The status of the Espagnolinae (Rehn 1948) and other subfamilies of the Episactidae (Descamps 1973) (Eumastacoidea, Caelifera, Orthoptera), with description of two new genera, Paralethus and Neibamastax

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The status of the Espagnolinae (Rehn 1948) and other subfamilies of the Episactidae (Descamps 1973) (Eumastacoidea, Caelifera, Orthoptera), with description of two new genera, *Paralethus* and *Neibamastax*

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Abstract

The phallic anatomy of all the modern Hispaniolan eumastacids and of representative species of all genera of the Central American Episactinae has been examined. Two new genera, *Neibamastax* from the Dominican Republic and *Paralethus* from El Salvador, are erected to accomodate species which were found to have very divergent phallic morphology. Additionally, we have examined isolated species of the Teicophryinae and Miraculinae. A cladistic analysis of the Central American and Hispaniolan genera was performed, which divides these into two well-supported monophyletic clades, corresponding to the two areas of distribution. These we equate with the Episactinae Burr 1903 and the Espagnolinae Rehn 1948, and offer diagnoses of these two subfamilies. We present new data from the Teicophryinae which supports their inclusion in the Episactidae as well.

Key words

Eumastacid grasshoppers, systematics, Hispaniola, Central America

Introduction

The recent description of eight new species and three new genera of Hispaniolan eumastacoids (Perez *et al*. 1997 a, b; Perez & Rowell 2006, this issue) and the acquisition of new specimens of the previously described Hispaniolan species *Antillacris explicatrix* and *Espagnola darlingtoni* (both Rehn & Rehn 1939) allow resolution of a disputed issue. Is the Espagnolinae Rehn 1948 a valid subfamily, adequately differentiated from the related Episactinae of Central America?

The Episactinae were originally recognized by Burr (1899, as group Episacti) and raised to subfamily status in Burr 1903. They currently comprise three Central American genera (*Episactus* Burr 1899 (Costa Rica, Guatemala, Mexico, El Salvador); *Gymnotettix* Bruner 1901 (Guatemala, Honduras); *Lethus* Rehn & Rehn 1934 (=*Mayamastax* Uvarov 1940) (Honduras, Mexico, Nicaragua). All are apterous and have numerous distinctive shared features; their phylogenetic unity has never been questioned. An additional genus of this subfamily (*Paralethus* n.gen., El Salvador) is described below.

Rehn & Rehn (1939) originally placed the then newly discovered Hispaniolan *Antillacris* in the Episactinae. Their sole specimen was a larval female, and the subfamilial attribution was made primarily on general morphological similarity and the fact that *Antillacris*, like all known Episactines, is apterous. For *Espagnola*, however, they erected a new group, Espagnolae, raised later to the subfamily Espagnolinae by Rehn (1948), because it is fully winged (and also on the structure of the male subgenital plate, with its membranous final sternite). This partitioning of the only two known Hispaniolan genera into two different subfamilies was provisionally retained by Descamps (1973) in his review of the superfamily, though he pointed out that the attribution of *Antillacris* was "very dubious". He grouped the two subfamilies, together with the then poorly known Mexican Teicophryinae Rehn 1948 and the Madagascan Miraculinae Bolivar 1903 into a new family Episactidae, and noted that the Cuban Masynteinae Decamps 1973 could be placed there too, if only phallic characters were considered. [Decamps' Miraculinae incorporated as a tribe the Malagassinae Rehn 1948; the Madagascan genus *Malagassa* was originally placed in the Episactinae by Saussure (1903), but was later given its own subfamily by Rehn & Rehn (1945)]. Descamps (1973) placed his Episactidae and the Afro-Asian Chorotypidae in his division Cryptophalli (the name referring to the small size of the endophallus in all these taxa, which also share various other characters, most obviously spinous dorsal margins of the first tarsal segment of the hind foot and a tendency to spinous ornament of the ectophallus).

Amedegnato (1993, and pers. comm.) disagreed with Descamp's (1973) scheme. She considered the Miraculinae to be unrelated to the other taxa, and suggested collapsing the remaining subfamilies (other than the Teicophryinae) to a unitary Episactinae which she then placed in the family Eumastacidae *s. str.*, along with all other New World eumastacoids. Amedegnato presented no evidence or arguments in support of this arrangement, but her opinions were accepted by Perez et al. at the time of their description of the new Hispaniolan taxa (1997a, b), which they accordingly placed in the Episactinae.

However, molecular systematic investigations using mitochondrial ribosomal RNA genes (Matt 1997, Rowell & Flook 1998), showed the Hispaniolan genera *Tainacris*, *Espagnolopsis* and *Antillacris* to be a monophyletic clade, with *Episactus* as their sister-group, but (*contra* Amedegnato 1993) to show no clear linkage with the Eumastacidae *s. str.*, but rather with the Asian *Erianthus* (Chorotypidae), thus supporting Descamp's (1973) arrangement. The Teicophryinae, the Miraculinae and the Masynteinae were not included in the sample studied with molecular techniques.

In the present study we have examined the external morphology and internal genitalia of both sexes of all known Hispaniolan eumastacoids (other than the fossil *Paleomastacris* (Perez *et al.* 1997), of representative species of all the Central American episactine genera, of two species of the Teicophryinae, of one species of Miraculinae, one species of Eruciinae (family Chorotypidae) and of numerous species of one genus of Eumastacinae. The data on the Central American and Hispaniolan Episactinae have been analysed cladistically. The results support the retention of the two separate subfamilies Episactinae and Espagnolinae, for which we provide diagnoses; the latter comprises all the Hispaniolan taxa, including

Antillacris, and none of the Central American genera. We consider these two subfamilies to be closely related and to comprise the Episactidae *s. str.* The position of the Teicophryinae and Miraculinae is unclear, owing to our having insufficient material at our disposal for analysis, but Descamps' (1973) placement of these taxa in the Episactidae *s.l.* seems at least a good preliminary hypothesis. We find no morphological evidence for a close relationship between the Episactidae and the Eumastacidae.

Materials and methods

Much of the material examined was from the authors' personal collections. Hispaniolan specimens collected in the Dominican Republic between 2001 – 2004 will ultimately be shared between the Academy of Natural Sciences, Philadelphia (ANSP), the United States National Museum of Natural History, Washington (USNM), and the Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic (MHND). Where necessary, we supplemented our materials with loans from the following institutions: Entomology Department, University of California at Riverside (UCR); California Academy of Sciences, San Francisco (CAS); the Entomology Museum, Utah State University at Logan (EMUS), the ANSP and the USNM.

We have examined the outer morphology and the internal genitalia of both sexes of the following taxa:

Episactidae Descamps 1973
  Episactinae Burr 1903
    Episactus tristani Rehn & Rehn 1934
    Episactus brunneri Burr 1899
    Episactus eremites Rehn & Rehn 1934 (male only)
    Gymnotettix lithocolletus Rehn & Rehn 1934
    (*G. occidentalis* Bruner 1901 has been examined externally, but not its internal genitalia.)
    Lethus nicaraguae Descamps 1974
    Lethus maya Rehn & Rehn 1934
    Lethus oresterus Rehn & Rehn 1934 (male only)
    Paralethus insolitus n. g., n. sp.

  Espagnolinae Rehn 1948
 (The justification for allotting the new Hispaniolan genera to this subfamily is given later in this paper.)
    Espagnola darlingtoni Rehn & Rehn 1939
    Espagnolopsis ornatipennis Perez *et al.* 1999
    E. breviptera Perez *et al.* 1999
    E. exaltata Perez & Rowell 2006, this issue
    Espagnoleta microptera Perez *et al.* 1999
    Antillacris explicatrix Rehn & Rehn 1939
    A. inflaticercus Perez *et al.* 1997
    A. eumenes Perez *et al.* 1997
    Tainacris nitaina Perez *et al.* 1997
    T. quisqueiana Perez *et al.* 1997
    T. divergentis Perez *et al.* 1997 (here transferred to *Neibamastax* n. gen.).

  Teicophryinae Rehn 1948
    Teicophrys robertsi (Rehn & Rehn 1939), male only
    Teicophrys bolivari Descamps 1976

  Miraculinae Bolívar 1903
    Malagassa tridens Rehn & Rehn 1945

Descamps (1965) split the Miraculinae into three tribes; the species examined belongs to the Malagassini, and to the genus placed by Saussure (1903) in the Episactinae.

Chorotypidae Stål 1876
  Eruciinae Burr 1903
    Erucius erianthoides C. Bolívar 1944 (male only)

Eumastacidae Burr 1899
  Eumastacinae Burr 1903
    Homeomastax Descamps 1979 (approx. 20 species—see Rowell & Bentos-Pereira 2000a for details). Nonmacerated dissection of the female system (see below) was performed on *H. surda* Burr 1899.

Methods

Male internal genitalia were dissected from relaxed specimens and prepared by conventional techniques, involving maceration in warm 5% KOH solution, staining in acid fuchsin in 5% acetic acid, differentiation in water, and clearing in glycerine. The endophallus was examined after making a lateral or ventral cut along the length of the ectophallic membrane.

The spermatheca of females was rapidly damaged or completely destroyed by treatment with alkali, which also distorted the course of the spermatophore duct in the intact animal by removing the surrounding tissues. Relaxed females were therefore dissected initially in water, thereafter in a dilute solution of acid fuchsin in 5% acetic acid. The ventral ovipositor valves and the medial common oviduct, together with the spermatheca and its duct, were dissected free of the subgenital plate, and the latter pinned flat for examination and drawing. For lateral views (to show the form of the medial process or egg guide) the plate was unpinned and restored to its its original convex form. Drawings were made using a drawing tube under 50× magnification.

For cladistic analysis, all genera of the Episactinae and Espagnolinae, plus the genera *Erucius* and *Homeomastax* (represented by the species listed above) were scored for 45 morphological characters, mostly derived from the male reproductive system. The character descriptions and data matrix are given in the Appendix. Parsimony analysis was conducted in Paup* 4.0 (D.L. Swofford 2003) version beta 10 and the resultant trees examined in MacClade 4.08 (Maddison & Maddison 2005). Trees were rooted using the Eumastacine *Homeomastax*. We did not have enough material to justify the inclusion in the formal analysis of the Teicophryinae or the Miraculinae.

Results

We first present the results of the phallic examinations, including the erection of two new genera (Part 1), and proceed from there to a cladistic analysis of the New World Episactidae *s. str.* (Part 2).

1. PHALLIC ANATOMY

In order to perform this revision it was necessary to investigate in some detail the Episactid phallic mechanism, which has been only very briefly (Rehn & Grant 1958, Descamps 1973) described previously. The starting point was the previous description (Rowell & Bentos-Pereira 2002) of the phallic complex of *Homeomastax* (Eumastacinae, Eumastacidae), to which the reader is referred for terminology. The general organisation of the Episactine phallus is

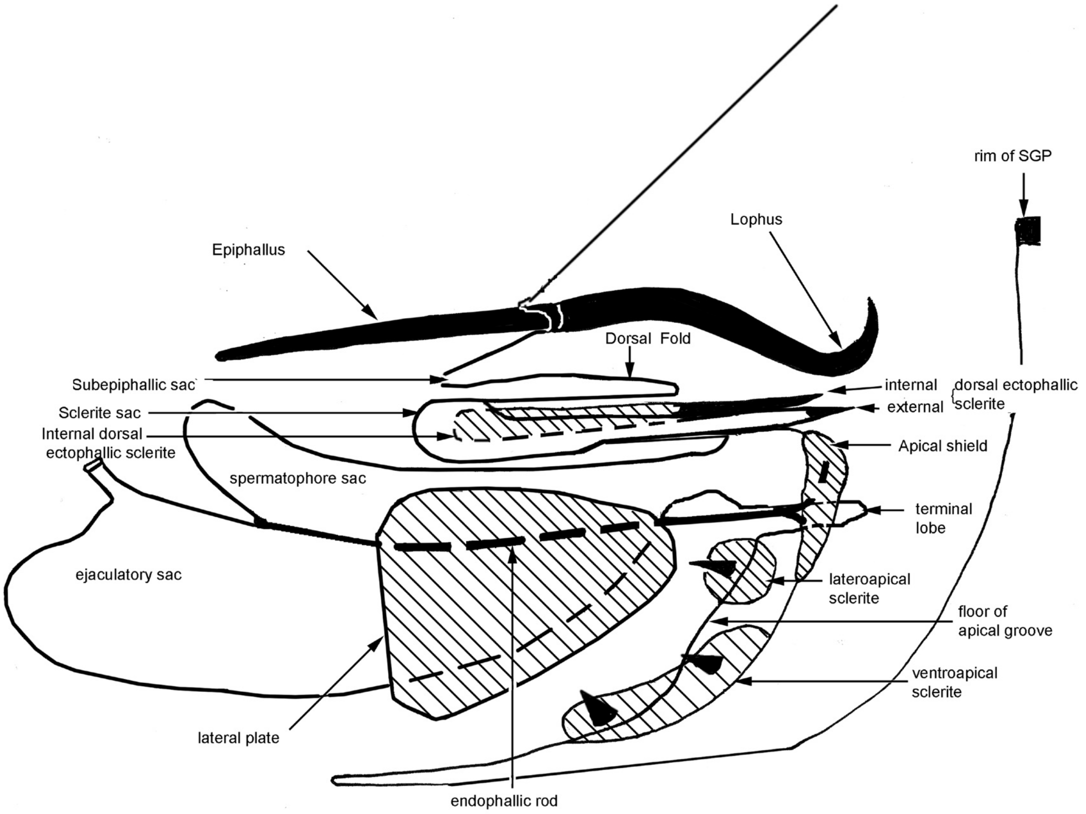


Fig. 1. Generalized diagram of the episactine phallus. The structure is shown in parasagittal section; sclerotised areas are shown hatched or filled with black. The spermatophore and ejaculatory sacs are drawn approximately twice their real size. Further explanation in text.

similar to that of *Homeomastax*, but with a number of important differences.

1A. Anatomy of the phallic complex of the Central American Episactinae

Fig. 1 shows a generalised diagram of the phallus in this subfamily, in its details most closely resembling that of *Episactus tristani*. The spermatophore and ejaculatory sacs are drawn disproportionately large (about double their real size) for clarity.

In the Episactinae the endophallic plate [the "penis" of Descamps (1973)] is reduced to two weakly sclerotised rods, tenuously joined proximally to form the typical Eumastacid "hairpin" structure, lying in the lower surface of the spermatophore sac. They occasionally insert posteriorly into the ectophallus at the apex of the phallus (see below), but are not otherwise connected to each other or to any other sclerotized structure. This reduced plate will be referred to here as the *endophallic rods*. The overall length of the rods is short in relation to the overall length of the phallus, especially as compared to the endophallic plate of a eumastacine such as *Homeomastax*.

A further difference in organization is that the spermatophore sac (which lies dorsal to the endophallic rods) does not open dorsally to any large extent, but rather apically. The genital trough (which opens dorsally in the main in the Eumastacinae) starts dorsally but is further produced right down over the end of the phallus, forming a deep vertical *apical groove,* containing the genital aperture; on either side of it, the ectophallic walls are sclerified and ornamented, and often produced into *lips* bordering the groove.

As a consequence of its apical opening, the spermatophore sac is long and tubular, and provided with longitudinal folds running its full length, suggesting that it is greatly dilated by the spermatophore when this is formed. [In the Eumastacines, where the sac opens both dorsally and apically, the spermatophore can project dorsally from the genital trough – see Rowell & Bentos-Pereira (2002)].

The ectophallus bears a variety of sclerifications. As in the Eumastacinae, the dorsal margins of the genital trough (the dorsal prolongation of the apical groove), are typically edged with bar-shaped longitudinal ectophallic sclerites which usually extend anteriorly into a sclerite sac lying medially above the spermatophore sac, and posteriorly end in spines or processes projecting beyond the tip of the phallus. To distinguish them from the numerous other paired ectophallic sclerites of this subfamily (below), they are here referred to as the *dorsal ectophallic sclerites* [they were called simply "ectophallic sclerites" in the Eumastacine paper; Descamps (1973) calls them ectophallic valves]. In *Episactus* and *Paralethus* n.g. there are two pairs of sclerites in this region, here called the *internal* and *external dorsal ectophallic sclerites*. The internal sclerites indeed seem to be homologous with those of the Eumastacines. The external sclerites, in contrast, appear to be merely apically sclerotised evaginations of the ectophallic membrane arising at the outer corners of the aperture of the sclerite sac, which lies above the anterior extremity of the trough. Their sclerotised portions do not extend into the sac itself, unlike the internal sclerites.

The sclerified margins of the middle zone of the apical groove are apparently homologous with the *apical shields* of the Eumastacinae, as the endophallic rods sometimes insert into them. Although they

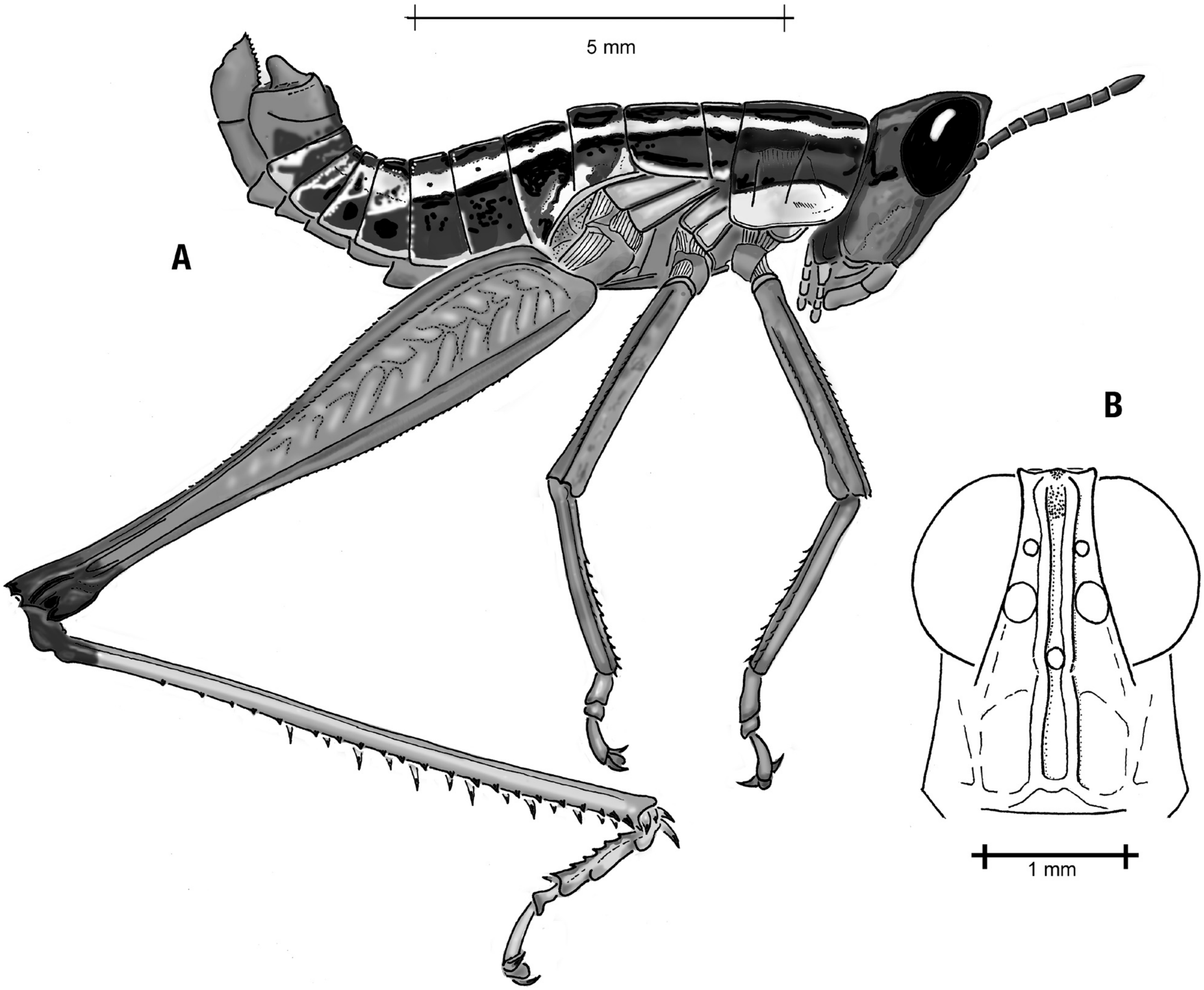


Fig. 2. *Episactus tristani*, male. A. Habitus, B. Head, frontal view.

are more often lip-like than actual shields, we will continue to use the eumastacine name here. In *Gymnotettix* and *Episactus eremites* their ornamentation may include spines. Laterally to them, in *Gymnotettix* and *Episactus*, are a separate pair of spined ectophallic sclerites, here called *apicolateral* sclerites. It is not clear to what extent these are derived from the apical shield, or whether they are quite independent ectophallic structures. The ventral part of the apical groove, where the medial ventroapical evagination would be in a eumastacine, is flanked laterally by a further pair of ectophallic sclerites (the *apicoventral sclerites*), which are usually armed with spines. Sometimes *(Episactus tristani)* there can be more than one pair of such sclerites. The same questions about their separate identity from the apical shield arise here as in the case of the apicolateral sclerites (above).

The lateral parts of the ectophallic membrane are more or less sclerified. In *Lethus* and *Paralethus* they form large robust *lateral ectophallic plates*, in the other genera the resultant structure is more tenuous. In *E. eremites* the plates connect the apicoventral and apicolateral sclerites with the sclerotisations of the apical shield, obscuring their boundaries.

The anterior region of the genital trough is covered dorsally by a median evagination of ectophallic membrane, the *dorsal fold* (as in Eumastacines), which is however rather short and tightly appressed. Above this, in most genera there is a small subepiphallic sac (also a prominent structure in some Eumastacinae). This sac is absent in *Paralethus*; instead of being medially invaginated to form a sac, the ectophallic membrane there merges directly with the posterior ventral margin of the epiphallus. From the posterior dorsal margin of the epiphallus a membrane runs posteriorly and dorsally to the base of the paraprocts.

The epiphallus itself is large and flat, roughly shield shaped in dorsal view in most genera (other than in *Lethus*, where it is roughly circular), narrower at the posterior end than the anterior. It is invariably deeply medially emarginate on its anterior edge, and often has membranous fenestrations elsewhere. The lophi are pointed, upwardly hooked, and usually large. The anterior margin of the epiphallus does not lie in the plane of the epiphallic membrane, but hangs from it into the haemocoel.

The episactine pallium does not cover the dorsal surface of the opening of the subgenital plate (as in *Homeomastax*, but unlike other eumastacines). Instead, this aperture is sheltered by the combination of supra-anal plate, recurved cerci and the variously produced edges of the subgenital plate, which imbricate to form a roof, especially well developed in *Lethus* and *Paralethus*.

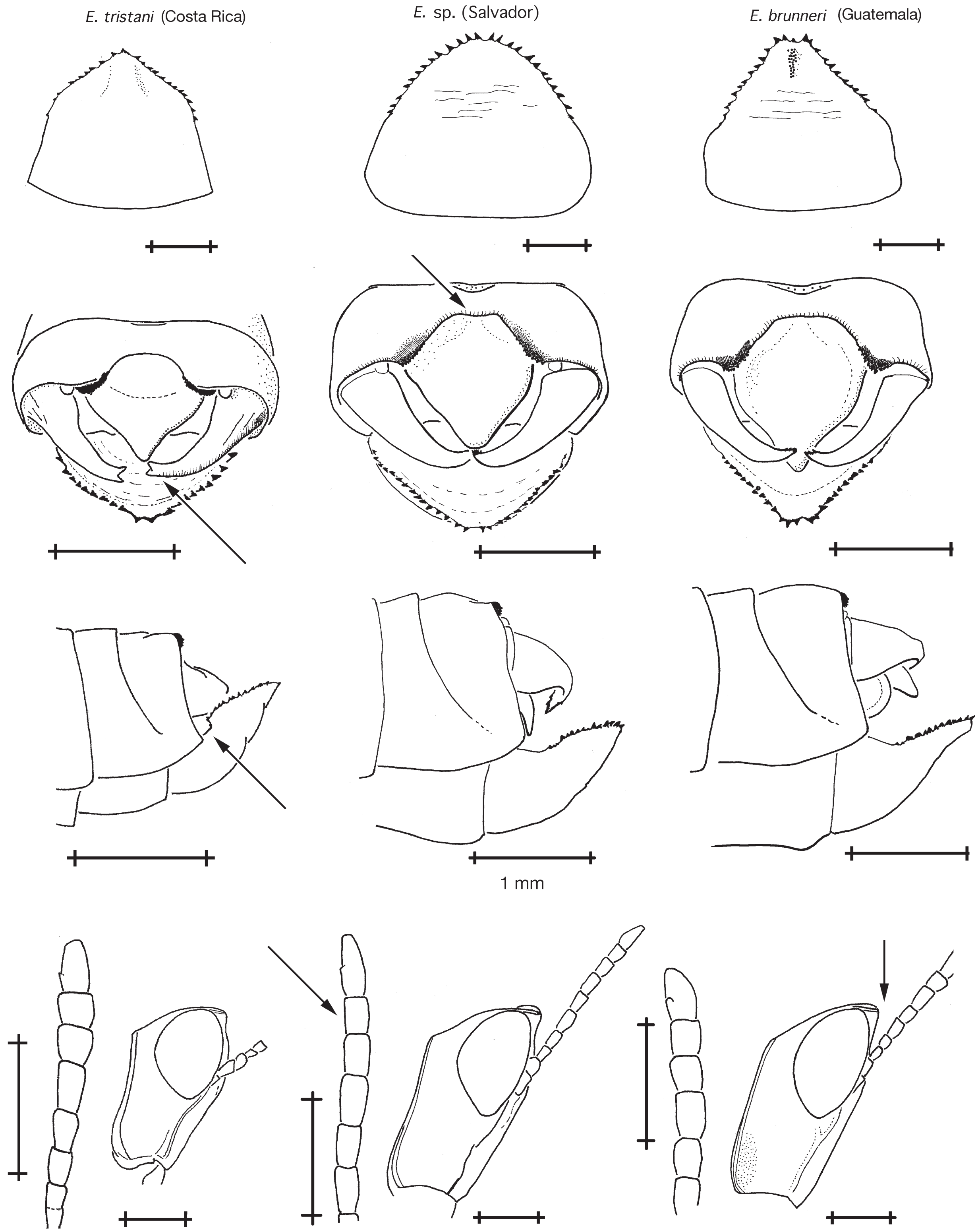


Fig. 3. External morphological differences between *Episactus* individuals from Costa Rica (*E. tristani* Rehn) (left hand column); Guatemala (*E. brunneri* Burr) (right hand column); and an unnamed intermediate form from Salvador (center column). The arrows indicate differentiating structures. Upper row; rear axial view of male subgenital plate. Second row: male cerci, supra-anal plate and furcula. Third row: tip of male abdomen, lateral view. Bottom row: head in lateral view to show profile of fastigium; antennae in dorsal view. Scale bars, 1 mm.

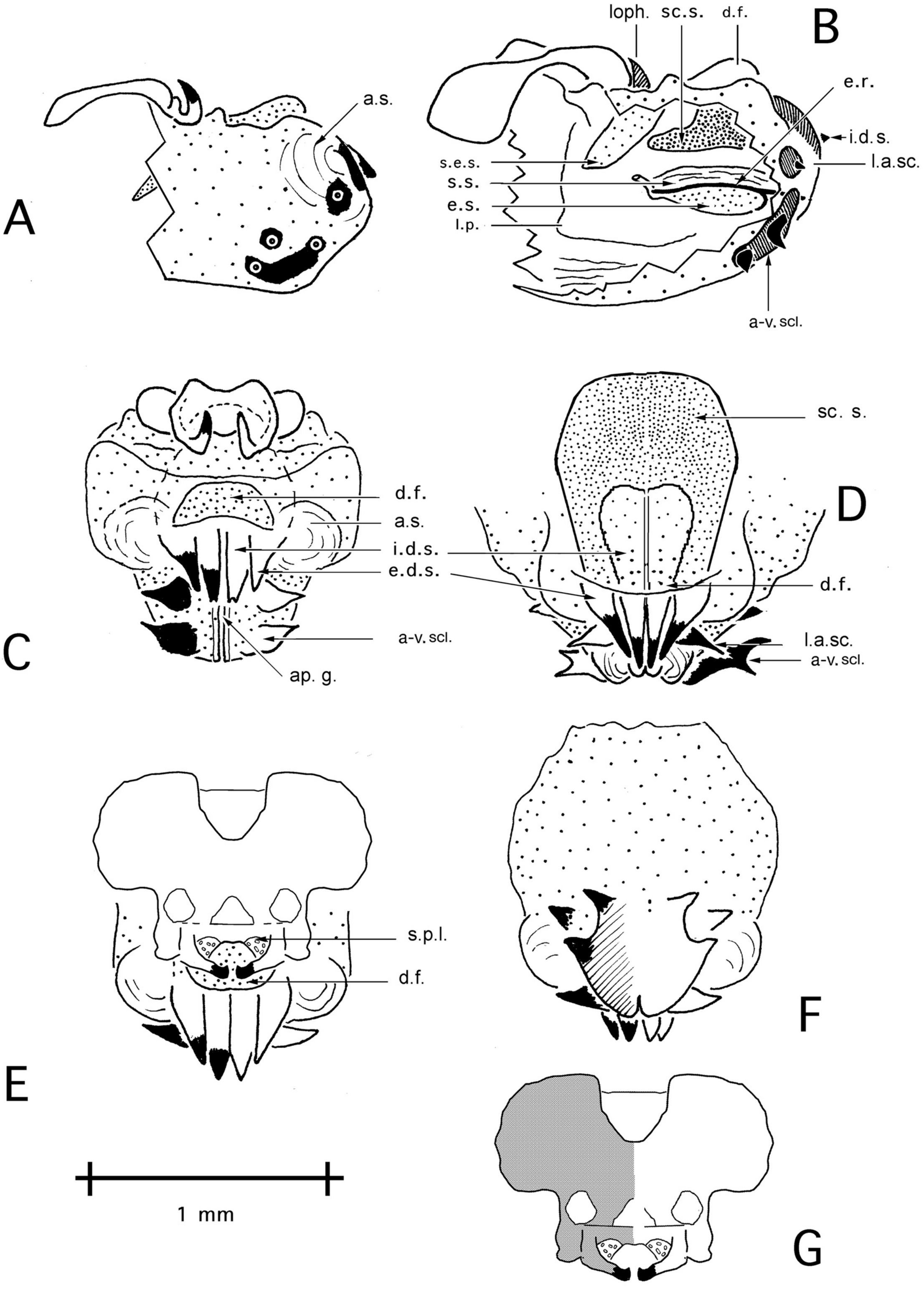


Fig. 4. *Episactus*, phallic structures. A-G, *E. tristani*. A. Lateral view of phallus. B. As A, in another preparation. Most of the near-side ectophallic membrane has been removed to show internal structures. Abbreviations: •a.s. - apical shield •d.f. - dorsal fold •e.r. - endophallic rod •e.s. - ejaculatory sac •l - lophus •l.p. - edge of lateral plate, seen from the inside (in this species the plate is merely thickened membrane with little or no sclerification) •s.a.s. - ventroapical sclerite •s.e.s. - subepiphallic sac •s.s. - spermatophore sac •sc.s. - sclerite sac. C. Phallus, frontal view. Abbrev.: •d.f. - dorsal fold •a.s. - apical shield •i.d.s. - internal dorsal ectophallic sclerite •e.d.s. - external dorsal ectophallic sclerite. D. Phallus, dorsal view. E. As D, in another preparation, to show the range of variation in the sclerites and their development. F. Phallus, ventral view. G. Epiphallus, dorsal view.

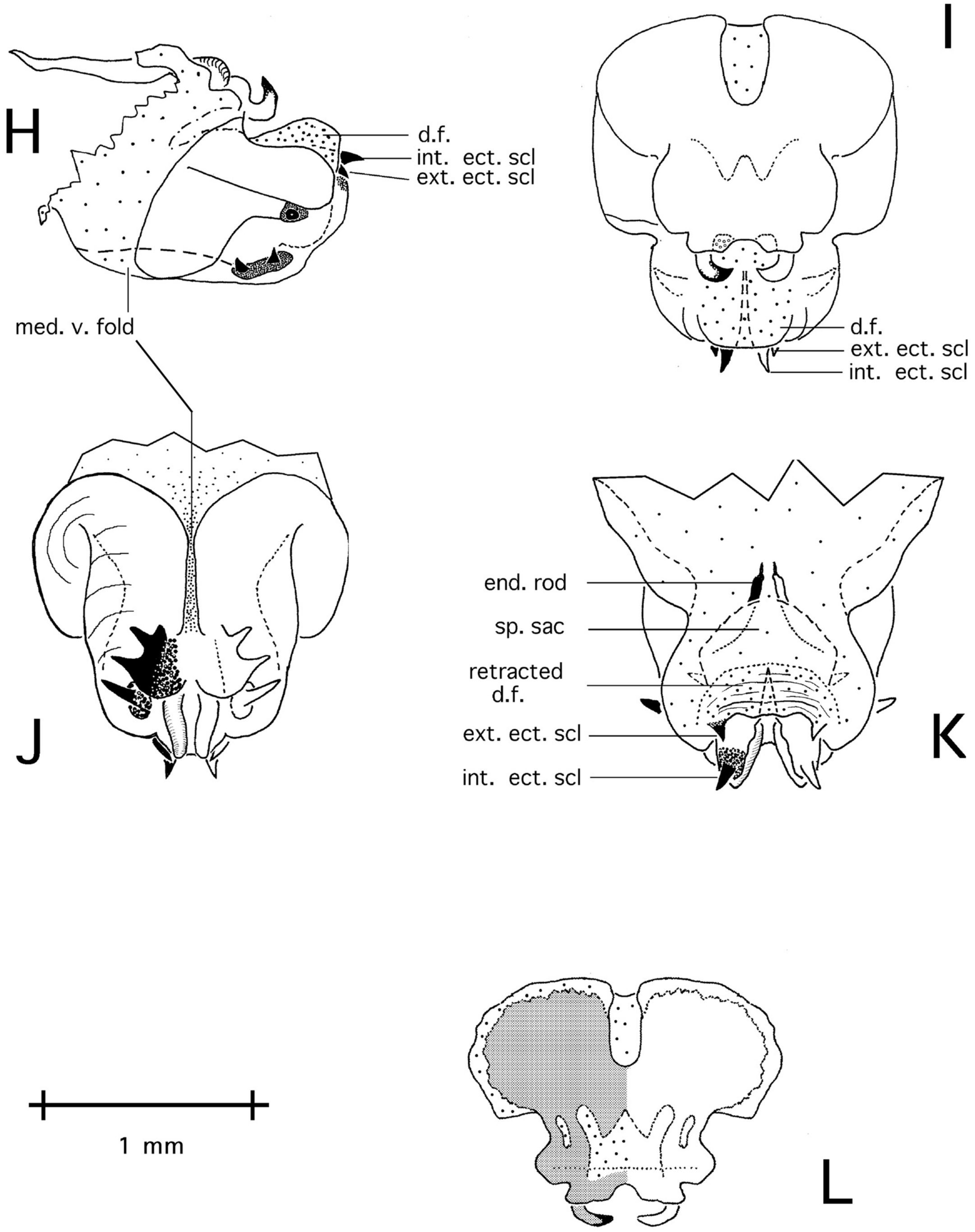


Fig. 4. contin. *Episactus*, phallic structures. H-L, *E. brunneri.* H. Lateral view of phallus, retracted state. I. As H, dorsal view. J. As H, ventral view. K. Dorsal view of ectophallus in extended state. L. Epiphallus.

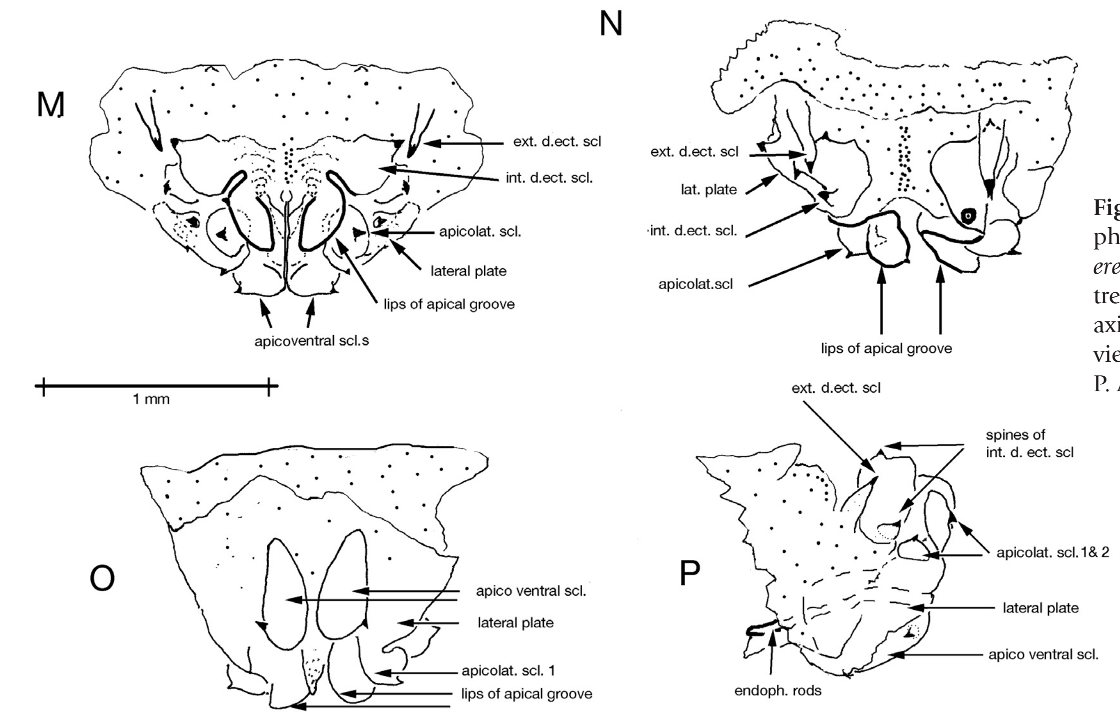


Fig. 4. contin. *Episactus*, phallic structures. M-P. *E. eremites*. M. Posterior extremity of phallic complex, axial view. N. As M, dorsal view. O. As M, ventral view. P. As M, lateral view.

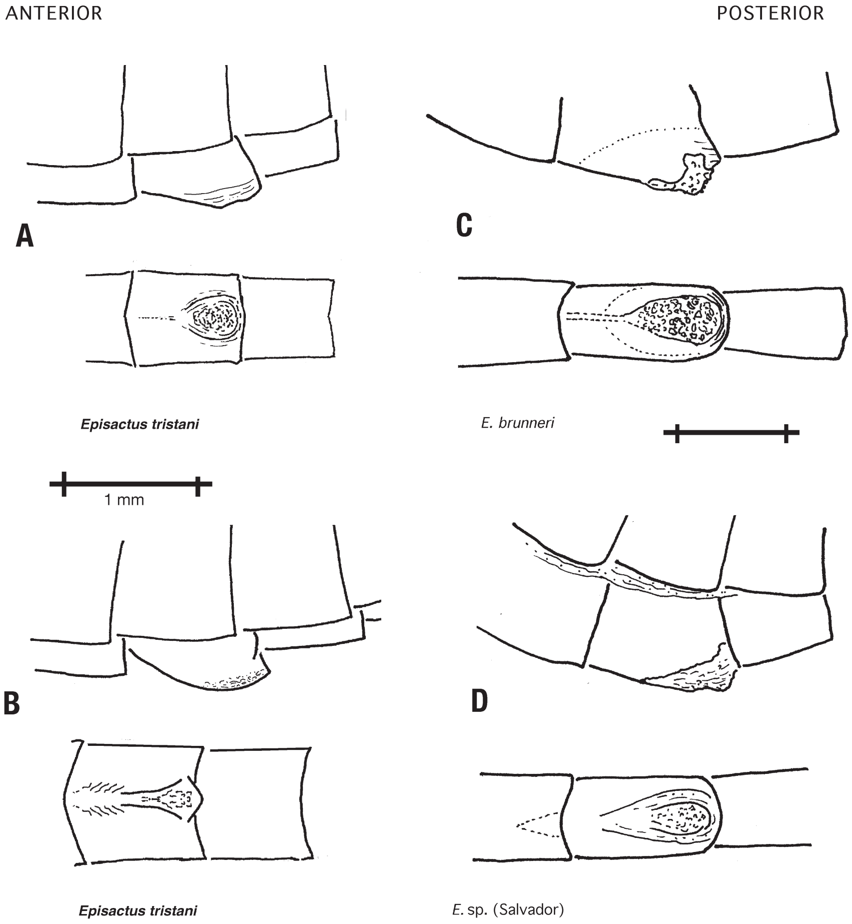


Fig. 5. Specialisation of 4th abdominal sternites of male *Episactus*. Each figure shows the same structure laterally (top) and in ventral aspect (bottom). A, B. *E. tristani*; C. *E brunneri*; D. *E.* sp. (El Salvador). In *E. eremites* there is little or no modification of the sternites.

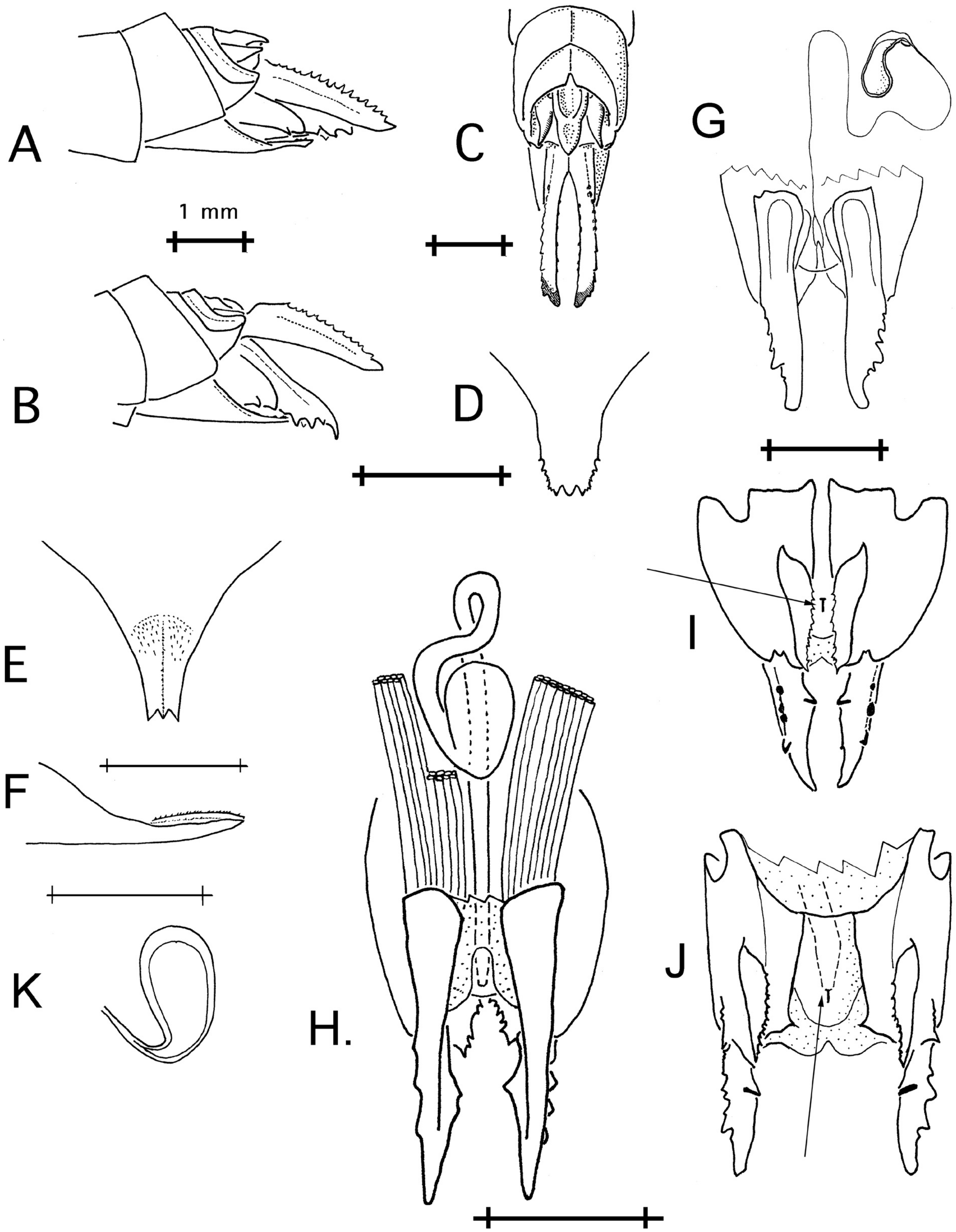


Fig. 6. *Episactus tristani*, female genitalia. A. Tip of female abdomen in resting position, lateral view. B. As A, with valves parted. C. As A, dorsal view. D. Tip of female subgenital plate, dorsal view. E. As D, in a different specimen. F. As E, lateral view. G. Ventral ovipositor valves and spermatheca, desheathed. H. As G, but not desheathed. I, J. Dorsal roof of genital chamber in ventral view to show papilla with T-shaped aperture of spermathecal duct (arrows) (two different specimens). K. Desheathed spermatheca showing spermatodose within. Scales 1 mm throughout.

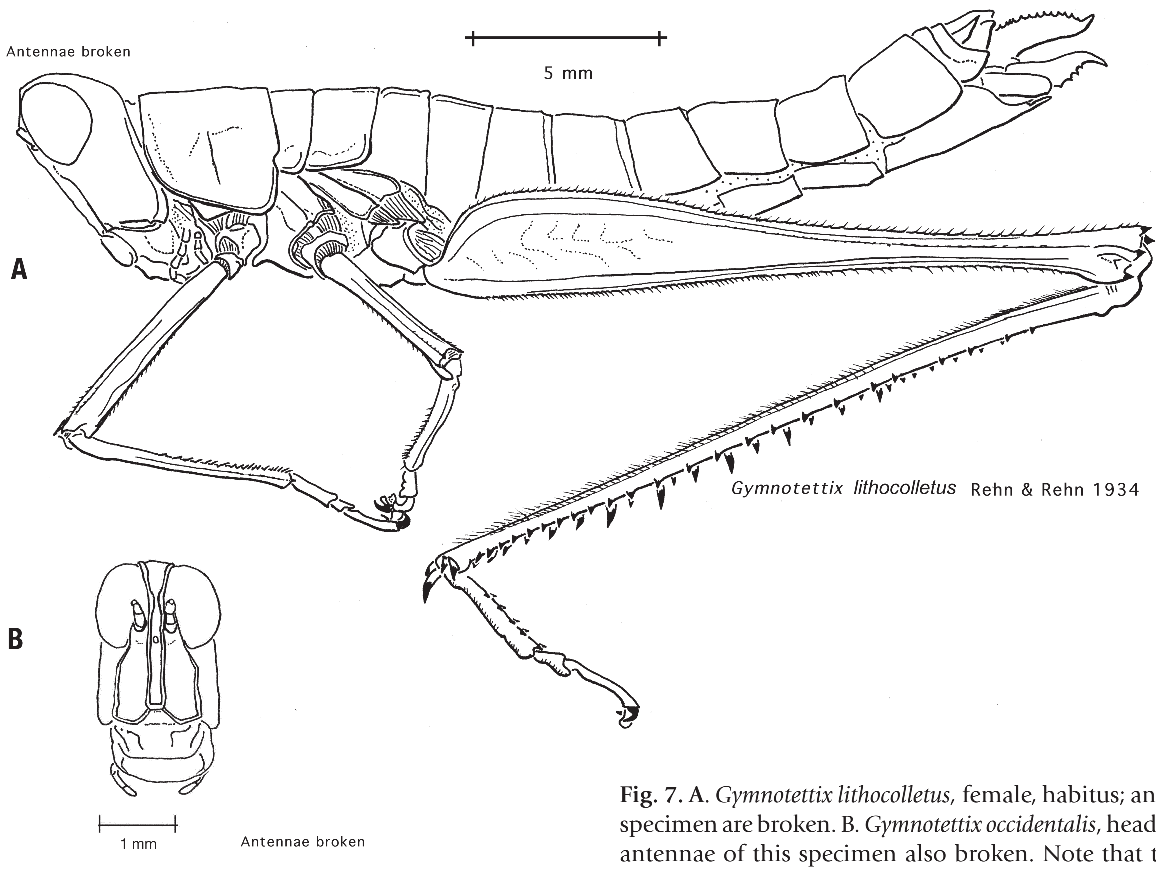


Fig. 7. A. *Gymnotettix lithocolletus*, female, habitus; antennae of this specimen are broken. B. *Gymnotettix occidentalis*, head, frontal view; antennae of this specimen also broken. Note that the carinae of the fastigium are here continuous with those of the frontal ridge (compare with Fig. 11B).

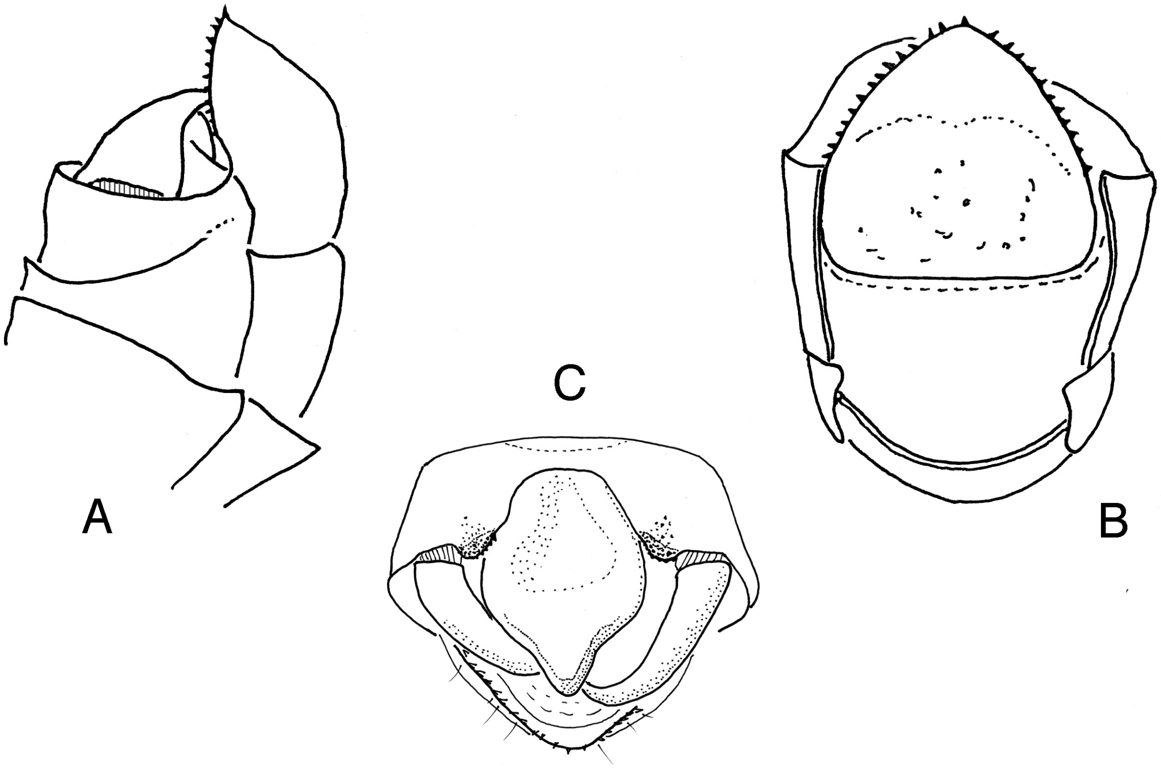


Fig. 8. *Gymnotettix lithocolletus*, male. A. Tip of abdomen, lateral view. B. Same, axial (posterior) view. C. Same, dorsal view.

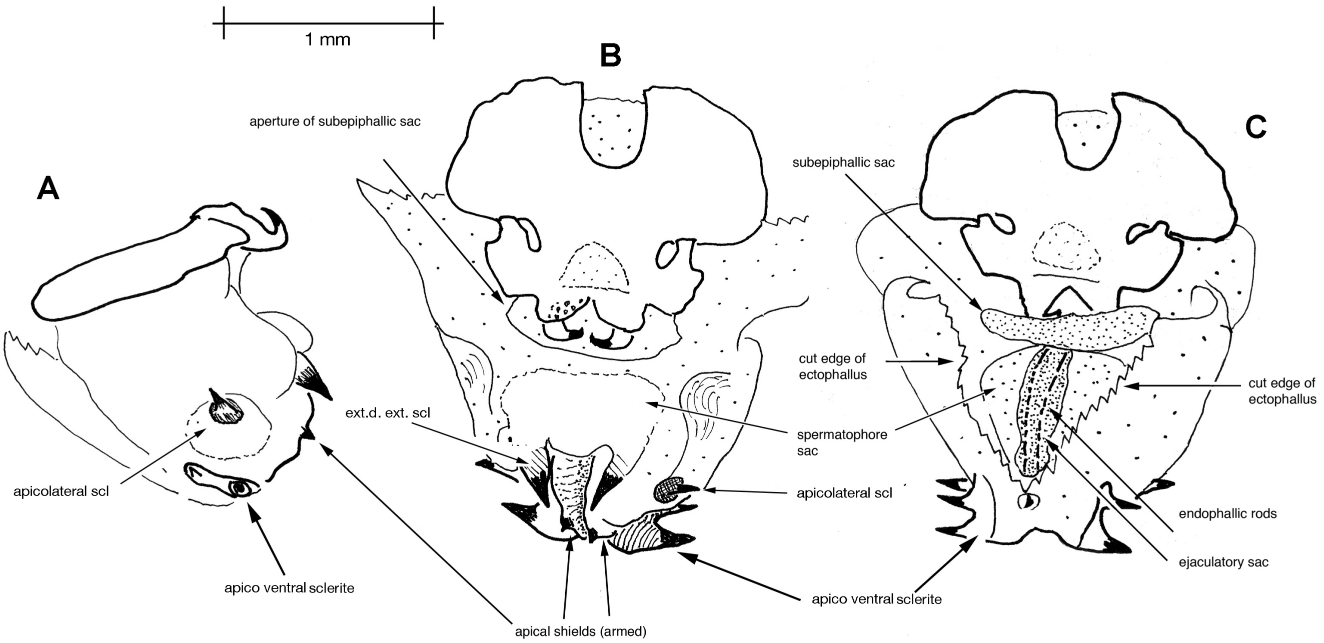


Fig. 9. *Gymnotettix lithocolletus*, phallus. A. Phallic complex, lateral view. B. As A, dorsal view. C. As A, ventral view, ectophallic membrane cut medially to show endophallus and subepiphallic sac.

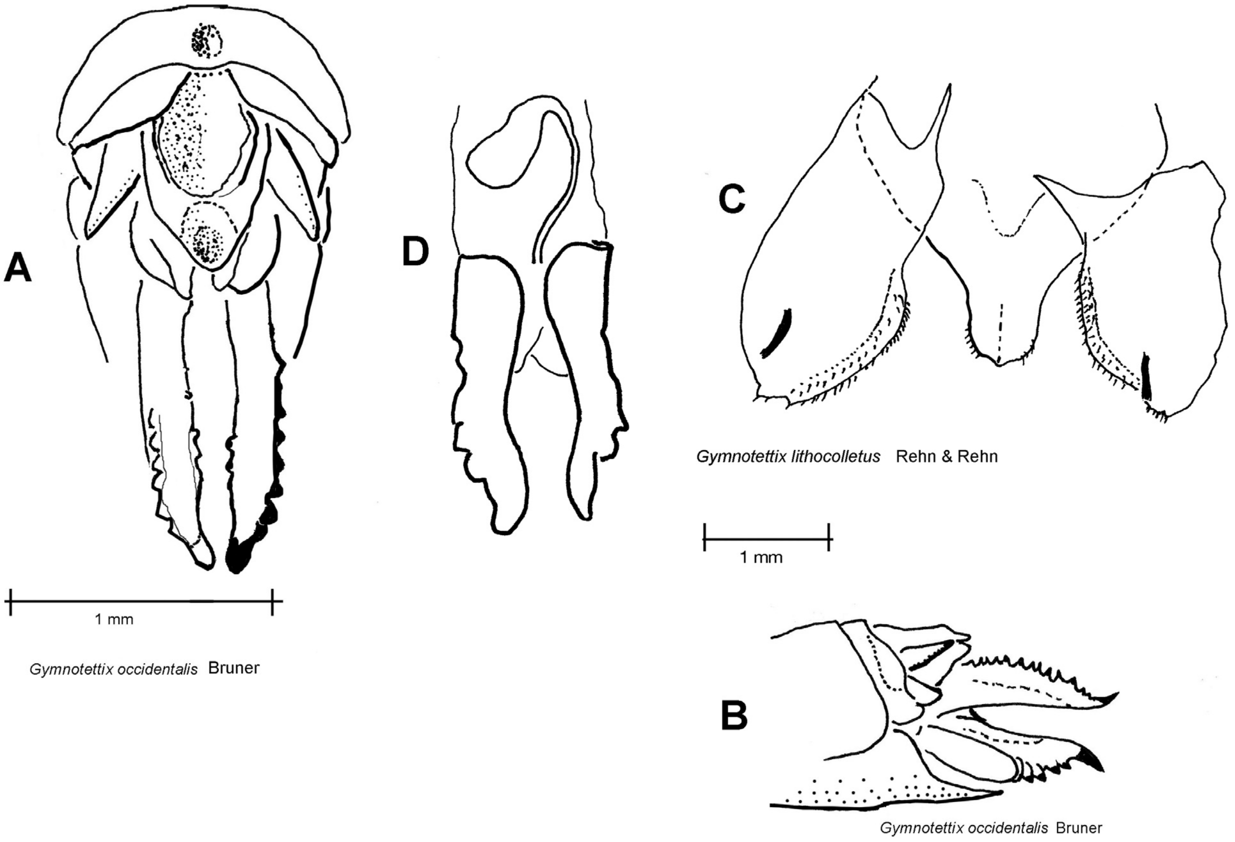


Fig. 10. *Gymnotettix*, female genitalia. A. *G. occidentalis*, tip of female abdomen, dorsal view. B. As A, lateral view. C. *G. lithocolletus*, *f*emale subgenital plate, dorsal view. D. *G. lithocolletus*, ventral ovipositor valves and spermatheca.

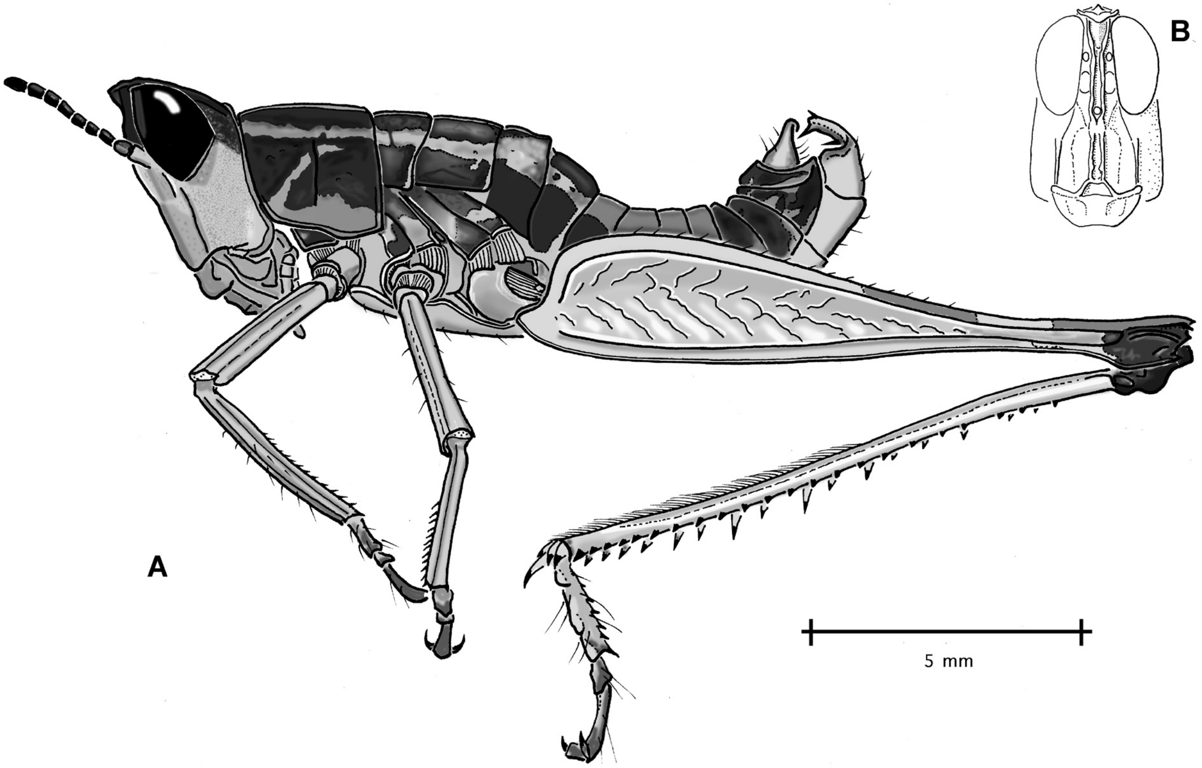


Fig. 11. *Lethus nicaraguae,* male. A. Habitus. B. Head, frontal view. Note that the carinae of the frontal ridge here abut, but are not continuous with, the carinae of the fastigium (compare with Fig. 7B).

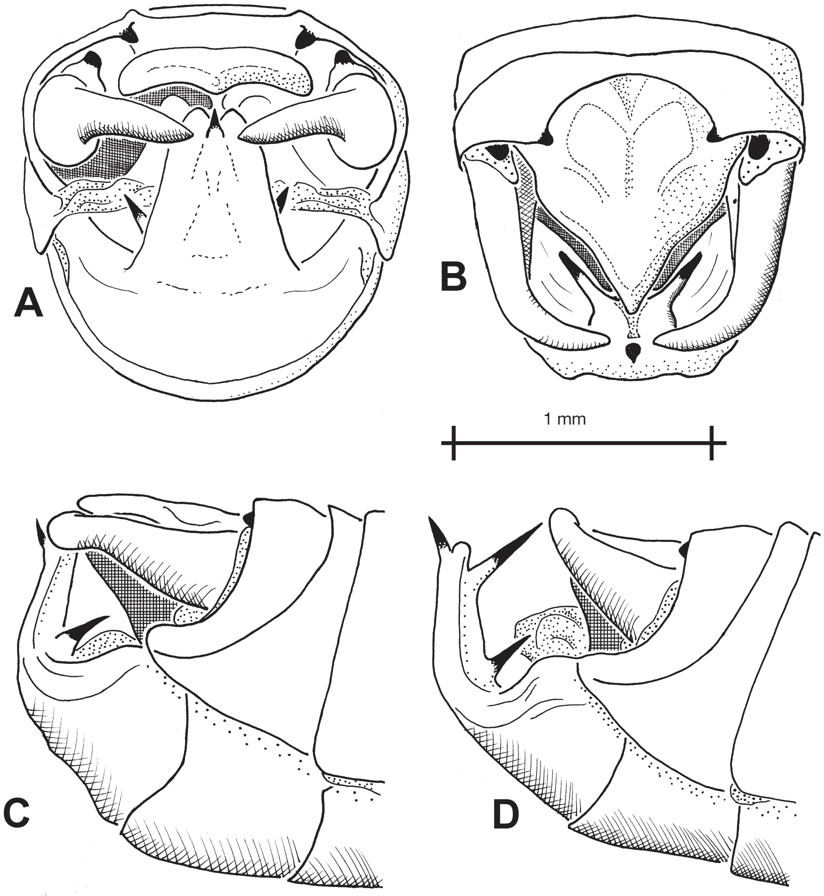


Fig. 12. *Lethus nicaraguae,* male, external genitalia. A. Tip of male abdomen, axial view. B. Dorsal view. C. Lateral view, normal posture. D. Lateral view, with prolongation of subgenital plate extended to disclose phallus.

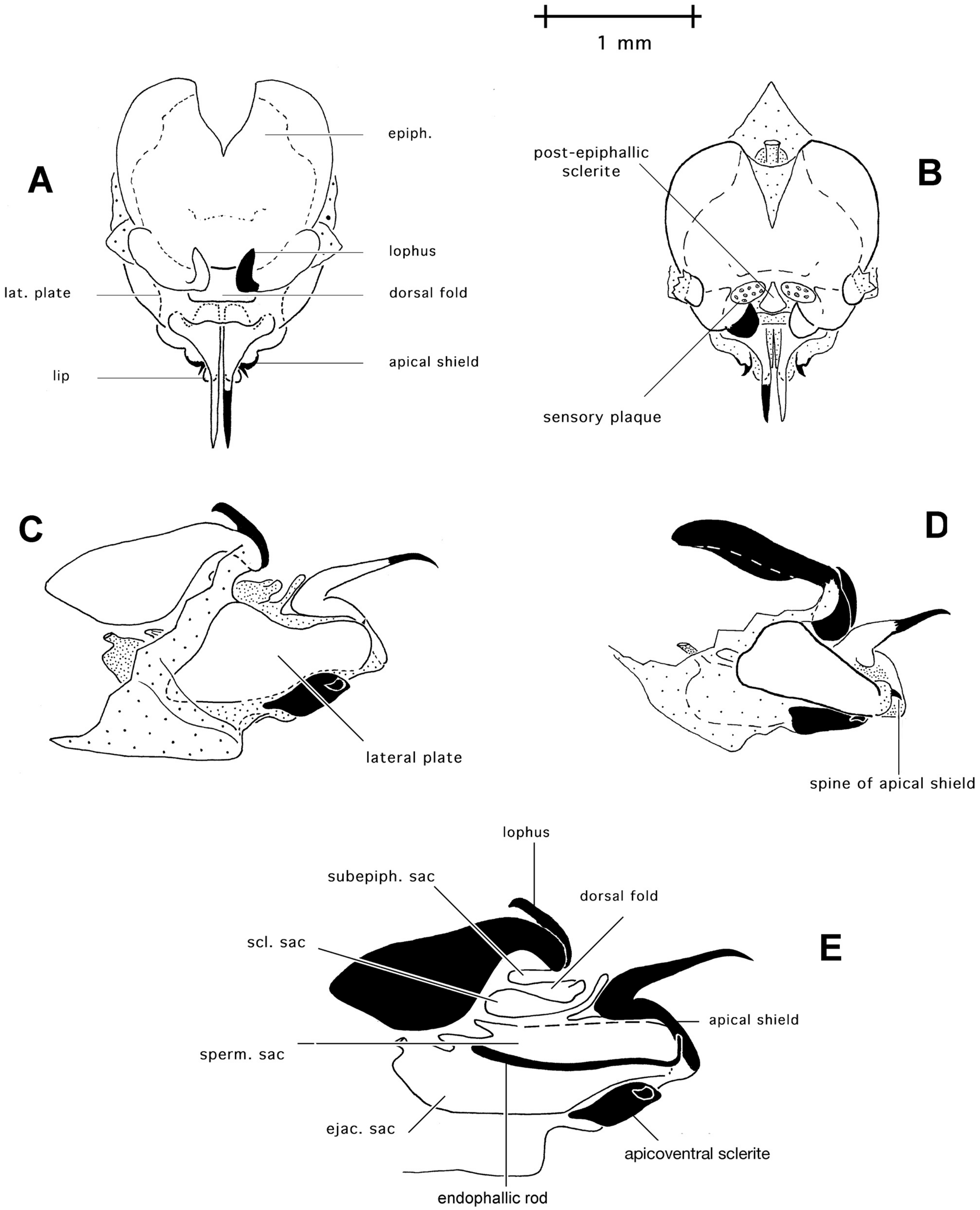
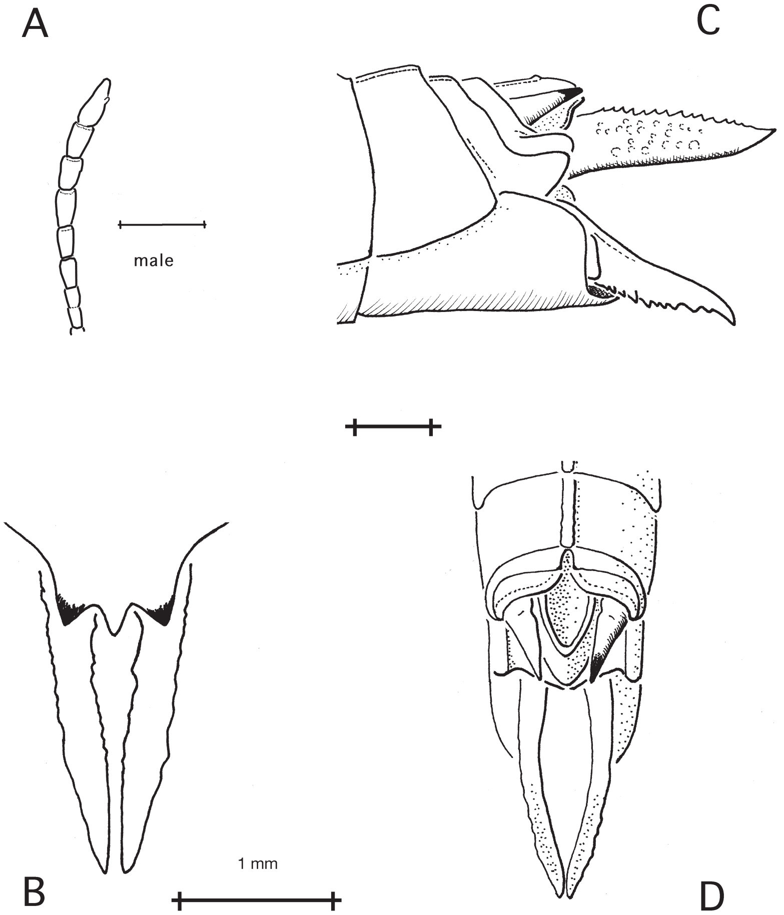


Fig. 13. A. *Lethus nicaraguae*, phallus. A. Phallic complex, dorsal view. B. As A but epiphallus retracted to show postepiphallic sclerite. C. Phallic complex, lateral view, extended. D. As C, retracted. E. Parasagittal section to show endophallic structures.

Fig. 14. *Lethus nicaraguae*. A. Male antenna. B-D. Female external genitalia. B. Posterior margin of female subgenital plate. C. Tip of abdomen, lateral aspect. D. Tip of abdomen, dorsal aspect.



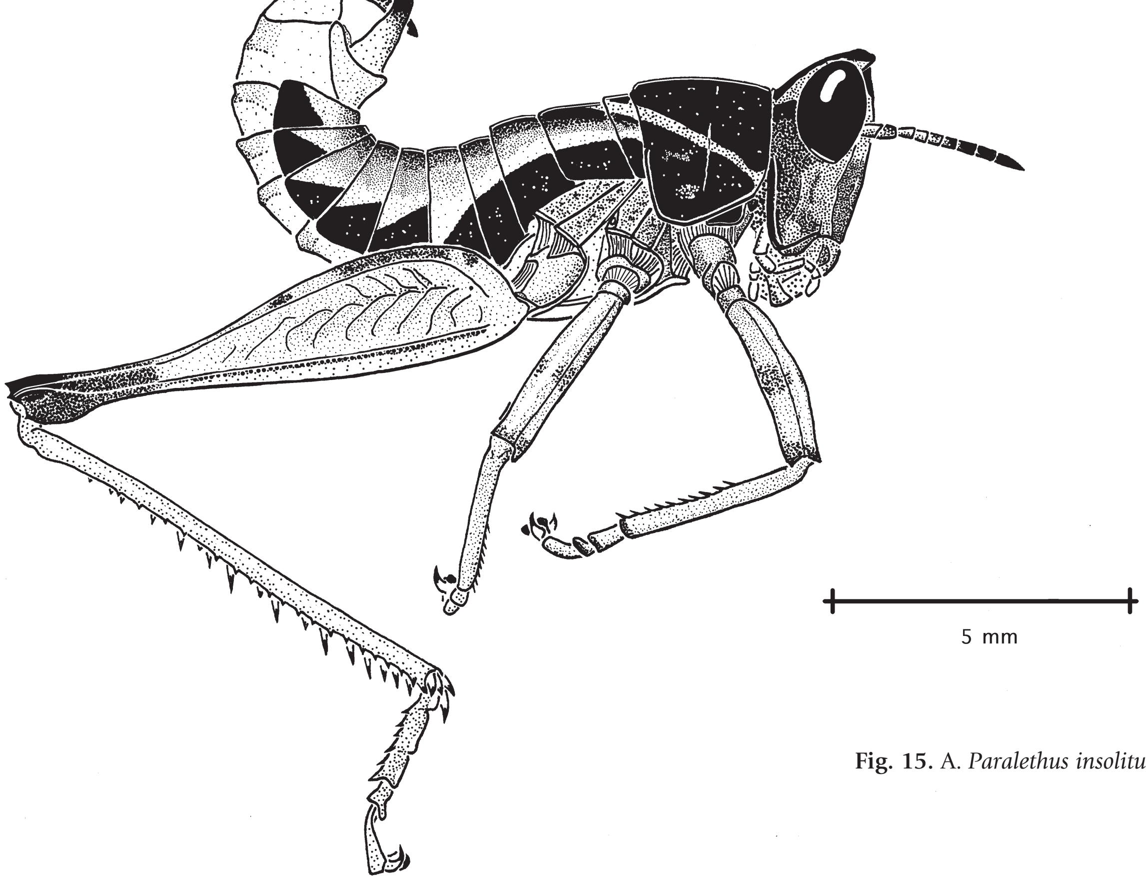


Fig. 15. A. *Paralethus insolitus* n. sp. male, habitus.

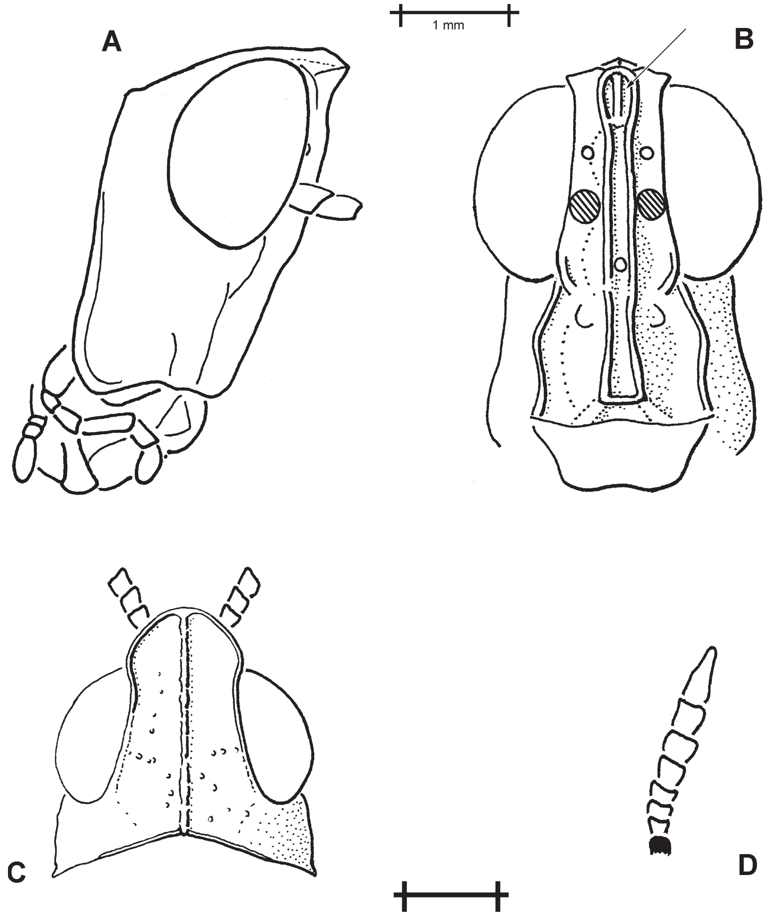


Fig. 16. *Paralethus insolitus* n. sp male. A. Head, lateral aspect. B. Head, frontal aspect. Note small medial carina in dorsal part of frontal ridge (arrow). C. Head dorsal view. D. Antenna.

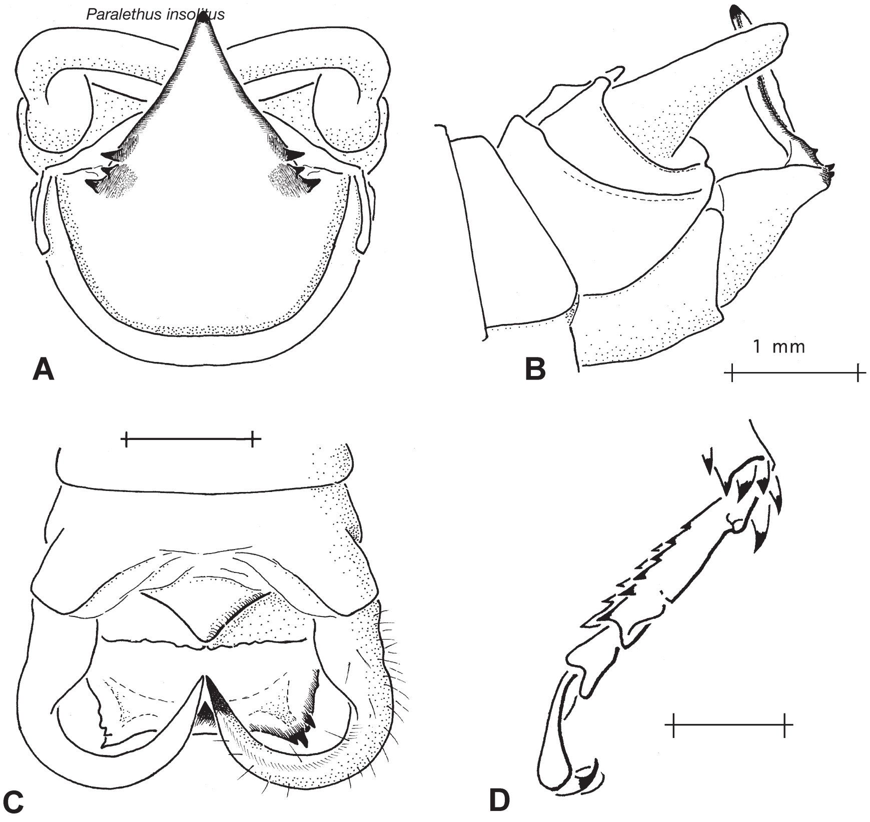


Fig. 17. *Paralethus insolitus* n. sp. male, A-C. Male external genitalia. A. Axial (posterior) view. B. Lateral view. C. Dorsal view. D. Right-hand side hind foot and tibial apex.

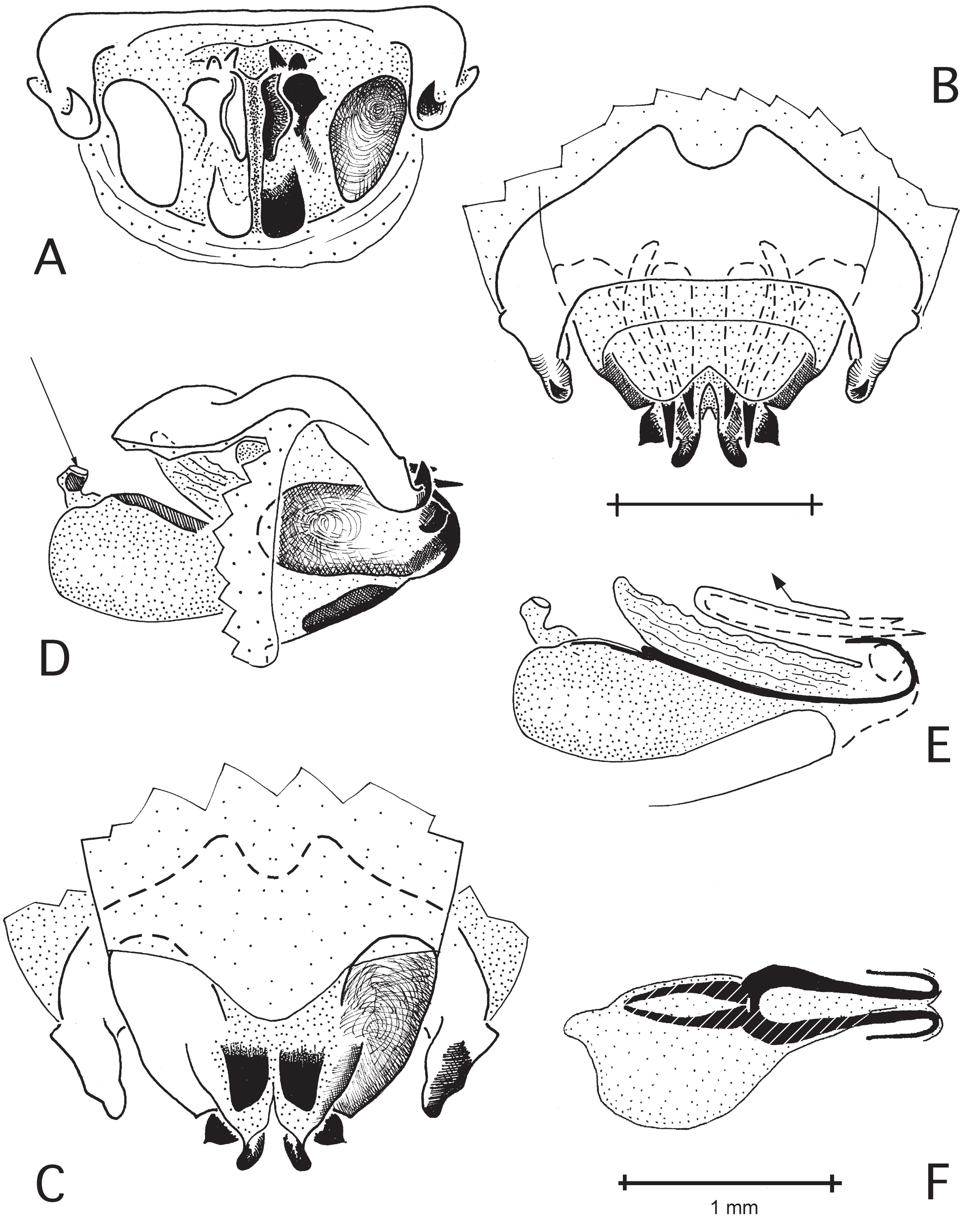


Fig. 18. *Paralethus insolitus* n. sp. Phallus. A. Phallic complex, axial (posterior) aspect. B. Dorsal aspect. C. Ventral aspect. D. Lateral aspect. Arrow shows ejaculatory duct with U-shaped sclerite. E. Endophallus, lateral aspect. F. Endophallus, dorsal aspect. The spermatophore sac has been displaced to the (animal's) left-hand side. Note paired anterior processes running over the ejaculatory sac.

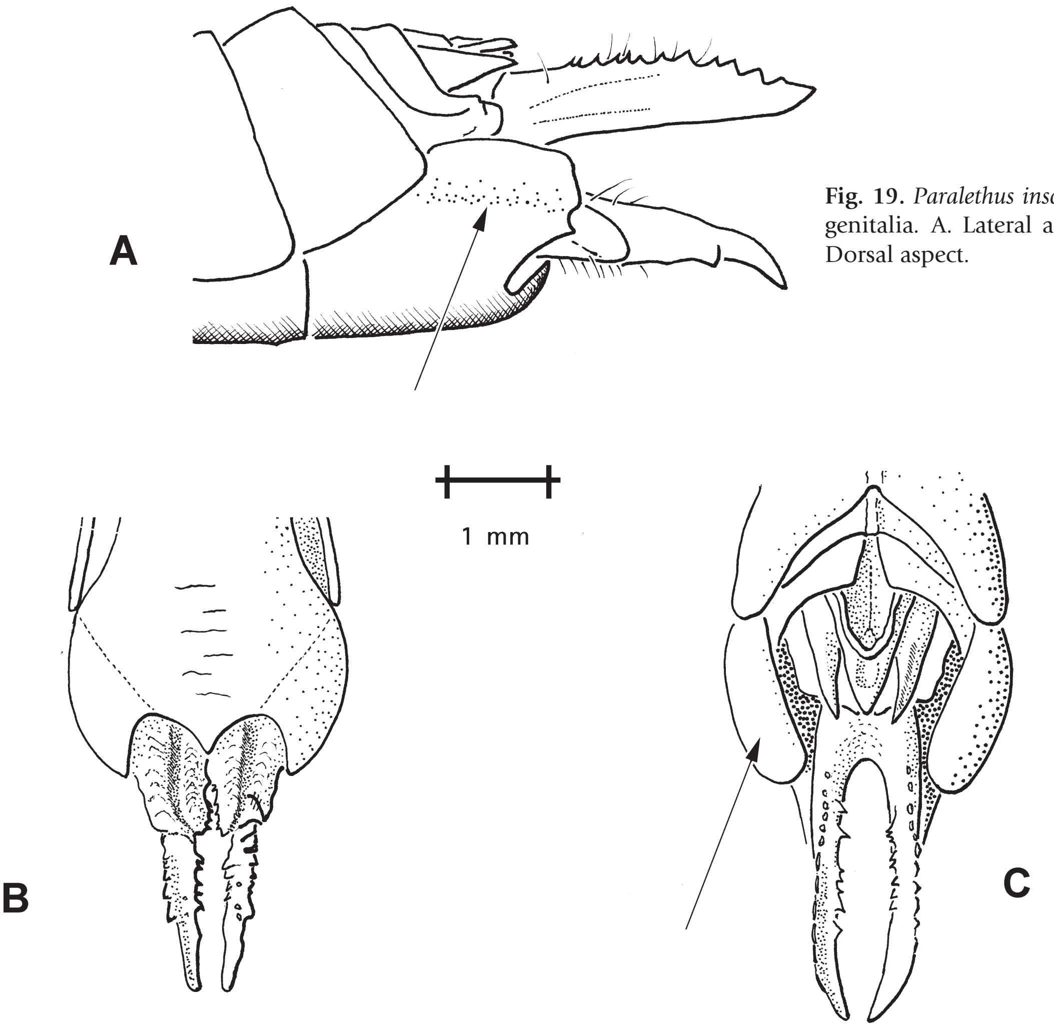


Fig. 19. *Paralethus insolitus* n. sp. Female external genitalia. A. Lateral aspect. B. Ventral aspect. C. Dorsal aspect.

1B. Notes on the Episactid female system, especially the spermatheca

The female system seems to be very uniform throughout the subfamily, and apart from the subgenital plate, has no obvious taxonomic utility.

The subgenital plate always has a prominent medial process or egg-guide, similar to that found in Acridoidea. It is usually densely sclerotized and pointed. In most cases there are also lateral lobes, which may be toothed or otherwise ornamented, and commonly are species specific in form.

The ovipositor valves are normal. Between and ventral to the proximal (internal) parts of the lower valves there is an elongate fleshy papilla, into which the duct of the spermatheca runs, without widening into a bursa copulatrix. Presumably there is an opening at its end or on its ventral surface, but this can rarely be seen clearly. The papilla varies somewhat in length among the genera (see Figs 6, 24, 29, 33, 35).

The spermatheca is positioned in contact with the anterior rim of the ventral ovipositor valves (Figs 6, 24). The spermatheca and its duct are contained in a complex sheath of connective tissue and trachea, and anchored to (at least) the muscles of the ventral ovipositor valve and the terminal abdominal ganglion. This network stabilises its position and prevents strain on the very delicate duct. The duct is relatively short, and there is no bursa copulatrix, nor even a widening of the duct near its confluence. It runs from the ventral papilla, mentioned above, forward along the right hand side of the spermatheca, across its top from right to left, then turns under itself and runs back again from left to right and down the right hand side of the spermatheca, which it enters near the bottom (Figs 21D, 33 E, F). The duct is bound to the spermatheca by a thin membrane. When this is removed, it is seen that both sac and duct are further enclosed in a thick pigmented sheath. The duct itself is extremely fine, but can be seen within the sheath by staining in acid fuchsin. The pigmented sheath can be dissected from the sac and sometimes from the duct too (Fig. 21.) The sac is then seen as a transparent balloon, thinner towards the posterior end. The duct runs into this balloon, turns towards the anterior, and frequently terminates in a spermatodose (see Vahed 2003) (Figs 6G, 33H, 21E, G).

There is no diverticulum of the spermatheca, and no obvious muscle, which could serve as a sperm pump, such as that found in *e.g.*, the Chrysomelidae (*e.g.* Chaboo 2002), attaching to the spermatheca.

As there is no bursa, and the phallus lacks an intromittent structure, presumably sperm (or a spermatophore) is deposited in the genital chamber - the space between subgenital plate and the ventral ovipositor valves, into which the ventral papilla projects. The rear of this space is closed by the membrane attaching the subgenital plate to the ventral surface of the oviduct, and this membrane is pouched forward, giving a well-defined cavity. From there sperm is presumably aspirated by the spermatheca—or the duct is invaded actively by the sperm. An amazing performance at all events, because the opening in the papilla and the lumen of the duct itself are VERY small.

1C. Individual Episactine genera

The different episactine genera are now illustrated and commented upon, using the above terminology.

1. *Episactus* Burr 1899: 254
Type species*:* *E. brunneri* Burr 1899, designated Rehn 1905: 801.
Rehn & Rehn 1934: 21.
Type genus of Episactinae, designated Rehn 1948: 123.
Descamps 1971: 110.
Type genus of Episactidae, designated Descamps 1973: 200.
Descamps 1973; Plate XIV (illustrations of male genital anatomy).

Etymology.— Replacement name for *Epeisactus* Brunner von Wattenwyl 1893 (invalid, as no type species indicated).

Episactus is the most gracile genus of the subfamily (Fig. 2, habitus) and the most widely distributed, extending from Mexico to Costa Rica.

There are three described species, *brunneri* Burr 1899 (Guatemala), *eremites* Rehn & Rehn 1934 (Mexico: Chiapas), and *tristani* Rehn & Rehn 1934 (Costa Rica).

A further form, intermediate between *brunneri* and *tristani*, and distinct from *eremites,* occurs in El Salvador. Material examined: EL SALVADOR: Los Aguilares: 23.06.1958; (no collector given), one late larval male (USNM). Los Chorros, 20.06.1963, ME Irwin & DQ Cavagnaro, adult male, specimen #71244 (UCR). Same data as previous specimen, specimen no. 2002010 (RC). This Salvadorian form is slightly larger than Costa Rican *tristani*, but otherwise very similar. *E. tristani* is the species best represented in collections and the best studied anatomically.

E. eremites is known only from the type specimens, and it differs markedly from the other members of the genus in its general form, resembling at first sight the genus *Lethus.* (Indeed, Rehn's handwritten holotype label bears the name *Lethus eremites*; obviously his final assignment to *Episactus*, which is confirmed by the present investigation, was a second thought). The phallus (Fig. 4) is similar to that of other *Episactus* species, and very different from that of *Lethus*. Also, as pointed out by Rehn and Rehn (1934), the distal margin of the prolongation of the male subgenital plate bears minute teeth similar to those seen in other *Episactus* spp., but unlike the large thornlike spines of *Lethus*.

The distinctions between the other species of the genus are sometimes subtle (Fig. 3), and there is insufficient material available to judge how distinct they really are. Conceivably they are an intergrading cline. *E. brunneri* and *E. tristani* do show small differences in epi- and ectophallic structures (Fig. 4). The external morphological differences are figured in Rehn & Rehn 1934, Figs 16-33, here supplemented by Fig. 3.

The phallic complexes of *E. tristani* and *E. brunneri* are shown in Fig 4. The two species differ in the details of the fenestration of the epiphallus and of the shape of the tips of the dorsal ectophallic sclerites, and in other minor details (see caption to Fig. 4). Both conform quite closely to the generalised schema for the subfamily shown in Fig. 1.

The epiphallus (Figs 4G, L) is flat and plate-like, deeply notched on its anterior border, and fenestrated at its posterior end anterior to the lophi, which are short and hooked and inwardly inflected.

There is a simple subepiphallic sac (Fig. 4B), but no subepiphallic or postepiphallic sclerites are associated with it. Below the ventral margin of the subepiphallic sac the membrane is evaginated to form a robust dorsal fold, overlying the anterior part of the genital trough.

The sclerotized tips of the internal dorsal ectophallic sclerites are small, spatulate and tend towards the bifid condition (Fig. 4C). The external dorsal ectophallic sclerites are large, pointed and thorn-shaped, backwardly directed (Fig. 4C). Two pairs of apicolateral sclerites are present (Fig. 4A), both armed with points directed laterally. The ventroapical sclerites are well developed and each bears two large laterally directed spines.

The endophallus is small and membranous, situated axially in the tip of the ectophallus.The endophallic rods run in the floor of the small spermatophore sac and are downward curving at their tips (Fig. 4B), with the ends lying free in the membrane of the ejaculatory sac.

The phallus of *E. eremites* (Figs 4M-P) agrees with much of the above description, but also differs considerably in various ways. The internal dorsal ectophallic sclerites are not of the usual bar-like type, but instead are broad and short, roughly triangular in dorsal aspect, and ornamented with two to three spines each (asymmetric in the specimen examined). The external dorsal ectophallic sclerites are represented by slender tubular membranous evaginations, which end in sclerotised points (single or double, again asymmetric). The lips of the apical groove are large, undulated, and ornamented with occasional spines, and the tips of the endophallic rods insert into their lower parts. Apicoventral and apicolateral sclerites are present and armed, and there are additional small spines on the lateral plate which runs between these structures.

All species of the genus have a specialisation of the integument of the male abdominal sterna, which may overlie glandular tissue, as it often appears to be covered with a dry secretion. Its exact form varies between individuals within a population (Fig. 5). It is most conspicuous on the 3rd abdominal sternite, but also present to some extent on the 2nd and 4th. This feature is least well developed in *E. eremites*.

Female reproductive structures are summarized in Fig. 6. Both spermatheca and ovipositor valves are typical for the subfamily as a whole.

2. *Gymnotettix* Bruner 1901: 20.

Type species *G. occidentalis* Bruner 1901, designated Rehn 1905: 801.
Rehn & Rehn 1934: 8.
Rehn & Grant 1958: 317, and Plate 29 (drawings of phallic structure *of L. lithocolletus)*.
Descamps 1971: 110.
Descamps 1973: Plate 14 (drawings of phallic structure *of L. lithocolletus)*.
Descamps 1974: 557.

Etymology.— Greek *gymnis*, bare, naked: *tettix*, cicada, conventionally used for grasshopper. Presumably a reference to the glabrous smooth cuticle.

There are 3 described species: *G. occidentalis* Bruner 1901 (Belize); *G. lithocolletus* Rehn & Rehn 1934 (Honduras); *G. moralesi* Descamps 1974 (Honduras).

Similar in both morphology and habitus (see Figs 7, 8) to *Episactus*, though more robust and more elongate. The phallus (Fig. 9) compares to that of *Episactus* as follows:

a. Epiphallus of similar type, notched on the anterior border, and fenestrated anterior to the lophi, which are sharp, upwardly directed, hooks. A simple subepiphallic sac is present.

b. Ectophallus usually with only one pair of armed apicolateral sclerites (Fig. 9A). Some variation between individuals is seen; Descamps (1973: Fig. 234) shows two pairs of such sclerites). Internal dorsal ectophallic sclerites absent. The external dorsal sclerites are of the same type as in *Episactus*, as are the apicoventral sclerites. Endophallic rods reflexed dorsally at their posterior ends, running in the margins of the genital trough. The apical shields are armed with small single spines on their posterior margins (Fig. 9B). The lateral plates are only weakly developed.

3. *Lethus* Rehn & Rehn 1934: 37.

Uvarov (1940) proposed the replacement name *Mayamastax* for *Lethus,* claiming the latter was preoccupied. This was vigorously disputed by Rehn & Rehn (1940). Subsequent authors have used either name. Descamps (1974), in the most recent review, used *Lethus.*

Etymology.— Acccording to Rehn & Rehn, the name of a Pelasgian prince, an ally of Troy. The applicability is not obvious!

Type species.— Lethus oresterus Rehn & Rehn 1934, by original designation.

Lethus and the following genus *Paralethus* resemble each other closely and differ in habitus from the previous two genera: they are ground dwelling, sombrely colored, laterally compressed species (Fig. 11) without the bright markings of the forb-dwelling genera. *Lethus* currently comprises four species:

L. oresterus Rehn & Rehn 1934 (Honduras)
L. maya Rehn & Rehn 1934 (Mexico, Chiapas)
L. carbonarius Desc.1974 (Guatemala)
L. nicaraguae Desc.1974 (Nicaragua & Honduras)

At least one other undescribed species (Guatemala) is known from female-only material:
Guatemala: Chimaltenango: Yepocapa, May 1948, (H.T. Dalmat) (USNM).

Lethus was reviewed by Descamps (1974), who then described two new species.

Externally, *Lethus* is characterised by the structure of the male subgenital plate (Fig.12). The plate's distal prolongation is sharply reflexed upwards and forwards, and imbricates with the inwardly recurved cerci and the supra-anal plate, together forming a closed roof over the dorsal aperture of the subgenital plate. The distal extremity of the subgenital plate is ornamented with a few large sharp thorn-like spines, in form quite unlike the numerous minute teeth which ornament the distal rim of the subgenital plate of *Episactus* or *Gymnotettix*. The third abdominal sternum of the male bears a medial boss, as in *Episactus*.

The phallic structure (Fig.13) is also characteristic. The epiphallus is flattened and disc-, rather than shield-, shaped, notched on its anterior margin, fenestrated posteriorly; the lophi are strong and hooked, upwardly and inwardly directed. There is a very small subepiphallic sac and a small postepiphallic sclerite in the membrane joining this to the ectophallus, a unique feature in this subfamily (Fig. 13B). The endophallic rods are reflexed upwards at their posterior tips and fuse with the apical shields where these form the lips of the genital aperture. In *Lethus* there is only a single pair of major ectophallic sclerites, which do not extend forwards into a sclerite sac, but are produced upwards and posteriorly in an extravagant curved projection differing slightly between the species (see Descamps 1974, Figs 16-23); it is probable that these structures are elaborations of the apical shields, as the similar structures of the Espagnolinae are taken to be, rather than homologous with the internal dorsal ectophallic sclerites of *Episactus*. The apicoventral sclerites are well developed and spined, as in *Episactus* and *Gymnotettix*. There are no separate apicolateral sclerites, but the apical shield bears two small spines laterally to the apical groove. The lateral regions of the ectophallus are sclerified into rigid concave sheets (lateral plates in Figs 13C & D). Descamps (1974: 553-554) remarks on the close similarity of the phalli in all four species of the genus *Lethus*, which serves to emphasize its distinctness from the following genus.

4. *Paralethus* n. gen.

Type species.— Paralethus insolitus Rowell & Perez-Gelabert, by original designation.

Etymology.— *para* (Greek), near, or similar to; *Lethus*, the generic name of a superficially closely similar Episactine grasshopper.

Diagnosis.— (see Fig. 15. Habitus).

Small-medium sized grasshoppers, body length 13 to 19 mm; F_{male} 8 to 9 mm, F_{female} unknown. Sexual dimorphism in size (P_{male}/P_{female}) = 0.75. Apterous. Antenna with seven to eight flagellar segments, segments four to six somewhat expanded laterally, shorter than wide, the terminal segment long and tapering to a rounded point, and bearing the antennal organ. Fastigium smoothly rounded in dorsal view (Fig. 16C), slightly projecting in lateral view (Fig. 16A), with a medial carina (Fig. 16C), which continues over the vertex. Frontal ridge (Fig. 16B) medially sulcate, more or less parallel-sided, extending almost to the clypeal suture; dorsally slightly diverging, enclosing a short medial carina just below the fastigium. Infraorbital carinae well developed. Pronotum with medial carina well developed, somewhat arcuate in lateral view; without true lateral carinae, but lateral lobes with a weak raised ridge running diagonally from dorsal posterior to ventral anterior, barely cut by a vertical sulcus which starts near the ventral edge of the lobe and terminates just dorsal to this ridge; no sulcus on pronotal disc. Abdominal segments all medially carinate dorsally. Posterior margin of fourth abdominal sternum of male somewhat thickened and inflated in the midline. Fore and middle femora and tibiae subrectangular in section; the dorsal carinae of the femora do not terminate in spines; tibiae with 9 to 10 pairs of ventral spines. Hind femora long, about 4× as long as pronotum, and narrow (ratio maximum length to maximum width = 4.7:1); hind knee with three weak spines corresponding to the ends of the dorsomedial and both ventrolateral carinae; both ventral lobes of knee also terminate in small weak spines. Hind tibia with 17 to 18 short external spines, 21 longer internal ones (biseriate). Four tibial spurs, the most interior being the longest. Hind tarsus with first segment longer than the other two together, foot formula 52: 16:32; the first tarsal segment has six spines on its external dorsal margin and five on the internal one (Fig. 17D).

Male supra-anal plate (Fig. 17C) triangular, wider than long, very small, almost vestigial; male cerci thickened at base, tapering abruptly, acutely pointed, hook-shaped in dorsal view, recurving inwards through almost 180° to meet in the midline. Male subgenital plate (Figs 17A, B) elongated and pointed, the distal end sharply reflexed upwards and forwards by more than 90°; on either side of the resulting fold two to three pairs of minute marginal spines; distal edges of prolongation of subgenital plate melanized, but devoid of spines. In the normal position in life the tip of the subgenital plate is lodged between and behind the tips of the cerci (Fig. 17C).

Phallus.— (Fig. 18). Epiphallus much wider than long, neither disc- nor shield-shaped in dorsal view, medially excavated on its anterior edge, not fenestrated, the rather small upwardly hooked lophi borne on long lateral processes, the distance between them comfortably exceeding the maximum width of the ectophallus. Internal and external dorsal ectophallic sclerites present, both projecting slightly posteriorly as sharp points, anteriorly widening and thickening within the sclerite sac. One pair of armed apicolateral sclerites present, apicoventral sclerites present but unarmed. Lateral plate present; sclerotized and concave. Dorsal part of apical groove bordered by produced, undulant, sclerotized lips. Tips of endophallic rods do not fuse with the lips of the apical groove, but are reflexed upwards and backwards, bordering the apical groove internally. The zone of fusion of the endophallic rods (the apex of the 'horseshoe', lying between the spermatophore sac and the ejaculatory sac, gives rise to two short converging proceses which run anteriorly in the dorsal wall of the ejaculatory sac (Figs 18E, F), a structure seen nowhere else in the subfamily. The ejaculatory duct contains a small semicircular sclerite in its wall just prior to joining the ejaculatory sac (Fig. 18D, arrow).

Female (Fig. 19) tenth abdominal tergite deeply notched. Female supra-anal plate triangular, long thin and pointed, proximally and medially excavated, the resulting hollow surrounded by a raised rim(Fig. 19C). Cerci thin, pointed, slightly longer than supra-anal plate. Ovipositor valves very similar to those of *Episactus*: long, laterally compressed, somewhat pointed, toothed on their margins; dorsal valves thin, slightly incurved and excavated at the tips, forceps-like. Subgenital plate with dorsal margins inflated (arrows in Figs 19A, C), forming two prominent ridges below the cerci; ventrally the posterior margin is smoothly notched at either side of the triangular medial process, which is inflected upwards at about 45°.

Female internal reproductive structures not examined, to avoid damaging the unique specimen.

1. *Paralethus insolitus* n. sp.

Holotype male.— El Salvador: (Provincia Sa. Ana:) Cerro Verde, 29.06.1963, Irwin ME & Cavagnaro DQ, specimen number UCR Ent 71241. Paratypes: one male, number 71242, one female, number 71243 (all property of the University of California at Riverside Entomological Museum; the holotype and female paratype are now on permanent loan to the Academy of Natural Sciences, Philadelphia).

Etymology.— *insolitus* (Latin), uncommon, strange, surprising, unexpected.

Description.—As the only known species, the generic diagnosis applies. The unique female specimen lacks both hind legs.

Phallic complex.—(Fig. 18). Epiphallus as in generic diagnosis, short and much wider than the rest of the phallic complex, closely appressed to phallus. Subepiphallic sac absent. Dorsal fold short, weakly bilobed, closely appressed to ectophallus. Ectophallus quite heavily sclerotized. Internal and external dorsal ectophallic sclerites present, projecting posteriorly as sharp points. Apical shields large, consisting of a sclerotized margin to the apical slit and laterally a rounded boss armed with a single spine, which may be homologous with the apicolateral sclerite of *Episactus*. Apicoventral sclerites present, but (uniquely in the subfamily) unarmed. The lateral walls of the ectophallus, under the arms of the epiphallus, are weakly sclerotized to form two lateral plates, concave in section (Fig. 18D). Endophallic rods and sacs very large for the family, extending anteriorly beyond the anterior edge of the epiphallus. The proximal end of the endophallic plate gives rise to paired sclerotised processes that run anteriorly in the wall of the ejaculatory sac (Fig. 18F). Distally, the endophallic rods turn upwards and touch the ectophallic apical shields at the ventrolateral margins of the genital aperture, then turn forwards, running along the dorsal edges of the genital aperture, and ultimately appear to fuse with the posterior ends of the exterior ectophallic sclerites, ventral to the pointed processes of the latter.

Dimensions.— see Table 1.

Coloration.—(Derived from dried specimens, not seen alive) Male: eyes dark brown, probably black in life. Antenna and head black; palps light yellow-brown. Prothorax blackish; a lighter mark follows the line of the raised oblique ridge which curves across the lateral lobes of the pronotum (see generic diagnosis). Abdominal segments yellow-brown above, darker in the dorsal midline, black laterally and ventrally. Femora marbled brown; tibiae and tarsi light brown. Tips of cerci black. The female is an almost uniform blackish brown, somewhat darker dorsally and lighter ventrally.

Natural history.—Unknown. The sombre coloration and the fact that the specimens were originally rather thickly coated with mud suggests that they live on the ground, as do the related genus *Lethus* (Rehn & Rehn 1934) and most of the Hispaniolan episactids.

Distribution.—Known only from the type locality, on the border between El Salvador and Guatemala, on the Pacific slope.

Discussion.—Superficially *P. insolitus* closely resembles the species of *Lethus*, especially in habitus, laterally flattened form, dull coloration, and in possessing a reflexed tip to the male subgenital plate. It differs externally from *Lethus* in having only minute spines at the base of the distal portion of the subgenital plate, and none elsewhere on that structure; the femur of the male is also relatively shorter and broader than in *Lethus*. The dorsal extremity of the frontal ridge is medially carinate (Fig. 16B), whereas in *Lethus* it is merely angled. This feature also distinguishes it from the superficially similar and *Lethus*-like *Episactus eremites*. The females differ from *Lethus* in the inflated dorsal margins to the subgenital plate, and the form of its extremity. The resemblance to *Lethus oresterus* Rehn & Rehn is particularly striking; however, Descamps (1974) examined and figured the phallus of that species and showed it was of the same type as the other *Lethus* species, and quite different from that of

Paralethus, a finding confirmed in the present study by dissection of a paratype *of L. oresterus*.

The major differences from *Lethus* are in phallic structure. The extremely wide and short epiphallus is distinctive. In the number and disposition of the dorsal ectophallic sclerites *Paralethus* resembles *Episactus* much more closely than *Lethus*: there are both external and internal sclerites, and these are simple, short, bluntly pointed at their posterior end, and the internal sclerites extend anteriorly into a sclerite sac. In *Lethus* there is only a single pair of dorsal sclerites, which do not extend appreciably into a sclerite sac, and which are probably elaborations of the apical shields; the ventroapical sclerites are spined and not unarmed as in *Paralethus*. The endophallus of *Paralethus*, however, is similar to that of *Lethus*, though larger and more robust and with unique anterior processes.

The major phallic differences in respect to *Episactus*, apart from the unique epiphallus, are in the type of endophallus (upward-curving and fused apically to the ectophallic sclerites, whereas that of *Episactus* is downward curving, with (in *E. tristani*) the ends lying free in the membrane of the ejaculatory sac) and in its much larger size; the absence of spines on the ventrolateral sclerites; the absence of a subepiphallic sac; and the wider bilobed dorsal fold, compared to the narrow rectangular one of *Episactus*. The general appearance of *Paralethus*, however, is very like that of *E. eremites*.

1D. Anatomy of the phallic complex of the Hispaniolan Episactidae (Espagnolinae)

The external characters, habitus, distribution and natural history of the various Hispaniolan eumastacids have been recently covered in detail by Perez *et al.* (1997a & b) and are not discussed further here. For purposes of comparison with the Central American Episactinae, however, the male phallic structures need further examination.

Endophallus.— In the Espagnolinae the endophallus is of small size but less reduced than in the Episactinae. It has the characteristic hairpin shape seen also in, *e.g.*, the Eumastacinae, and is formed in the ventrolateral wall of the spermatophore sac. In contrast to the situation in the other two subfamilies, however, the ends of the "legs" of the hairpin, *i.e.*, the endophallic rods, neither insert into the apical shield sclerites of the ectophallus, nor end freely on the walls of the ejaculatory sac. Instead they curve upwards and then backwards, running as fine rods bordering the aperture of the spermatophore sac, and sometimes continuing along the dorsal edges of the genital trough, more or less in the position of the internal ectophallic sclerites of the Episactinae. Among the Episactinae, only *Paralethus* approaches this condition. The lumen of the spermatophore sac opens to the exterior between the posterior upwardly curved portions

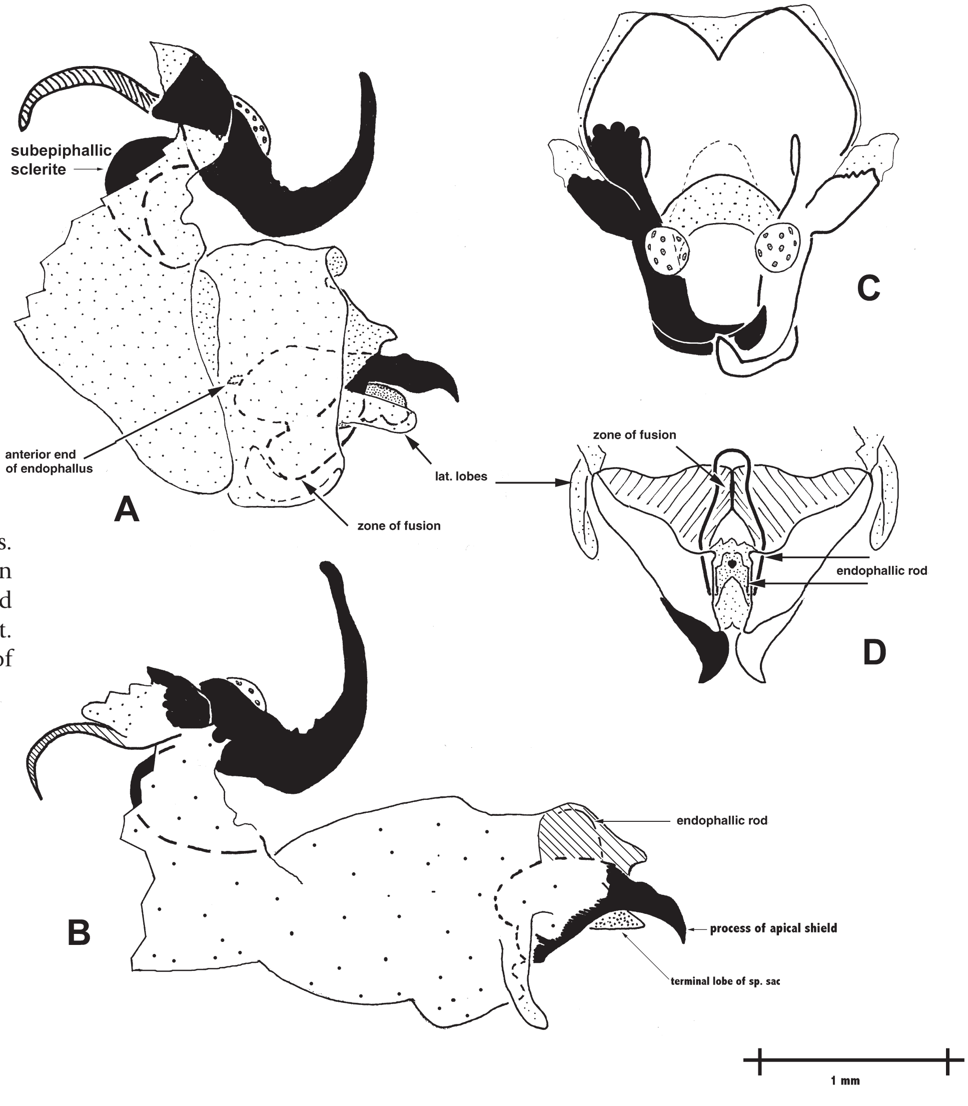


Fig. 20. *Espagnola darlingtoni*, phallus. A. Lateral view of phallic complex, in retracted position. B. As A, in extended position. C. Epiphallus, dorsal aspect. D. Endophallus and ventral surface of ectophallus, from above.

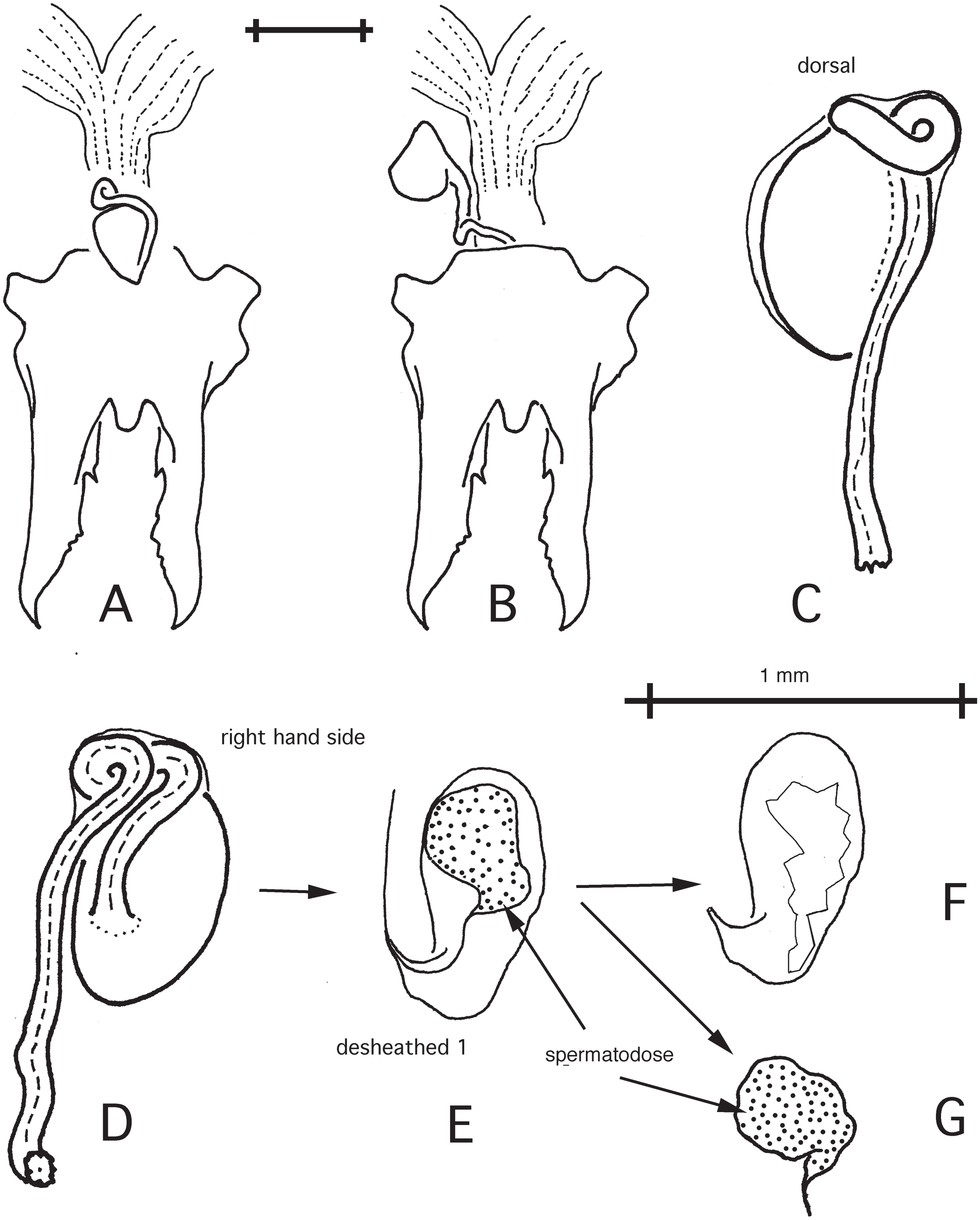


Fig. 21. *Espagnola darlingtoni.* Spermatheca. A, B. Spermatheca *in situ*, A. Prior to removing stabilising membranes. B. Afterwards. C, D. Closer views of spermatheca showing detail of insertion of duct. E. Spermatheca desheathed, revealing two components, the transparent bladder (F) and the spermatodose that this contains (G).

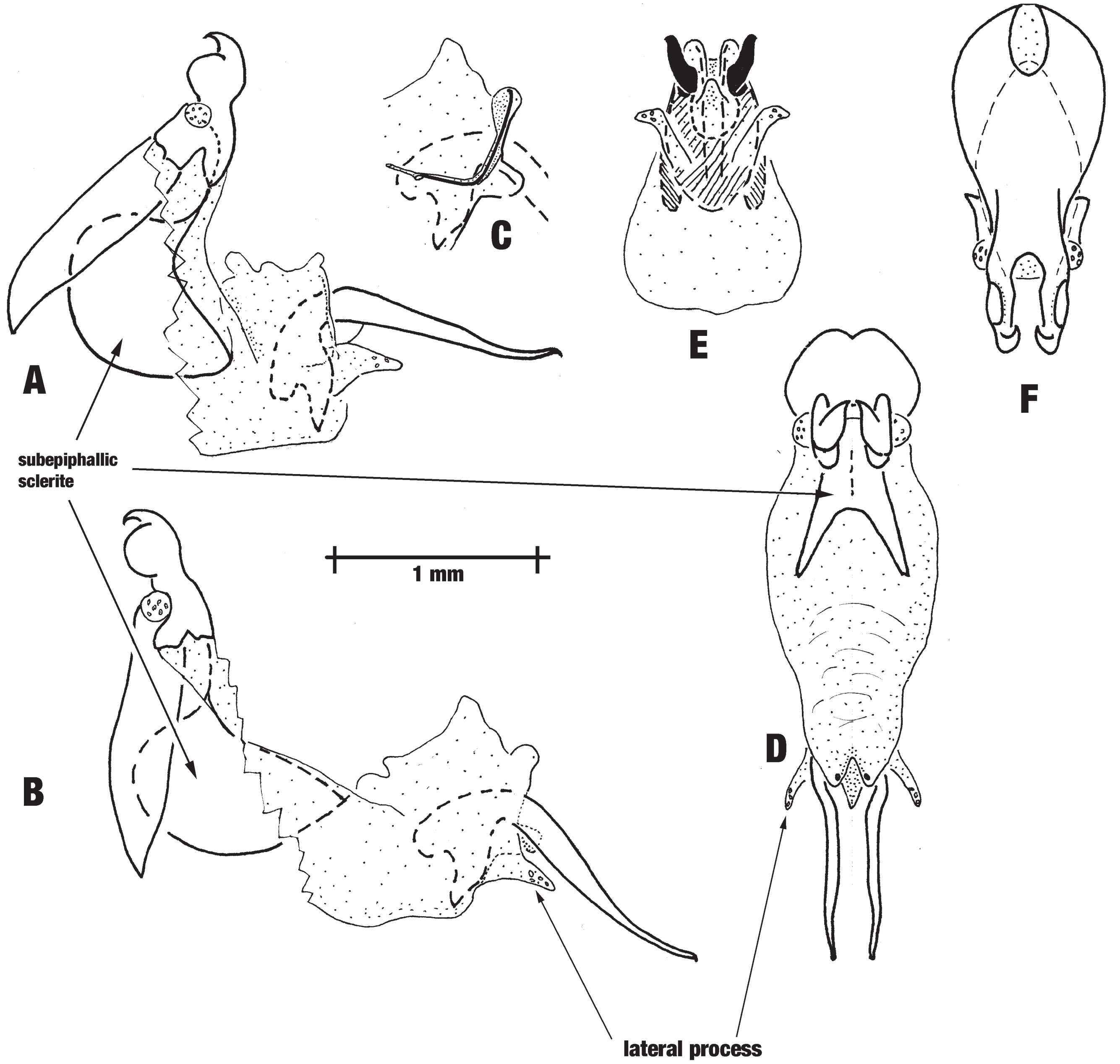


Fig. 22. *Espagnolopsis ornatipennis*, phallus. A. Lateral view of phallic complex, in retracted position. B. As A. in extended position. C. Tips of endophallic rods, lateral aspect. D. As B, dorsal aspect. E. Tip of ectophallus, axial view. F. Epiphallus, dorsal aspect.

of the endophallic rods, and may be apical (*Espagnolopsis*) or more commonly dorsoapical in position. The membrane of the floor of the spermatophore sac is produced distal to the rods in the form of a soft 'terminal lobe of the spermatophore sac'. This is of variable size, and often bilobed. Relative to the situation in the Episactinae or the Eumastacinae both the ejaculatory and spermatophore sacs are very small, comparable to those of the Teicophryinae.

Ectophallus.— The multiple ectophallic sclerites, often spinous, which are seen in the Episactinae, are absent in the Espagnolinae. In all but one genus (*Neibamastax*), there is only a single pair of large paired sclerites, apparently corresponding to the apical shields of the Eumastacinae and Episactinae, typically bearing elongate processes projecting to the rear. Unlike the situation elsewhere, these two sclerites fuse in the midline apically below the aperture of the spermatophore sac; or they (*Tainacris*) are joined together by a plate of lightly sclerotized membrane in the same region, or (*Espagnola*) fuse ventrally, or (*Antillacris*) are joined dorsally by a bar anterior to the genital trough. In all cases there seems to be some structure to make the complex rigid, perhaps associated with the fact that the endophallus doesn't insert apically on the ectophallus. Only in *Neibamastax* is there a different arrangement. Here there is no obvious apical shield, and instead there are internal dorsal ectophallic sclerites very similar to those found in the Episactines, pointed at their posterior tips, extending forward into a sclerite sac, where they (oddly!) cross over each other in the midline. These sclerites are overlaid dorsally by two further sclerites with inwardly curving hooked extremities, conceivably derived from a modified subepiphallic sclerite. These structures have no parallel elsewhere in the subfamily. As in most Espagnoline genera the aperture of

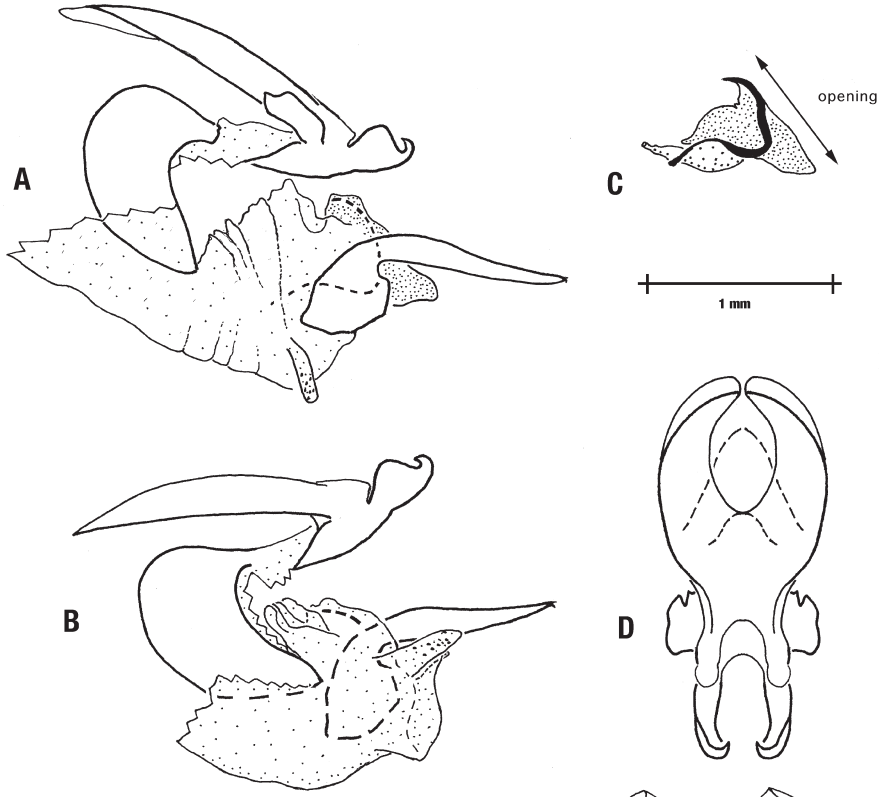


Fig. 23. *Espagnolopsis breviptera*, phallus. A. Lateral view of phallic complex, in semi-extended position. B. As A in retracted position. C. Tips of endophallic rods, lateral aspect. D. Epiphallus, dorsal aspect.

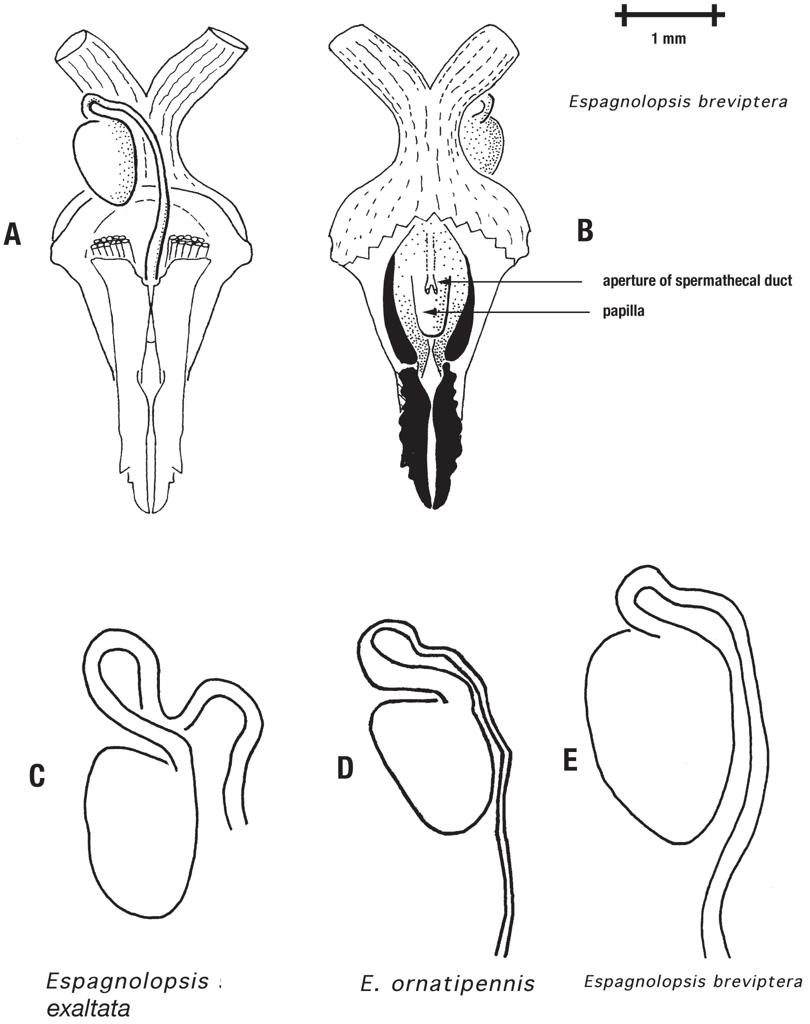
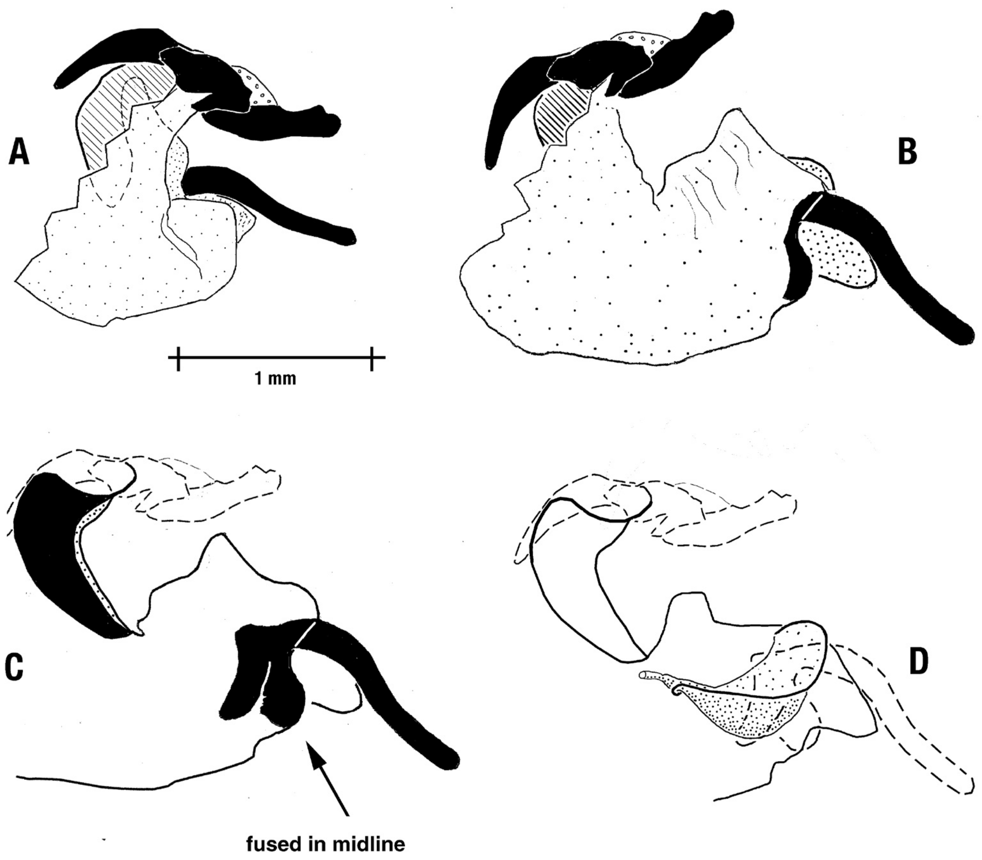


Fig. 24. *Espagnolopsis*, female genitalia. A. *E. breviptera.* Lower ovipositor valves and spermatheca, dorsal aspect. B. *E. breviptera.* Lower ovipositor valves and spermatheca, ventral aspect, to show papilla and aperture of spermathecal duct. C, D, E. Spermatheca and spermathecal duct in three species of *Espagnolopsis*.



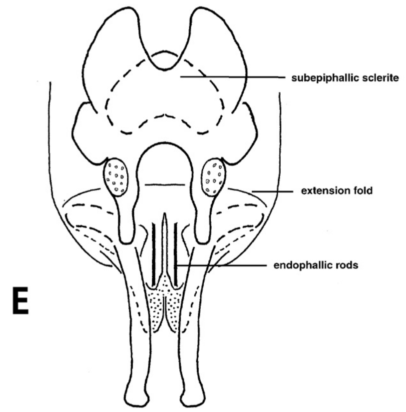


Fig. 25. *Espagnoleta microptera*, phallus. A. Lateral view of phallic complex, in retracted position. B. As A, in extended position. C. As B, to show detail of sclerites obscured in B by other structures. D. As B, to show endophallus. E. Phallic complex in dorsal aspect.

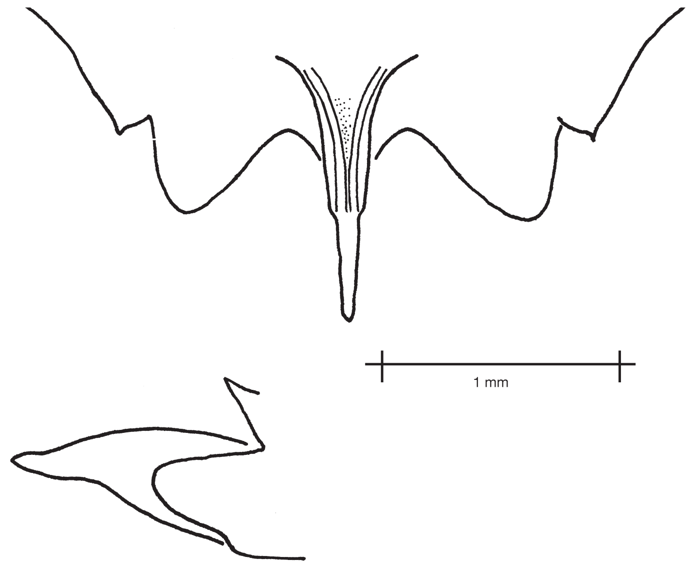


Fig. 26. *Espagnoleta microptera*, female subgenital plate. A. Dorsal aspect of posterior margin. B. Lateral aspect.

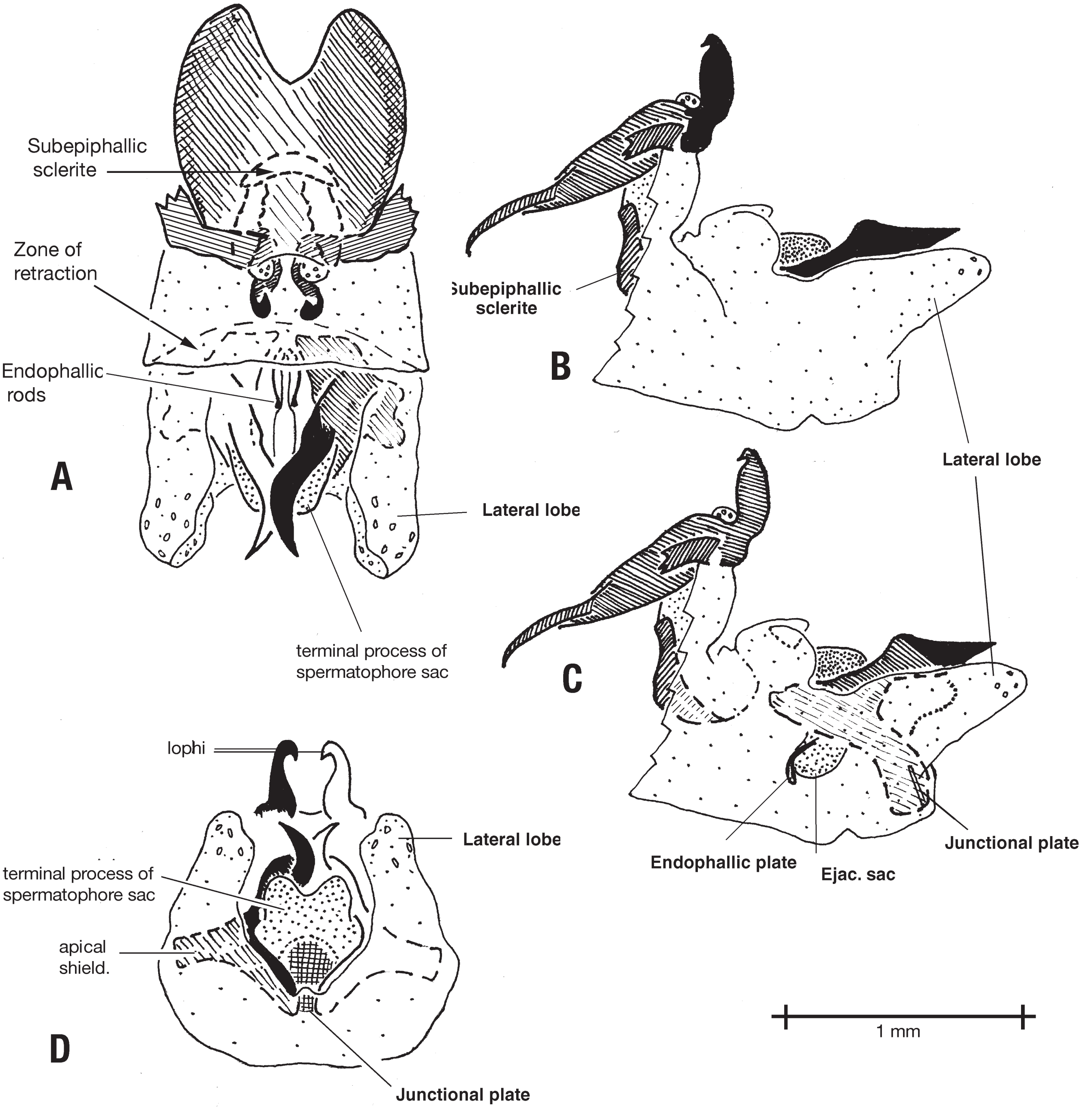


Fig. 27. *Tainacris quisqueiana*, phallus. A. Phallic complex, dorsal aspect. B. Phallic complex, lateral aspect. C. As B, to show subepiphallic sclerite and endophallus. D. Phallus, axial (posterior) aspect.

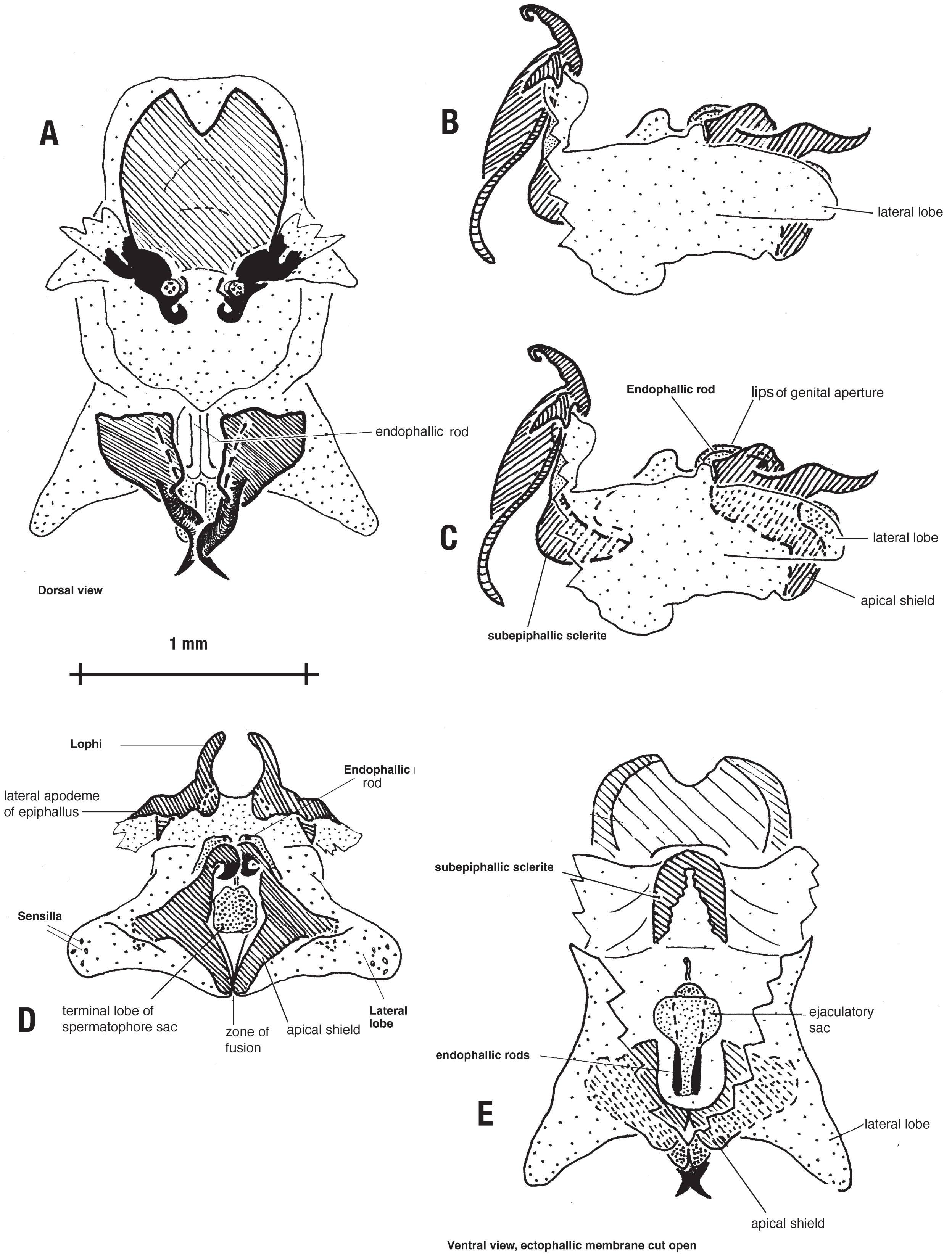


Fig. 28. *Tainacris nitaina*, phallus. A. Phallic complex, dorsal aspect. B. Phallic complex, lateral aspect. C. As B, to show subepiphallic sclerite and apical shield. D. Phallus, axial (posterior) aspect. E. Phallus, ventral aspect; ectophallic membrane cut open to show endophallus and subepiphallic sclerite.

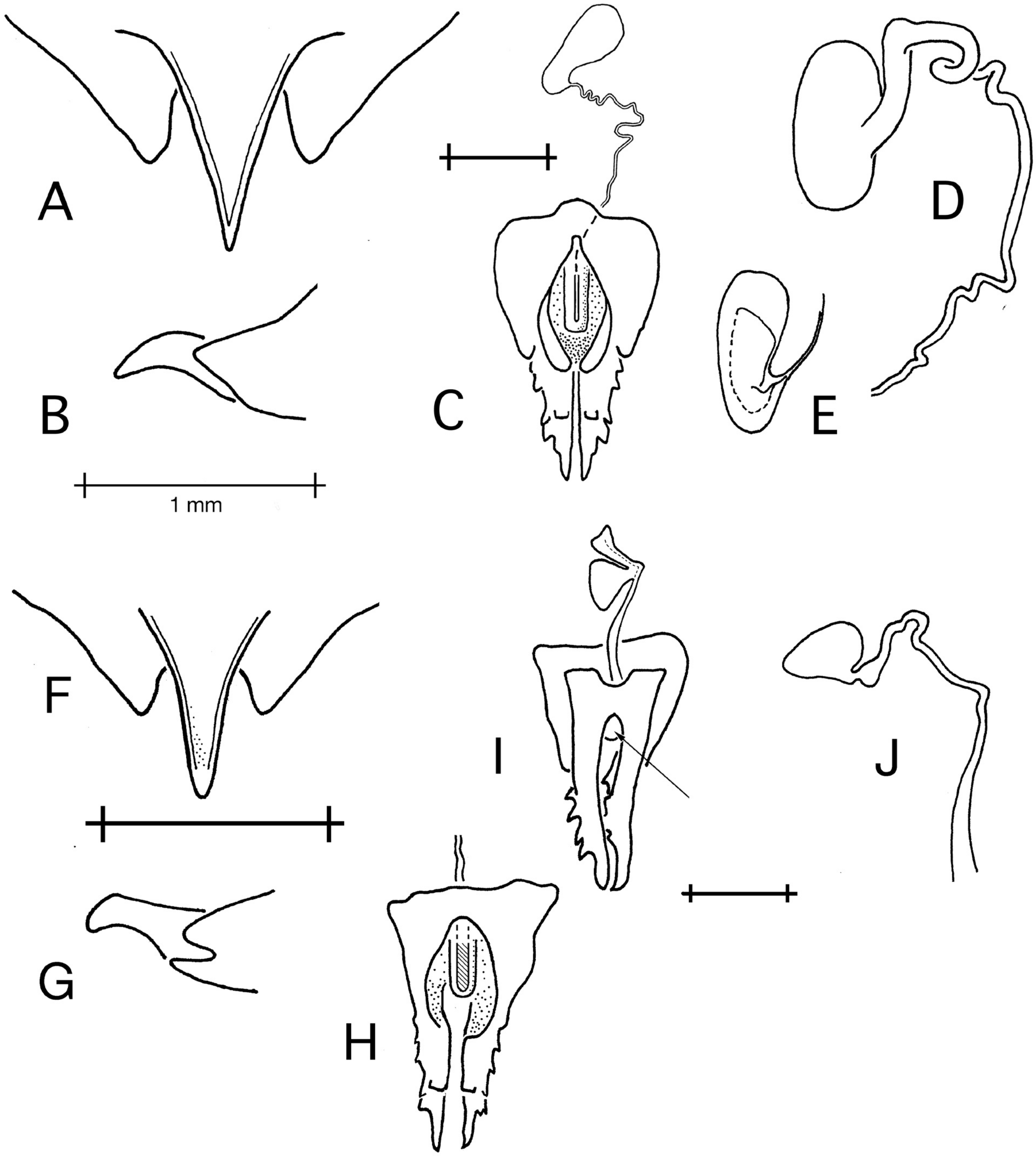


Fig. 29. *Tainacris quisqueiana,* female genitalia. A. Posterior margin of subgenital plate, dorsal aspect. B. The same, lateral aspect. C. Ventral ovipositor valves and spermatheca, ventral aspect, to show papilla and aperture of spermathecal duct. D. Detail of spermatheca. E. Spermatheca to show spermatodose within. F. Posterior margin of subgenital plate, dorsal view. G. As F, lateral view. H. As C, but a different individual. I. Same preparation as H, dorsal view, before desheathing spermatheca and duct. Arrow marks end of the papilla. J. Spermatheca and duct as in I, after desheathing. The smaller scale bar applies.

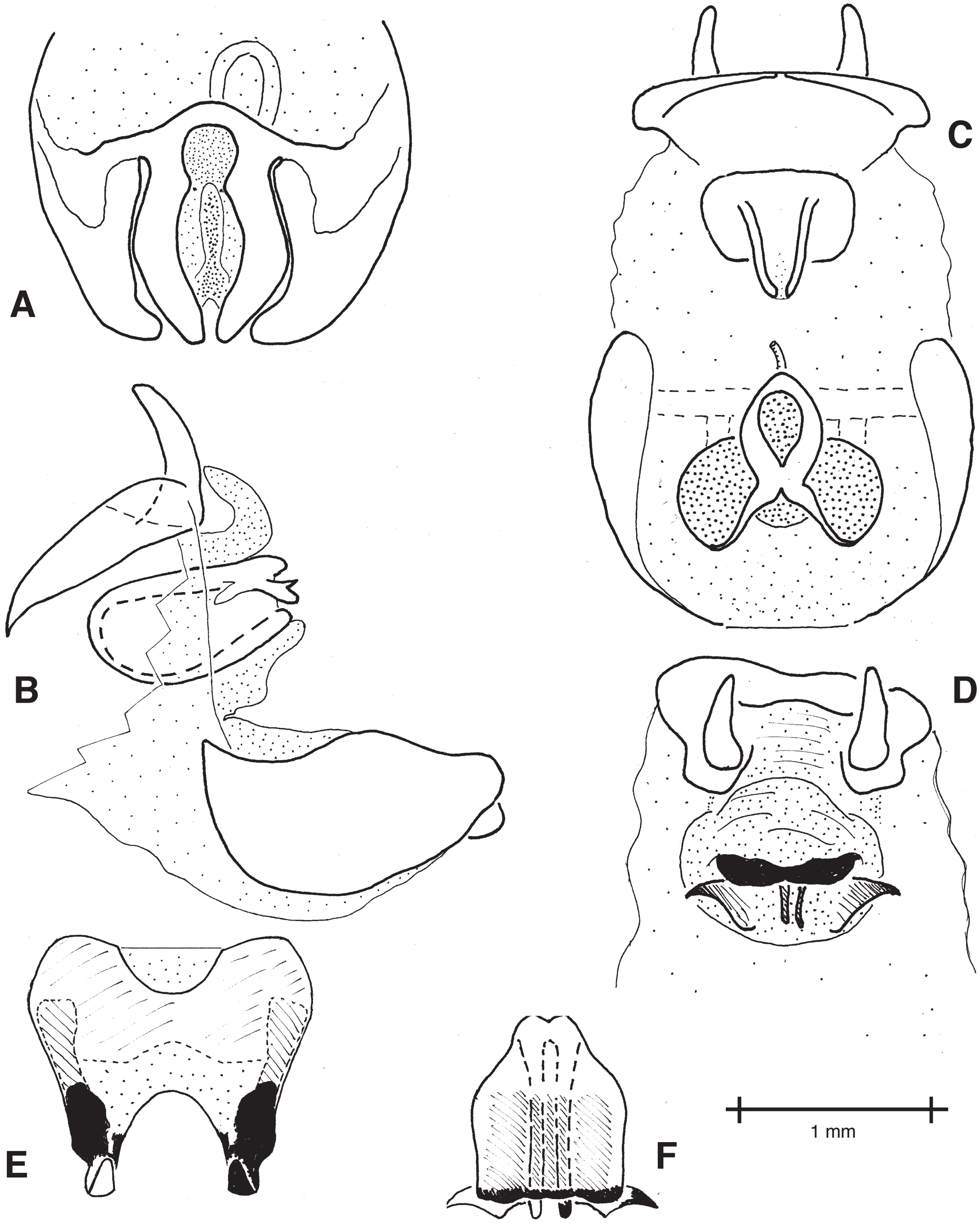


Fig. 30. *Antillacris inflaticercus*. Phallus. A. Tip of ectophallus, dorsal aspect, showing the sclerotised bar joining the the apical shields dorsally, and the sclerotised lateral processes. B. Lateral aspect. C. Ventral aspect with ectophallic membrane removed to show endophallus and subepiphallic sclerite. D. Axial view of epiphallus and subepiphallic sclerite. E. Epiphallus, dorsal aspect. F. Subepiphallic sclerite, dorsal aspect.

the spermatophore sac is not strictly apical, but instead is rotated dorsally, opening between the ectophallic sclerites. This positioning in turn suggests that the 'dorsal ectophallic sclerites' of *Neibamastax* are actually modified apical shields. It is of course not excluded that this is true in all taxa showing these sclerites.

The ectophallus is developed in some members of this subfamily (*e.g., Espagnola*) into a long protrusible sleeve of membrane, bearing at its tip the apical shields and the endophallus which they enclose. At rest, this structure is folded telescopically, giving rise to the complex folds of membrane seen in this condition (Fig. 20 — see also Descamps 1973, Fig. 240). A similar but less elaborate arrangement is seen in *Espagnoleta* and *Espagnolopsis*. In *Tainacris* there is only a single fold, and the phallus is protrusible for only about an extra 20% of its length. In *Antillacris* and *Neibamastax* there is nothing of this sort, and in the former genus the ectophallus is largely sclerotized and not at all extensible.

The ectophallic dorsal fold that covers the genital trough in, e.g., the Eumastacinae and Episactinae, is absent in the Espagnolinae, though the telescopic fold mentioned above can overlap the genital area somewhat, and in *Antillacris* it is covered by a fold of membrane

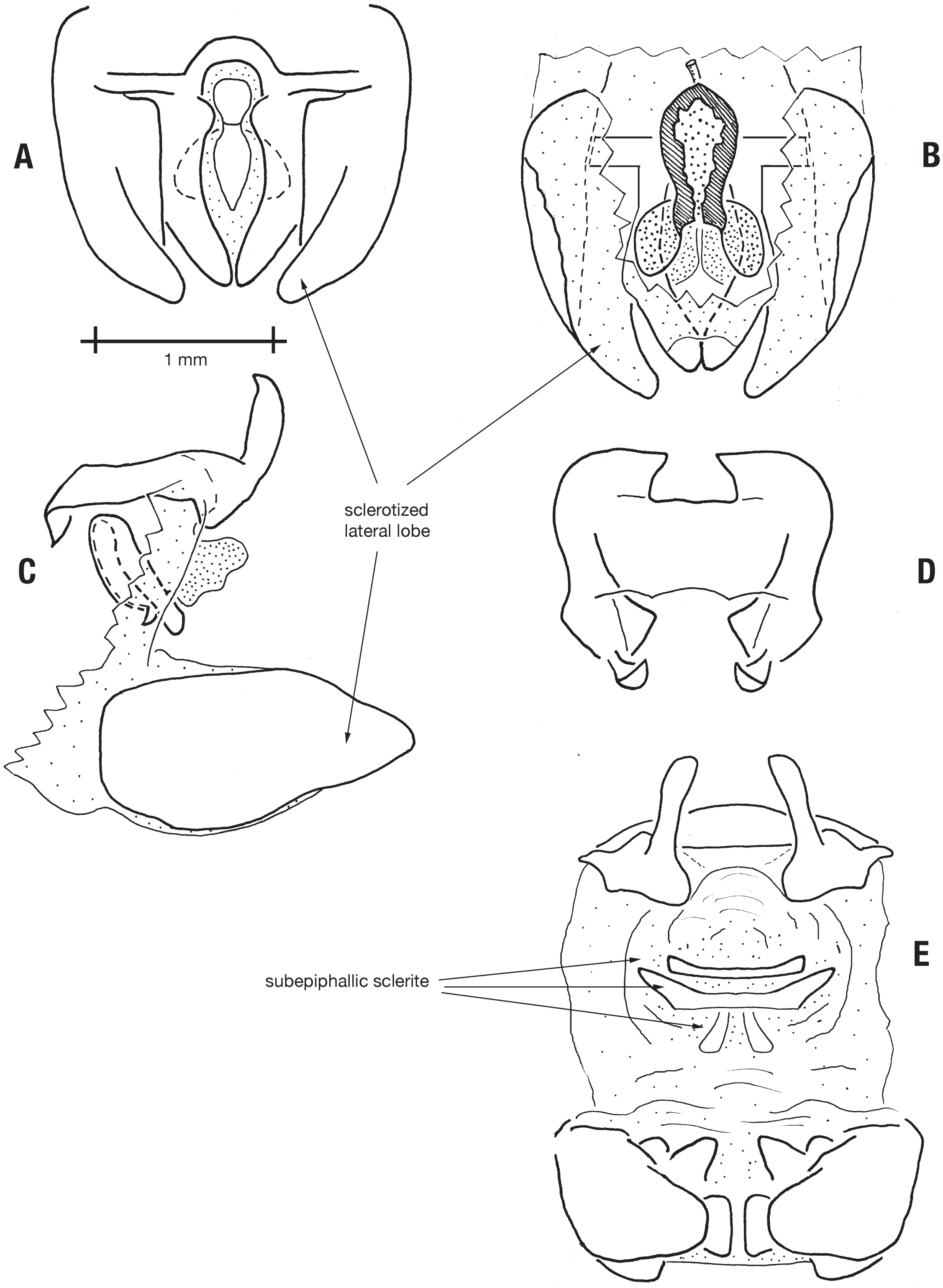


Fig. 31. *Antillacris eumenes*. Phallus. A. Tip of ectophallus, dorsal aspect, showing the sclerotised bar joining the the apical shields dorsally, and the sclerotised lateral processes. B. Ventral view with ectophallic membrane cut away to show endophallus. C. Lateral aspect. D. Epiphallus, dorsal aspect. E. Phallic complex, axial (posterior) aspect.

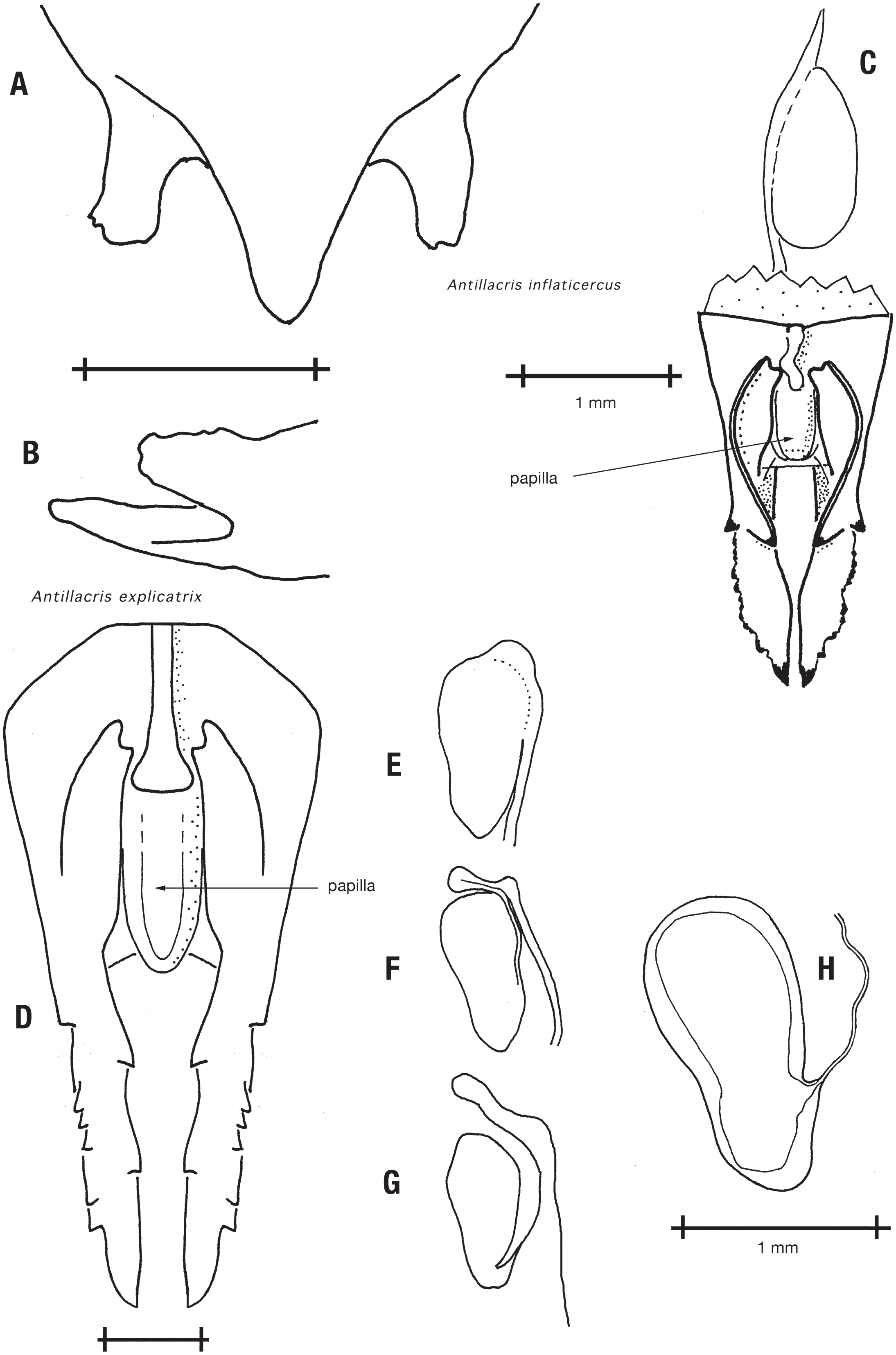


Fig. 32. *Antillacris.* Female genitalia. A-C *A. inflaticercus:* A. Posterior margin of subgenital plate, dorsal aspect. B. Lateral aspect. C. Ventral ovipositor valves and spermatheca, ventral aspect. D-H. *A. explicatrix.* D. Ventral ovipositor valves and spermatheca, ventral aspect. E-G. Spermatheca in progressive stages of desheathment. H. Spermatheca, desheathed, to show spermatodose within.

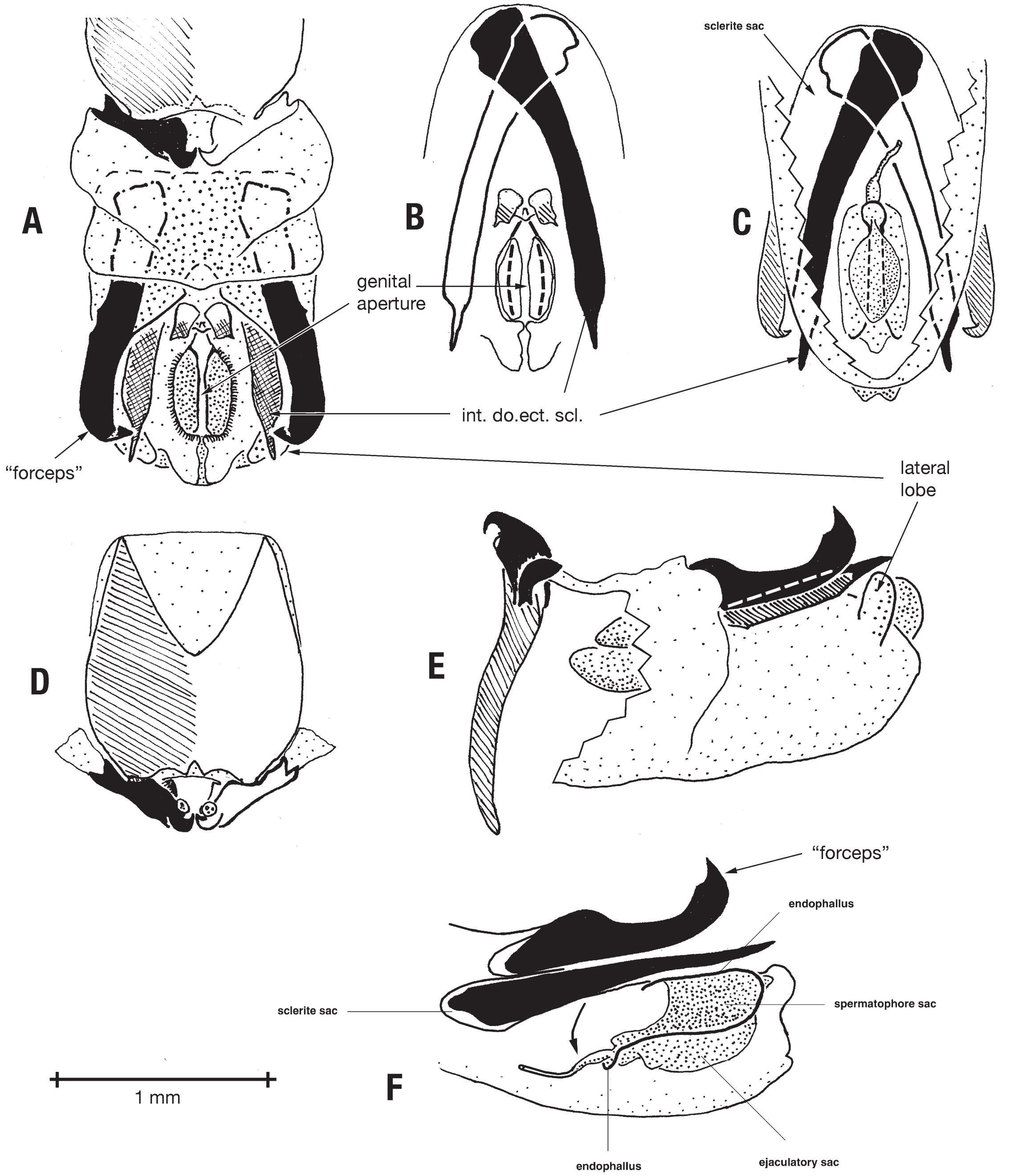


Fig. 33. *Neibamastax divergentis*. Phallus. A. Posterior portion of phallus, dorsal aspect. B. Dorsal ectophallic sclerites and genital aperture, dorsal aspect. C. Endophallus and dorsal ectophallic sclerites, ventral aspect. Ectophallic membrane has been cut away in midline to expose these structures. D. Epiphallus, dorsal aspect. E. Phallic complex, lateral aspect. F. As E, but parasagittal section to show endophallus and sclerites. The ejaculatory duct has been forceably depressed (curved arrow) to stretch and make visible the spermatophore sac; in life it lies just under the surface of the ectophallus. The sclerites labelled 'forceps' are unique to the genus and probably represent a greatly modified subepiphallic sclerite [compare with Fig 31F, and Fig. 5F, G of Perez & Rowell 2006 (this issue)]

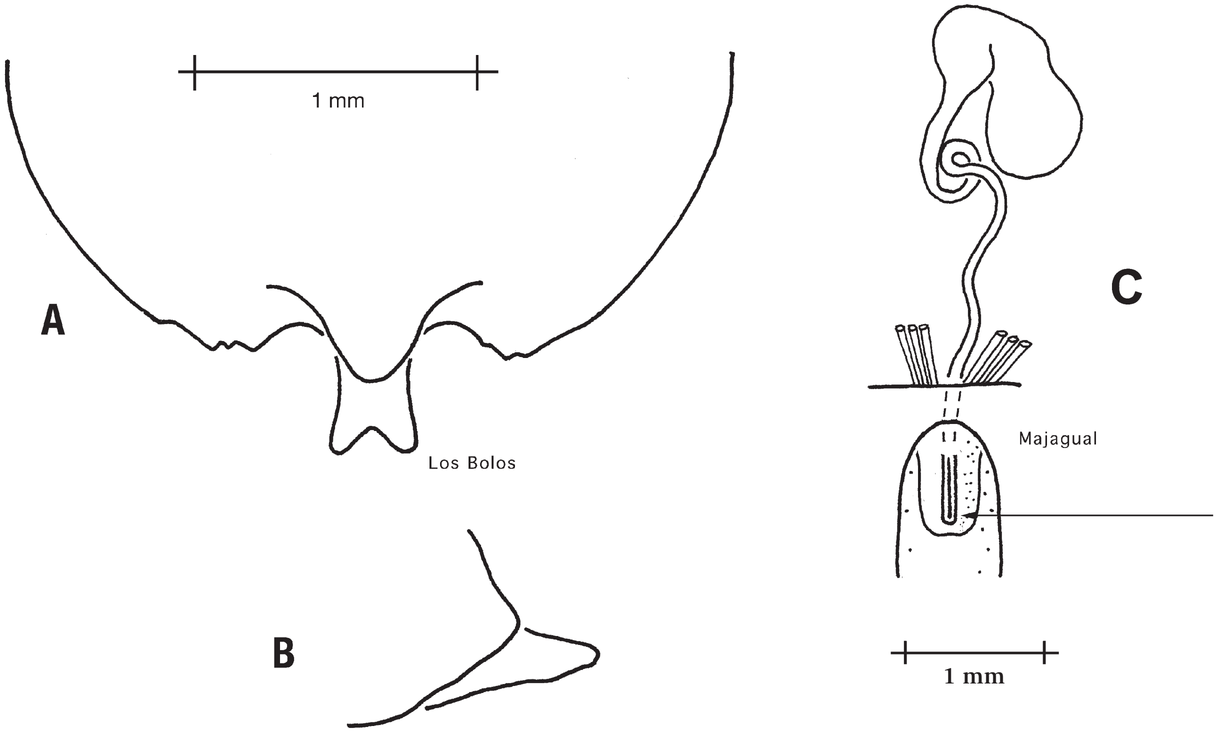


Fig. 34. *Neibamastax divergentis*. Female genitalia. A. Posterior margin of subgenital plate, dorsal aspect. B. The same, lateral aspect. C. Spermtheca and duct, ventral aspect.Arrow indicates the ventral papilla and opening of spermathecal duct. The specimens drawn originate from two different localities, corresponding to the place names on the diagram. Scale bar, 1 mm.

attached to the posterior ventral edge of the epiphallus.

In all genera except *Espagnoleta* the ectophallic membrane is produced into two lateral lobes at either side of the phallic complex. They bear sensilla on their tips. What appear to be homologous structures are just thin tubular processes in *Espagnola*, more robust in *Tainacris*; in *Antillacris* they are very large and sclerotized and larger than the apical shields. No episactine has similar structures.

Epiphallus.— The epiphallus *per se* is similar to that of the Eumastacinae or Episactinae, thin and roughly shield-shaped, with large hooked lophi, usually bearing transparent domes of sensilla at their bases. In the Espagnolinae, however, the subepiphallic sac, which is purely membranous and of variable size in the other subfamilies, is large and to a greater or lesser degree sclerified. It forms a subepiphallic sclerite (Perez *et al.* 1997) having the shape of a basin or cup opening posteriorly — the dorsal rim of this sclerite connects via membrane with the ventral posterior edge of the epiphallus between the lophi, and its lower rim is contiguous with the dorsal membrane of the ectophallus. This appears to be an apomorphy of the subfamily, distinguishing it from Episactines, though something similar seems to occur in at least one species (*T. robertsi*) of the Teicophryinae too.

This subepiphallic sclerite is very variable in shape and development, but there always seems to be a lumen, even if flattened and narrow (as in *Antillacris*). In its simplest form it appears just to provide a space into which the phallus can be withdrawn when the system is at rest. Often its ventral surface is emarginate or split open in the midline. The dorsal rim is often thickened and robust, and in *Antillacris* the ventral rim is provided with paired spines. (In *Neibamastax* the subepiphallic sclerite as found in other genera is absent, but there is a large forceps-like structure, unique to this genus, which may be derived from these spines.) The membrane connecting the epiphallus to the upper rim of the subepiphallic sclerite is hypertrophied in *Antillacris*, forming a flap of membrane which covers the posterior end of the retracted phallus, just as the ectophallic dorsal fold does in the Eumastacinae (or an epiphallic fold in Ommatolampine Acridids such as *Rhachicreagra* or *Microtylopteryx*, for that matter!).

1E. Individual Hispaniolan genera:

Previous illustrations.— Perez *et al.* 1997a & b figured the phallic complexes of the Espagnoline genera described below, but in general only considered their external aspects and did not examine their separate components. The phallus *of Espagnola darlingtoni* was figured by Descamps (1973). The following paragraphs summarise their properties.

1. *Espagnola* Rehn & Rehn 1939: 190.
Rehn 1948: 122.
Descamps 1971: 110.
Descamps 1973: 268, & Figs 239-241 – Drawings of phallus.
Perez *et al.* 1997a: Figs. 19a-e, n.

Figs 20 & 21: Epiphallic lophi long and hooked, crossing in the midline. Sensory plaques of lophi large, situated on dorso-internal face of lophal bases. Subepiphallic sclerite simple, cup shaped. Apical shields large, fused ventrally and anteriorly, separated dorsally. Processes of apical shields pointed, inflected downwards and outwards. Lateral lobes present, small thin and membranous.

Ectophallus is telescopic, allowing a 2-3× extension. Endophallic rods reflexed through 180°: tips flank the dorsally opening genital aperture.

2. *Espagnolopsis* Perez *et al.* 1997b: 155.

Type of genus: *E. ornatipennis* Perez *et al.*

Figs 22-24: There are three described species, with very similar phallic complexes. They are best distinguished by the form of the female subgenital plate. Phallus laterally compressed, especially the dorsal surface very narrow. Lophi very short, laterally compressed, with a semicircular vertical 'fin' — tips short and strongly hooked. Sensory plaques on dorso-external face of base of lophi. Subepiphallic sclerite simple, cup shaped, ventral face strongly emarginate. Apical shields fused ventral to terminal lobe of the spermatophore sac. Processes of apical shields long, thin subparallel pointed. Lateral lobes present, small, thin, membranous, similar to those of *Espagnola*. Ectophallus telecopic and extensible, but not so markedly as in *Espagnola*. Endophallic rods reflexed through only 90°; tips flank the posteriorly opening genital aperture.

3. *Espagnoleta* Perez-Gelabert 2000:116

Type of genus, *E. microptera*. There is only a single described species. (The genus was originally called *Espagnolina* Perez *et al.* 1997b: 154, but that name was preoccupied (Perez-Gelabert 2000).

Figs 25,26: Phallus of normal proportions. Lophi quite long, horizontal, not hooked. Sensory plaques on dorso-external face of base of lophi. Subepiphallic sclerite simple, cup shaped, (ventral face strongly emarginate). Apical shields fused immediately ventral to terminal lobe of the spermatophore sac. Processes of apical shields long, thin, subparallel, not pointed. Lateral lobes absent. Ectophallus telescopic and extensible, but not so markedly as in *Espagnola*. Endophallic rods reflexed through 180°, tips flank the dorsally opening genital aperture.

4. *Tainacris* Perez *et al.* 1997a: 140.

Type of genus, *T. nitaina*. There are three described species, one of which, *T. divergentis*, is here transferred to *Neibamastax* n. gen. Figs 27 -29.

Phallus of normal proportions. Lophi quite moderately long, vertical, sharply hooked, laterally compressed. Basal apodemes well developed. Sensory plaques on dorso-internal face of base of lophi. Subepiphallic sclerite simple, cup shaped, ventral face strongly emarginate. Apical shields fused ventral to lip of genital aperture. Processes of apical shields long, thin subparallel pointed, and outwardly inflected at the tip. Lateral lobes present, very large, membranous. Ectophallus somewhat extensible, but not so markedly as in *Espagnola*. Endophallic rods reflexed through 180°; tips flank the dorsally opening genital aperture.

5. *Antillacris* Rehn & Rehn 1939: 199.

Type of genus *A. explicatrix* Rehn & Rehn. There are three described species. The previously unknown male of *A. explicatrix* is described and figured in Perez and Rowell 2006, Fig. 5 (this issue), to which the reader is referred; the other two species are shown in Figs 30-32: phallus of normal proportions. Lophi moderately long, vertical, weakly hooked. Sensory plaques apparently absent from base of lophi. Subepiphallic sclerite flattened, complex; dorsal and ventral surfaces thickened, dorsal rim curved and sclerotized, ventral rim weak, but provided with two laterally flared sclerotized points and longitudinal anterior-posterior ribs: dorsal membrane voluminous, forming a tongue overlying the genital trough. Apical shields confined to dorsal surface, joined together by a crossbar anterior to genital aperture. Processes of apical shields short and blunt. Lateral lobes present, very large, sclerotised, and filled with muscle, flanking the genital area completely. Ectophallus not at all telescopic. Endophallic rods broader and heavier than in other genera of this subfamily; reflexed through 180°; tips flank the dorsally opening genital aperture.

6. Neibamastax n. gen.

Type species.— Tainacris divergentis Perez *et al.* 1997a by original designation.

Figs 33, 34: The genus is raised to accomodate a single species, previously described under the genus *Tainacris* Perez *et al.* The external morphology of the genus is very similar to that of *Tainacris* s. str.; it is differentiated on its highly aberrant phallic structure. In this taxon there is neither apical shield nor subepiphallic sclerite. Instead, there is a well-developed but unusually shaped pair of internal dorsal ectophallic sclerites, and a unique pair of forceps-like sclerites, hooked at the tip, lying in a membrane flap overlying the genital trough. As both biogeography and all other morphological features speak for *Neibamastax* being a member of the same group of genera as the remaining Hispaniolan eumastacids, and thus presumably sharing with them a common ancestor, we postulate that there has been an evolutionary transformation and that the apical shield is represented by the dorsal sclerites and the subepiphallic sclerite by the forceps. The longitudinal ribs and the paired spines of the ventral face of the subepiphallic sclerite of *Antillacris* (Figs 5F, G in Perez & Rowell 2006; Fig. 30F, this article) may well represent the antecedents of the forceps of *Neibamastax*. Phallus of normal proportions. Lophi short and strongly hooked. Sensory plaques on dorso-interior face of base of lophi, but small. Subepiphallic sclerite either absent, or (see above) formed into a very different structure, comprising a membrane flap overlying the genital trough and two large embedded sclerites, flattened, hooked at the tip and inflected inwards, nearly as long as the apical shields; an apomorphy of the genus. Apical shields reduced to two long ectophallic sclerites lying along margins of genital trough, crossing each other anterior to the trough, and contained in a membranous sclerite sac. Posterior processes of apical shields sharply pointed, straight. Lateral lobes present, small and membranous. Ectophallus only slightly telescopic. Endophallic rods reflexed through 180°; tips flank the dorsally opening genital aperture.

1F. Notes on the Teicophryinae and their phalli

The Teicophryinae, confined to southern Mexico, differ from the Episactid taxa so far described in three major external characters which allow their instant recognition: they have long antennal flagella (>20 segments); the lateral carinae of the frontal ridge are continuous with those of the fastigium, and they converge and fuse below the medial ocellus and run to the clypeal suture as a single medial carina (Fig. 35B); and the dorsal carinae of the hind femur are spined (as is commonly the case in the Chorotypidae and in the

Miraculinae). In other respects their external morphology (Fig. 35 A) accords well with the other Episactidae: they are apterous, have the typical spinous hind first tarsal segment, and in many species (*e.g., T. strigilecula)* the posterior rim of the male subgenital plate is prolonged and spinous, as in the Episactinae. The phallic complex of the species previously described, however, differs considerably from that of the remaining Episactidae. Here we show that in at least one species of the genus the phallus is much closer to the Episactid norm.

The genus was partially revised by Descamps (1976), who at that time erected several new species, but unfortunately could not reexamine all of those previously described by other authors. So the data presented are not complete. He considered that the nine described species represented some four different genera, but did not define or erect these, leaving all of them in *Teicophrys* Bruner 1901, and even synonomizing *Cadomastax* Rehn & Rehn 1939 with that genus.

In most of these taxa the phallus appears to be of the type represented by Descamps' (1973, 1976) description *of T. bolivari* (erroneously called *T. strigilecula* in his 1973 work). The phallus of that species [Fig. 36; Descamps (1973): Figs 218-222] differs considerably from that of the Episactinae or Espagnolinae. The epiphallus is large and bridge shaped, with very wide, flat, inwardly directed lophi. There is no well-defined subepiphallic sac. The ectophallus is almost entirely membranous, and is open ventrally, except at its posterior extremity; sclerotization of the ventral edge of the ectophallic membrane forms a U-shaped sclerite, the "armature" of Descamps. The posteriorly directed arms of this U are reflexed upwards, running inside the ectophallic membrane for a short distance and emerging dorsally as two flattened spatulate sclerites more or less in the position where one would expect to find dorsal ectophallic sclerites in the Episactinae (Fig. 36C). There are no other ectophallic sclerites. The endophallic tube is reduced to a small terminal sac opening at the posterior extremity of the ectophallus. Embedded in its floor are small paired sclerites which appear to represent greatly reduced endophallic rods, and were interpreted as endophallic sclerites by Descamps.

In *T. robertsi* [not apparently examined by Descamps (1976)] the phallus (Fig. 37) is of a different nature, and much easier to homologize with that of the other two subfamilies. The epiphallus is again bridge shaped, but the lophi are narrow, vertically directed hooks, similar to those of the other subfamilies (Fig. 37E). A further sclerite lying ventrally to the epiphallus appears to be a subepiphallic sclerite similar to that seen in the Espagnolinae (Figs 37A-C, G). A heavy U-shaped armature is formed in the walls of the ectophallus, again ending in spatulate dorsal processes, here rounded rather than squared as in *T. bolivari* (Fig. 37F). The two lateral pieces of this armature are joined anteriorly and dorsally by the subepiphallic sclerite (Fig. 37 A-C), suggesting that in the other species of the genus the latter structure has been incorporated into the armature. Paired apicoventral sclerites are present (Figs 37 D, F), as in the Episactinae, and the ectophallus is a conventional tube, not open at the bottom at its anterior end. The endophallus is similar to that of the Episactinae, being much larger than that of *T. bolivari,* of hairpin form, running in the ventral wall of the spermatophore sac. The ends of the arms of the hairpin are reflexed upwards and extend along the dorsal margins of the genital aperture, in a typically episactid manner.

All in all the phallus of *T. robertsi* presents a structure almost exactly intermediate between the Episactine phallus and that of *T. bolivari*, which may suggest that it is plesiomorphic within its subfamily. It should be stressed that in its external morphology *T. robertsi* is very similar to *T. bolivari* and the other species of the genus: its phallic differences are much greater. Descamps (1973) considered that the Teicophryinae belonged to the Episactidae; the phallus of *T. robertsi* strongly reinforces that view.

Phallic characters of the subfamily.—Epiphallus large, bridge shaped, with or without hooked pointed lophi. Subepiphallic sclerite and apical ventrolateral sclerites sometimes present. Dorsal ectophallic sclerites absent, ectophallus largely membranous, supported by a U-shaped armature with backwardly directed arms. Endophallic sclerites either in form of endophallic rods, reflexed upwards at their tips to border the genital cleft, or reduced to small sclerifications in the wall of the spermatophore sac.

1G. Notes on the Miraculinae and their phallus

The Madagascan Miraculinae (Figs 38-41) are the last subfamily placed by Descamps (1973) in the Episactidae. They differ from the other included taxa as follows: antennae with 15-20 segments, the antennal organ being on the third or fourth segment from the tip. The dorsal carinae of the hind femora are spinous. The spines on the inner dorsal margin of the first tarsal segment of the hind foot are very fine. In other respects the Miraculinae resemble the other subfamilies, *e.g.*, in being apterous. They comprise only six genera in all, and it is not obvious that these must be divided into three different tribes, as Descamps has done. These differ primarily in the shape of the fastigium, the position of the antennal organ and the direction of curvature of the endophallus.

For this work we have been able to examine only one genus: *Malagassa* Saussure 1903 (Figs 38-41).

The phallic structure (Fig. 40) recalls that of the Episactinae, but there are differences:

1. The epiphallus is fenestrated behind its posterior margin, and bears prelophal spines at its posterior lateral angles. Dorsal ectophallic sclerites and an associated sclerite sac are both present.
2. Subepiphallic sac and sclerite both absent.
3. Ectophallic lateral processes present, reminiscent of the Espagnolinae.
4. All other ectophallic sclerites absent, including the apical shields.
5. Endophallic sclerite hairpin-shaped, ends not reflexed. Decamps (1973) reports that in other genera they are often reflexed ventrally (Malagassini) or dorsally (Heteromastacini). This is the same range of variation as is seen in the Episactinae.
6. Dorsal fold present. Ventral face sclerified. Descamps 1973 says "an invagination present above the dorsal fold, everting in copulation; ventral face of this invagination with 1-3 sclerites".

The spermatheca is relatively small, but its shape, position, and the course of its duct (Fig. 41C) are very similar to those of the episactid subfamilies.

The posterior dorsal margin of the male subgenital plate (Fig. 49B) is produced in a manner very reminiscent of the Episactinae.

On purely morphological characters, there seems no good reason to dispute Descamps' placement of the Miraculinae in the Episactidae. It falls well within the definition of the Cryptophalli; the well developed epiphallus and the relative lack of ectophallic ornamentation seems to preclude the inclusion of the subfamily in the predominantly Asian Chorotypidae, which would raise fewer biogeographic problems (see below). Only the epiphallus, with its

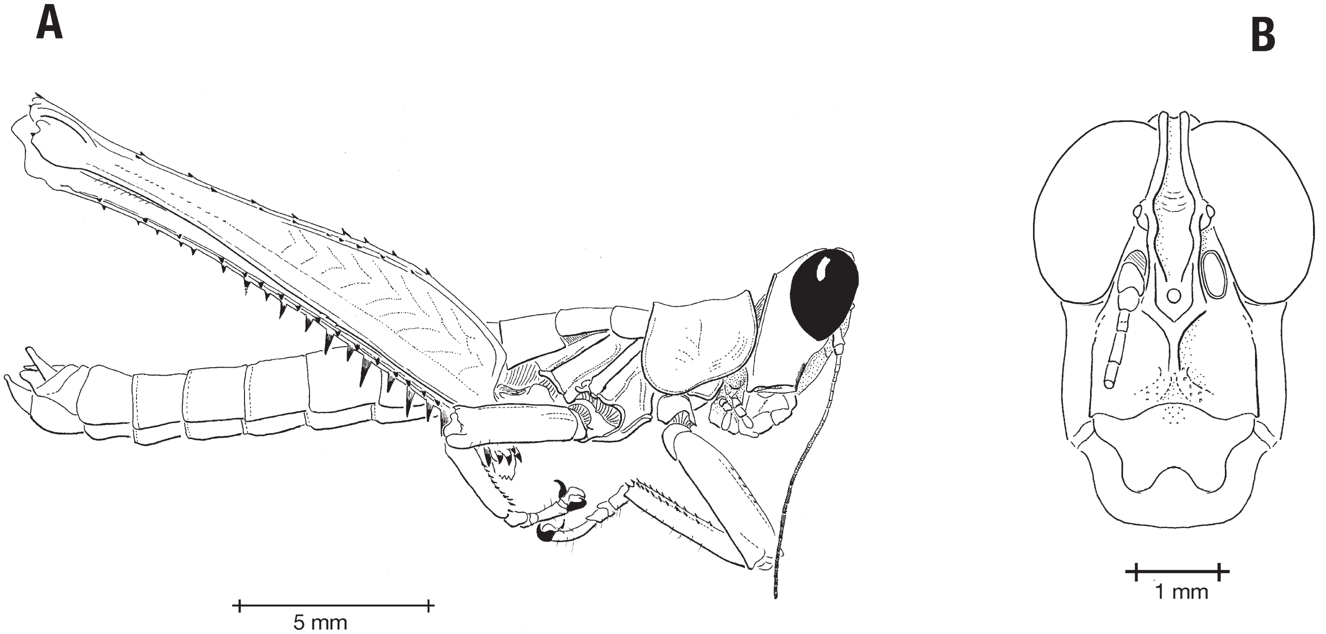


Fig. 35. *Teicophrys robertsi*, male. A. Habitus. B. Frontal view of head. Note single medial carina below the medial ocellus, a characteristic of the subfamily.

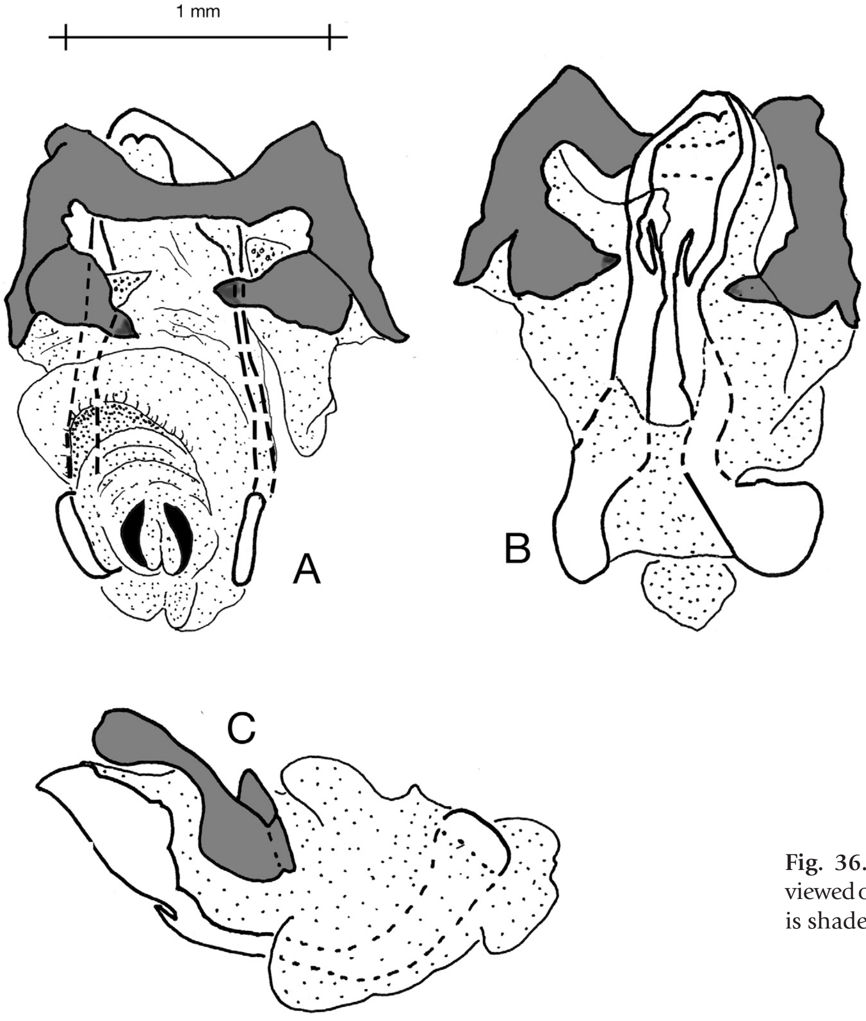


Fig. 36. *Teicophrys bolivari*, male. A. Phallic complex, viewed obliquely from posterior and above. The epiphallus is shaded. B. Ventral aspect. C. Lateral aspect.

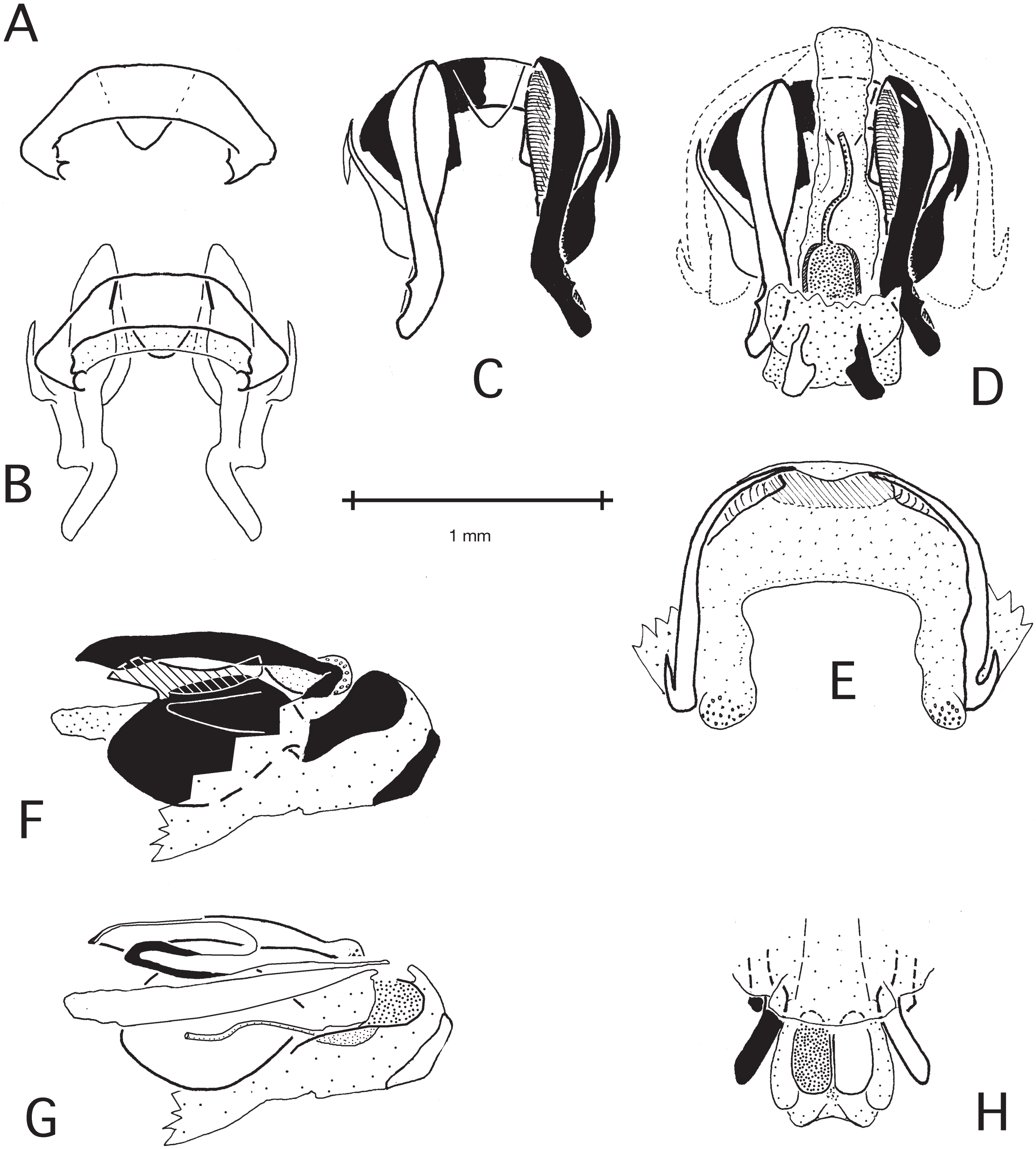


Fig. 37. *Teicophrys robertsi*. Phallic complex. A. Subepiphallic sclerite, dorsal aspect. B. As A, to show relations with armature. C. Armature and subepiphallic sclerite, seen from ventral surface. D. As C, but remaining phallic structures shown; the ectophallic membrane is cut away ventrally to show the endophallus and the ejaculatory duct. Dotted lines show outline of epiphallus. E. Epiphallus, dorsal view. F. Phallic complex, lateral view. Epiphallus and armature and apicoventral sclerites in black; subepiphallic sclerite hatched. G. As F, but parasagittal section to show endophallic rods and sacs. Subepiphallic sclerite in black. H. Tip of ectophallus in dorsal view, to show genital aperture.

prelophal spines, seems different in kind from what one sees in the other subfamilies.

The main objection to a placement in the Episactidae has always been biogeographical. Even with a liberal invocation of plate tectonics as currently understood, it is not easy to reconcile the exclusively Madagascan occurrence of the Miraculinae with the otherwise New World distribution of the rest of the family, especially considering that no related forms are known from either Africa or India. This issue is likely to remain unresolved until new molecular evidence can be brought to bear, indicating whether the similarities with the Episactidae are due to common ancestry or merely represent convergence of an otherwise unrelated lineage.

2. PHYLOGENETIC ANALYSIS

2A. Choice of in- and outgroups

We did not have sufficient material available to justify including either the Teicophryinae or the Miraculinae in the analysis. The ingroup consisted therefore only of the Central American Episactinae and the Hispaniolan taxa.

According to Descamps (1973), the sister group of the Episactidae is the Chorotypidae, and these would therefore constitute the most suitable outgroup for our purpose. We had unfortunately only one specimen of this group available (a male *Erucius*), and our hopes of obtaining adequate character descriptions from the literature (*e.g.*, Descamps' reviews of the Eumastacoidea (1973) or of the genus *Erianthus* (1975), proved overly optimistic, as these works supply almost exclusively autapomorphies of the taxa. Our character matrix descriptions of *Erucius* or of the Chorotypidae are accordingly very weak, and unsuitable for use as a sole outgroup. We therefore employed *Homeomastax* (Eumastacinae, Stenophalli) for which we had adequate data, despite its remoter relationship to the ingroup, either as a sole outgroup or in conjunction with *Erucius*.

2B. Procedure

Morphological data were coded (Appendix, Table 1) and entered into MacClade 4.8 (Maddison & Maddison 2005). All characters were coded as unordered and equally weighted. Most of them were derived from the male internal or external genitalia. We excluded from the matrix characters which varied between the species of a genus (*e.g.*, form of the female subgenital plate), and which would have therefore introduced polymorphic coding into the matrix. PAUP 4.0 version b10 (Swofford 2003) was used for phylogenetic analysis of the resulting data matrix (Table 1, Appendix). We obtained most-parsimonious reconstruction (MPR) trees using the branch and bound algorithm with the following settings: no limit to MAXTREES; branches collapsed if minimum length is zero. Branch support was assessed with nonparametric bootstrap (Felsenstein 1985) by conducting 1000 branch and bound replicates with the above settings. We used MacClade to examine the distribution of characters on the phylogenetic trees obtained in PAUP*.

2C. Results

Thirteen of the 45 coded characters were parsimony uninformative, leaving 32 to contribute to the analysis. Parsimony analysis of the full set of taxa produced eight MPRs (Fig. 42) of 98 steps with CI = 0.704, RI = 0.701, RC = 0.494, and HI = 0.296. Their majority rule consensus tree is shown in Fig. 43. Bootstrapped over 1000 replicates, the 50% majority rule consensus tree (Fig. 44) is similar but slightly less well-resolved. Its length is 104 steps, CI= 0.663, RI = 0.639, RC = 0.424, HI = 0.327. Both trees divide the Episactidae into two monophyletic clades, one (bootstrap support 92%) corresponding to the Central American Episactinae (Burr 1903) and a second clade (bootstrap support 73%) containing *Espagnola* and all the other Hispaniolan genera, which can be equated with the Espagnolinae Rehn 1948. When rooted on *Homeomastax*, the sis-

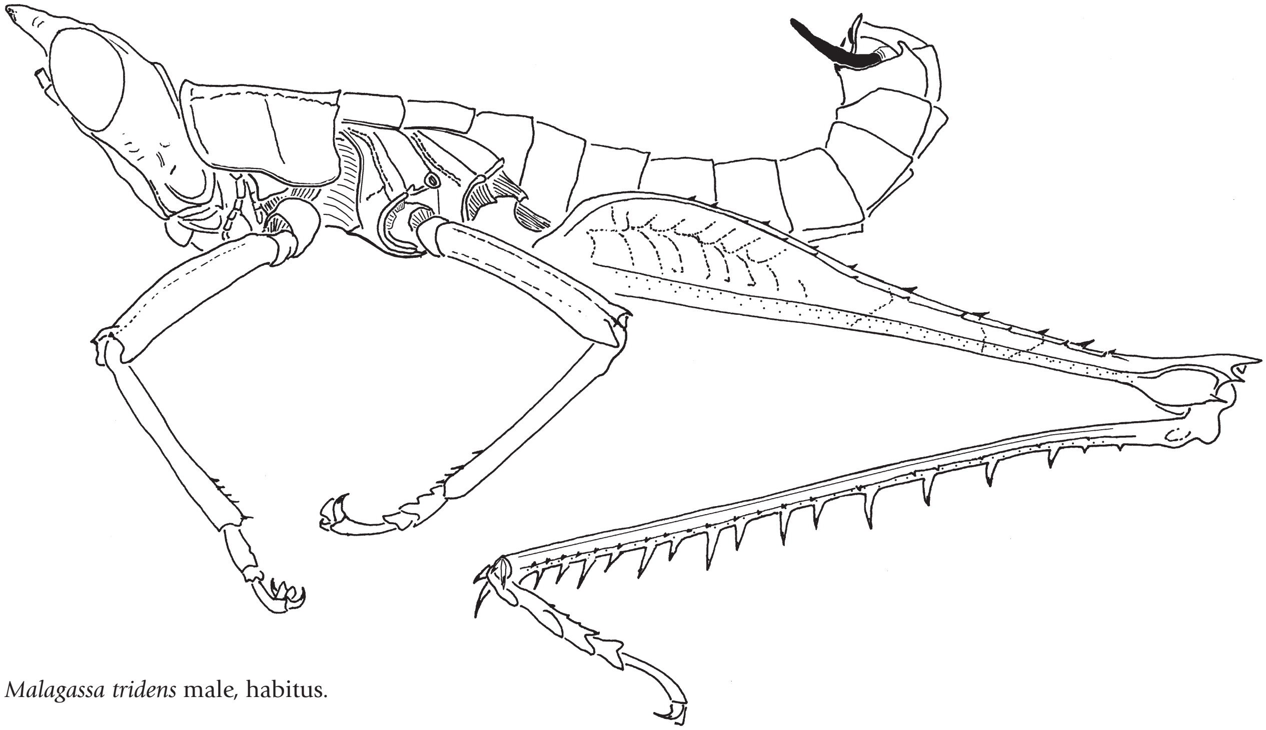


Fig. 38. *Malagassa tridens* male, habitus.

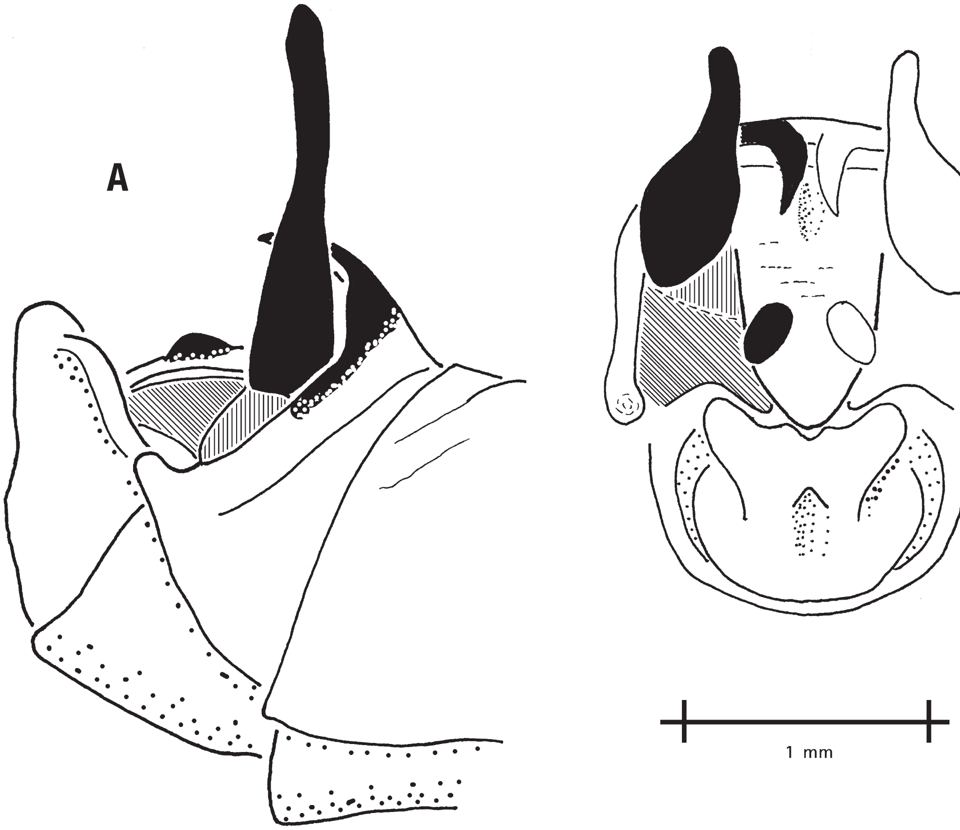


Fig. 39. *Malagassa tridens* male terminalia. A. Lateral view. B. Dorsal view, showing furcula and melanized bosses on supra-anal plate, the prolongation and reflexing of distal margin of subgenital plate .

ter group of the Episactidae is shown as *Erucius*, representing the Chorotypidae. These topological results concur with the molecular systematic findings of Matt (1998), and support the arrangement of Descamps (1973).

If *Erucius* is excluded from the analysis one obtains 2 equally parsimonious trees (Fig. 45) of length 88 steps (CI =0.705, RI = 0.714, RC = 0.583, HI = 0.295). The majority rule consensus of these (Fig. 46) again shows the Episactinae and the Espagnolinae as separate monophyletic clades, each with 100% occurrence. Non parametric bootstrapping (1000 replicates branch and bound) gives 80% and 88% support for the two clades (Fig. 47).

The only difference in ingroup topography brought about by the exclusion of *Erucius* is that one of the most parsimonious trees now puts *Paralethus* and not *Gymnotettix* as the most basal member of the Episactine clade. This is understandable, as *Gymnotettix* and *Erucius* share some unusual character states, such as continuous fastigial and frontal carinae.

The number of unequivocal character changes on the most parsimonious tree (with no characters or taxa excluded) are illustrated in Fig. 48. *Neibamastax* or *Antillacris* are resolved as the most basal members of the Espagnolinae, and *Paralethus* as the most basal of the Episactinae. However, as mentioned above, the latter result is strongly dependent on the outgroup taxa and the composition of the ingroup. Both are interesting placements, as these taxa differ rather markedly from the rest of their clades and from each other, suggesting that the clades have diverged strongly from the plesiomorphic condition, especially in their phallic characters. It is also interesting to recall that Rehn & Rehn (1939: 201) called their species of *Antillacris* "*explicatrix*" because they felt that it "clearly demonstrated" an origin of this West Indian genus among the Central American Episactinae. On the other hand, they also speculated (their p.190) that *Espagnola* (which we find to be the most derived member of its clade) might be ancestral to the Episactinae!

2D. Discussion, diagnoses

On the basis of the results presented above, we support the inclusion of at least the following subfamilies within the Episactidae (Descamps 1973):

Episactinae Burr 1903.
Included genera:
Episactus Burr 1899
Gymnotettix Bruner 1901
Lethus Rehn & Rehn 1934
Paralethus n. gen.

Espagnolinae Rehn 1948.
Included genera:
Antillacris Rehn & Rehn 1939
Espagnola Rehn & Rehn 1939
Espagnolopsis Perez *et al.* 1997
Espagnoleta Perez-Gelabert 2000
Tainacris Perez *et al.* 1997
Neibamastax n. gen.

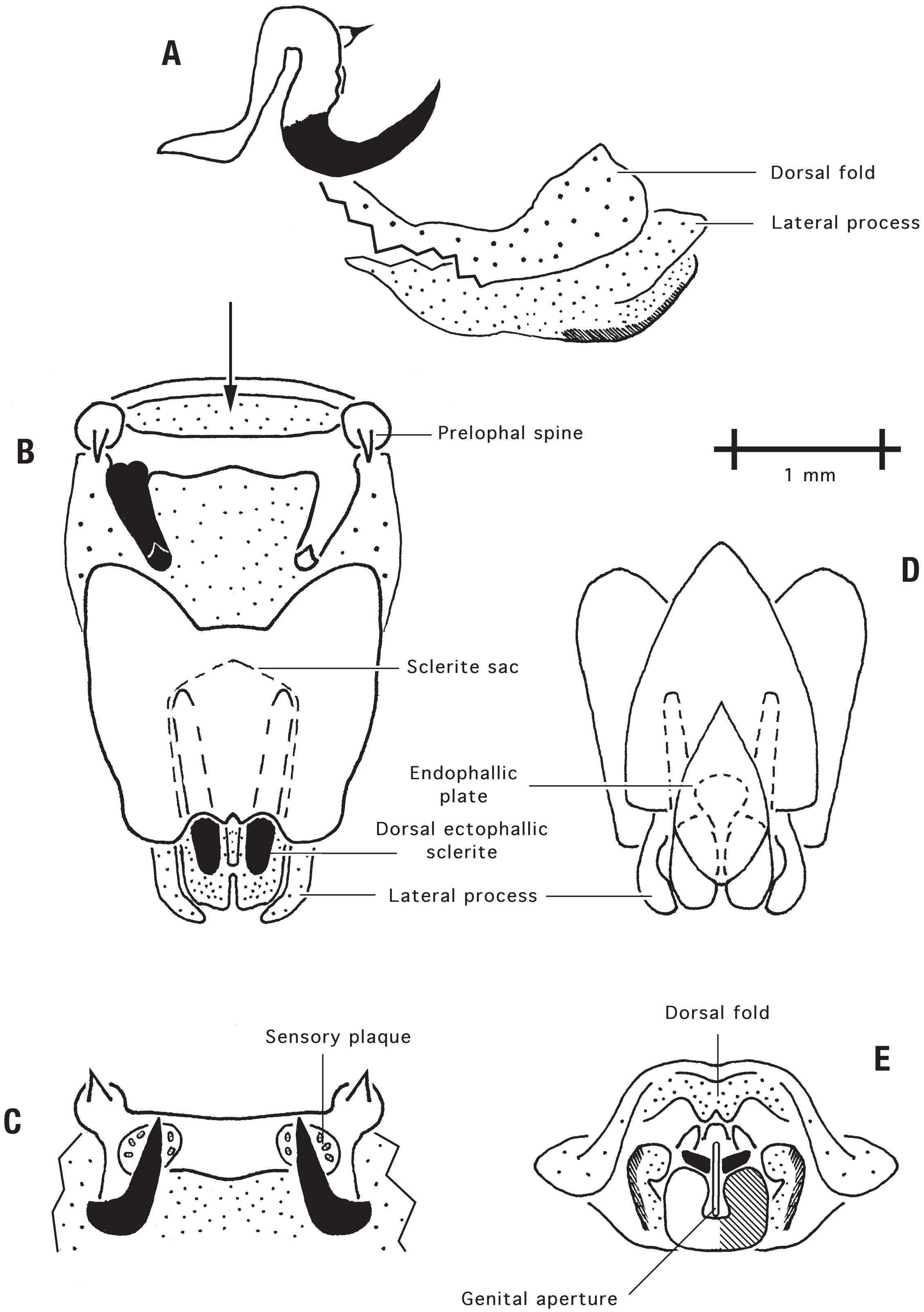


Fig. 40. *Malagassa tridens.* Phallic complex. A. Phallic complex, lateral view. B. As A, dorsal view. C. Epiphallus, axial view (from behind). D. Phallic complex, ventral aspect, showing position of endophallic rods. E. Phallic complex, axial view.

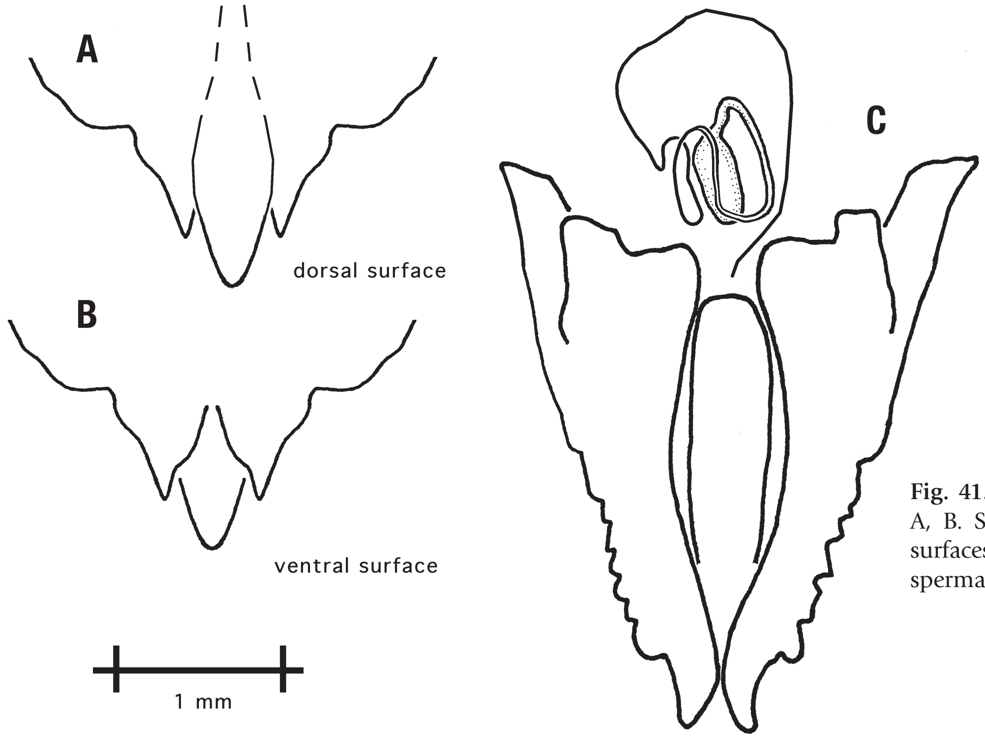


Fig. 41. *Malagassa tridens* female genitalia. A, B. Subgenital plate, dorsal and ventral surfaces. C. Ventral ovipositor valves and spermatheca.

Teicophryinae Rehn 1948.
Included genera:
Teicophrys Bruner 1900

We see no morphological reasons to exclude the Miraculinae Bolivar 1903, but recommend withholding judgment until molecular evidence becomes available.

Diagnoses.—Descamps (1973) gives a key to the higher divisions of the Eumastacidae as a whole.

All members of the Cryptophalli have: dorsal margins of first tarsal segment of hind foot spined. Endophallus small, usually shorter than half the length of the ectophallus.

Characters defining the Episactidae clade of the Cryptophalli are: male SP clearly divided by a suture between sterna nine and 10. Epiphallus always distinct and well developed. Longest tibial spur no. 4 (most internal). Secondary lateral carinae of pronotum often present. Lateral carinae of frontal ridge not continuous with those of fastigium (except in *Gymnotettix*).

Episactinae characters

Characters defining the Episactinae clade of the Episactidae are the following [the initial number of each sentence refers to the list of characters (Table 2)]:
3. Seven or eight flagellar antennal segments.
13. Pronotal hind margin truncate, medially broadly emarginate.
23. Apical position of genital aperture.
All the above characters are unique, and uniform in the phylogenetic tree above their acquisition point. They are accordingly diagnostic within the sample treated here.

The following characters, in contrast, are typical, but not diagnostic of the Episactinae — they occur elsewhere, or they are not universal among the Episactinae:

5. Aptery (also in some Espagnolinae, Teicophryinae, *etc.*).
4. Fastigium a little produced beyond vertex, wide, bluntly rounded in dorsal aspect (except *Gymnotettix*).
11. Dorsal carinae of hind femora not spinous.
14. Subgenital plate of male not membranous (also in Teicophryinae).
15. Usually some male abdominal sterna bossed.
16. Male subgenital plate rim spinous (also in some Teicophryinae).
18. Usually with male furcula (except *Paralethus)*.
24. Usually with subepiphallic sac (except *Lethus* and *Paralethus*).
25. Internal dorsal ectophallic sclerites usually present (except *Lethus* and *Gymnotettix*).
41. Lateral ectophallic plate present (except *Episactus* and *Gymnotettix*).
42 and 43. Dorsoapical and ventroapical armed sclerites present on ectophallus (except *Paralethus.*)
44. Endophallic rods fuse with apical shields (not *Episactus* or *Gymnotettix*).

b. General description.

Fastigium of vertex wide, usually slightly produced in front of eyes, its border carinate, fastigio-facial angle acute (except *Gymnotettix*); frontal ridge deeply sulcate, its lateral edges carinate, the carinae abutting but not continuous with the fastigial marginal carinae (except *Gymnotettix)*; median ocellus patent. Carinae of frontal ridge continue below medial ocellus, diverging basally to form a supraclypeal triangle or trapezium. Antennal flagellum with seven

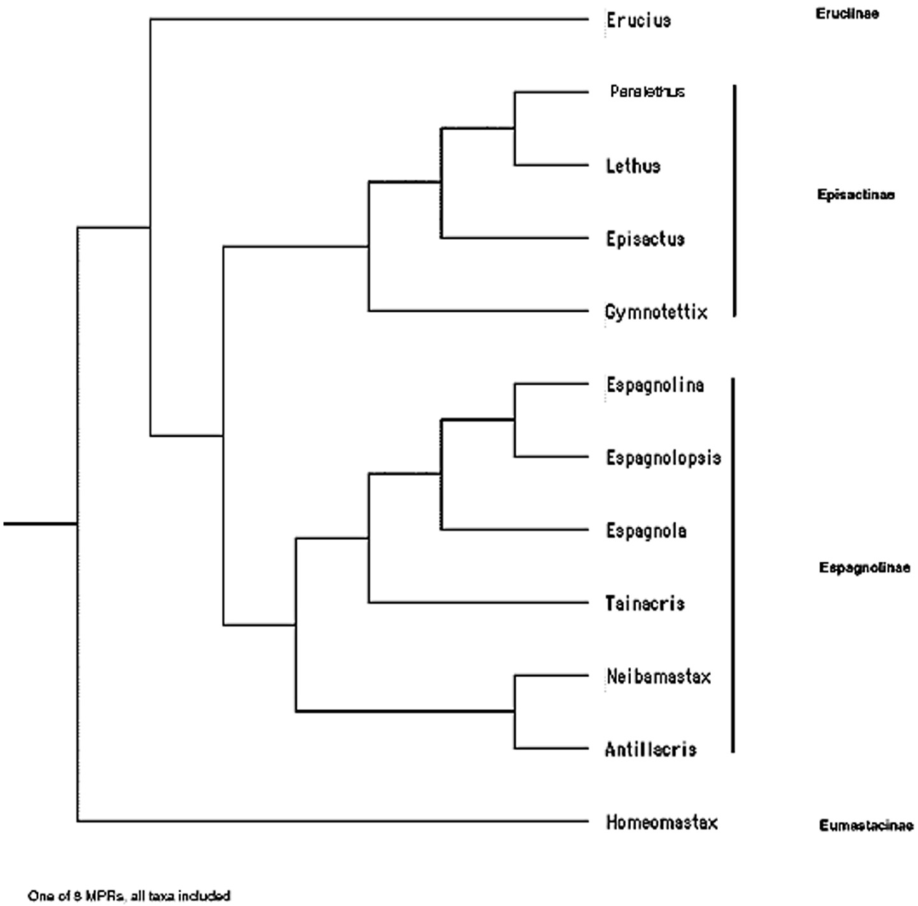


Fig. 42. One of eight maximally parsimonious reconstructions of the morphological data shown in matrix form in Table 2. Tree rooted on *Homeomastax*.

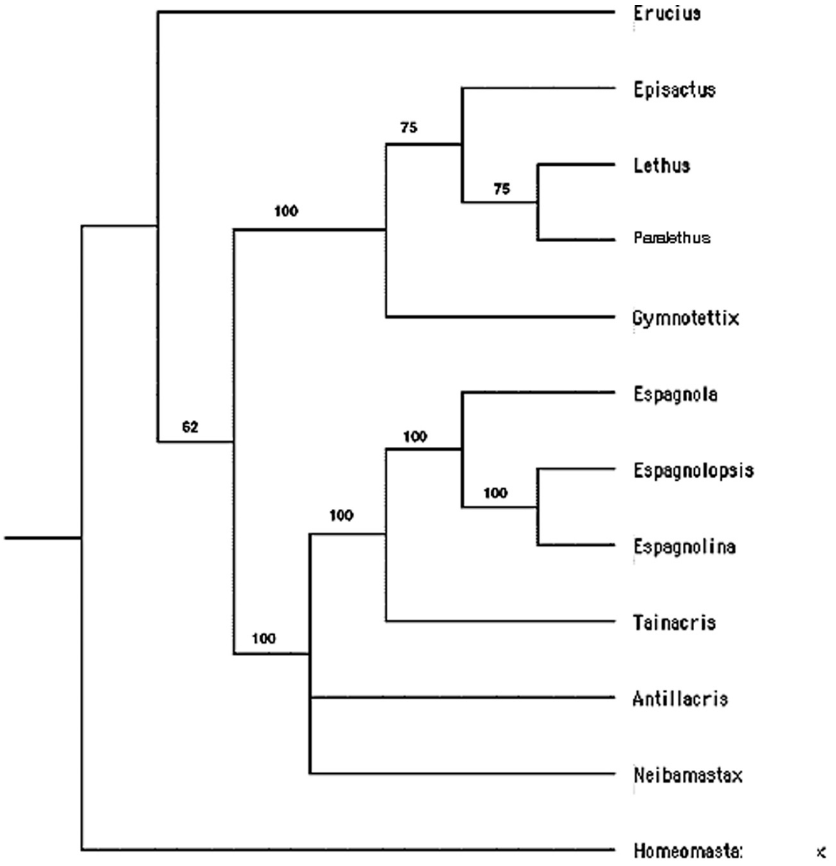


Fig. 43. Majority rule consensus tree of all eight maximally parsimonious reconstructions. Tree rooted on *Homeomastax.*

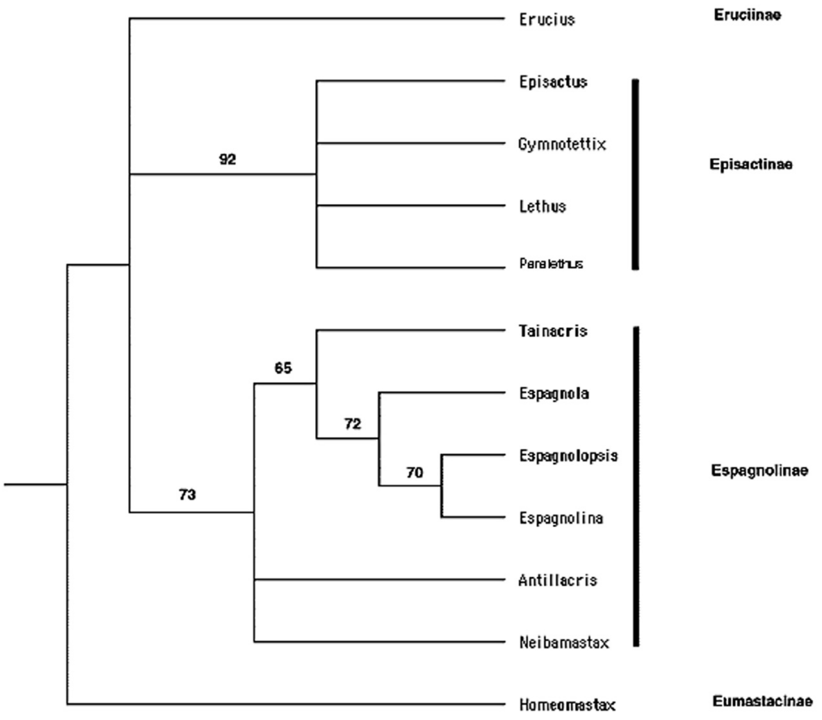


Fig. 44. Majority rule consensus tree with bootstrap values (1000 replicates). Tree rooted on *Homeomastax*.

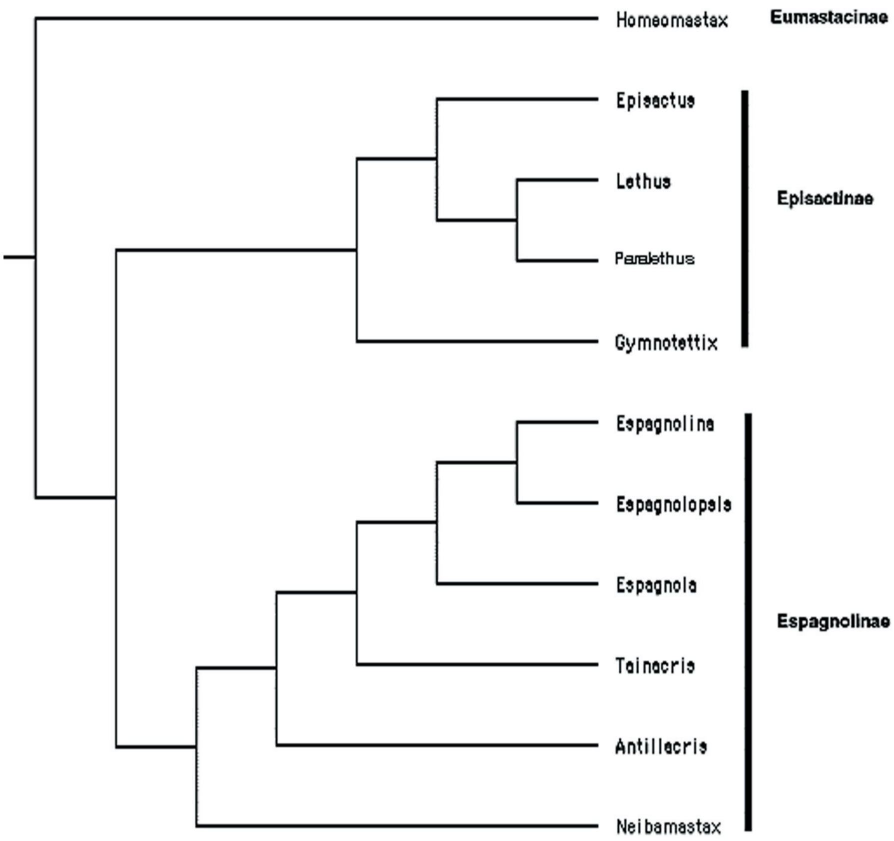


Fig. 45. One of two maximally parsimonious reconstructions of the morphological data shown in matrix form in Table 2, omitting *Erucius*. Tree rooted on *Homeomastax*. The other MPR (not shown) has *Paralethus* as the basal Episactine, instead of *Gymnotettix* as shown here.

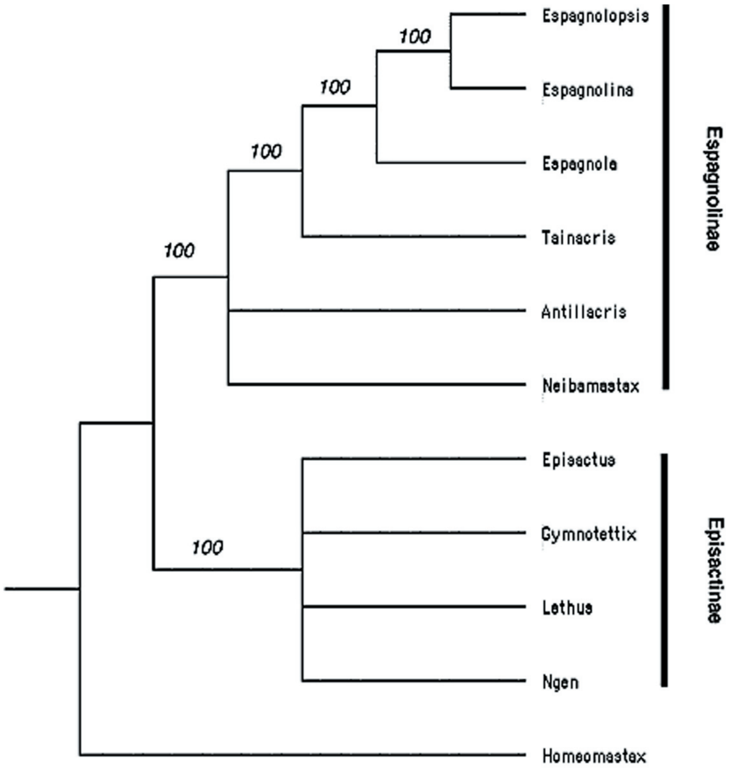


Fig. 46. Majority rule consensus tree of both maximally parsimonious reconstructions obtained after exclusion of *Erucius*. Tree rooted on *Homeomastax*.

to eight segments (of which the two most proximal are indistinctly separated); antennal organ on the ultimate, most distal segment.

Pronotum medially carinate, posterior border truncate and broadly V-emarginate. True lateral carinae of PN absent, but a secondary ridge, especially marked in *E. eremites*, traverses the pronotal lobes obliquely in all genera except *Gymnotettix* and is cut by one lateral sulcus. No sulci cross pronotal disc. Anterior ventral angle of pronotal lobe rounded, obtuse; posterior ventral angle rounded rectangular. Invariably apterous. Femora of fore and middle legs subquadrate in cross section, dorsal surface somewhat excavated, its margins carinate, the carinae usually (except *Paralethus*) ending distally in small spines. Fore and mid tibiae with two rows of ventral spines. Dorsal margin of hind femur usually minutely denticulate (except *Paralethus*) but never spinous. Hind tibiae with 17 to 26 external spines, and 18 to 27 biseriate internal spines. Tibae with two pairs of terminal spurs, of which the most interior spur (the fourth) is largest. Both internal and external dorsal margins of first hind tarsal segments armed with five to six spines. Thoracic sterna with a surrounding carina.

Proximate abdominal segments always medially carinate. Tenth abdominal tergite always medially emarginate, in male often with a small furcula. Some abdominal sternites of male, especially segments two, three and/or four, usually with a boss of thickened, possibly glandular, integument. Supra-anal plate triangular, varying in relative length and width between taxa, in females elongate and rounded at tip. Male subgenital plate cupuliform with no membranous areas, the dorsal rim sometimes produced, and always ornamented with large or small spines. Male cerci incurved, sometimes reflexed through 180˚. Aperture of subgenital plate normally covered by imbricating subgenital plate, supra-anal plate and cerci.

Phallus.— Epiphallus shield or disc-shaped, sometimes (*Paralethus*) much wider than rest of phallus, always emarginate on anterior margin, often fenestrated. Lophi upturned and hook-shaped. Subepiphallic sac usually present, subepiphallic sclerite always absent. Small medial postepiphallic sclerite occasionally *(Lethus*) present. Genital aperture apical, endophallus small, its sclerites reduced to a pair of endophallic rods which may or may not be inserted into ectophallic structures apically. Both internal and external dorsal ectophallic sclerites sometimes present (either can however be missing, as in *Lethus* and *Gymnotettix*), normally pointed and protruding at their posterior extremity. Ectophallus usually decorated with one to four pairs of armed sclerites. Lateral processes of ectophallus absent.

Female cerci simple, tapering, straight. Dorsal ovipositor valves usually long, forceps-like, the tips curving inwards and excavated at their apices; ventral valves shorter and straighter. External margins of both valves sharply toothed. Posterior margin of female subgenital plate usually more or less trifid; egg guide weakly developed. Spermatheca a simple oval bladder, the spermathecal duct running obliquely forward from a papilla in roof of genital chamber and then reflexed 180˚ on itself, to run backwards to enter the spermatheca near its posterior extremity. Bursa copulatrix absent. No appreciable differences seen between genera, the spermatheca is not a taxonomically useful structure in this subfamily.

Espagnolinae characters

Characters defining the Espagnolinae clade of the Episactidae are the following:

4. Elongate fastigium, always produced and pointed in dorsal view.
35. Lateral lobes of ectophallus present (except *Espagnoleta*) (though may be sclerified.)
7. Oblique secondary lateral carina on PN lobes, (except *Espagnoleta)*.
31. Subepiphallic sclerite present (also in some Teicophryinae).
23. Dorsoapical position of genital aperture.

5. Usually winged, though commonly flightless with reduced wings. *Antillacris* is the only known apterous member of the subfamily, *Espagnola* the only genus certainly capable of flight. [Perez has seen *Espagnola* fly at Monte Diego de Ocampo: it was a short (no more than 1 m) displacement in an arching trajectory].
13. Posterior margin of PN produced backwards, generally smoothly rounded (except *Tainacris)*.
3. Antennal flagellum with 10 segments (as in Chorotypidae).
15. Abdominal sterna lacking glandular bosses.
14. Male subgenital plate with membranous area.
16. Rim of male subgenital plate always devoid of spines.
26. Post epiphallic sclerite always absent.

Phallus usually lacking dorsal ectophallic sclerites, but with armed apical shields which are fused together at some midline point (except *Neibamastax*). Ectophallus has no sclerites other than apical shields (except *Neibamastax*). Subepiphallic sac absent, subepiphallic sclerite usually, perhaps always, present. Endophallic rods never end on endophallic sacs, nor do they insert into apical shields, but are reflexed upwards and usually forwards to encompass genital aperture.

Furcula if present quite large, ninth and tenth tergites sometimes decorated with ornamental processses.

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Table 1. Dimensions of selected Episactine species (mm). Abbreviations are as follows: P: length of pronotum in midline. L: overall length from tip of fastigium to tip of abdomen. Ant: length of antennal flagellum. IOS: width of inter-ocular space. E-e: maximun width across the compound eyes. Fast B: breadth of fastigium (in dorsal view). Fast L: Length of fastigium (from anterior margin of compound eyes to tip of fastigium, in dorsal view). F: length of each of the three hind tarsal segments. FD: maximum width of hind femur. Ta 1-3: length of each of the three hind tarsal segments.

Specimen, No.		Locality	P	L	Ant	IOS	E-E	Fast B	Fast L	F	FD	Ta1	Ta2	Ta3	Ta1+2+3
Paralethus insolitus															
Males	UCR 71241	Cerro Verde	2.25	curled	2.68	0.74	2.32	0.86	0.37	8.27	1.79	1.63	0.49	0.98	3.10
	UCR 71242	Cerro Verde	2.15	13.53	2.04	0.80	2.28	0.80	0.36	8.96	1.88	1.69	0.47	1.08	3.24
		MEAN	2.20	13.53	2.36	0.77	2.30	0.83	0.37	8.62	1.84	1.66	0.48	1.03	3.17
Female	UCR 71243	Cerro Verde	2.86	18.78	2.31	1.02	2.55	1.09	0.58	no data	no data	no data	no data	no data	no data
		Sex. Dimorph	0.77	0.72	1.02	0.76	0.90	0.76	0.63						
Lethus nicaraguae															
Males	UCR 71248	NP La Muralla	2.37	14.29	2.41	0.87	2.56	0.87	0.39	12.47	2.34	1.97	0.55	1.51	4.03
	UCR 71249	NP La Muralla	2.46	12.78	2.46	0.86	2.49	0.86	0.32	11.48	2.30	1.96	0.60	1.41	3.97
	2002008	NP La Muralla	2.44	15.39	2.77	0.95	2.69	0.95	0.41	12.28	2.33	1.97	0.68	1.49	4.14
		MEAN	2.42	14.15	2.55	0.89	2.58	0.89	0.37	12.08	2.32	1.97	0.61	1.47	4.05
Females	UCR 71252	NP La Muralla	2.52	19.87	2.34	1.04	2.98	1.04	0.45	12.84	2.74	2.13	0.60	1.46	4.19
	UCR 71253	NP La Muralla	3.11	22.35	2.12	1.11	2.95	1.18	0.53	12.13	2.56	1.97	0.55	1.42	3.94
	UCR 71251	NP La Muralla	3.08	20.92	2.50	1.12	2.96	1.12	0.57	12.55	2.62	1.88	0.65	1.58	4.11
		MEAN	2.90	21.05	2.32	1.09	2.96	1.11	0.52	12.51	2.64	1.99	0.60	1.49	4.08
		Sex. Dimorph	0.83	0.67	1.10	0.82	0.87	0.80	0.72	0.97	0.88	0.99	1.02	0.99	0.99
Episactus tristani (Costa Rica)															
Males	RC 91013	Changuita	1.70	10.50	1.94	0.50	1.97	0.57	0.19	8.92	1.62	1.35	0.42	1.20	2.97
	97163	Fila Diamante	1.97	12.36	2.16	0.55	2.20	0.61	0.22	10.28	1.71	1.78	0.53	1.32	3.63
	2000.003	R. Tabor	1.68	10.95	2.04	0.56	2.03	0.55	0.20	9.88	1.46	1.55	0.46	1.30	3.31
	91178	V. Cacao	1.85	11.05	1.97	0.59	2.10	0.55	0.20	9.31	1.51	1.71	0.46	1.12	3.29
	93292	Tres Rios	1.67	10.52	1.70	0.55	2.08	0.55	0.19	8.77	1.52	1.52	0.45	1.06	3.03
	27106	Los Cartagos	1.58	11.23	2.11	0.55	1.95	0.55	0.17	9.07	1.58	1.36	0.40	1.01	2.77
		Mean	1.74	11.10	1.99	0.55	2.06	0.56	0.20	9.37	1.57	1.55	0.45	1.17	3.17
		Min	1.58	10.50	1.70	0.50	1.95	0.55	0.17	8.77	1.46	1.35	0.40	1.01	2.77
		Max	1.97	12.36	2.16	0.59	2.20	0.61	0.22	10.28	1.71	1.78	0.53	1.32	3.63
		N	6	6	6	6	6	6	6	6	6	6	6	6	6
Females	RC 97164	Fila Diamante	2.28	18.25	1.71	0.81	2.52	0.81	0.29	12.05	2.10	1.99	0.56	1.42	3.97
	91014	Changuita	1.76	15.60	1.99	0.60	2.14	0.64	0.19	8.97	1.71	1.53	0.44	1.20	3.17
	27105	Los Cartagos	1.82	15.46	1.68	0.61	2.09	0.66	0.21	9.64	1.73	1.71	0.50	1.31	3.52
	2001. 013	Tarbaca	1.75	14.22	1.53	0.71	2.19	0.71	0.25	9.28	1.55	1.60	0.42	1.15	3.17
	93287	Tres Rios	1.88	16.33	1.82	0.67	2.13	0.70	0.28	10.72	1.79	1.90	0.46	missing	
	91180	V. Cacao	2.20	17.24	1.52	0.72	2.39	0.73	0.35	11.15	2.00	1.92	0.53	1.27	3.72
		Mean	1.95	16.18	1.71	0.69	2.24	0.71	0.26	10.30	1.81	1.78	0.49	1.27	3.51
		Min	1.75	14.22	1.52	0.60	2.09	0.64	0.19	8.97	1.55	1.53	0.42	1.15	3.17
		Max	2.28	18.25	1.99	0.81	2.52	0.81	0.35	12.05	2.10	1.99	0.56	1.42	3.97
		N	6	6	6	6	6	6	6	6	6	6	6	5	5
		Sex. dimorph.	0.89	0.69	1.16	0.80	0.92	0.80	0.75	0.91	0.86	0.87	0.93	0.92	0.90
Episactus sp. ?tristani? El Salvador:															
Males	UCR Ent 71244	Los Chorros	2.30	13.58	2.66	0.60	2.33	0.63	0.21	11.91	1.99	2.12	0.55	1.40	4.07
	RC 2002010	Los Chorros	2.18	13.62	2.81	0.59	2.28	0.63	0.25	12.18	2.05	2.00	0.61	1.52	4.13
		Mean	2.24	13.60	2.74	0.60	2.31	0.63	0.23	12.05	2.02	2.06	0.58	1.46	4.10
		Larger than CR population: but no diffs. in proportions, other than smaller E-E/P.													
Episactus brunneri		Guatemala													
Male	USNMNH	Est. de la Virgen	2.14	13.63	1.98	0.55	2.22	0.60	0.29	11.77	2.28	1.87	0.50	1.20	3.57

Table 1. (contin.) Abbrev: L/P *etc*.: Length (or other measure) divided by length of pronotum. F/FD: the 'aspect ratio' of the femur, i.e., its length divided by its width. Ta1 - 3/F: ratio of length of hind foot to length of hind femur. Fast L/B: the 'aspect ratio' of the fastigium i.e., its length divided by its breadth. Ext. or Int. spines: number of external or internal spines on tibia. The population value is here expressed as the median, not the mean. Foot formula: the lengths of the three hind tarsal segments expressed as percentages of their sum.

Ratios:

L/P	Ant/P	IOS/P	E-E/P	Fast B/P	Fast L/P	F/P	FD/P	Ta1/P	Ta2/P	Ta3/P	Ta1-3/P	F/FD	Ta1-3/F	Fast L/B	Foot formula				Ext spines	Int Spines
no data	1.19	0.33	1.03	0.38	0.16	3.68	0.80	0.72	0.22	0.22	1.38	4.62	0.37	0.43	53%	16%	32%		21	17
6.29	0.95	0.37	1.06	0.37	0.17	4.17	0.87	0.79	0.22	0.22	1.51	4.77	0.36	0.45	52%	15%	33%		21	18
6.29	1.07	0.35	1.05	0.38	0.17	3.92	0.84	0.76	0.22	0.22	1.44	4.69	0.37	0.44	52%	15%	32%		21	18
6.57	0.81	0.36	0.89	0.38	0.20	No data	No data	No data	No data	No data	No data	No data	No data	0.53					no data	no data
0.96	1.32	0.98	1.17	0.99	0.82									0.83						
6.03	1.02	0.37	1.08	0.37	0.16	5.26	0.99	0.83	0.23	0.23	1.70	5.33	0.32	0.45	49%	14%	37%		24	18
5.20	1.00	0.35	1.01	0.35	0.13	4.67	0.94	0.80	0.24	0.24	1.61	4.99	0.35	0.37	49%	15%	36%		23	18
6.31	1.14	0.39	1.10	0.39	0.17	5.03	0.96	0.81	0.28	0.28	1.70	5.27	0.34	0.43	48%	16%	36%		23	19
5.84	1.05	0.37	1.07	0.37	0.15	4.99	0.96	0.81	0.25	0.25	1.67	5.20	0.34	0.42	49%	15%	36%	Median:	23	18
7.89	0.93	0.41	1.18	0.41	0.18	5.10	1.09	0.85	0.24	0.24	1.66	4.69	0.33	0.43	51%	14%	35%		23	17
7.19	0.68	0.36	0.95	0.38	0.17	3.90	0.82	0.63	0.18	0.18	1.27	4.74	0.32	0.45	50%	14%	36%		24	19
6.79	0.81	0.36	0.96	0.36	0.19	4.07	0.85	0.61	0.21	0.21	1.33	4.79	0.33	0.51	46%	16%	38%		22	18
7.29	0.81	0.38	1.03	0.39	0.18	4.36	0.92	0.70	0.21	0.21	1.42	4.74	0.33	0.46	49%	15%	36%	Median:	23	18
0.80	1.30	0.98	1.03	0.96	0.87	1.14	1.04	1.17	1.21	1.21	1.18	1.10	1.03	0.90	1.00	1.02	1.00		1.00	1.00
6.18	1.14	0.29	1.16	0.34	0.11	5.25	0.95	0.79	0.25	0.71	1.75	5.51	0.33	0.33	45%	14%	40%		22	19
6.27	1.10	0.28	1.12	0.31	0.11	5.22	0.87	0.90	0.27	0.67	1.84	6.01	0.35	0.36	49%	15%	36%		22	19
6.52	1.21	0.33	1.21	0.33	0.12	5.88	0.87	0.92	0.27	0.77	1.97	6.77	0.34	0.36	47%	14%	39%		22	19
5.97	1.06	0.32	1.14	0.30	0.11	5.03	0.82	0.92	0.25	0.61	1.78	6.17	0.35	0.36	52%	14%	34%		23	20
6.30	1.02	0.33	1.25	0.33	0.11	5.25	0.91	0.91	0.27	0.63	1.81	5.77	0.35	0.35	50%	15%	35%		21	18
7.11	1.34	0.35	1.23	0.35	0.11	5.74	1.00	0.86	0.25	0.64	1.75	5.74	0.31	0.31	49%	14%	36%			
6.39	1.15	0.32	1.18	0.32	0.11	5.40	0.90	0.89	0.26	0.67	1.82	5.99	0.34	0.35	49%	14%	37%	Median:	22	19
5.97	1.02	0.28	1.12	0.30	0.11	5.03	0.82	0.79	0.25	0.61	1.75	5.51	0.31	0.31	45%	14%	34%		21	18
7.11	1.34	0.35	1.25	0.35	0.12	5.88	1.00	0.92	0.27	0.77	1.97	6.77	0.35	0.36	52%	15%	40%		23	20
6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6		5	5
8.00	0.75	0.36	1.11	0.36	0.13	5.29	0.92	0.87	0.25	0.62	1.74	5.74	0.33	0.36	50%	14%	36%		21	19
8.86	1.13	0.34	1.22	0.36	0.11	5.10	0.97	0.87	0.25	0.68	1.80	5.25	0.35	0.30	48%	14%	38%		22	19
0.34	0.92	0.34	1.15	0.36	0.12	5.30	0.95	0.94	0.27	0.72	1.93	5.57	0.37	0.32	49%	14%	37%		21	19
8.13	0.87	0.41	1.25	0.41	0.14	5.30	0.89	0.91	0.24	0.66	1.81	5.99	0.34	0.35	50%	13%	36%		20	20
8.69	0.97	0.36	1.13	0.37	0.15	5.70	0.95	1.01	0.24			5.99		0.40					20	20
7.84	0.69	0.33	1.09	0.33	0.16	5.07	0.91	0.87	0.24	0.58	1.69	5.58	0.33	0.48	52%	14%	34%		20	20
6.98	0.89	0.35	1.16	0.37	0.13	5.29	0.93	0.91	0.25	0.65	1.80	5.68	0.34	0.37	50%	14%	36%	Median:	21	20
0.34	0.69	0.33	1.09	0.33	0.11	5.07	0.89	0.87	0.24	0.58	1.69	5.25	0.33	0.30	48%	13%	34%		20	19
8.86	1.13	0.41	1.25	0.41	0.16	5.70	0.97	1.01	0.27	0.72	1.93	5.99	0.37	0.48	52%	14%	38%		22	20
6	6	6	6	6	6	6	6	6	6	5	5	6	5	6	5	5	5		6	6
0.92	1.29	0.90	1.02	0.89	0.84	1.02	0.97	0.97	1.04	1.03	1.01	1.05	0.98	0.94	0.98	1.03	1.02		1.07	0.97
5.90	1.16	0.26	1.01	0.27	0.09	5.18	0.87	0.92	0.24	0.61	1.77	5.99	0.34	0.33	52%	14%	34%		25	22
6.25	1.29	0.27	1.05	0.29	0.11	5.59	0.94	0.92	0.28	0.70	1.89	5.94	0.34	0.40	48%	15%	37%		25	23
6.08	1.22	0.27	1.03	0.28	0.10	5.38	0.90	0.92	0.26	0.65	1.83	5.96	0.34	0.37	50%	14%	36%		25.00	22.50
			smaller																	
6.37	0.93	0.26	1.04	0.28	0.14	5.50	1.07	0.87	0.23	0.56	1.67	5.16	0.30	0.48	52%	14%	34%		28	23

Table 2. The character matrix used for cladistic analysis. The characters are numbered progresssively along the first row, and their number corresponds to that in the "Annotated list of characters" in the Appendix. Shaded characters are cladistically uninformative in the current analysis.

Characters:	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Taxa																						
Erucius	1	2	2	0	1	2	0	1	1	1	1	2	0	0	0	0	2	2	0	0	2	2
Homeomastax	1	3	3	0	1	1	0	0	-	1	0	1	0	0	0	0	1	0	0	1	1	1
Episactus	2	1	1	1	2	1	1	1	0	1	0	2	1	0	1	1	1	1	0	1	1	2
Gymnotettix	1	1	1	0	2	1	0	1	0	1	0	2	1	0	1	1	1	1	0	1	1	2
Lethus	2	1	1	1	2	1	1	1	0	1	0	2	1	0	1	1	1	1	0	1	1	2
Paralethus	2	1	1	1	2	1	1	1	0	0	0	2	1	0	1	1	1	0	0	1	1	2
Espagnola	2	1	2	2	1	1	1	1	0	0	0	2	0	1	0	0	1	2	0	1	1	2
Espagnolopsis	2	1	2	2	1	1	2	1	0	2	0	2	0	1	0	0	1	2	1	1	1	2
Espagnoleta	2	1	2	2	1	1	0	1	0	0	0	2	0	1	0	0	1	0	1	1	1	2
Tainacris	2	1	2	2	1	1	2	1	0	1	0	2	0	1	0	0	1	0	0	1	1	2
Antillacris	2	1	2	2	2	1	1	1	0	1	0	2	0	1	0	0	1	0	1	1	1	2
Neibamastax	2	1	2	2	1	1	2	1	0	1	0	2	0	1	0	0	1	0	0	1	1	2

Characters:	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**
Taxa																							
Erucius	3	0	0	?	1	-	?	-	0	?	?	?	?	0	1	?	1	?	?	?	?	?	0
Homeomastax	1	1	1	0	1	2	2	2	0	0	0	?	0	0	2	0	1	1	0	?	?	1	0
Episactus	2	1	1	1	1	1	2	2	0	0	0	0	0	0	1	0	2	0	1	1	2	0	0
Gymnotettix	2	1	0	1	1	1	2	2	0	0	0	3	0	0	1	0	2	0	1	1	2	0	0
Lethus	2	1	0	0	1	1	2	?	0	0	0	2	0	0	1	1	2	0	2	1	2	1	0
Pralethus	2	0	1	1	1	3	2	?	0	0	0	1	0	0	2	2	1	0	2	1	1	1	1
Espagnola	3	0	0	0	1	3	2	2	1	1	3	1	1	2	1	2	3	2	0	0	0	0	0
Espagnolopsis	3	0	0	0	2	1	2	1	1	1	2	2	1	1	1	1	3	2	0	0	0	0	0
Espagnoleta	3	0	0	0	1	2	1	1	1	1	2	2	0	1	1	2	3	2	0	0	0	0	0
Tainacris	3	0	0	0	1	2	2	2	2	1	2	1	2	1	1	2	2	2	0	0	0	0	0
Antillacris	3	0	0	0	1	2	2	0	2	2	1	0	3	0	2	2	3	0	0	0	0	0	0
Neibamastax	3	0	1	0	1	1	2	2	3	2	0	0	1	0	1	2	2	1	0	0	0	0	0

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Appendix 1. Annotated list of characters. The number of each paragraph refers to a matrix column (Table 2). An asterisk indicates a phylogenetically uninformative character in the present analysis.

Head.

1. Fastigial/frontal carinae. The frontal ridge is edged by carinae. These may be either continuous with the fastigial marginal carinae dorsally (1), or separate from them (2) (they can be separate but abutting, however!)

2*. Position of antennal organ on antenna. The antennal organ is a cylindrical projection of unknown function found on one (exceptionally, on more than one) of the antennal segments. Present on distal segment of flagellum (1) or 3rd segment from apex (2) or on both the 4th and 7th segments from apex (3).

3. Number of antennal segments. The number of segments in the antennal flagellum varies systematically. The scape and pedicel (segments 1 and 2) are always present. Episactinae have 7 or 8 flagellar segments (1), *Erucius* and the Hispaniolan genera have 10 (2), Eumastacinae have 11-12 flagellar segments (3).

4. Form of fastigium: not projecting appreciably beyond vertex (0), little produced beyond vertex, in dorsal view wide, bluntly rounded (1); thin and elongated, sharply rounded at tip, projects well above or in front of vertex (2). State 1 is characteristic of most Episactinae, state 2 of the Hispaniolan genera.).

Thorax, wings and legs.

5. Winged (1) or apterous (2). Winged forms can be macropterous, brachypterous or micropterous.

6*. Median carina of pronotum absent (0), present and continuous (1), present but discontinuous (2).

7. Secondary lateral carinae of pronotum. Absent (0), present (1), weakly developed (2). Many Eumastacids have no lateral carinae of the pronotal disc, or only a rudiment at the posterior margin of the disc, but some have a secondary ridge, sometimes ornamented with tubercles, running obliquely from the upper posterior corner of the lateral lobe to its anterior ventral corner. This has been called a "secondary lateral carina" by previous authors (Rehn, Descamps).

8*. Dorsal margins of hind 1st tarsal segment armed with multiple spines: no (0), yes (1). All the families of the Cryptophalli are characterised by having multiple spines on the dorsal edges of the first hind tarsal segment. In *Homeomastax* the dorsal margins of the 1st hind tarsal segment terminate distally in spines, but the margin itself is unarmed.

9*. Tarsal spines (see 8.) slewed onto outer face of tarsus (1), or follow strictly the dorsal edge of the segment to its distal end (0). State 1 is an apomorphy of the Eruciinae. *Homeomastax* has no tarsal spines, so coded as (-) .

10. Dorsal carinae of legs 1 and 2 end in spines: no (0), yes (1), in one sex only (2).

11*. Dorsal carina of hind femur spined: no (0), yes (1). State 1 is an apomorphy of the Chorotypidae.

12*. Longest tibial spur. Eumastacids, like other grasshoppers, have four movable spurs at the distal extremity of the hind tibia, two internal and two external. In *Homeomastax* the largest spur is the third one, i.e., the more medial (closer to the long axis of the tibia) of the inner pair (1). In the other taxa it is the innermost spur of the inner pair, the fourth one (2).

13. Posterior margin of PN disc: produced backwards, rounded, even if sometimes narrowly notched at tip (0), or, truncate, broadly medially emarginate (1). State 0 is typical of winged forms, state 2 of the wingless Episactinae.

Abdomen.

14. Male subgenital plate membranous? In some Eumastacid taxa the distal sternite of the subgenital plate is completely sclerified (0), in others it is partially membranous (1).

15. Abdominal sternites with (1) or lacking (0) medial boss. In some Episactines the males have medial thickened bosses on the abdominal sterna, especially on segments 3 or 4. These may overlie glandular tissue, as they are often covered with dry powdery deposit. Their function is unknown.

16. Rim of male subgenital plate spinous (1) or not spinous (0). The rim of the subgenital plate in Episactines bears either numerous small teeth or a few large thornlike spines. In the other taxa there are no spines on the rim.

17*. Distal portion of male subgenital plate simple (1) or deeply trifid, with a triangular central lobe covering the genital apparatus and elaborate bifid lateral lobes (2). This latter condition is typical of the Eruciinae.

18. Male furcula absent (0), small (1) or large and well developed (2). The furcula is small in Episactines, larger in a few Hispaniolan genera, e.g., *Espagnola*, and very large indeed in the Eruciinae. *Homeomastax* has no furcula.

19. Ninth or 10th abdominal terga simple (0), or decorated with horns or projections (1).

Male genitalia.

20*. Epiphallus present, of normal form (1) or absent (0). State 0 is characteristic of the Chorotypidae.

21*. Male subgenital plate clearly separated into two sternites by a well-defined suture (1), or not clearly separated (2).

22*. Endophallic sacs large (1) or small (2). In the present sample, only *Homeomastax* (being a Stenophalline, and not a Cryptophalline), has a relatively large endophallic apparatus.

23. Position of male genital aperture? Dorsal (1), apical (2), dorsoapical (3). The spermatophore sac opens through the wall of the ectophallus. This aperture is mostly dorsal in the eumastacines, apical in the episactines, and dorso-apical in the Hispaniolan genera.

24. Subepiphallic sac? Absent (0), or present (1). This sac is common in the Eumastacines and in the Episactines, but is replaced by (probably transformed into) a sclerite (character 34) in the Hispaniolan genera.

25. Internal dorsal ectophallic sclerites absent (0), or present (1). These are defined as sclerites bordering the dorsal genital trough, usually entering a sclerite sac at their anterior end. (Note the coding (1) for *Neibamastax* involves an assumption about the homology of this structure in that taxon: see discussion in the text).

26. External dorsal ectophallic sclerites absent (0), present (1). These lie lateral to the internal dorsal ectophallic sclerites (#25), arise from near the posterior corners of the sclerite sac, and do not extend into it.

27*. Phallus normally proportioned (1) or laterally compressed (2) The modified condition is found only in *Espagnolopsis*.

28. Size of lophi: small (1), medium (2), large (3). As *Erucius* has no epiphallus, it also has no lophi, coded as (-). Most *Homeomastax* lophi are of moderate length, coded as 2.

29*. Orientation of lophi? Lophi horizontal (1) or vertically inflected (2). Only *Espagnoleta* has state 1.

30. Sensory plaques of lophi. Absent (0), external (1) or internal (2). In *Homeomastax* the plaques are mostly internal – coded as 2.

31. Nature of subepiphallic sclerite. Absent (0) simple (1), complex (2) or hypercomplex (3). (Note this coding 3 assumes that the *Neibamastax* forceps structure is a modified subepiphallic sclerite! Discussion in text).

32. Membrane of subepiphallic sclerite absent (0), normal (1) or hypertrophied (2).

33. Position of zone of fusion between L and R apical shields. None (0), dorsal and anterior (1), apically below genital aperture (2), or ventrally (3).

34. Form of processses of apical shields. A (0), short and outwardly inflected (1), long and straight (2) or short spines (3). *Homeomastax* coded as (?) Short processes of the lips of the apical groove (as in Episactines) are included here, as well as large dorsal or terminal processes as in Espagnolinae.

35. Lateral lobes of ectophallus absent (0), small (1) large and membranous (2), or large and sclerotized (3).

36. Ectophallus not extensible (0), somewhat extensible (1) or telescopic (2).

37. Endophallus gracile (1) or robust (2).

38. Shape of endophallic rods: straight or reflexed downwards (0), reflexed upwards 90° (1), or reflexed upwards and backwards 180° (2).

39. Shape of male cerci: simple, tapering, straight (1) incurved through 90° or less (2), recurved through 90-180° (3).

40. Apical lobe of spermatophore sac: absent (0), present (1), well developed (2).

41. Ectophallic lateral plate: absent (0), slightly developed (1), highly developed (2).

42. Lateroapical sclerite absent (0), present (1) duplicated (2).

43. Ventroapical sclerite absent (0), present (1), or armed (2).

44. Endophallic rods free at tips (0), or fused with other sclerite (1).

45*. Postepiphallic sclerite absent (0), present (1). In this sample, such a sclerite occurs only in *Lethus*.