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Kaindipsocinae are the sister taxon of the rest of Psocidae (Insecta: Psocodea: 'Psocoptera')

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Abstract. The systematic status of Kaindipsocinae (formerly Kaindipsocini) is revised based on morphology of the male terminalia and on molecular data. *Clematostigma*, *Lasiopsocus*, and *Tanystigma* are newly assigned to this subfamily. The *Blaste lunulata* species group is also placed within Kaindipsocinae and is probably closest to *Kaindipsocus*. Both morphological and molecular data provide strong support for monophyly of Kaindipsocinae and molecular data support a sister relationship between this subfamily and the rest of Psocidae.

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Introduction

The family Psocidae is the most diverse family of the free-living members of Psocodea ("Psocoptera") (Lienhard & Smithers, 2002). Many different higher-level classification schemes have been proposed for this diverse family (see Yoshizawa & Johnson, 2008 for review), but the classification proposed by Mockford (1993) is now generally accepted (Lienhard & Smithers, 2002; Yoshizawa & Johnson, 2008). Differing from the earlier classifications, which placed greater importance on homoplastic wing vein characters, Mockford's system emphasized more phylogenetically relevant characters, such as male genitalic structures. However, Mockford's system was established based mainly on the Nearctic species and many genera from other regions were not assigned to subfamily or tribe at that time. Later, all unclassified genera of Psocidae were assigned to the subfamilies and tribes of Mockford's system (Lienhard & Smithers, 2002; Mockford, *in litt.* 2001).

One such genus is the *Kaindipsocus* Smithers & Thornton, 1981. This genus was originally assigned to the subfamily Psocinae and its affinity with Amphigerontiinae was explicitly rejected (Smithers & Thornton, 1981). New (in New & Lienhard, 2007) accepted this taxonomic treatment and assigned the genus to the tribe Ptyctini of Psocinae. Previously, however, Lienhard & Smithers (2002) had assigned *Kaindipsocus* to the subfamily Amphigerontiinae without mentioning the basis for this placement. Later, the placement of *Kaindipsocus* in Amphigerontiinae was confirmed morphologically (Lienhard, 2008) and, based on molecular phylogenetic analyses, a unique tribal status within Amphigerontiinae was given to the genus (Yoshizawa & Johnson, 2008).

Problems remain with the systematic placement of Kaindipsocini, however. First, although the placement was not rejected statistically, results from the molecular phylogeny suggested that the tribe does not form a monophyletic group with the rest of Amphigerontiinae (Yoshizawa & Johnson, 2008). Kaindipsocini may represent the most basal divergence event within Psocidae. Thus, the tribe occupies a very important systematic position in understanding the origin, evolution, and biogeography of the family Psocidae. Second, although the tribe is currently represented by a single genus, additional genera may also belong to this tribe. *Kaindipsocus* has its center of diversity in the Australian region (Lienhard, 2008), and the higher level classification of psocid genera of this region is poorly established. For example, the genus *Lasiopsocus* Enderlein, 1907 of the subfamily Amphigerontiinae is nearly endemic to

Australia, but its placement within the subfamily has not been tested (Li, 2002; Yoshizawa & Johnson, 2008). The genera *Clematostigma* Enderlein, 1906 and *Tanystigma* Smithers, 1983 are nearly endemic to the Australian region, as well. Both genera are now only tentatively assigned to the tribe Ptyctini of the subfamily Psocinae, without a detailed examination of their morphological characters (Lienhard & Smithers, 2002: "Assigned to Ptyctini (for present): Mockford, *in litt.* 2001"). Given their unique distributional pattern, these three genera may share a close affinity with Kaindipsocini.

In this study, we estimate the systematic placements of these Australian psocids based on a highly informative character system, morphology of the male terminalia. We also evaluate the systematic placement of these Australian psocids with molecular data in a combined analysis of nuclear 18S rDNA, Histone 3 and Wingless and mitochondrial 12S rDNA, 16S rDNA and COI.

Materials and Methods

Taxa examined are listed in Appendix 1. Specimens stored in either 80% or 99% ethanol were used. For specimens stored in 80% ethanol, the abdomen was removed and soaked in 10% KOH at room temperature for one night before morphological observation. For those stored in 99% ethanol, the abdomen was placed in Proteinase K solution from a Qiagen DNeasy Tissue Kit for both DNA extraction and to clear the tissues for morphological observation. See Yoshizawa & Johnson (2008) for further procedures for preparation of DNA data and Yoshizawa (2005) for methods of morphological observation, illustration, and terminology.

We performed maximum parsimony (MP) and maximum likelihood (ML) analyses using the portable version of PAUP* 4b10 (Swofford, 2002) and Bayesian MCMC using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). For MP analysis, all data were weighted equally, and TBR branch swapping was performed with 100 random-addition replicates. For ML analyses, TBR branch swapping was performed using the equally parsimonious trees obtained from the MP analysis as starting trees. Parameters for ML analysis were estimated using Modeltest 3.7 (Posada & Crandall, 1998) on the basis of Akaike information criterion (Akaike, 1974). As a result of Modeltest, the GTR+I+G model was selected (unequal base frequencies: A = 0.3232, C = 0.1529, G = 0.1826, T = 0.3413; six substitution categories: A-C = 1.4006, A-G =

4.9710, A-T = 2.9758, C-G = 1.3901, C-T = 8.3099, G-T = 1; gamma distributions shape parameter = 0.5856 based on four rate categories; proportion of invariant sites = 0.5478). Bootstrap support was calculated using 100 replicates with TBR branch swapping, but TBR rearrangement was limited to 3,000 for ML bootstrapping because full TBR rearrangements were unacceptably time consuming. We also applied a constraint strategy to expand tree search space (Yoshizawa & Johnson, 2008). Modeltest-estimated parameters were also adopted for ML bootstrapping. The confidence in monophyly of Amphigerontiinae was also tested using the approximately unbiased test (AU test: Shimodaira, 2002) using CONSEL 0.1h (Shimodaira & Hasegawa, 2001). For Bayesian analyses, we performed two runs each with four chains for 2,000,000 generations, and trees were sampled every 1000 generations. The first 200 trees were excluded as burnin, and we compared a 50% majority consensus tree of the remaining trees to estimate posterior probabilities of branches in the tree.

Result

Morphology of the male terminalia

"Blaste" lunulata species group

Eighth sternum (Fig. 1B) with weak but broad sclerotization fused to hypandrium posteriorly. Posterodorsal margin of clunium (Figs 1B, 2B) weakly extended posteriorly, with epiproct articulated at posterior margin; posterolateral margin without extension (Fig. 1B). Epiproct (Figs 1B, 3A) with well-developed single lobe extended from anterior margin. Hypandrium (Fig. 1B) fused to clunium laterally, rounded posteriorly, with pair of lateral, incurved, posteriorly projecting processes. Phallosome (Fig. 4B) open posteriorly; phallobase V-shaped, with elongated anterior apodeme, and sometimes with long sclerotized rods laterally arising from base of anterior apodeme and extended posteriorly (erroneously interpreted as "outer paramere" by New, 1974, Smithers, 1984 and Schmidt & Thornton, 1993); paramere ("inner paramere" of the above authors) articulated with phallobase anteriorly, almost straight, and pointed apically.

Kaindipsocus

See Lienhard (2008) for illustrations. Eighth sternum with weak but broad sclerotization

fused to hypandrium posteriorly. Posterodorsal margin of clunium weakly extended posteriorly with epiproct articulated at posterior margin; posterolateral margin without extension. Epiproct with well developed single lobe arising from anterior margin. Hypandrium fused to clunium laterally. Phallosome open posteriorly. Phallobase V- or U-shaped, with short anterior apodeme, paramere articulated with phallobase, strongly curved outwardly, pointed apically.

Tanystigma

Eighth sternum (Fig. 1CD) without sclerotization. Posterodorsal margin of clunium (Figs 1CD, 2CD) with weak extension, with epiproct articulated at posterior margin; posterolateral margin with (Fig. 1D) or without (Fig. 1C) posterior extension. Epiproct (Fig. 3BC) with pair of well developed lobes anterolaterally, their anterior surfaces membranous, and with less- to well-developed sclerotized lobe medially. Hypandrium (Fig. 1CD) articulated with clunium. Phallosome (Fig. 4CD) open posteriorly; phallobase V- or U-shaped, without conspicuous anterior apodeme; paramere articulated with phallobase, almost straight or slightly curved outwardly, and pointed or bifurcated apically.

Lasiopsocus

Eighth sternum (Fig. 1E) with weak sclerotization fused to hypandrium posteriorly. Posterodorsal margin of clunium (Figs 1E, 2E) with flap-like extension strongly extended posteriorly, with epiproct articulated at posterior margin; posterolateral margin with strong posterior extension (Fig. 1E). Epiproct (Fig. 3D) with pair of well-developed lobes anterolaterally, their anterior surfaces membranous. Hypandrium (Fig. 1E) articulated with clunium. Phallosome (Fig. 4E) open posteriorly; phallobase V-shaped, with short anterior apodeme; paramere articulated with phallobase, short, directed outwardly and bifurcated apically.

Clematostigma

Eighth sternum (Fig. 1F) with weak but broad sclerotization, fused to hypandrium posteriorly and to clunium laterally. Posterodorsal margin of clunium (Figs 1F, 2F) with flap-like extension strongly extended posteriorly, with epiproct articulated at posterior margin; posterolateral margin (Fig. 1F) with strong posterior extension. Epiproct (Fig. 3E) with pair of

well-developed lobes anterolaterally, their anterior surfaces membranous. Hypandrium (Fig. 1F) articulated with clunium. Phallosome (Fig. 4F) closed posteriorly; phallobase U-shaped, without conspicuous anterior apodeme; paramere articulated with phallobase, very long, curved, and bifurcated apically.

Molecular phylogeny

The MP, ML, and Bayesian trees recovered from the present analyses were highly congruent with each other (available online) and with the trees estimated previously (Yoshizawa & Johnson, 2008). Fig. 5 shows the ML tree with branch support values obtained from bootstrapping (BP: MP and ML) and Bayesian MCMC (PP). Here, we primarily discuss the position of taxa added to the analyses of the previous study (Yoshizawa & Johnson, 2008).

Representatives of the "*Blaste*" *lunulata* group, *Kaindipsocus*, *Tanystigma* and *Clematostigma* composed a clade with weak to strong statistical support (100% PP, 35% ML-BP and 62% MP-BP). The support value for this clade from the ML analysis was extremely low in comparison to those from the MP and Bayesian analyses, but this is likely due to missing data in a sample and the tree searching strategy. The ML analysis is very time consuming, and a NJ tree is employed here as a starting tree for each bootstrap replicate. Also, 100 replicates of full TBR was too time consuming and thus a rearrangement limit of 3000 was used for each bootstrap replicate. Such limited searching strategies worked well for the relatively complete data set (Yoshizawa & Johnson, 2008). However, a newly added taxon, *Tanystigma* sp. 2, included only 2 of the 6 genes used in phylogenetic analysis (see Appendix 2), and there are no data for comparing this sample and *Atlantopsocus personatus*, *Oreopsocus buholzeri*, *Kaindipsocus* sp. KY379 and *Clematostigma* sp. KY418 (see Appendix 2 and Yoshizawa & Johnson, 2008). Therefore, placement of this sample within the initial NJ tree could not be calculated correctly, which had the effect of destabilizing the ML bootstrap analysis. By excluding this sample from the ML bootstrapping, monophyly of *lunulata* group + *Kaindipsocus* + *Tanystigma* + *Clematostigma* received very strong ML-BP support (91%). Exclusion of *Tanystigma* sp. 2 also improved support values for *Kaindipsocus* + *lunulata* group (43 -> 51% ML-BP) and *Clematostigma* + *Tanystigma* (39 -> 99% ML-BP). The *lunulata* group + *Kaindipsocus* + *Tanystigma* + *Clematostigma* clade was sister to the remainder of the family Psocidae, and monophyly of the remainder of Psocidae received strong

support from the Bayesian analysis (100% PP) but was weakly supported by MP and ML analyses (<50% BP). Monophyly of Amphigerontiinae including Kaindipsocini was never recovered, but results from the AU test did not reject the possibility (P=0.108 by full data set and 0.154 by excluding *Tanystigma* sp. 2).

Within the *lunulata* group + *Kaindipsocus* + *Tanystigma* + *Clematostigma* clade, *Tanystigma* and *Clematostigma* composed a clade with strong statistical support (93% MP-BP, 39% full ML-BP, 99% ML-BP ex. *Tanystigma* sp. 2, 100% PP). ML and Bayesian trees both supported monophyly of "*Blaste*" *lunulata* group + *Kaindipsocus*, but statistical support was weak (at most 54% BP and 78% PP).

Discussion

The molecular phylogeny strongly supports the clade composed of the "*Blaste*" *lunulata* group, *Kaindipsocus*, *Tanystigma* and *Clematostigma* (termed Kaindipsocini *sensu* Yoshizawa & Johnson, 2008 in the following discussion). This clade is further divided into two subclades: *lunulata* group + *Kaindipsocus* and *Tanystigma* + *Clematostigma*. Although a morphology-based cladistic analysis was not performed, the molecular tree and past morphological analyses (Lienhard, 2008; Yoshizawa, 2002, 2005; Yoshizawa & Johnson, 2008) allow us to evaluate morphological apomorphies supporting this result.

The Kaindipsocini are characterized by the following features: 1) posterodorsal margin of clunium with posterior extension at which epiproct is articulated (Figs 1B-F, 2B-F); 2) male epiproct with well developed lobes anteriorly (Fig. 3); 3) parameres articulated with the phallobase (Fig. 4B-F). The state of Character 1 apparently represents a derived condition, as it is unique to Kaindipsocini among the Psocetae (= infraorder including Psocidae). A similar posterodorsal extension of the clunium is also observed in some Psocidae including all members of Psocini, Atrichadenotecnini, Metylophorini, and Thyrsophorini, some species of *Indiopsocus* and *Trichadenotecnum* of Ptyctini, and *Glossoblaste amamiensis* of Amphigerontiinae (Figs 1A, 2A). However, in all these latter cases, the clunial extension always extends over the epiproct (Fig. 2A) and thus these structures are not directly articulated with each other, which clearly differs from the clunial extensions of Kaindipsocini. Therefore, character 1 provides unambiguous morphological support for the monophyly of Kaindipsocini. The state of Character 2 is also considered to be apomorphic (e.g., Mockford, 1993), but

similar conditions evolved many times independently and several reversals are also evident (Yoshizawa & Lienhard, 2004). In addition, the shape of the epiproct lobe is significantly different between two subclades of *Kaindipsocini* (Fig. 3A vs. B-E). Therefore, character 2 provides only ancillary support for *Kaindipsocini*. Character state 3 probably represents a plesiomorphy (see below).

The "*Blaste*" *lunulata* group and *Kaindipsocus* share an apomorphy: the single tongue-shaped epiproct lobe strongly extended dorsally (Figs 1B, 2B, 3A: Lienhard, 2008). The hypandrium of this group is fused to the clunium (Fig. 1B). The presence of clunial-hypandrial articulation is likely the ground plan condition for Psocidae (Fig. 1A, C-F: Yoshizawa, 2002), and a similar condition is also widely observed in Myopsocidae (Lienhard, 2004; Yoshizawa, personal observation). Therefore, the clunial-hypandrial fusion of the *lunulata* group and *Kaindipsocus* can be regarded as a synapomorphy. In addition to the male terminal characters, these two groups share an apomorphic character of stalked-eyes (Smithers & Thornton, 1981; Smithers, 1984; Schmidt & Thornton, 1993; Lienhard, 2008; Bess & Yoshizawa, present observation)

Monophyly of *Tanystigma* + *Clematostigma* is supported strongly by molecular data. *Lasiopsocus*, which was not included in the molecular analysis, shares a morphological apomorphy with these two genera: the epiproct with a pair of anterolateral lobes with their anterior surfaces membranous (Fig. 3B-E). *Lasiopsocus* also shares the above-mentioned morphological apomorphies of *Kaindipsocini*. Similar paired epiproct lobes are also observed in some species of *Trichadenotecnum* but, in all cases, the paired lobes are well sclerotized and are developed as accessory lobes of the main epiproct lobe (e.g., *T. auritum* Yoshizawa & Lienhard, 2004 and *T. barrerai* Yoshizawa, García-Aldrete & Mockford, 2008). *Trichadenotecnum* is also phylogenetically distant from *Kaindipsocini* (Fig. 5), and the lack of homology of these features is obvious. Therefore, the paired and well-developed epiproct lobe is a prominent autapomorphy of the *Tanystigma* + *Lasiopsocus* + *Clematostigma* subclade.

Within this subclade, the following morphological features support the close relationship of *Lasiopsocus* and *Clematostigma*: 1) posterodorsal extension of the clunium well developed (Figs 1EF, 2EF); 2) posterolateral margin of the clunium with posterior extension (Fig. 1EF); 3) paramere bifurcated apically (Fig. 3EF). Among them, Characters 2 and 3 are very prominent and apparently autapomorphic character states. However, these states are also

observed in at least one species of *Tanystigma* (e.g., *T. latimentula* examined here: Fig. 1D for the clunial extension; Fig. 4D for the bifurcated paramere). The genus *Tanystigma* is characterized by the shallow pterostigma in the forewing, but such a wing venational character is also observed in other genera of Psocidae (e.g., *Camelopsocus* of Ptyctini). Therefore, *Tanystigma* is possibly paraphyletic. Character 1 is a quantitative character that requires careful observation, but the difference in this character between *Tanystigma* and *Lasiopsocus* + *Clematostigma* is obvious (Fig. 2CD vs. EF). Therefore, Character 1 provides additional support for the latter clade.

The above mentioned relationships are supported by molecular data and male morphological characters, and females might be difficult to assign to this subfamily morphologically. However, all genera assigned to Kaindipsocini have previously been defined based on both sexes (e.g., Smithers, 1983) which will help to allocate females to this subfamily. "*Blaste*" *lunulata* group can be characterized by the stalked eyes in both sexes.

The most important finding of the present analyses concerns the sister relationship of Kaindipsocini with the remainder of Psocidae. Based on the detailed analysis of a species of *Kaindipsocus*, Lienhard (2008) concluded that the genus belongs to the subfamily Amphigerontiinae. The broadly sclerotized 8th sternum was considered to be the most important synapomorphy between *Kaindipsocus* and other genera of Amphigerontiinae. However, *Tanystigma* lacks sclerotization on the 8th sternum (Fig. 1CD), and sclerotization on the 8th sternum of the *lunulata* group and other genera of Kaindipsocini is much less developed compared to other Amphigerontiinae. For example, lateral margins of the 8th sternum always overlap the clunium in other Amphigerontiinae (Yoshizawa, 2010: Fig. 1A). This condition was never observed in Kaindipsocini (Fig. 1B-F) including *K. splendidus* Lienhard, 2008, on which interpretation by Lienhard (2008) was based. The 8th sternum functions as an attachment of the retractor muscles of the phallosome (Badonnel, 1934) and sclerotization of the 8th sternum has evolved many times independently in Psocidae, probably associated with function of the phallosome. For example, a broadly sclerotized 8th sternum fused to the hypandrium posteriorly evolved at least three times independently within a single genus, *Trichadenotecnum* (Yoshizawa et al., 2008). Therefore, this character state only provides weak evidence for Kaindipsocini + other Amphigerontiinae. Lienhard (2008) also pointed out the posteriorly open phallosome as an additional shared character between *Kaindipsocus* and other genera of

Amphigerontiinae. However, the phallosome of *Clematostigma* is closed posteriorly (Fig. 4F), which indicates that this character state is inconsistent within Kaindipsocini. Molecular data fail to support monophyly of Kaindipsocini + other Amphigerontiinae. Monophyly of Amphigerontiinae including Kaindipsocini was not rejected by the AU test. However, a sister relationship between Kaindipsocini and the remainder of Psocidae received very strong support in Bayesian analysis (100% PP), that is robust within a variety of taxon sampling schemes (Yoshizawa & Johnson, 2008). Therefore, we conclude that subfamilial status (i.e. Kaindipsocinae) should be given to this group to clarify its significant morphological differences from the other Amphigerontiinae, and also to indicate its distinctiveness from the rest of Psocidae.

Is there any morphological evidence supporting this basal split between Kaindipsocinae and the rest of Psocidae? This is a very difficult question to answer, and more extensive and detailed morphological analysis is needed. However, the phallosomal character (Fig. 4: listed as Character 3 of Kaindipsocini above) may provide support for this divergence. In all species of Kaindipsocinae, the parameres are articulated basally with the phallobase (Fig. 4B-F). This represents the ground plan condition of Psocodea (Yoshizawa & Johnson, 2006). In the rest of Psocidae, the parameres are either fused to the phallobase (Fig. 1A) or absent (Yoshizawa, 2003, 2005, 2010) which suggests that the articulated condition as observed in Kaindipsocinae represents a plesiomorphy and thus supports their exclusion from the rest of Psocidae. However, interpretation of this character state is not straightforward, because the parameres of many psocomorphan families are fused to the phallobase (Yoshizawa, 2005). The infraorder Epipsocetae often is placed as sister to Psocetae in molecular phylogenies (Johnson et al., 2004; Yoshizawa & Johnson, 2010), and movable parameres are retained in some groups of Epipsocetae (Casasola-González & García-Aldrete, 2002; Yoshizawa personal observation). However, the phylogenetic placement of Psocetae is far from stable. Further detailed study of Psocidae and the establishment of a stable higher level classification of Psocomorpha are critical to understanding the origin and diversification of the family.

In conclusion, based on the present morphological and molecular analyses, the classification scheme as shown in Table 1 and Fig. 5 is proposed here for the family Psocidae. It is evident from the present study that an independent genus should be established for the "*Blaste*" *lunulata* group. However, we postpone this action for two reasons. First, we only

examined a single undescribed species of the group in this study. Second, judging from the literature, other Australian "*Blaste*" are also quite distinctive from the "typical" members of the genus (e.g., New, 1974; Smithers, 1984), and an official nomenclatural act should also consider those heterogeneous species.

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Appendix 1. Specimens examined

"*Blaste*" sp. (09.20.2007.11.2) (*lunulata* species group): morphology & molecular

Clematostigma maculiceps (Enderlein, 1903): morphology

Clematostigma sp. KY418 (Brisbane, Australia): morphology & molecular

Kaindipsocus splendidus Lienhard, 2008 (= *Kaindipsocus* sp.: Yoshizawa & Johnson, 2008):
morphology & molecular

Kaindipsocus sp. KY379 (Cameron Highland, Manalaysia): molecular (available by females
only)

Lasiopsocus dicellyus : morphology

Tanystigma latimentula: morphology

Tanystigma sp. 1 (09.20.2007.13): morphology & molecular

Tanystigma sp. 2 (09.20.2007.18): morphology & molecular

Appendix 2. GenBank accession numbers for sequence data taken from Kaindipsocinae (see Yoshizawa & Johnson, 2008 for other sequences). "-" indicates missing data.

<u>Species</u> <u>Gene</u>	<u>18S</u>	<u>H3</u>	<u>Wg</u>	<u>16S</u>	<u>12S</u>	<u>COI</u>
" <i>Blaste</i> " sp. (cf. <i>lunulata</i>)	-	-	JF820383	JF820381	JF820378	JF820373
<i>Clematostigma</i> sp.KY418	JF820388	JF820387	-	JF820380	JF820377	-
<i>Kaindipsocus splendidus</i>	EF662270	EF662149	EF662194	EF662109	EF662236	EF662072
<i>Kaindipsocus</i> sp. KY379	-	JF820386	-	-	JF820376	-
<i>Tanystigma</i> sp. 1	-	-	JF820384	JF820382	JF820379	JF820374
<i>Tanystigma</i> sp. 2	-	-	JF820385	-	-	JF820375

Table 1. Higher level systematics of Psocidae newly proposed here. For tribes and genera of Amphigerontiinae and Psocinae, see Yoshizawa & Johnson (2008)

Family Psocidae

Subfamily Kaindipsocinae

"Blaste lunulata" species group

Clematostigma

Kaindipsocus

Lasiopsocus

Tanystigma

Subfamily Amphigerontiinae

Subfamily Psocinae

Figure captions

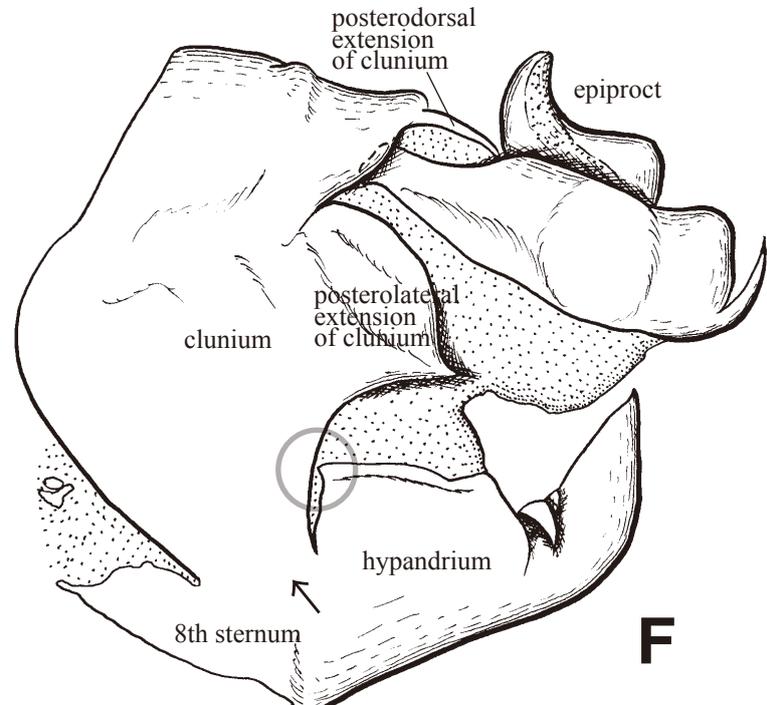
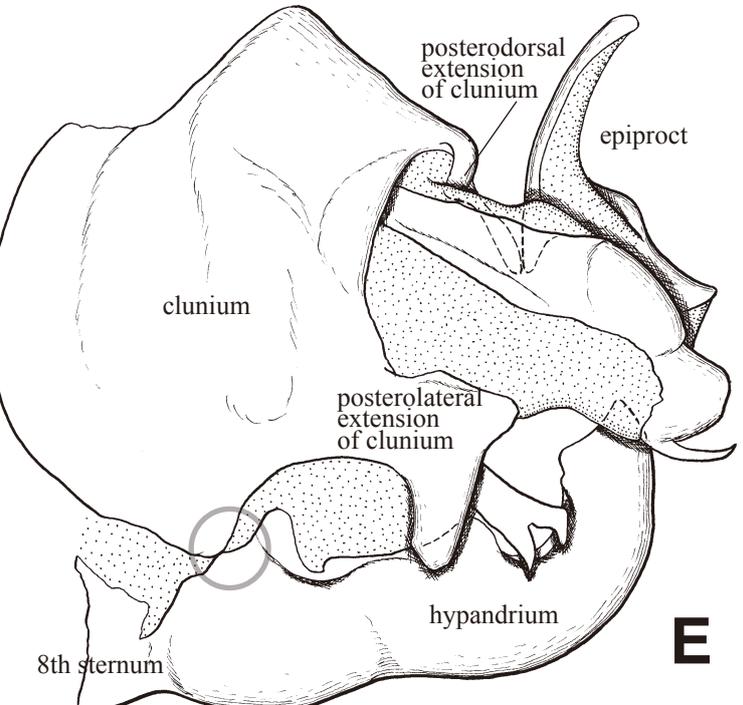
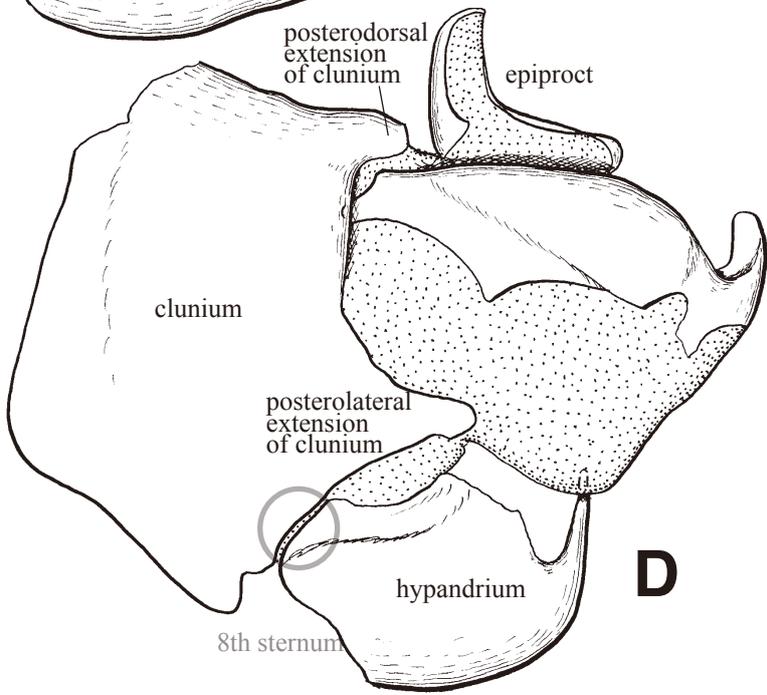
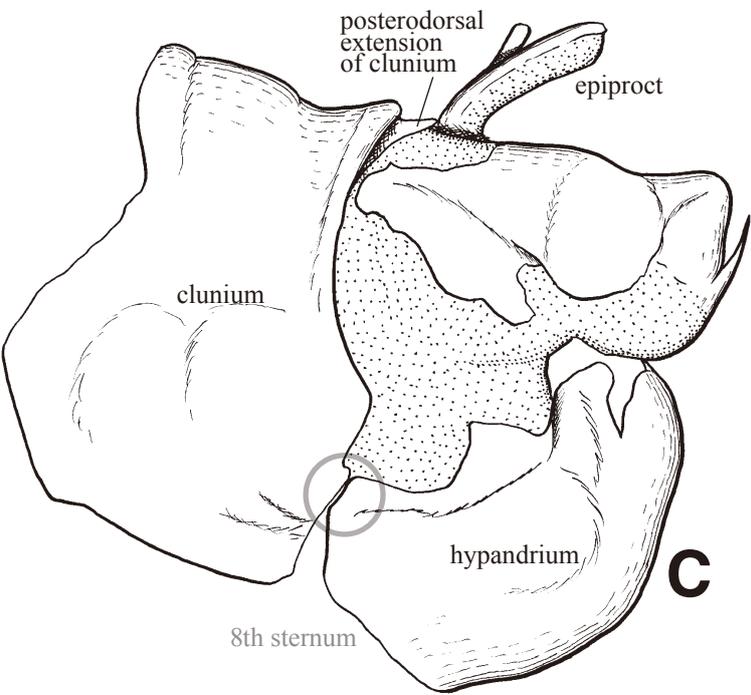
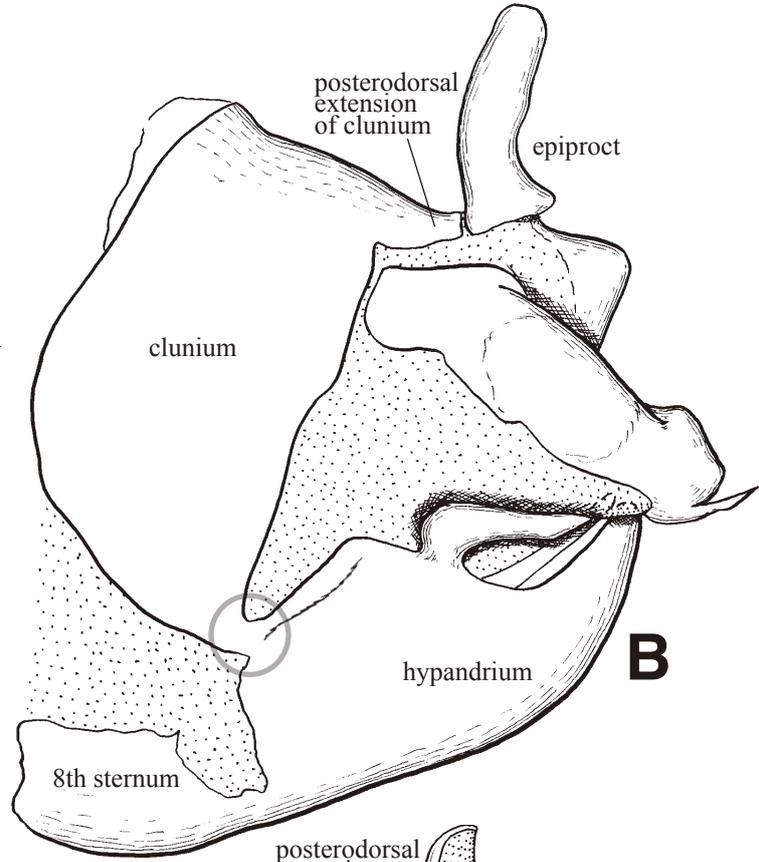
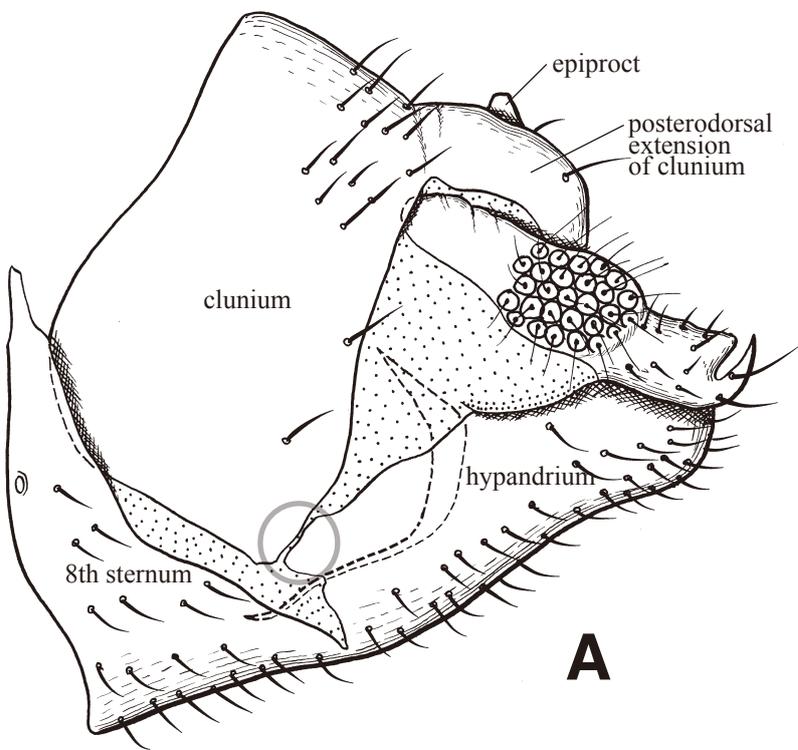
Fig. 1. Male terminalia, lateral view. A. *Glossoblaste amamiensis*, B. "*Blaste*" sp. (*lunulata* species group), C. *Tanystigma* sp. 2, D. *Tanystigma latimentula*, E. *Lasiopsocus dicellyus*, F. *Clematostigma* sp. KY379. Circles indicate the clunium-hypandrium fusion/articulation. The arrow in F indicates the clunium-8th sternum fusion which is not homologous with those indicated by circles.

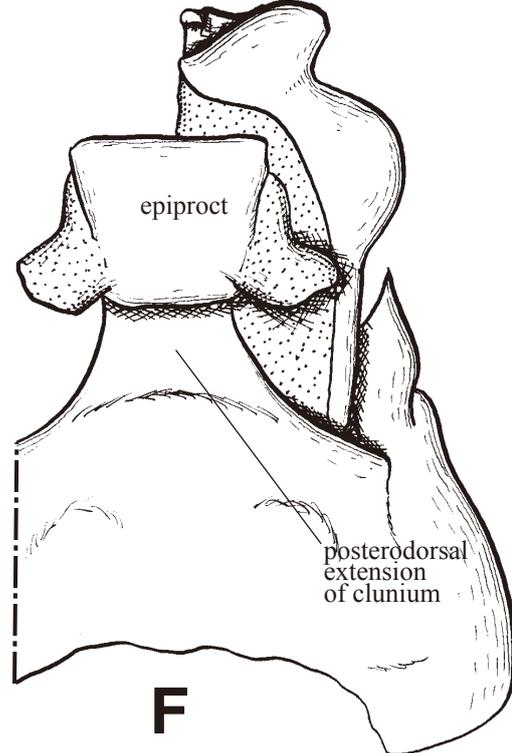
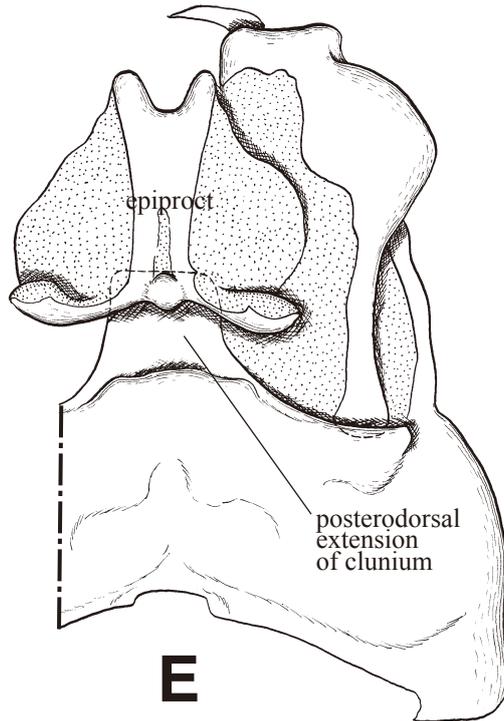
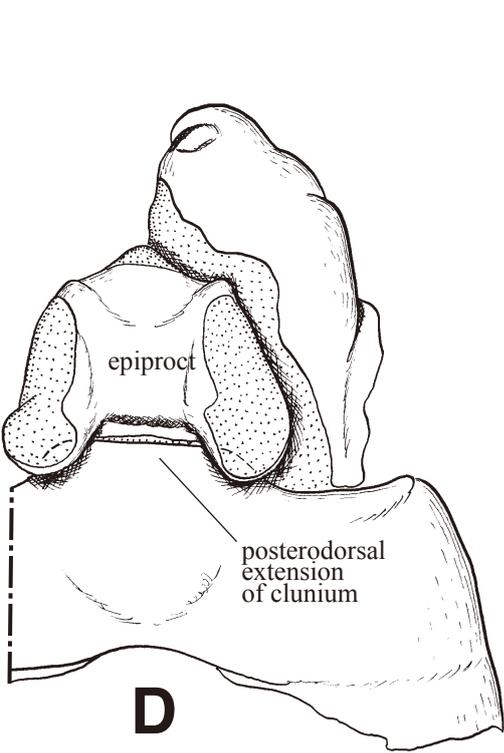
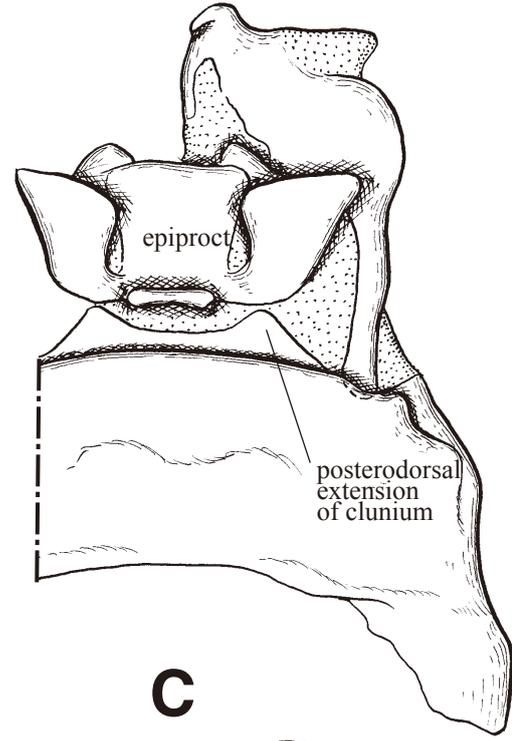
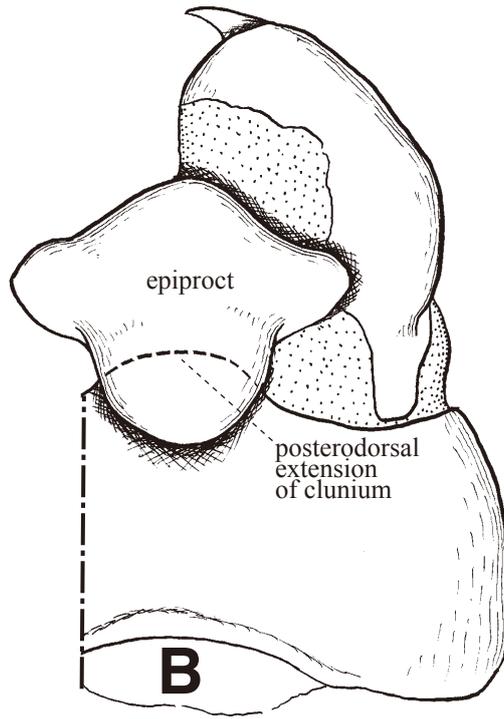
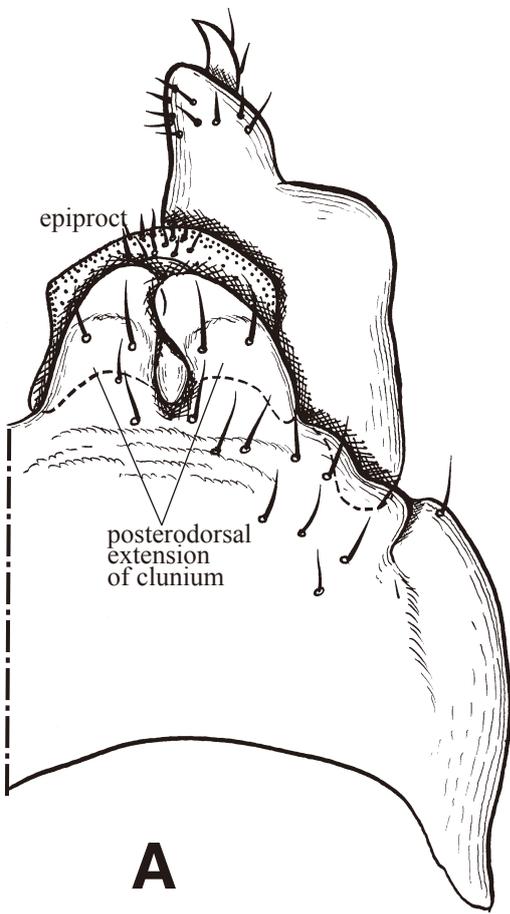
Fig. 2. Male terminalia, dorsal view. A. *Glossoblaste amamiensis*, B. "*Blaste*" sp. (*lunulata* species group), C. *Tanystigma* sp. 2, D. *Tanystigma latimentula*, E. *Lasiopsocus dicellyus*, F. *Clematostigma* sp. KY379.

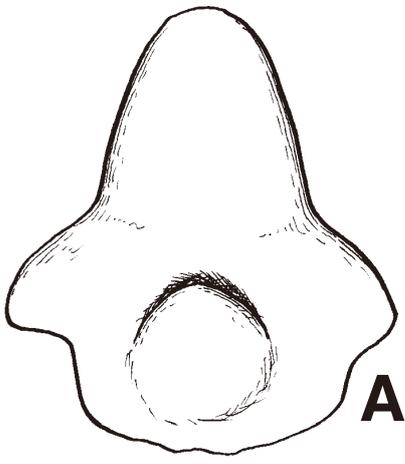
Fig. 3. Male epiproct, posterior view. A. "*Blaste*" sp. (*lunulata* species group), B. *Tanystigma* sp. 2, C. *Tanystigma latimentula*, D. *Lasiopsocus dicellyus*, E. *Clematostigma* sp. KY379.

Fig. 4. Phallosome, ventral view. A. *Glossoblaste amamiensis*, B. "*Blaste*" sp. (*lunulata* species group), C. *Tanystigma* sp. 2, D. *Tanystigma latimentula*, E. *Lasiopsocus dicellyus*, F. *Clematostigma* sp. KY379.

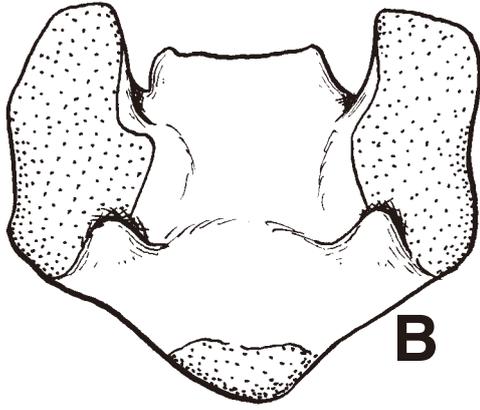
Fig. 5. The ML tree estimated from the data set including all taxa. Branch lengths are proportional to ML estimated branch lengths. The numbers above the branches are Bayesian posterior probability/ML bootstrap/MP bootstrap support values and those below the branches are ML bootstrap support from the data set excluding *Tanystigma* sp. 2. The label "con" indicates the constrained branches (see Materials and Methods).



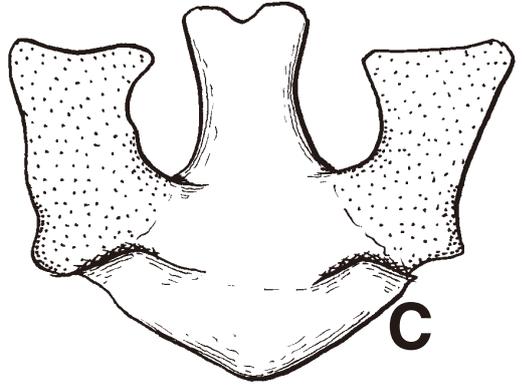




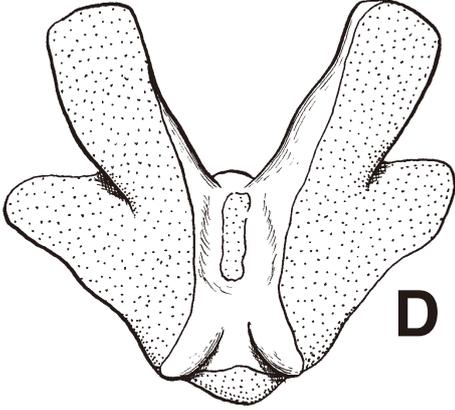
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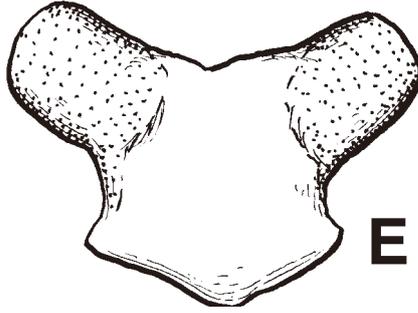
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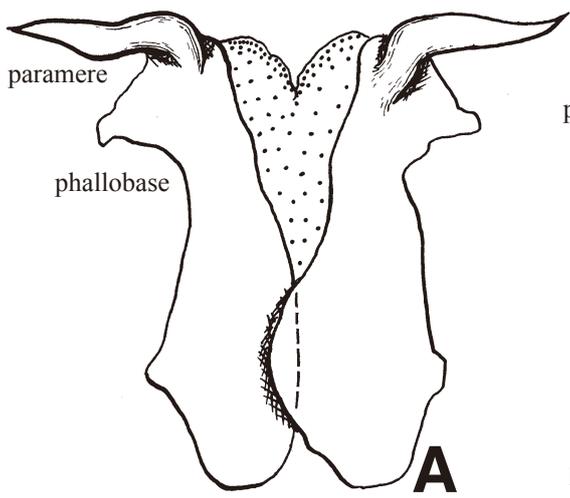
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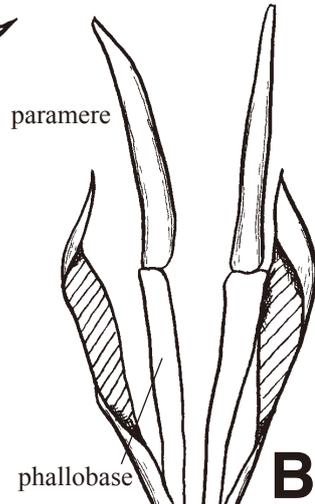
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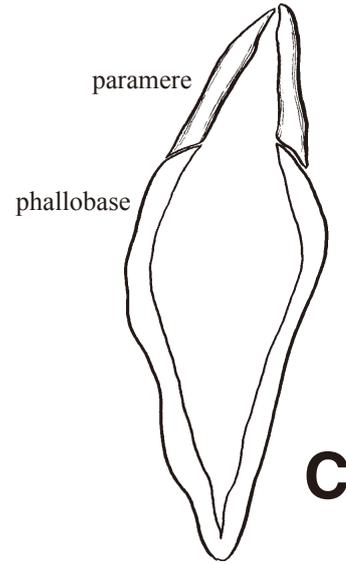
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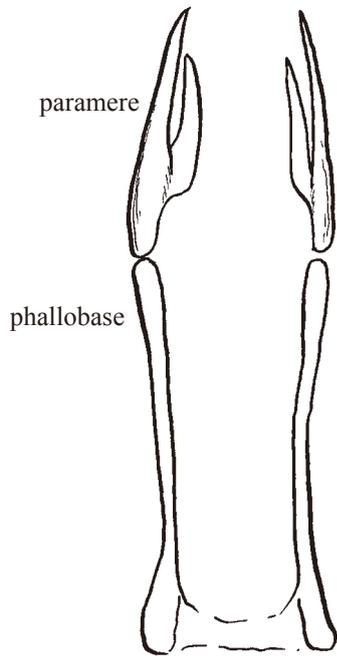
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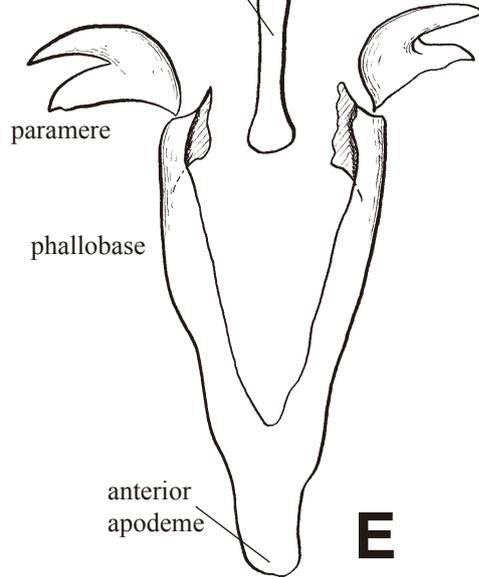
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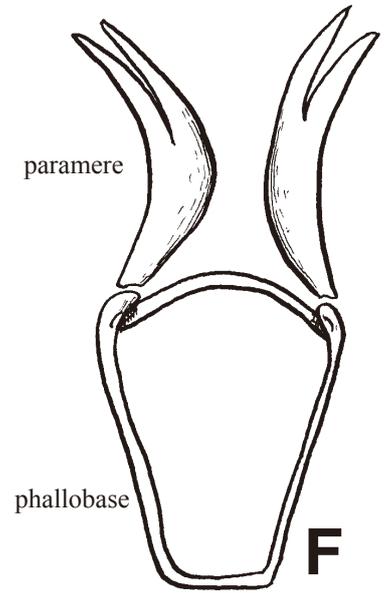
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D



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F

