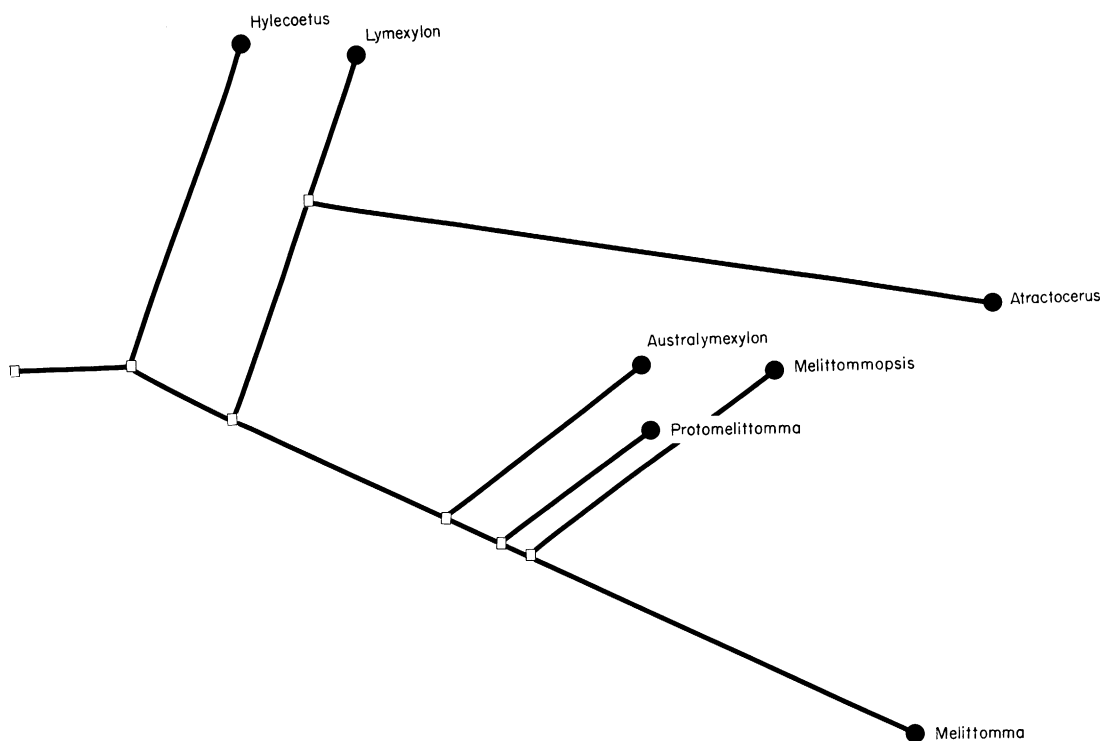
FIG. 300.   Degree of divergence branching diagram. Clades are drawn to lengths representative of the number of synapomorphs or autapomorphs since last node. Angle of clades not informative. See text for discussion.

mexylon + Atractocerus). I use this subfamily in a restricted sense compared to Crowson (1955) and Boving and Craighead (1931); it is supported by the following synapomorphs: presence of tertiary branches on the maxillary palporgan (10), sharp lateral margins on the pronotum lost (12), tongue-and-groove locking mechanism of elytra lost (29), crossvein 1a-2a of hindwing incomplete (33), larval abdominal segment IX large, bulbous, membranous (67), and abdominal segment IX of larva with asperites (68).

Subfamily Melittomminae, New Subfamily (Australymexylon + Melittommopsis + Protomelittomma + Melittomma). Synapomorphs include the serrate antennae (6), supracoxal slot in prohypomeron (13), slotted procoxa (14), elevation of anterior part of mesepisternum (21), mesepimeron with depressed lateral area (23), and abdominal seg-

ment IX of larva round, truncate, heavily sclerotized (69).

Melittomma Complex. Three of the genera of Melittomminae are particularly closely associated. This complex shares elevation of the anterior area of the mesosternum (18) and a short, broad lamina of the metendosternite (43).

The carinal margin of the mesepimeral depression supports a sister-group relation of Melittomma and Protomelittomma, as does the proximal location of the proctigeral baculi of the female genitalia (50). However, the presence of large paratergites on male abdominal segment IX (85) indicates a sister-group relationship between Melittommopsis and Melittomma. Because of the unusual and structurally complex nature of the latter character, I regard it as more compelling evidence of cladogenesis (Wheeler, 1986).
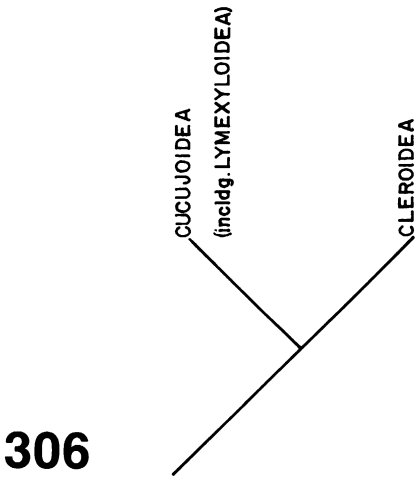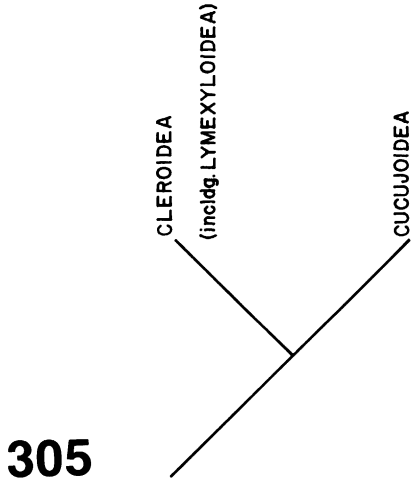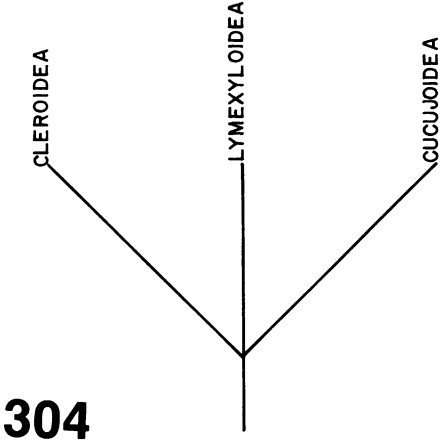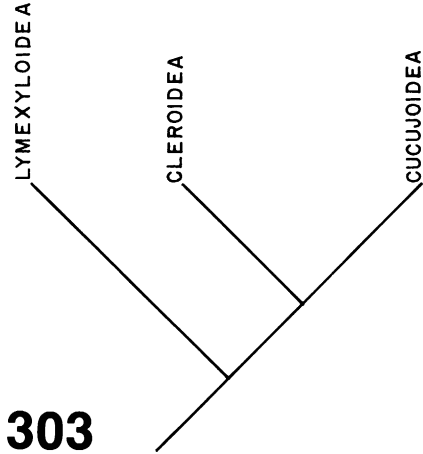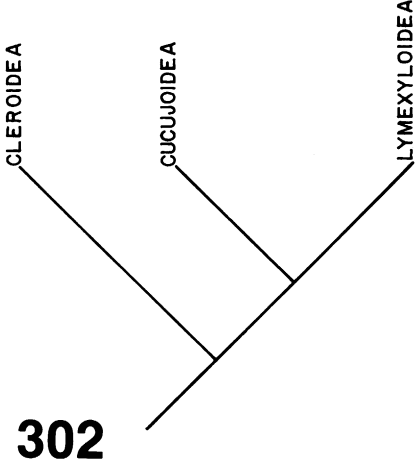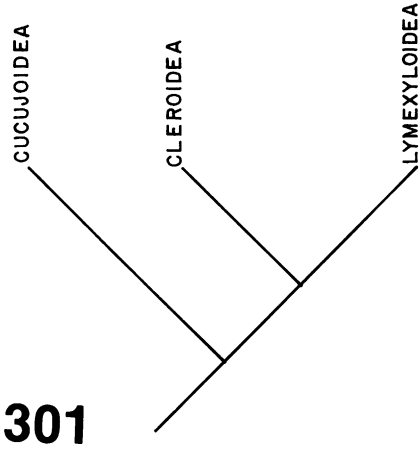
FIGS. 301–306. Cladograms showing possible relationships among Lymexyloidea, Cleroidea, and Cucujoidea.

Family Lymexylidae. Assuming that the absence of maxillary palporgans in *Australymexylon* is a secondary loss, then the palporgans provide the strongest synapomorph for the family. Other evidence includes the partial division of the coxites of the female genitalia, the membranous, setose mesal margin of the maxillary mala, and the large, superior ninth abdominal segment of the larvae.

Superfamily Lymexyloidea. Relations of the lymexyloids have already been mentioned, and remain enigmatic. It is generally agreed that they are related in some unspecified way to the Cleroidea and the Cucujoidea (in its broad, modern sense including both Clavicornia and Tenebrionoidea). There are a number of possible relations, summarized in figures 301–306. Crowson (1960, 1981) has suggested that they be regarded as part of a trichotomy with the Cleroidea and Cucujoidea (fig. 304), a position adopted here as a course of convenience. Several workers studying adult characters have conjectured a relation between lymexyloids and cleroids (fig. 301). At least some of the similarities shared by cleroids and lymexyloids, particularly the soft integument, dense setose covering, and short adult life-span are generally associated with chemically active beetles (see Crowson, 1964). Boving and Craighead (1931), studying larvae, noted the resemblance of lymexyloids and cucujoids (fig. 298). But the possibility that lymexyloids are themselves the sister of both cleroids and cucujoids cannot be eliminated at present, nor inclusion of the lymexyloids *within* one of these related superfamilies.

Progress in studies of Cleroidea (Crowson, 1964) and Tenebrionidae and related families by J. T. Doyen, J. F. Lawrence, J. C. Watt and others indicate an improving climate for asking questions about higher relationships within the Cucujiformia (Lawrence and Newton, 1982). Ultimate resolution of such questions, however, will likely be associated with continued growth of our knowledge of both the Tenebrionoids and the Clavicorns.

GEOGRAPHIC HISTORY

Procedures for estimating the geographic histories of taxa have improved dramatically with the infusion of cladistic theory into biogeography (e.g., Nelson and Platnick, 1981; Platnick and Nelson, 1978). The first step in any such analysis is to assess the geographic pattern exhibited by the taxon under study, without direct reference to other taxa or geologic evidence (Humphries, 1981). Thus, this discussion of Lymexylidae geographic history is divided into two parts. A description of present patterns; and a comparison of this pattern to those available for other organisms and for earth history.

LYMEXYLIDAE GEOGRAPHIC PATTERNS

The simplest measure of historical patterns in a taxon is derived by replacing terminal taxon designations with summaries of those taxa's extant distributions. No one supposes that ranges have not changed in what is probably many millions of years in the Lymexylidae. This is just recognition of the limitations of data in taxa for which fossil records are minimal. Figure 307 shows an area cladogram transcribed from the accepted taxon cladogram (fig. 299). This area cladogram is particularly confused by the two Pantropical genera, *Lymexylon* and *Atractocerus*. These taxa are relatively uninformative with regard to historical patterns, since they embrace most areas now occupied by other and endemic taxa. A simplified area cladogram can be achieved by setting these taxa aside, as in figure 308. The possible implications for the Pantropical taxa will be discussed below, but for now it is interesting to ask whether those taxa with endemic distributions are informative about some broad historic pattern.

COMPARISONS OF CLADOGRAMS

With the global scale of lymexylid distributions, the obvious place to look for concordant patterns is in plate tectonic data from geologists and from patterns seen in other global taxa. Rosen (1978) presented a geo-

N. AMERICA
EUROPE
ASIA

EUROPE
ASIA

PANTROPICS

AUSTRALIA

S. AMERICA

MADAGASCAR

PANTROPICS

307

N. AMERICA
EUROPE
ASIA

EUROPE
ASIA

AUSTRALIA

S. AMERICA

MADAGASCAR

308
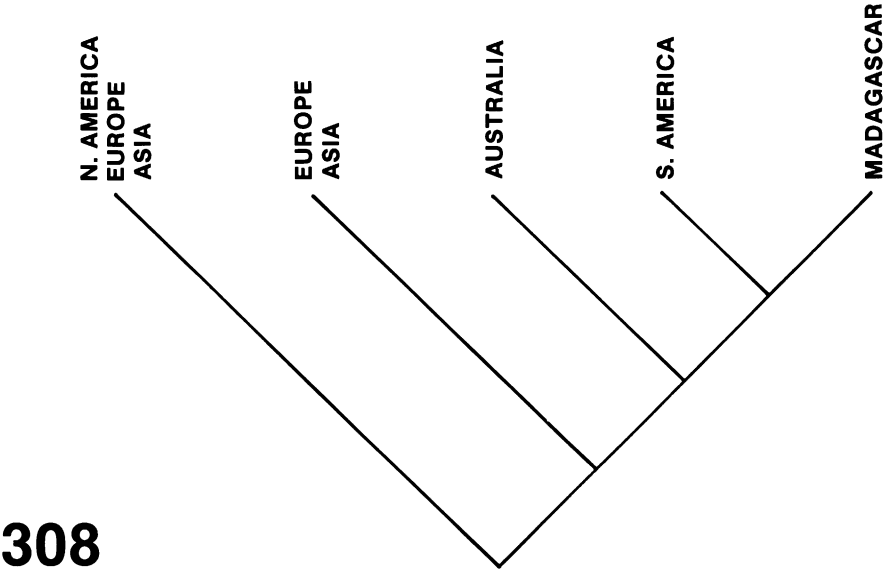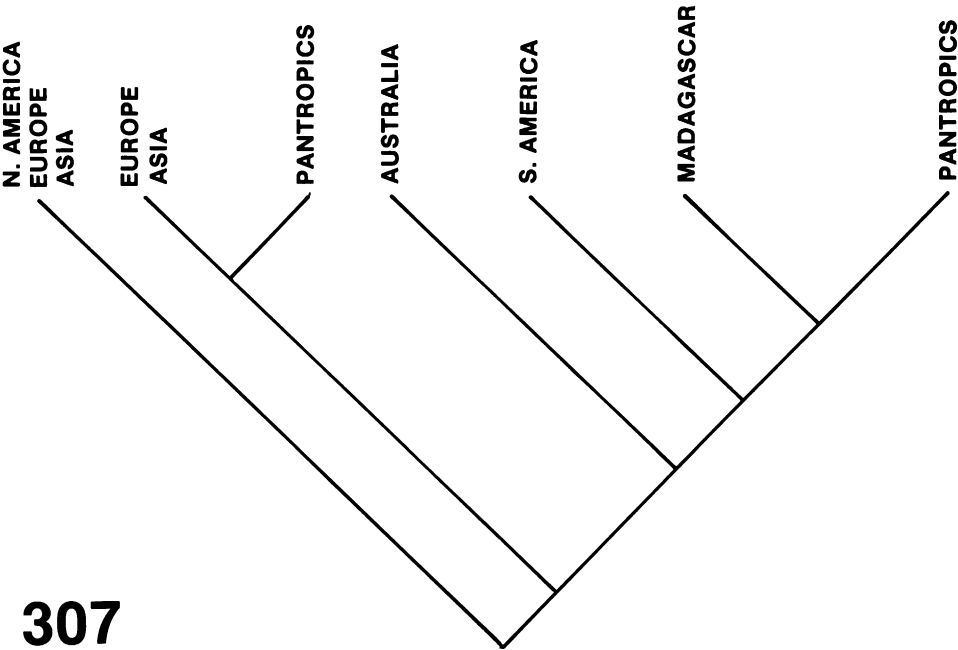
FIGS. 307, 308. Area cladograms. **307.** Branching pattern from cladogram (fig. 299), taxa replaced by area statements. **308.** Reduced area cladogram. Pantropical distributions omitted to simplify relative relations among endemic taxa.

cladogram based on the maps of Dietz and Sproll (1970), Rich (1975), and Ballance (1976), which can be summarized in the following set notation:

(LAU + (AFR + (NZ + ((E.ANT. + AUS)
          + (W.ANT. + SAM)))))

in which the following acronyms are used: LAU (Laurasia), AFR (Africa), NZ (New Zealand), E.ANT. (Eastern Antarctica), AUS (Australia), W.ANT. (Western Antarctica), and SAM (South America).

This sequence agrees little with the simplified area cladogram for Lymexylidae, with the exception of a basal Laurasian-Gondwanaland rift. Owen's (1976) geologic evidence can be summarized in the following set notation, with the acronyms used above plus IND for India and MAD for Madagascar:

(LAU + (IND + (AFR + MAD))
          + (AUS + SAM))).

This pattern too is not significantly in agreement with the lymexylid data.

Evidence from Shields (1979), however, shows a little more congruence. His data, simplified from its presentation by Humphries (1981), can be expressed in this set notation:

(LAU + (IND + (SAM + AFR + MAD)
          + AUS))).

In this case, South America and Madagascar are more recently associated with one another than with Australia, the pivotal aspect of the lymexylid data in conflict with the evidence given by Rosen and Owen above. It differs, however, in having Australia separate after Madagascar + South America, whereas the lymexylid data imply that Australia was isolated first, followed by a fractioning of South America–Madagascar. Again, a significant difference of implication.

Comparing the lymexylid data with a survey of area cladograms based on a diversity of taxa by Humphries (1981) and with family-level taxa of lizards by Presch (1983) also failed to find any strong correlation of patterns with the lymexylid data.

CONCLUSIONS

What does this incongruence of lymexylid data mean? There are several possibilities.

First, the taxon cladogram for the Lymexylidae may be wrong and the taxa, if correctly analyzed, would conform to continental rifting patterns supported by geologists and at least some area cladograms, derived from biogeographical data. With no additional characters to test the cladograms, this is not a productive line of reasoning for the present, albeit an everpresent possibility. Assuming that the cladogram is essentially correct, what are the possibilities? Clearly there are a number of possible historic causes for such a distribution pattern, none of which would lend credence to correlations with known patterns of continental drift, with the possible exception of a Hylecoetinae isolation correlated with the isolation of Laurasia from Gondwanaland (and Lymexylinae + Melittomminae). Crowson (1981) has hypothesized a lower Jurassic origin for the family Lymexylidae, implying that at least some of the higher taxa may have predated the major breakup events of Gondwanaland.

The Pantropical distributions of *Melittomma* and *Atractocerus* are problematical. They could be due to a primitive cosmopolitanism, but with few exceptions the species involved are (in general respects) relatively more apomorphic than those of their sister taxa. One might not reasonably expect to see relictual morphologies preserved in such groups with any consistency if they were truly ancient in origin, but the constant absence of paleoendemism of form is somehow subjectively bothersome. The other possibility for these two taxa (which, incidentally, are the most speciose of all lymexylid genera) is that their present, Pantropical patterns arose from dispersal events. *Atractocerus* beetles are powerful fliers, and both these species and those of *Melittomma* are undeniably effectively vagile since many individual species are transcontinental or wider in their distributions, as for example, widespread species in Central and South America, Africa and Madagascar, the Indo-Malaysian area, and Southeast Asia. Thus, I am inclined to hypothesize that both taxa were later in origin, and that their present distributions largely result from their own movements.

Similarly, the incongruence of endemic genera with "known" geologic and other taxonomic data suggests that these patterns too may be the end product of beetle dis-

persal. At least this is one conclusion of such geographic incongruities (Platnick and Nelson, 1978). If this is the case, then there is little immediate hope of elucidating the origin of the pattern beyond reading the sequence from figure 307 (or 308), and guessing dispersal events from area to area. Perhaps detailed analyses of the extant and historic distribution patterns of the species within each of the genera of the family will contribute to unraveling the general pattern of area occupation origins. It may well be that some intrageneric vicariance events can be credibly linked with other taxon patterns and "known" geologic sequences, limiting (channelizing) possible readings of the generic level patterns.

TABLE 4
A Phyletic Sequence Classification of the Subfamilies and Genera of Lymexylidae

Subfamily Hylecoetinae Boving and Craighead, 1931
　Genus *Hylecoetus* Latreille, 1806
Subfamily Lymexylinae Boving and Craighead, 1931
　Genus *Lymexylon* Fabricius, 1775
　Genus *Atractocerus* Palisot de Beauvois, 1801
Subfamily Melittomminae Wheeler, new subf.
　Genus *australymexylon* Wheeler, new genus
　"*Melittomma* Complex"
　　Genus *Protomelittomma* Wheeler, new genus
　　Genus *Melittommopsis* Lane, 1955
　　Genus *Melittomma* Murray, 1867

CLADISTIC CLASSIFICATION

A formal classification of the genera of Lymexylidae is proposed that conforms in all important respects to my cladistic analysis (above). The classification is summarized in table 4. It includes three subfamilies: Hylecoetinae, including the single genus *Hylecoetus* Latreille; Lymexylinae, here restricted to two genera, *Lymexylon* Fabricius and *Atractocerus* Palisot de Beauvois; and Melittomminae, new subfamily, including *Melittomma* Murray, *Melittommopsis* Lane, *Protomelittomma* Wheeler, new genus, and *Australymexylon* Wheeler, new genus.

All described species are assigned as accurately as possible to these genera (in the discussion of each), an effort greatly facilitated by museum studies in Europe in 1982. These placements, and the generic reclassification, should make eventual taxonomic studies of lymexylids easier and immediate storage of biological information more useful.

APPENDIX

Taxonomic Outgroup Taxa

Dermestoidea
　Derodontidae (*Derodontus*)
Cleroidea
　Peltidae (*Decamerus, Eronyxa, Peltis, Thymalus*)
　Trogossitidae (*Lophocateres, Tenebroides*)
　Chaetosomatidae (*Chaetosoma*)
　Melyridae (*Dasytes, Collops*)
　Cleridae (*Thaneroclerus*)

Cucujoidea
　Byturidae (*Byturus*)
　Cucujidae (*Laemophloeus, Brontes, Telephanus*)
　Rhizophagidae (*Rhizophagus*)
　Sphindidae (*Sphindus*)
　Nitidulidae (*Cateretes, Pallodes*)
　Bothrideridae (*Deretaphrus*)
　Cerylidae, Colydiidae (*Monoedus, Bitoma*)
　Tetratomidae (*Penthe*)
　Inopeplidae (*Inopeplus*)

LITERATURE CITED

Alexopoulos, C. J., and C. W. Mims
1979. Introductory mycology, 3rd ed. New York, Wiley, 632 pp.

Arnett, R. H.
1971. The beetles of the United States. Ann Arbor, American Entomological Institute, 1112 pp.

Baehr, M.
1976. Das Prothorakalskelett von *Atractocerus* (Lymexylidae) und seine Bedeutung für die Phylogenie der Coleopteren, besonders der Polyphagen (Insecta: Coleoptera). Zoomorphology, vol. 85, pp. 39–58.

Balfour-Brown, J.
1961. The metendosternite in the Coleoptera. Jour. Linn. Soc. London (Zool.), vol. 44, pp. 337–354.

Ballance, P. F.
1976. Evolution of the Upper Cenozoic magmatic arc and plate boundary in northern New Zealand. Earth and Planetary Sci. Lett., vol. 28, pp. 356–370.

Barber, H. S.
1952. Notes on *Telegeusis* and some relatives (Coleoptera: Lymexylidae). Pan-Pacific Ent., vol. 28, pp. 163–170.

Batra, L. R.
1967. Ambrosia fungi: a taxonomic revision, and nutritional studies of some species. Mycologia, vol. 59, pp. 976–1017.

Batra, L. R., and H. Francke-Grosmann
1961. Contributions to our knowledge of ambrosia fungi. I. *Ascoidea hylecoeti* sp. nov. (Ascomycetes). Amer. J. Bot., vol. 48, pp. 453–456.
1964. Two new ambrosia fungi: *Ascoidea asiatica* and *A. africana*. Mycologia, vol. 56, pp. 632–636.

Beeson, C. F. C.
1961. The Ecology and Control of Forest Insects in India and the Neighboring Countries. Gov. of India, Delhi, 767 pp.

Benick, L.
1952. Pilzekäfer und Käferpilze. Acta Zool. Fennica, vol. 70, pp. 1–250.

Blackburn, T.
1891. Further notes on Australian Coleoptera, with descriptions of new genera and species. Trans. Roy. Soc. S. Austr., vol. 14, pp. 292–345.
1898. Further notes on Australian Coleoptera, with descriptions of new genera and species. Trans. Roy. Soc. S. Austr., vol. 23, pp. 22–101.

Blackwelder, R. E.
1957. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. U.S. Natl. Mus. Bull., vol. 6, no. 185.

Blair, K. G.
1936. A new species of *Melittomma* (Col., Lymexylidae) from India. Ent. Mon. Mag., vol. 72, p. 154.

Blatchley, W. S.
1910. An illustrated descriptive catalog of the Coleoptera or beetles (exclusive of Rhyncophora) known to occur in Indiana. Indianapolis, Bull. Indiana Geol. Nat. Res., 1386 pp.

Boheman, C. H.
1851. Insecta Caffraria . . . , vol. 1, pt. 2, pp. 299–625.

Boudreaux, H. B.
1979. Arthropod phylogeny with special reference to insects. New York, Wiley, 320 pp.

Bourgeois, J.
1905. Voyage du Dr. W. Horn a Ceylon: Malacodermes et Lymexylonides. Ann. Soc. Ent. Fr., vol. 74, pp. 127–133.
1909. Malacodermes et Lymexylonides de Ceylon. Ann. Soc. Ent. Fr., vol. 78, pp. 423–439.

Boving, A. G., and F. C. Craighead
1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. Ent. Amer., vol. 11, pp. 1–351.

Bright, D. E.
1979. Cleroidea. *In* H. V. Danks, Canada and its insect fauna. Mem. Can. Ent. Soc., no. 108, p. 377.

Britton, E. B.
1970. Coleoptera. *In* I. M. Mackerras (ed.), The insects of Australia. Victoria, Melbourne Univ. Press, pp. 495–621, 112 figs.
1974. Key to families of Coleoptera based on larvae. *In* The Insects of Australia, Suppl. Carleton, Melbourne Univ. Press, pp. 72–89.

Brown, E. S.
1954. The biology of the coconut pest *Melittomma insulare* (Col., Lymexylonidae), and its control in the Seychelles. Bull. Ent. Res., vol. 45, pp. 1–66.

Buchner, P.
1928. Holznahrung und Symbiose. Berlin, Springer, 64 pp.
1953. Endosymbiose der Tiere mit pflanzlich-

en Mikroorganismen. (English translation, 1965, Wiley, New York.) Basel, Birkhauser, 909 pp.

Champlain, A. B., and J. N. Knull
1923. Fragmentary notes on forest Coleoptera. Can. Ent., vol. 55, p. 112.

Chenu, J. C.
1860. Encyclopedie d'histoire naturelle. Coléoptères, vol. 1. Paris, 312 pp.

Chevrolat, L. A. A.
1844. In F. E. Guérin-Méneville, Iconographie du Règne Animal de G. Cuvier, vol. 7, Insectes. Paris, 576 pp.

Clark, J.
1925. Forest pests. The pin-hole borer (Atractocerus kreuslerae Pasc.). Jour. Dept. Agric. W. Austr., vol. 2, pp. 138–142.
1931. A new species of Lymexylonidae (Coleoptera). Proc. Roy. Soc. Victoria, vol. 43 (n. s.), pp. 120–122.

Collart, A.
1952. Hylecoetus dermestoides L. en Belgique. Bull. Ann. Soc. Ent. Belg., vol. 88, pp. 164–166.

Cooreman, J.
1952. Histiogaster hylecoeti, n. sp. (Acarien, Tyroglyphidae). Description de la deutonymph migratrice vehiculee par Hylecoetus dermestoides L. Bull. Ann. Soc. Ent. Belg., vol. 88, pp. 234–240.

Craighead, F. C.
1950. Insect enemies of eastern forests. USDA Misc. Publ., no. 657, 679 pp.

Crowson, R. A.
1938. The metendosternite in Coleoptera: a comparative study. Trans. Roy. Ent. Soc. London, vol. 87, pp. 397–415.
1944. Further studies on the metendosternite in Coleoptera. Trans. Roy. Ent. Soc. London, vol. 94, pp. 273–310.
1955. The natural classification of the families of Coleoptera. London, Lloyd, 187 pp.
1960. The phylogeny of Coleoptera. Ann. Rev. Ent., vol. 5, pp. 113–310.
1964. A review of the classification of Cleroidea (Coleoptera), with descriptions of two new genera of Peltidae and of several new larval types. Trans. Roy. Ent. Soc. London, vol. 116, pp. 275–327.
1981. Biology of the Coleoptera. London, Academic Press, 802 pp.
1984. Associations of Coleoptera with Ascomycetes. In Q. Wheeler and M. Blackwell (eds.), Fungus-insect relationships, pp. 256–285. New York, Columbia Univ. Press, 514 pp.

Dietz, R. S., and W. P. Sproll
1970. Fit between Africa and Antarctica: a continental drift reconstruction. Science, vol. 167, pp. 1612–1614.

Dominik, J.
1957. Drwionki-Lymexylonidae. Klucze do Oznaczania Owadów Polski, Część XIX, Chrząszcze - Coleoptera, Zeszyt 44. Polski Związek Entomologiczny, Warsaw, pp. 13–22.
1975. Uwagi ó biologii i zwalczaniu rytla (Hylecoetus dermestoides L., Col., Lymexylonidae) na tle obserwacji prowadzonych w latach 1953–1973 w lasach doświadczalnych ar w rogowie. Zeszyty Naukowe Adademii Rolniczej w Warszawie, Leśnictwo, 21, Warsaw, pp. 93–98.

Dominik, J., and S. Kinelski
1976. Bradania nad chemiczną dezynsekcją surowca opanowanego przez rytla (Hylecoetus dermestoides L. Col. Lymexylonidae). Zeszyty Problemowe Postępów Nauk Rolniczych 1976, vol. 178, pp. 129–133.

Donisthrope, H. J. K.
1939. A preliminary list of the Coleoptera of Windsor Forest. London, Lloyd, 126 pp.

Doyen, J. T.
1966. The skeletal anatomy of Tenebrio molitor (Coleoptera: Tenebrionidae). Misc. Pub. Ent. Soc. Amer., vol. 5, pp. 103–150.

Egger, A.
1974. Beiträge zur Morphologie und Biologie von Hylecoetus dermestoides L. (Col., Lymexylonidae). Anz. Schadl. Planz.-Umwelt., vol. 47, pp. 7–11.

Eldredge, N.
1979. Cladism and common sense. In J. Cracraft and N. Eldredge (eds.), Phylogenetic patterns and the evolutionary process. New York, Columbia Univ. Press, pp. 165–198.

Eldredge, N., and J. Cracraft
1980. Phylogenetic patterns and the evolutionary process. New York, Columbia Univ. Press, 349 pp.

Erichson, W. F.
1842. Beitrag zur Insecten-Fauna von Vandiemensland. Arch. Naturg., vol. 8, pp. 83–287.

Fabricius, J. C.
1775. Systema entomologiae. Lipsiae, 832 pp.
1781. Species insectorum, vol. 1. Kilonii, 552 pp.
1787. Mantissa insectorum sistens eorum species nuper detectas, vol. 2. Hafniae, 382 pp.

Fairmaire, L.
    1882.   Description d'une espèce nouvelle du genre *Atractocerus*. Notes Leyden Mus., vol. 4, pp. 217–218.
    1885.   Malacodermes, Lymexylides et Heteromeres nouveaux recueillis par M. Deby a Sumatra et a Borneo. Ann. Soc. Ent. Belg., vol. 29, pp. cv–cxii.
    1887.   Coléoptères nouveaux ou peu connus du Musée de Leyde. Notes Leyden Mus., vol. 9, pp. 145–162.
    1889.   Coléoptères de l'interieur de la Chine. Ann. Soc. Ent. Fr., ser. 6, vol. 9, p. 45.
    1891.   Notes sur quelques Coléoptères de l'Afrique intertropicale et descriptions d'espèces nouvelles. Ann. Ent. Soc. Fr., vol. 60, pp. 231–274.
    1893.   Communications, Seance du 13 decembre 1893. Bull. Ent. Soc. Fr., vol. 1893, pp. cccxxiii–cccxxiv.
    1901.   Materiaux pour la faune coléoptèrique de la Région Malgache (lle note). Rev. Ent., vol. 20, pp. 101–248.

Fleming, J.
    1821.   Insecta. Supplement to the Encyclopaedia Britannica, vol. 5, pp. 41–56. Originally published as a whole (1824) as "Supplement to the Fourth, Fifth, and Sixth Editions of the Encyclopaedia Britannica, with Preliminary Dissertations on the History of Sciences."

Forbes, W. T. M.
    1922.   The wing venation of Coleoptera. Ann. Ent. Soc. Amer., vol. 15, pp. 328–352.
    1956.   Note on *Atractocerus*. Col. Bull., vol. 10, p. 10.

Foursow, N. I.
    1935.   Zwei neue Arten aus Fam. Lymexylonidae (Coleoptera) von Kaudasus und Ost-Siberien schadlich in der Fortwirtschaft. Bull. Soc. Nat. Moscou, Sci. Biol., vol. 44, pp. 92–93.

Francke-Grosmann, H.
    1953.   Über Larvenentwicklung unter Generationsverhaltnisse bei *Hylecoetus dermestoides* L. (Coleoptera, Lymexylonidae). Trans. Ninth Int. Congr. Ent., pp. 735–741.
    1967.   Ectosymbiosis in wood-inhabiting insects. *In* S. M. Henry (ed.), Symbiosis. New York, Academic Press, pp. 141–205.

Fulmek, L.
    1931.   Zur Kenntnis der Entwicklung von *Atractocerus emarginatus* Cast. (Coleopt.-Lymexylonidae). Treubia, vol. 12, pp. 389–394.

Gahan, C. J.
    1908.   On the larvae of *Trictenotoma childreni* Gray, *Melittomma insulare* Fairmaire, and *Dascillus cervinus* Linn. Trans. Ent. Soc. London, vol. 1908, pp. 275–282.

Gardner, J. C. M.
    1934.   On some coleopterous larvae from Uganda. Bull. Ent. Res., vol. 25, pp. 149–154.
    1935.   A new Indian species of *Atractocerus* (Col., Lymexylonidae). Stylops, vol. 4, pp. 69–70.
    1936.   A new Indian species of *Atractocerus* (Col., Lymexylonidae). Proc. Roy. Ent. Soc. London (B), vol. 5, pp. 181–182.
    1937.   Immature stages of Indian Coleoptera. 22. Ind. For. Rec., vol. 3, pp. 127–140, 2 pls.
    1944.   On some coleopterous larvae from India. Ind. Jour. Ent., vol. 6, pp. 111–116.

Germer, F.
    1912.   Untersuchungen über den Bau und die Lebensweise der Lymexyloniden, speziell des *Hylecoetus dermestoides* L. Zeitschr. Wiss. Zool., vol. 101, pp. 683–735.

Germer, F., and O. Steche
    1912.   Über ban und Bedentung der Kopfgliedmassen bei den Lymexyloniden (Col.). Ent. Mitt., vol. 1, pp. 295–300.

Gerstaecker, C. E. A.
    1873.   Die Gliederthier-Fauna des Sansibar-Gebietes. Leipzig und Heidelberg, C. F. Winter, 542 pp.

Gestro, F.
    1874.   Descrizione di tre specie nuove del genere *Atractocerus* appartenenti alle collezioni del Museo Civico di Genova. Ann. Mus. Civ. Stor. Nat. Genova, vol. 6, pp. 544–547.

Gistel, J. N. F. X.
    1857.   Achthundert und zwanzig neue oder unbeschriebene wirbellose Thiere. Straubing, Schorner, 94 pp.

Gorham, H. S.
    1881.   Insecta, Coleoptera. Lycidae, Lampyridae, Telephoridae, Lymexylonidae, Melyridae. *In* F. D. Godman and O. Salvin, Biologia Centrali-Americana. Zoology, vol. 3, pt. 2, pp. 25–112, London.
    1886.   Insecta, Coleoptera. Supplement to Malacodermata. *In* F. D. Godman and O. Salvin, Biologia Centrali-Americana. Zoology, vol. 3, pt. 2, pp. 313–360, London.

Graham, K.
    1967.   Fungal-insect mutualism in trees and

timber. Ann. Rev. Ent., vol. 12, pp. 105–126.

Grandi, G.
1961. *Hylecoetus dermestoides* L. (Coleoptera Lymexylonidae), morphologia larvale, la larva neonata. Bull. Inst. Ent. Univ. Degli Stud. Bologna, vol. 24, pp. 39–51.

Guérin-Méneville, F. E.
1844. Iconographie du Regne Animal de G. Cuvier, vol. 7, Insectes. Paris, 576 pp.

Gyllenhal, L.
1808. *In* C. J. Schonherr (ed.), Synonymia insectorum, vol. 1, pt. 2. Stockholm, C. F. Marquard, 424 pp.
1827. Insecta Suecica, vol. 1, pt. 4. Lipsiae, 761 pp.

Harris, T. W.
1841. A report on the insects of Massachusetts, injurious to vegetation. Cambridge, Folsom, Wells and Thurston, 459 pp.

Hennig, W.
1966. Phylogenetic systematics. Urbana, Univ. Illinois Press, 263 pp.
1981. Insect phylogeny. New York, Academic Press, 515 pp. [transl. A. C. Pont, rev. notes D. Schlee].

Herbst, J. F. W.
1784. Kritisches Verzeichnis meiner Insecten-Sammlung. Arch. Insectengesch., vol. 5, pp. 68–151.

Heyden, L. F. J. D., E. Reitter, and J. Weise
1891. Cat. Col. Eur. Modling. 424 pp. [as cited in Schenkling, 1915].

Hopkins, A. D.
1894. Notes on some discoveries and observations of the year in West Virginia. Insect Life, vol. 7, pp. 145–153.

Humphries, C. J.
1981. Biogeographical methods and the southern beeches (Fagaceae: *Nothofagus*). *In* V. A. Funk and D. R. Brooks (eds.), Advances in cladistics, vol. 1, pp. 177–207. Bronx, New York Botanical Garden, 250 pp.

Jacquelin du Val, P. N. C.
1863. Genera des Coléoptères, vol. 3. Paris, 464 pp.

Jeannel, R., and R. Paulian
1944. Morphologie abdominale des Coléoptères et systematique de l'order. Rev. Fr. Ent., vol. 11, pp. 65–110.

Kalshoven, L. G. E.
1964. Observations of Lymexylonidae in Indonesia and Malaya. Ent. Ber., vol. 24, pp. 184–186.

Karny, H. H.
1922. Zur Kenntnis der Orientalischen *Atrac-tocerus*-Arten (Col., Lymexylonidae). Treubia, vol. 3, pp. 6–13.

King, E. W.
1955. The phylogenetic position of *Atractocerus* Palis. Coleopt. Bull., vol. 9, pp. 65–74.

Kinzelbach, R.
1971. Morphologische Befunde an Fächerflüglern und ihre phylogenetische Bedeutung (Insecta: Strepsiptera). Zoologica, vol. 41, no. 119, pp. 1–256.

Kono, H.
1938. Die Lymexyloniden, schadlich an Sachalintannen und Ezofichten in Sachalin und Hokkaido. Trans. Sapporo Nat. His. Soc., vol. 15, pp. 199–201.

Kraatz, G.
1895. Zwei neue *Atractocerus*-arten von Togo. Deutsch. Ent. Zeit., vol. 1895, p. 163.

Kristensen, N. P.
1981. Phylogeny of insect orders. Ann. Rev. Ent., vol. 26, pp. 135–157.

Kurosawa, Y.
1949. Description of a new Lymexylidae of the genus *Lymexylon* Fabricius from Japan. Ent. Rev. Jap., vol. 1, pp. 26–28.
1956. A new genus and species of the family Lymexylonidae with the additional notes on some Japanese species (Coleoptera). Bull. Nat. Sci. Mus., Tokyo, vol. 3, pp. 80–82.
1985. Revisional notes on the family Lymexylonidae (Coleoptera) in Eastern and Southeastern Asia. Bull. Natl. Sci. Mus., Tokyo, ser. A, vol. 11, pp. 109–119.

Kuschel, G.
1979. The genera *Monotoma* Herbst (Rhyzophagidae) and *Anommatus* Wesmael (Cerylidae) in New Zealand (Coleoptera). N. Z. Ent., vol. 7, pp. 44–48.

Lacordaire, J. T.
1830. Mémoire sur les habitudes de insectes Coléoptères de l'Amerique meridionale. Ann. Sci. Nat., vol. 20, pp. 185–291.
1857. Histoire Naturelle des Insectes. Paris, 579 pp.

Lane, F.
1955. Novos gêneros e espécies de Coleoptera Lymexylonidae e notas sôbre *Melittomma* Murray, 1867. Pap. Avul. Dept. Zool., Secr. Agric., S. Paulo, vol. 12, pp. 141–163.

Laporte, F. L. N. de
1832. Mémoire sur cinquante espèces nouvelles ou peu connues d'insectes. Ann. Soc. Ent. Fr., vol. 1, pp. 386–415.

1836. Études entomologiques, out descriptions d'insectes nouveaux et observations sur la synonymie. Rev. Ent., vol. 4, pp. 5–60.

1840. Histoire naturelle et iconographie des insectes Coléoptères, vol. 3. Paris, P. Dumenil.

Latreille, P. A.
1806. Genera Crustaceorum et Insectorum, secundum ordinem naturalem in familias deposita, iconibus exemplisque plurimus explicata, vol. 1. Paris, 302 pp.

1825. Families naturelles du règne animal. Paris, 570 pp.

Lawrence, J. F.
1982. Coleoptera. In S. P. Parker (ed.), Synopsis and classification of living organisms, vol. 2, pp. 482–553. New York, McGraw-Hill.

Lawrence, J. F., and A. F. Newton, Jr.
1982. Evolution and classification of beetles. Ann. Rev. Ecol. Syst., vol. 13, pp. 261–290.

Lea, A. M.
1894. Descriptions of new species of Australian Coleoptera. Proc. Linn. Soc. N. S. Wales, ser. 2, vol. 4, pp. 589–634.

1912. Descriptions of new species of Australian Coleoptera, part IX. Proc. Linn. Soc. N. S. Wales, vol. 36, pp. 426–478.

1917. Notes on some miscellaneous Coleoptera, with descriptions of new species, part III. Trans. Roy. Soc. S. Austr., vol. 41, pp. 121–322, pls. xii–xv.

Leach, W. E.
1815. Insecta. In Brewster's Edinburgh Encyclopaedia, pp. 329–338.

1817a. Entomology. In Brewster's Edinburgh Encyclopaedia, pp. 329–338.

1817b. The zoological miscellany; being descriptions of new or interesting animals, vol. 3. London [illustr. R. P. Nadder].

LeConte, J. L.
1861–1862. Classification of the Coleoptera of North America. Smiths. Misc. Coll., no. 136, pp. 1–286.

Leng, C. W.
1920. Catalogue of the Coleoptera of America, north of Mexico. Mt. Vernon, N.Y., Sherman, 470 pp.

Lepeletier, A. L. M., and J. G. Audinet-Serville
1825. Atractocere. In Encyclopedie Methodique ... Entomologie, vol. 10, pt. 1. Paris, 344 pp.

Le Pelley, R. H.
1959. Agricultural Insects of East Africa. East African High Commission, Nairobi, 307 pp.

Lepesme, P.
1947. Les Insectes de Palmiers. Paris, 903 pp.

Lever, R. J. A. W.
1969. Pests of the Coconut Palm. FAO Agric. Stud., no. 77, pp. 1–190.

Lewis, G.
1896. On a new species of Hylecoetus (Lymexylonidae) from Japan. Ann. Mag. Nat. Hist., ser. 6, vol. 17, p. 65.

Lindroth, C. H.
1957. The principle terms used for male and female genitalia in Coleoptera. Opusc. Ent., vol. 22, pp. 241–256.

Linnaeus, C.
1758. Systema naturae, ed. 10, vol. 1. Holmiae, 823 pp.

1761. Fauna Suecica. Stockholm, 578 pp.

1766. Systema Naturae, ed. 12. Holmiae, pp. 533–1327.

Lohse, G. A.
1979. Familie: Lymexylonidae. In H. Freude, K. W. Harde, and G. A. Lohse (eds.), Die Kafer Mitteleuropas, Diversicornia. Krefeld, Goecke and Evers Verlag, 367 pp.

Lyngnes, R.
1956. Asymmetrical genital segments in Hylecoetus dermestoides L. (Col.). Norsk Ent. Tidskr., vol. 10, no. 1, pp. 221–235.

1958. Studier over Hylecoetus dermestoides L. under et angrep på bjørkestokker på Sunnmøre 1954–1955. Norsk Ent. Tidskr., vol. 10, pp. 221–235.

Melsheimer, F. E.
1853. Catalogue of the described Coleoptera of the United States. Washington, D.C., 174 pp.

Miwa, Y.
1935. Descriptions of two new species of Lymexylonidae from Formosa. Trans. Nat. Hist. Soc. Formosa, vol. 25, pp. 456–458.

Mulsant, E., and C. Rey
1863–1864. Histoire naturelle des Coléoptères de France, vol. 14, Colligeres. Paris, 24 pp.

Murray, A.
1867. List of Coleoptera received from Old Calabar, on the west coast of Africa. Ann. Mag. Nat. Hist., ser. 3, vol. 20, pp. 314–323.

Nakane, T.
1963. New or little-known Coleoptera from Japan and its adjacent regions. XXV. Sci. Rep. Kyoto Prefect. Univ. (Nat. Sci. Liv. Sci.), vol. 3, no. 5, pp. 221–226.

1985. On the Coleoptera occurring in Yakushima Island. Yakushima no Shizen,

Tokyo, pp. 587–631 [cited by Kurosawa, 1985].

Nelson, G., and N. Platnick
1981. Systematics and biogeography: cladistics and variance. New York, Columbia Univ. Press, 567 pp.

Nye, I. W. B.
1961. Control of the coconut pest *Melittomma insulare* (Coleopt., Lymexylidae) in the Seychelles. Bull. Ent. Res., vol. 52, pp. 489–499.

Olliff, A. S.
1889. Insect fauna. *In* Lord Howe Island: its zoology, geology, and physical characters. Austr. Mus. Mem., no. 2, pp. 75–98.

Owen, H. G.
1976. Continental displacement and expansion of the earth during the Mesozoic and Cenozoic. Phil. Trans., ser. B, vol. 281, pp. 223–291.

Palisot de Beauvois, C.
1801. Mémoire sur un nouveau genre d'insecte trouve en Afrique. La Decade Phil., Litt., Polit., vol. 9, no. 4, pp. 513–518, pl. 1.

Pascoe, F. P.
1860. Notices of new or little-known genera and species of Coleoptera. Jour. Ent., vol. 1, pp. 36–64, 98–132.
1864. Notices of new or little-known genera and species of Coleoptera. Proc. Ent. Soc. London, pp. 25–56.

Perty, J. A. M.
1830–1834. Delectus animalium articulatorum, fasc. I–II. Monachii, 224 pp.

Peterson, A.
1961. Larvae of insects, an introduction to nearctic species. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Ann Arbor, 416 pp.

Pfeil, O. A. E.
1859. Bemerkungen zur gattung *Hylecoetus* Latr. Stett. Ent. Zeitg., vol. 20, pp. 74–83.

Philippi, R. A.
1866. Einige Insekten von Chile. Stett. Ent. Zeitg., vol. 27, pp. 109–117.

Pic, M.
1936. Nouveautes diverses. Mélanges Exot.-Ent., Moulins, vol. 67, pp. 1–36.
1939a. Nouveaux Coléoptères de la presqu'ile Malaise. Jour. Fed. Malay St. Mus., Kuala Lumpur, vol. 18, pp. 372–376.
1939b. Diagnoses de Coléoptères exotiques. L'Echange, Rev. Linn., vol. 55, no. 577, pp. 31–32.

1944. Coléoptères du globe (suite). L'Echange, Rev. Linn., vol. 60, no. 496, p. 5.
1945. Coléoptères du globe (suite). L'Echange, Rev. Linn., vol. 61, no. 502, p. 31.
1948. Captures et Coléoptères nouveaux. Divers. Ent., vol. 3, pp. 12–16.
1949. Nouveaux Coléoptères de l'Ouest Africain. Bull. Inst. Fr. D'Afr. Noire, vol. 11, pp. 307–312.
1955. Contributions a l'étude de la fauna entomologique du Ruanda-Urundi, Part XII. Coleoptera. Ann. Mus. Roy. Congo Belg., vol. 35, pp. 125–135.

Platnick, N. I.
1979. Philosophy and the transformation of cladistics. Syst. Zool., vol. 28, pp. 537–546.

Platnick, N. I., and G. Nelson
1978. A method of analysis for historical biogeography. Syst. Zool., vol. 27, pp. 1–16.

Presch, W.
1983. The family-subfamily taxon in lizards: effects of plate tectonics on biogeographic patterns. *In* N. I. Platnick and V. A. Funk (eds.), Advances in cladistics, vol. 2, pp. 191–200. Columbia University Press, New York.

Redtenbacher, J.
1849. Fauna Austriaca. Die Kafer. Vienna, 883 pp.
1858. Fauna Austriaca. Die Kafer, 2nd ed. Vienna, 1017 pp.

Reitter, E.
1911. Fauna Germanica . . . , vol. 3, 436 pp., pls. 81–128.

Rich, P. V.
1975. Antarctic dispersal routes, wandering continents and the origin of Australia's non-passerine avifauna. Mem. Natl. Mus., vol. 36, pp. 63–126.

Richter, G.
1933. Beitrag zur biologie von *Hylecoetus dermestoides* L. Mitt. Forstwirtsch. u. Forstwiss., vol. 5.

Roonwal, M. L.
1972. Field observations on biology of salai borer, *Atractocerus reversus* Walk. (Coleoptera: Lymexylonidae) in India. Zeitschr. Ang. Ent., vol. 72, pp. 92–97.

Rosen, D. E.
1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool., vol. 27, pp. 159–188.

Rummukainen, U.
1947. Über das Auftreten des Laubholzbohrers, *Hylecoetus dermestoides* L., an Birken. Ann. Ent. Fenn., vol. 13, no. 2, pp. 144–148.

1949. Weiteres über das Auftreten des Laub-holzbohrers *Hylecoetus dermestoides* L. an Birken. Ann. Ent. Fenn., vol. 15, pp. 131–135.

Rymer-Roberts, A. W.
1930. A key to the principle families of Co-leoptera in the larval stage. Bull. Ent. Res., vol. 21, pp. 57–72.

Sanderson, M. W., and M. O. Glenn
1963. Note on behavior and distribution of *Melittomma sericeum* Harris (Coleop-tera, Lymexylonidae). Col. Bull., vol. 17, p. 52.

Say, T.
1835. Descriptions of new North American coleopterous insects, and observations on some already described. Boston Jour. Nat. Hist., vol. 1, no. 2, pp. 151–203.

Schaeffer, J. C.
1766. Elementa entomologica. Ratisbonae [from Horn].
1777. Elementorum entomolgicorum appen-dix V, insectorum nova genera exhi-bens. Ratisbonae. 140 pls. [from Horn].

Schaller, G.
1783. Neue Insekten beschrieben. Schrift. Na-turf. Gesell. Halle, vol. 1, pp. 217–328.

Schedl, K. E.
1958. Breeding habits of arboricole insects in Central Africa. Proc. 10th Internat. Congr. Ent., vol. 1, pp. 183–197.

Schenkling, S.
1914. Beiträge zur Kenntnis der Lymexyloni-den (Col.) I. Ent. Mitt., vol. 3, pp. 317–321.
1915. Lymexylonidae. *In* Coleopterorum Ca-talogus, vol. 10, pars 64. Berlin, W. Junk, pp. 1–13.

Schneider, D. H.
1791. Anmerkung des Herausgebers. Neues Mag. Leibh. Ent., vol. 1, p. 109.

Schneider-Orelli, O.
1920. Beiträge zur biologie des pilzzuchten-den Käfers *Hylecoetus dermestoides* L. Mitt. Schweiz. Ent. Gesell., Bern, vol. 13, pp. 64–67.

Selander, R. B.
1959. Additional remarks on wing structure in *Atractocerus*. Col. Bull., vol. 13, pp. 1–5.

Sharp, D., and F. Muir
1912. The comparative anatomy of the male genital tube in Coleoptera. Trans. Ent. Soc. London, vol. 1912, pp. 477–642.

Sherborn, C. D.
1937. Brewster's Edinburgh Encyclopaedia. J. Soc. Bibl. Nat. Hist., vol. 1, pt. 4, p. 112.

Shields, O.
1979. Evidence for initial opening of the Pa-cific Ocean in the Jurassic. Palaeogeogr., Palaeoclim., and Palaeoecol., vol. 26, pp. 181–220.

Simmonds, F. J.
1956. An investigation of the possibilities of biological control of *Melittomma in-sulare* Fairm. (Coleoptera, Lymexyloni-dae), a serious pest of coconut in the Seychelles. Bull. Ent. Res., vol. 47, pp. 685–702.

Sleeper, E. L.
1964. Notes on *Atractocerus brasiliensis* Le-peletier & Serville (Coleoptera: Tele-geusidae) in western Mexico. Bull. S. Calif. Acad. Sci., vol. 63, pp. 54–55.

Slifer, E. H., T. F. J. Gruenwald, and S. S. Sekhon
1975. The maxillary palp organs of a wood-boring beetle, *Melittomma sericeum* (Coleoptera, Lymexylonidae). Jour. Morph., vol. 147, pp. 123–136.

Spilman, T. J.
1971. Bredin-Archbold-Smithsonian biologi-cal survey of Dominica: Bostrichidae, Inopeplidae, Lagriidae, Lyctidae, Ly-mexylonidae, Melandryidae, Monomi-dae, Rhipiceridae, and Rhipiphoridae (Coleoptera). Smiths. Contrib. Zool., no. 70, pp. 1–10.

Stephens, J. F.
1832. Illustrations of British Entomology. London, Baldwin & Cradock, 448 pp.

Strohmeyer, H.
1907. Ueber die Lebensweise und Schad-lichkeit von *Hylecoetus dermestoides* L. Naturw. z. Land. Forstwirt, vol. 5, 624 pp.
1910. Zwei neue *Atractocerus*-Arten (Lymexy-lonidae), Ent. Rundschau, vol. 27, no. 1, p. 6.

Swabey, C.
1935. Notes on insect attack on mora (*Mora excelsa* Benth.) in Trinidad. Leaflet, Forest Dept.

Tanner, V. M.
1927. A preliminary study of the genitalia of female Coleoptera. Trans. Amer. Ent. Soc., vol. 53, pp. 5–50.

Thomsen, M.
1950. Contributions to the biology of *Xylo-terus domestidus* L. and *Hylecoetus der-mestoides* L. Proc.-Verbaux, 8th Inter-nat. Congr. Ent., Stockholm, pp. 804–811.

Thomson, M. J.
1858. Famille XIX. Lymexylonidae. *In* Ar-

chives Entomologiques II, Societe entomologique de France. Paris, 469 pp.

Thunberg, C. P.
1791. Char. Gen. Ins., Meyer (ed.), p. 26 (from Schenkling, 1915, p. 10).

Uddman, I.
1753. Novae Insectorum Species. Abo, J. Merckell, p. 24, fig. 4.

Vaurie, P.
1957. *Atractocerus brasiliensis* in Cuba. Col. Bull., vol. 10, p. 86.

Vessey-Fitzgerald, D.
1941. *Melittomma insulare* Fairm. (Col. Lymexylonidae), a serious pest of coconut in the Seychelles. Bull. Ent. Res., vol. 31, pp. 383–402.

Villiers, A.
1969a. Contributions a la connaissance de la faune entomologique de la Cote-D' Ivoire (J. Decelle, 1961–1964) XXXVI: Coléoptères Lymexylonidae. Ann. Mus. Roy. l'Afr. Central, Tervuren, vol. 175, pp. 133–136.
1969b. Contribution a la faune du Congo (Brazzaville). Mission A. Villiers et A. Descarpentries, LXXXIII. Coléoptères Lymexylonidae. Bull. Inst. Fond. D'Afr. Noire, ser. A, vol. 31, pp. 73–82.
1969c. Coléoptères Lymexylonidae de la collection du Musée Royal de l'Afrique Centrale. Rev. Zool. Bot. Afr., vol. 80, pp. 321–324.

Vitrac, L.
1913. Un nouveau Lymexylonide Americain, *Atractocerus antillarum,* nov. sp. (Ins. Coleopt.). Insecta, Rev. Illus. d'Ent., vol. 3, pp. 168–170.

Vrydagh, J. M.
1952. Observations sur l'*Hylecoetus dermes-*

toides L. Bull. Ann. Soc. Ent. Belg., vol. 88, pp. 166–168.

Walker, F.
1858. Characters of some apparently undescribed Ceylon insects. Ann. Mag. Nat. Hist., ser. 3, vol. 2, pp. 280–286.

Wasmann, E.
1902. Species nouveaux insectorum termitophilorum ex America meridionali. Tidjs. Ent., vol. 45, pp. 95–107.

Watrous, L. E., and Q. D. Wheeler
1981. The out-group comparison method of character analysis. Syst. Zool., vol. 30, pp. 1–11.

Wheeler, Q. D.
1981. The ins and outs of character analysis. Syst. Bot., vol. 6, pp. 296–307.
1986. Character weighting and cladistic analysis. Syst. Zool., vol. 35, pp. 102–109.

Wheeler, Q., and M. Blackwell
1984. Cladistics and the historical component of fungus-insect relationships. *In* Q. Wheeler and M. Blackwell (eds.), Fungus-insect relationships, pp. 5–41. New York, Columbia Univ. Press, 514 pp.

Wheeler, Q., and E. R. Hoebeke
1984. A review of mycophagy in the Eucinetoidea (Coleoptera), with notes on an association of the eucinetid beetle, *Eucinetus oviformis,* with a Coniophoraceae fungus (Basidiomycetes: Aphyllophorales). Proc. Ent. Soc. Washington, vol. 86, pp. 274–277.

Wiley, E. O.
1981. Phylogenetics. New York, Wiley, 439 pp.

Wilson, E. O.
1971. The insect societies. Cambridge, Belknap Press/Harvard Press, 548 pp.

INDEX OF SCIENTIFIC NAMES

Boldface page numbers refer to the description, main reference for each name, or (pp. 193–196) primary discussion of cladistic relations.

BULLETIN OF

THE AMERICAN MUSEUM

OF NATURAL HISTORY

VOLUME 183

1986

Edited by
BRENDA JONES

CONTENTS OF VOLUME 183