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Authors: Rowell, C. H. F., and Bentos-Pereira, A.

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Helicomastax, a new genus of Central American eumastacid grasshoppers

C.H.F. Rowell and A. Bentos-Pereira

(CHFR) Zoologisches Institut der Universität Basel, Switzerland. E-mail: hrowell@datacomm.ch
(ABP) Facultad de Ciéncias, Entomología, Universidad de la República, Montevideo, Uruguay. E-mail: bentos@fcien.edu.uy

Abstract

Helicomastax n. gen. is externally almost identical with *Homeomastax* Descamps 1979, but has radically different genital structures. In the male the ectophallic sclerites give rise on their anterior medial surface to a pair of chitinous filaments. These enter the spermatophore sac dorsally, run in a circular course within the sac and emerge from its opening ventrally and posteriorly as two fine whip-like projections, which extend dorsally above the ectophallic sclerites. The complex of spermatophore sac, endophallic plate and ectophallic sclerites, forms a sclerotized capsule; the posterior extremities of the ectophallic plate are not inserted into the ectophallic membrane, as in other eumastacine genera, but are free and project to the exterior. The spermathecal duct of the female is longer and more convoluted than in other eumastacine genera, presumably in association with the filaments of the male, which are hypothesized to be inserted into the duct during copulation. The genus is represented by two new species (*H. mnioides* and *H. copensis*) from the mountains of Central and Western Panama. Both are sympatric with local species of *Homeomastax*.

Keywords

Grasshoppers, Eumastacidae, Eumastacinae, new species, Panama, genitalia, taxonomy

Introduction

In a companion paper (Rowell & Bentos-Pereira 2001, p. 209-254 in this issue) we reviewed *Homeomastax*, the only eumastacine genus previously recorded from Central America and the most northerly parts of the Pacific coast of South America; we described seven new species from Costa Rica and Panama.

Among our collections made in Panama were two other species, which we initially assumed to be further members of the genus *Homeomastax*. Examination of the male internal genitalia, however, disclosed radical differences, which seem to us to necessitate the erection of a new genus, even though the external differences are minimal.

Abbreviations of depositories

ANSP Academy of Natural Sciences, Philadelphia.
MNHNP Musée National d'Histoire Naturelle, Paris.
RC The first author's collection.
UP Museo de Invertebrados G.B. Fairchild, Universidad de Panamá, República de Panamá.

***Helicomastax* gen. nov.**

Type species.— *Helicomastax mnioides* Rowell and Bentos-Pereira, by original designation.

Etymology.— Greek *helix, helikos* (feminine), whorl or spiral, relating to the course of the ectophallic filaments in lateral view; Greek *mastax, mastacos* (feminine), jaw or mouth, conventionally used as a suffix in the generic names of eumastacid grasshoppers, deriving from the original (but invalid) genus name *Mastax* Perty 1834 and its replacement *Eumastax* Burr 1899, the type genus of the family.

Diagnosis.— Outwardly practically identical with *Homeomastax* Descamps 1979. Distinguished externally by pronotal characters (Fig. 1). Pronotum in dorsal view somewhat squarer than in *Homeomastax*, less constricted anteriorly. Disc of pronotum with four slight swellings, bounding the lateral sulcus; *Homeomastax* shows maximally two of these. Median carina stronger, lateral carinae of metazona of pronotum more pronounced than in *Homeomastax*, and bordered ventrally by a more pronounced black stripe (but this also occurs in *Homeomastax cerciata* Hebard, Fig. 1C). The posterior part of the disc of the metazona is suffused with dark color, absent in *Homeomastax*. In about half of all individuals the posterior or anterior margin of the pronotum is minutely notched in the midline (as in Fig. 1), which does not occur in *Homeomastax*. The maximum number of external and internal hind tibial spines (22) is smaller than in most species of *Homeomastax*; all other measurements and proportions fall within the range of *Homeomastax* (see Rowell & Bentos-Pereira 2001). In one species (*mnioides*), the red coloration of the distal femora, always present in adult *Homeomastax*, is often absent.

Male phallus (Figs 4, 6) with two long chitinous filaments which arise anteriorly from the ectophallic sclerites and enter the spermatophore sac. Within the sac they run first anteriorly, then ventrally, then curve posteriorly and emerge ventrally and posteriorly from the genital trough as free filaments; these extend dorsally beyond the posterior

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extremities of the ectophallic sclerites, ending in fine flexible points.

Female subgenital plate (Fig. 5B) trilobed, lobes of subequal length, the lateral lobes broad, the medial lobe pointed (but the female of only one species is known to date). Female with duct of the spermatophore (Fig. 5A) appreciably longer and more coiled than in *Homeomastax*, probably in functional association with the filaments of the male phallic apparatus. Ovipositor valves (Fig. 5C) with hooked pointed tips, outer edges prominently toothed, similar to *Homeomastax*, not differentiating the genus.

Description. — See Fig 2. Externally very similar to *Homeomastax* Descamps 1979, even including color pattern in the case of *H. copensis*. Slightly brachypterous, (E/F = 0.84-0.88); moderately sexual dimorphic in size (M/F = 0.8). Proximal parts of carinae of hind femur thickened and melanized, as in *Homeomastax*. Two pale postgenicular stripes on the hind femur. In one species (*H. mnioides*) the cryptic larval coloration is retained in the adult.

Male phallic structure (Figs 4, 6). The two known species have effectively identical male internal genitalia; the following description applies to both of them. The terminology used is explained fully in our paper on *Homeomastax* (Rowell & Bentos-Pereira 2001).

Epiphallus oblong to trapezoidal in dorsal view, tending to be narrower at anterior end; anterior margin with slightly flared wing-like corners. Medial area membranous. Lophi hooked, rather smaller than in the genus *Homeomastax*, sensory plaques present at their base. Subepiphallic sac present, simple, wide, not elaborated. Dorsal fold small, in *H. copensis* lightly sclerotized (Figs 6A, B). Sclerite sac present, thick walled. Anterior ends of ectophallic sclerites diverging; posterior ends of ectophallic sclerites rounded and projecting in lateral view, straight and narrow in dorsal view, slightly concave longitudinally on their inner surface; apical shields absent. Ventroapical evagination present, small, pointed, medial apodeme absent. Ejaculatory sac small, narrow.

Endophallic plate and spermatophore sac remarkable and highly modified. Anterior end of endophallic plate slender and pointed, but surrounded by a rounded flange of thin cuticle (Figs 4E, 6D). Arms of plate running ventromedially, narrow, closely appressed, forming a medial gutter which ends in twin processes at the end of the genital trough, immediately above the ventroapical evagination. Lateral walls of the spermatophore sac variously sclerified, including the formation of two struts which run upwards and posteriorly, diverging laterally, and fuse with the ectophallic sclerites about halfway along their length (Figs 4B, 6B). The whole complex of endophallic plate, spermatophore sac and ectophallic sclerites forms a lightly sclerified capsule. Dorsally, the spermatophore sac gives rise to two semicircular lobes, which extend upwards on either side of the sclerite sac to above the dorsal edge of the ectophallic sclerites. These sclerites give rise on their dorsal medial surface to two long filaments, which enter the lobes of the spermatophore sac, then in a circular course run first anteriorly and ventrally, then posteriorly along the medial gutter and emerge at the ventral margin of the genital trough. From here they continue externally, curving dorsally and anteriorly, ending in fine points well above the ectophallic sclerites.

Female genitalia: similar to those of *Homeomastax*, but the duct of the spermatophore much longer and more convoluted (Fig. 5A), presumably in association with the filaments of the male described above.

Distribution.— Known to date only from the mountains of Western and Central Panama (Fig. 7). Both species known to date are sympatric with or overlap the distribution of species of *Homeomastax*.

Key to species

— Femora and tibia of mid-and forelegs banded with dark brown; hind femora with or without red band distally; male cerci shorter than subgenital plate, only slightly inwardly curving, somewhat flattened and rounded at tip in side view; subgenital plate of male strongly compressed laterally (Bocas del Toro, Chiriquí)..... *H. mnioides* n. sp.

— Mid-and forelegs clear green, not banded with dark color; hind femora conspicuously ringed with red distally; male cerci as long as subgenital plate, pointed, abruptly curved inwards and almost meeting in midline, in side view angled downwards midway to tip; subgenital plate of male not compressed laterally (Coclé)..... *H. copensis* n. sp.

***Helicomastax mnioides* sp. nov**.

Holotype.— ♂: PANAMA: Prov. Bocas del Toro: Quebrada Felix, 2 km NW of summit of rd from Fortuna to Chiriquí Grande, 900 m, coords N9723500_E365800, 26-9-1997 (Rowell CHF, Bentos-Pereira A), specimen no. 97545 (ANSP).

Paratypes.— Data as holotype, but 3 ♀♀, specimen nos 97449 97544 97546 (ANSP). Data as holotype, but 19-9-1999, 1♀, specimen no. 99146; 3 ♂♂, specimen nos 99148 99533 99534 (ANSP).

Data as holotype, but 22-9-1999, 1 ♂, specimen no. 99200 (MNHNP). Data as holotype, but 1 ♀, specimen no. 97568 (MNHNP). Data as holotype, but 1 ♀, specimen no. 97567, 1 ♂, specimen no. 99532 (RC). Data as holotype, but 22-9-1999, 1 ♂, specimen no. 99203 (RC).

Prov. Bocas del Toro, 1-3 km beyond watershed on rd from Fortuna to Chiriquí Grande, 850-1035 m, approx. coords N973000_E366000, 18-9-1999 (Rowell CHF, Bentos-Pereira A), 1♀, specimen no. 99118 (RC).

Prov. Chiriquí: Fortuna: Centro de Investigaciones Jorge L. Arauz (IRHE), 1300 m, 23-9-1997 (Rowell CHF, Bentos-Pereira A), specimen no. 97434 (RC).

Provs. Chiriquí/Bocas del Toro: Fortuna, División continental, 1050 m, 10-4-1999 (Cambra R, Santos A), 1♂, 1♀, specimen nos 99546 99547 (UP).

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Etymology.— Greek *mnion*, moss, and *-oides*, similar to, alluding to the moss-like coloration.

Diagnosis.— Male cerci (Figs 3A, B) short and blunt, somewhat widened towards the tip in side view, only slightly inwardly flexed in dorsal view. Male subgenital plate rather short, laterally compressed, narrow in axial view with a small medial carina dorsally; dorsal margins markedly convex in lateral view. Female subgenital plate (Fig. 5B) trilobed, the lateral lobes wide, almost as long as the medial lobe, and with small spines on the posterior margins. Ovipositor valves (Fig. 5C) similar to those of *Homeomastax*, outer edge of upper valve provided with 8-9 teeth.

Epiphallus (Fig. 4C) as long as wide, posterior margin straight or slightly concave. Dorsal fold (Fig. 4E) of male phallus weakly developed, not sclerotized. Spermatophore sac (Fig. 4B) very large, disc shaped in lateral view, filling much of the cavity of the ectophallus.

Description.—Dimensions: see Table 1. Both sexes with 17-18 inner and 20 outer hind tibial spines. Markedly sexually dimorphic in size, M/F = 0.80, but there are few differences between the sexes in proportions. E/F = 0.84 (males), 0.85 (females). Males are noticeably more variable in size than are females: the ratio of standard deviation to mean is 2-3X larger in males. This large range of variation is not seen in males of *H. copensis*.

Coloration: differs markedly from the other species of the genus and those of *Homeomastax* in retaining in the adult the typical cryptic larval coloration. General color light olive green, with banding and speckling in dark olive brown. Antennal flagellum black, basal segments yellow green. Face yellow green, clypeus and labrum tinged blue. Wings and elytra dusky brown. All femora with 4-5 broken bands of dark olive brown, 3-4 similar bands on fore and mid tibiae. The male is somewhat more brightly colored; the pleura of the abdomen bear a lateral yellow stripe and the subgenital plate is bluish, both features reminiscent of *Homeomastax*; on fore and midlegs, and on the the tibiae and distal femur of the hind leg, the olive green is replaced by grey-blue. Females (see also Fig. 2) have the abdominal tergites mottled olive brown and olive green; the yellow lateral stripe is restricted to the pterothorax. The red color characteristic of the distal hind femur of *Homeomastax* and *Helicomastax copensis* is not present in all individuals of *H. mnioides*, and when present is restricted and dull. When the red band is absent it is replaced by light olive green in females, light blue-grey in males.

Natural history.— On ferns in wet montane forest, on both sides of the Atlantic/Pacific watershed. The older fronds of ferns in the habitat are frequently overgrown with algae and mosses, and the coloration is highly cryptic on this background. Sympatric with *Homeomastax kressi* (Rehn & Rehn 1934) at lower altitudes (800 m) on the Atlantic slope.

***Helicomastax copensis* sp. nov.**

Holotype.— ♂: PANAMA: Prov. Coclé: Cerro Copé, 830 m, 20-9-1997 (Rowell CHF, Bentos-Pereira A), specimen no. 97401 (ANSP).

Paratypes.— As holotype, but 15-9-1999, three ♂♂, specimen nos 99073, 99074 (ANSP), 99075 (RC).
Female unknown.

Etymology.— *copensis*, coming from Cerro Copé, the type locality.

Diagnosis.— Male cerci (Figs 3C, D) markedly different from those of the previous species: long, reaching approximately to posterior margin of the subgenital plate, robust basally, thereafter thin, gently tapering to a fine point; in dorsal view divergent basally but inwardly flexed at about midlength, forceps-like; in lateral view curved ventrally downwards towards the tip. Subgenital plate (Figs 3C, D) pointed and rather slender in lateral view, dorsal margin slightly convex, thickened; in dorsal view the tip is produced to a rounded point; in axial view not at all compressed laterally, shallowly notched (corresponding to the convexity of the dorsal margin), in some but not all individuals with a fine medial carina.

Epiphallus and subepiphallic sac as in the generic description. Dorsal fold of male phallus (Figs 6A, D) well developed, lightly sclerotized, simple, convex on its posterior margin. The complex of endophallic plate, ectophallic sclerites and spermatophore sac is yet more unified than in *H. mnioides* and sclerotised throughout, forming a capsule (Fig. 6B). The total size of the spermatophore sac complex is however smaller than in *mnioides*, and in lateral view occupies only the upper half of the cavity bounded by the ectophallic membrane. The floor of the sclerite sac and the confluent roof of the spermatophore sac form two flap-like projections (Fig. 6C), narrow in dorsal view, wide and bilobed in lateral view, that appear to act as valves separating the cavity of the anterior part of the spermatophore sac from that of the genital trough proper. Similar structures are present in *H. mnioides* and in some species of *Homeomastax*, but are not so well developed as in *H. copensis*.

Description.—Dimensions: see Table 1. Slightly longer winged than *H. mnioides*, E/F = 0.88 (males). Male with 20-22 inner and outer hind tibial spines.

Coloration: similar to that of *Homeomastax*, the larval coloration is not retained as in *H. mnioides*. General color green with blue head and yellow lateral abdominal stripe. Frons and genae whitish in dried specimens, vertex with a prominent black V, clypeus, labrum and palps blue. A well-marked blackish stripe immediately ventral to lateral carina of the metazone of the pronotum. Elytra and wings suffused blackish. The red area of the hind femur is not clear, but shadowed by proximal and distal darker rings. Cerci bluish at base, black apically.

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Table 1. Dimensions (mm) and morphometric ratios of *Helicomastax* spp.

	E	F	P	E/F	F/P	E/P	E	F	P	E/F	F/P	E/P	F male/ F female	P male/ P female
	Males						Females							
Helicomastax nmioides														
Minimum	8.56	11.31	1.87	0.76	5.64	4.53	11.61	13.68	2.34	0.8	5.35	4.47		
Maximum	10.31	11.99	2.11	0.9	6.17	5.17	12.86	15	2.6	0.89	6.15	5.29		
Average	9.79	11.6	1.99	0.84	5.85	4.93	12.24	14.47	2.47	0.85	5.86	4.96	0.8	0.8
s	0.54	0.26	0.08	0.04	0.17	0.22	0.44	0.51	0.09	0.02	0.24	0.24		
s/mean	1.06	1.04	1.02	1.02	1.02	1.04	0.04	0.04	0.03	0.03	0.04	0.05		
n	9	9	9	9	9	9	10	10	10	10	10	10		
Helicomastax copensis														
Minimum	9.32	10.96	1.89	0.85	5.39	4.71								
Maximum	10.31	11.43	2.09	0.9	5.8	5.13								
Average	9.84	11.23	2.01	0.88	5.61	4.91			(No females)				?	?
s	0.47	0.2	0.08	0.03	0.18	0.17								
s/mean	0.05	0.02	0.04	0.03	0.03	0.04								
n	4	4	4	4	4	4								

E = length of elytron; F = length of hind femur; P = length of pronotum.

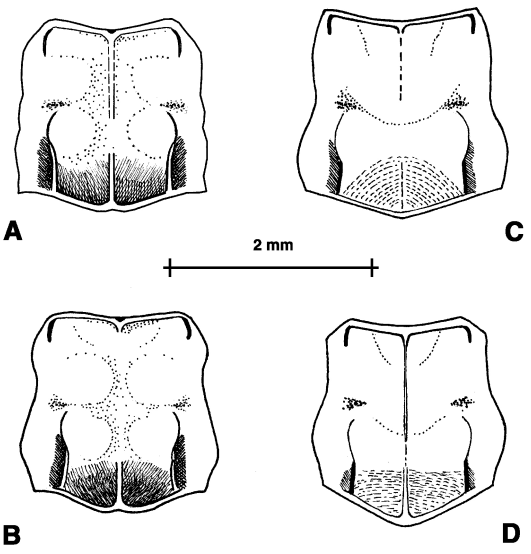


Fig. 1. Pronota of *Helicomastax* (A, B) and *Homeomastax* (C, D). **A**. *H. mnioides* n. sp. **B**. *H. copensis* n. sp. **C**. *H. cerciata* Hebard 1923. **D**. *H. brachyptera* Rowell & Bentos-Pereira 2001.

Natural history.— On ferns in montane forest, on both sides of the Atlantic/Pacific watershed. Sympatric with *Homeomastax brachyptera* Rowell & Bentos-Pereira, but much less common than that species. We noted no obvious ecological separation between the two.

Discussion

It is obviously undesirable in general to create genera which are defined solely on criteria requiring dissection. In the case of *Helicomastax* we offer slight differences in the shape of the pronotum as external characters discriminating the genus from *Homeomastax*, but if further collecting produces more species of the new genus, it may well transpire that these are not totally reliable. Even if this were to be the case, however, we feel that separate generic status is unavoidable, given the profound differences in genital morphology. Our situation is not unique: there are precedents for the creation of purely genitalic genera within the Caelifera. Examples are *Chloropseustes*/*Callistacris* and *Ophthalmolampis*/*Adrolampis* (Descamps 1977), *Abracris*/*Omalotettix* (Carbonell *et al.* 1980), the complex of genera formerly subsumed under *Catantops* (Jago 1984) and *Oxyaeida*/*Neritius* (Jago 1994).

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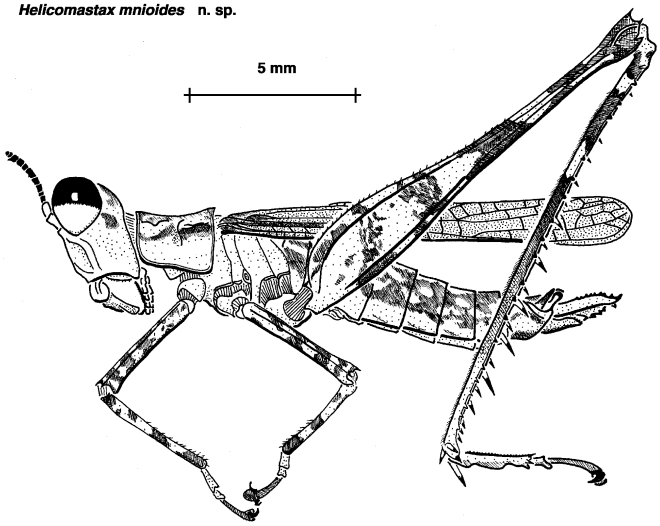


Fig. 2. *Helicomastax mnioides* n. sp., adult female, habitus.

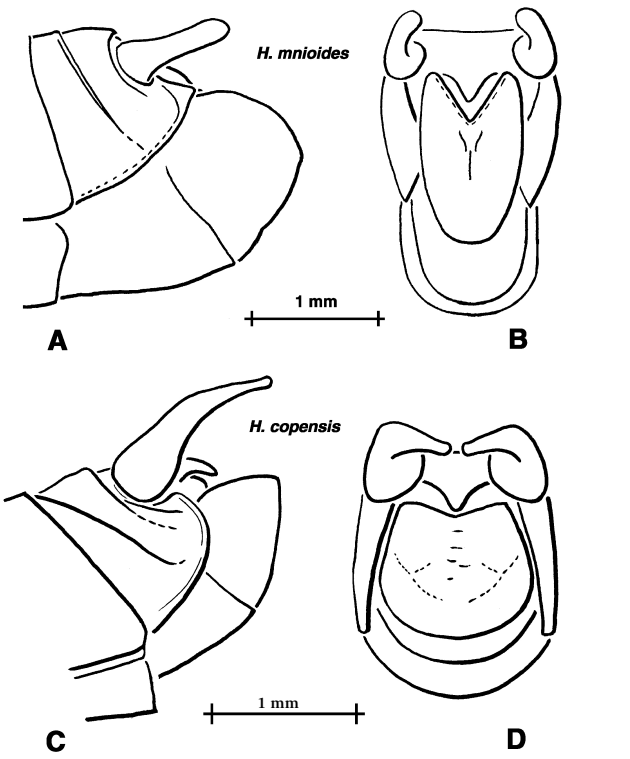


Fig. 3. *Helicomastax*, male external genitalia. **A.** *H. mnioides* n. sp., lateral view; **B.** axial view. **C.** *H. copensis* n. sp., lateral view; **D**. axial view.

One can only speculate on the circumstances which could allow such profound divergence in genitalia and such stasis in external morphology. The currently known range of *Helicomastax* is confined to Western and Central Panama. This is a very recent area geologically (about 3 million years old). If *Helicomastax* has differentiated from *Homeomastax* (the only related genus in the area at present) since the colonization of the new land by grasshoppers, genital evolution has been extremely swift. However, it is perhaps at least equally probable that the two genera were already present in South America prior to the formation of the isthmus, and some support for this would be afforded if *Helicomastax* were to be found there. Unfortunately, it is currently impossible to collect in Colombia.

It is of interest that whereas the numerous species of *Homeomastax* are rarely if ever sympatric, both known species of *Helicomastax* overlap spatially with a *Homeomastax* species. This suggests an ecological separation between the two genera, which, however, we have not been able to observe.

The spiral filaments of *Helicomastax* are unique within the Eumastacidae, but recall the extravagant processes found in the male genitalia of other eumastacoid taxa (especially the African Thericleidae — see Descamps (1973) for a review); these, however, are anatomically of different origin. A functional study of how such structures are deployed in copulation would be of great interest. Presumably they are inserted into the spermathecal duct of the female, as in other insects (see *e.g.*, Eberhardt 1985, Rodriguez 1995). The only other analogous examples within the Caelifera known to the authors are some taxa of Proctolabinae (*e.g.*, *Balachowskyacris*), where the ventral sclerites of the aedeagus are produced into long wire-like filaments.

Assuming that the *Helicomastax* phallus is derived from something similar to that of *Homeomastax* and other eumastacine genera, it is possible to reconstruct what has happened structurally in the course of evolution. It is clear that the junction of the arms of the endophallic plate with the apical shields (local sclerotizations of the ectophallic membrane) has been dissolved, and that the apical shields themselves have disappeared. The arms of the endophallic plate move ventrally with respect to their original position, and become more closely appressed medially, forming a chitinous gutter defining the ventral margin of the spermatophore sac. The lateral walls of the spermatophore sac are secondarily sclerotized to a variable extent, dorsally forming two well-marked struts which run upwards, diverging laterally, to fuse with the ectophallic sclerites. The filaments are thus contained entirely within the spermatophore sac, entering it dorsally, running along the medial gutter and emerging from the opening of the floor of the genital trough. These filaments appear to be extensions of the ectophallic sclerites. However, they arise medially from a point on the sclerite where laterally the endophallic plate fuses with it. It is therefore conceivable that the filaments are in fact derived from the endophallic plate; detailed developmental study would be necessary to resolve these alternatives. The distinction may however be trivial, as all the sclerotizations of the eumastacine phallus (other than the epiphallus and those associated with the ventroapical evagination, the floor of the ectophallic membrane or the dorsal fold), may be regarded as sclerotizations of the wall of the spermatophore sac in its wider sense. The distinction into endo- and ectophallic sclerites is currently simply one of convenience for taxonomists, not one reflecting developmental history.

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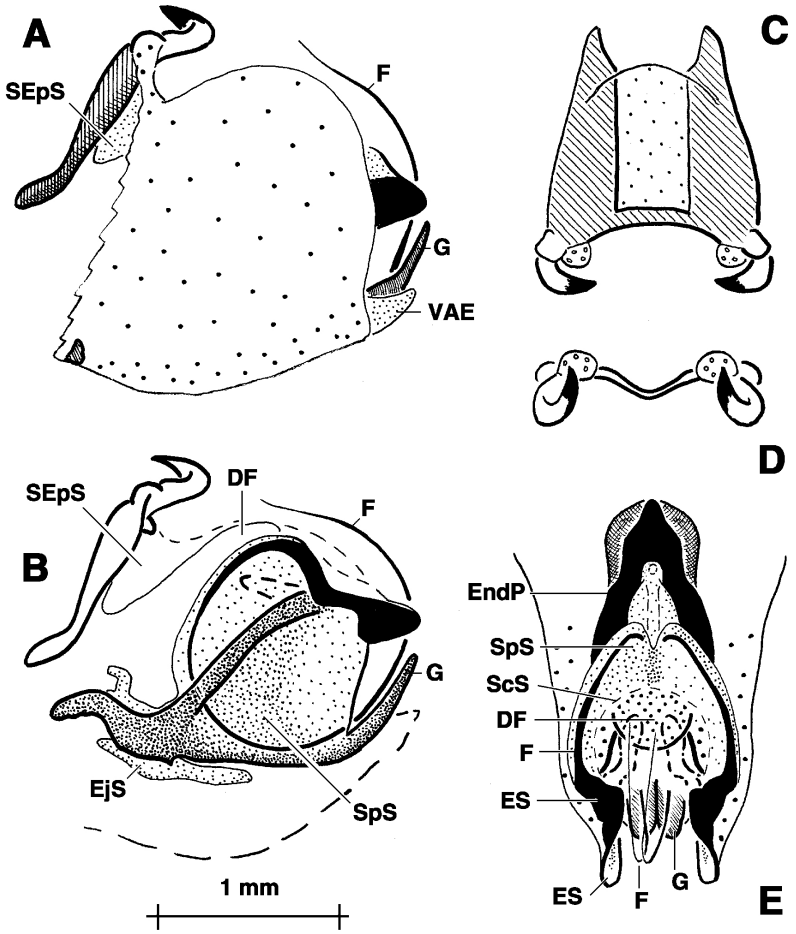


Fig. 4. *Helicomastax mnioides* n. sp., male internal genitalia. **A.** Phallic complex including epiphallus in side view. **B.** As A, but ectophallic membrane removed from right hand side to show subepiphallic sac and spermatophore sac/endophallic plate complex. **C.** Epiphallus, dorsal view. **D.** Epiphallus, axial view. **E.** Phallic complex with epiphallus retracted, dorsal view, semidiagrammatic. The ectophallic membrane is not shown dorsally, other than the dorsal fold. The complex is represented with the genital trough spread open, to show the included structures. Abbreviations: DF, dorsal fold; EndP, endophallic plate; ES, ectophallic sclerites; F, filaments; G, gutter; ScS, sclerite sac; SEpS, subepiphallic sac; SpS, spermatophore sac; VAE, ventroapical evagination.

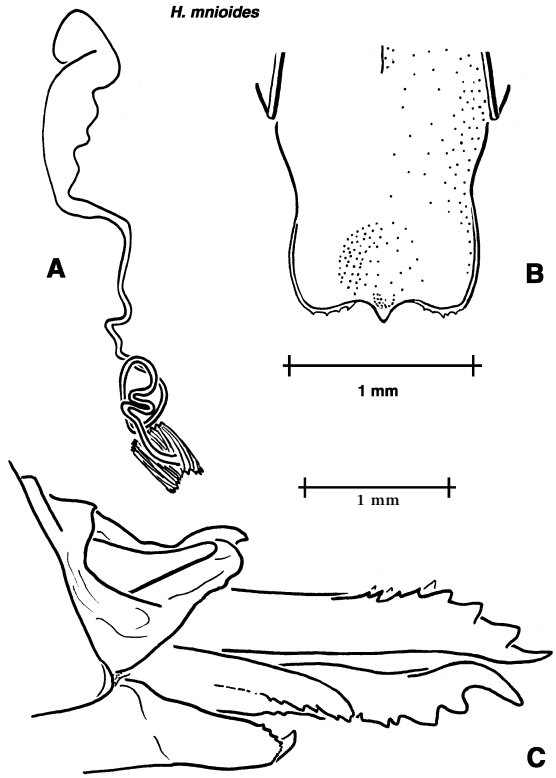


Fig. 5. *Helicomastax mnioides* n. sp., female genitalia. **A.** Spermatheca. **B.** Subgenital plate, ventral view. **C.** Ovipositor and cerci, lateral view. The upper scale bar refers to A & B.

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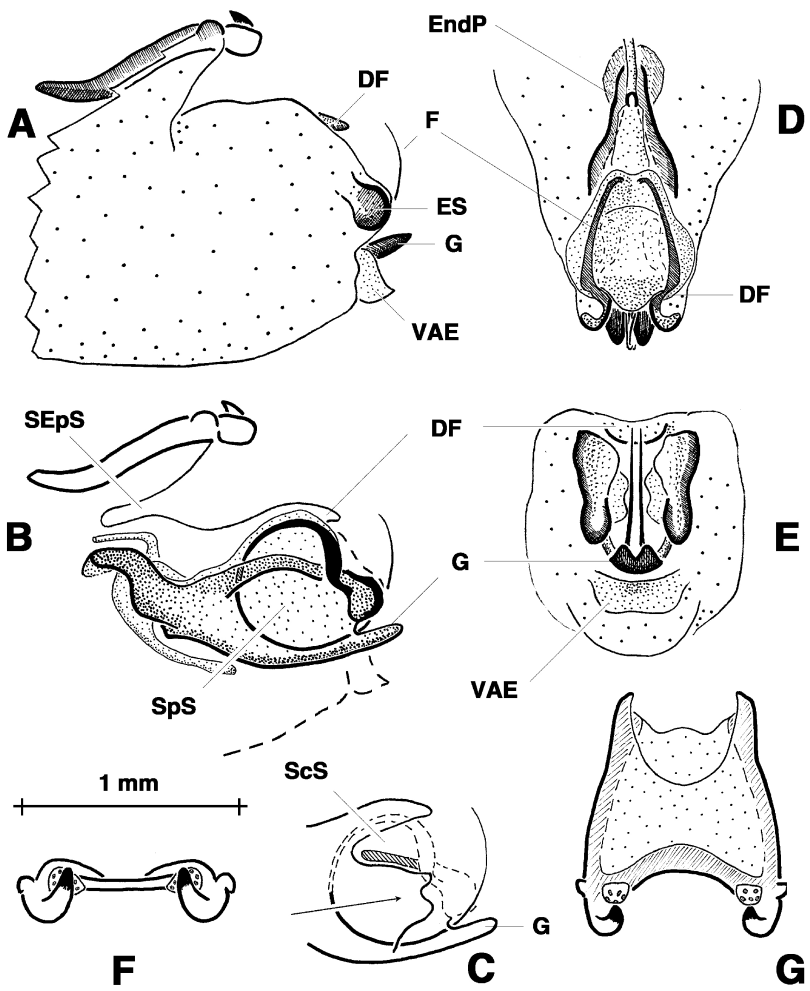


Fig. 6. *Helicomastax copensis* n. sp., male internal genitalia. **A.** Phallic complex including epiphallus in side view. **B.** As A, but ectophallic membrane removed from right hand side to show subepiphallic sac and spermatophore sac/endophallic plate complex. **C.** As B, but parasagittal section nearer midline, to show sclerite sac and membranous lobes (arrow) formed at junction of sclerite sac and spermatophore sac. **D.** Phallic complex with epiphallus retracted, dorsal view. **E.** Phallic complex without epiphallus, axial view. **F.** Epiphallus, axial view. **G.** Epiphallus, dorsal view.
Abbreviations: DF, dorsal fold; EndP, endophallic plate; ES, ectophallic sclerites; F, filaments; G, gutter; ScS, sclerite sac; SEpS, subepiphallic sac; SpS, spermatophore sac; VAE, ventroapical evagination.

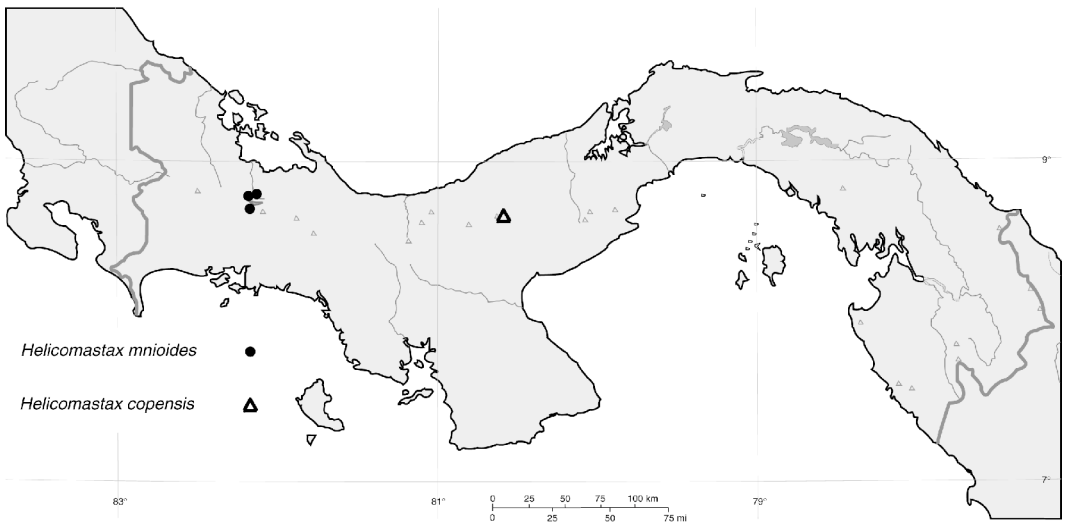


Fig. 7. Distribution map of *Helicomastax* spp.

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