Description of *Leptoomus janzeni*, n. gen. and n. sp. (Hymenoptera: Chalcidoidea) from Baltic amber, and discussion of its relationships and classification relative to Eupelmidae, Tanaostigmatidae and Encyrtidae

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Abstract

Leptoomus janzeni, **n. gen.** and **n. sp.**, is described from 5 females and 2 males in 7 pieces of Baltic amber. An enlarged acropleuron forming the entire mesopleuron places the taxon within Eupelmidae, Tanaostigmatidae or Encyrtidae (Chalcidoidea), but it has a unique combination of features that differentiates it from extant members of these families. Its structural features are compared with those that characterize the three families and it is postulated to be the sister group of Tanaostigmatidae *sensu stricto* + (*Cynipencyrtus* + Encyrtidae) based on relative structure of its pronotum, prepectus and mesothoracic spiracle, and retention of two other putative symplesiomorphies, the presence of complete furrowlike notauli and a protibial apical spicule. Conflicting character states indicate other possible relationships, including a sister-group relationship with *Cynipencyrtus* + Encyrtidae based on transverse-triangular axillae and a flagellum having only seven funicular segments, or with Tanaostigmatidae *s. s.* based on presence of an externally visible prepectal pouch, or possibly forming a monophyletic group with Tanaostigmatidae *s. s.* + *Cynipencyrtus* based on combined acropleural-metacoxal structure. Several features support the monophyly of Tanaostigmatidae *s. s.*, that is excluding *Cynipencyrtus* and *Leptoomus*, but these two genera are both classified in Tanaostigmatidae *sensu lato* until relationships are resolved more conclusively. Features possessed by different members of Neanastatinae (Eupelmidae) suggest that this subfamily may be closely related to Tanaostigmatidae *s. l.* + Encyrtidae, but possible relationships of Tanaostigmatidae *s. s.* are also discussed if its enlarged acropleuron and other skeletomusculature features associated with jumping are convergent to similar features in the other taxa.

Key words: Neanastatinae, Calosotinae, Eupelminae, *Cynipencyrtus*

Introduction

Chalcidoidea (Hymenoptera) are classified into 19 extant families, of which Eupelmidae, Tanaostigmatidae and Encyrtidae are diagnosed partly by the presence of a greatly enlarged, convex acropleuron. Among these three families, apomorphic states have been proposed to support the monophyly of Tanaostigmatidae and Encyrtidae, but not Eupelmidae (Gibson *et al.* 1999). Tanaostigmatidae is the least speciose of the three families and one of the smaller families of Chalcidoidea. About 95 species are classified in 9 genera, of which 4 are monotypic (Noyes 2003). One of these, *Cynipencyrtus* Ishii (1928), was described originally in Encyrtidae but was transferred to Tanaostigmatidae by LaSalle and Noyes (1985) because of a single apomorphy, the presence of a large prepectus that is distinctly swollen anteriorly. However, relative prepectal-pronotal structure of *Cynipencyrtus* differs substantially from other Tanaostigmatidae and could represent an intermediate stage in the evolution of the prepectal-pronotal structure of Encyrtidae (Gibson 1989). *Cynipencyrtus flavus* Ishii is a parasitoid of several species of Cynipidae (Cynipoidea) that form galls on *Quercus serrata* Murray (Fagaceae) (Tachikawa 1973), whereas other tanaostigmatids are phytophagous, most of them being gall-

formers (LaSalle & Noyes 1985). Members of Encyrtidae and Eupelmidae are primary or hyperparasitoids of a wide variety of insects and arachnids (Gibson *et al.* 1999).

Several years ago I received inclusions of Baltic amber for identification that purportedly contained specimens of Eupelmidae. Among the material was a single female that resembles extant species of the New World genus *Lambdobregma* Gibson (Neanastatinae), a single female similar to *Metapelma* Westwood (Neanastatinae), and two females that definitely represent an undescribed genus of Neanastatinae. Also included were five females and two males that I provisionally identified as belonging to Tanaostigmatidae even though they have a combination of features different from other members of the family, including *Cynipencyrtus*. Janzen (2002, fig. 318) published a dorsal image of one of the latter specimens under the family name Tanaostigmatidae and an image of the female resembling *Lambdobregma* under the family name Eupelmidae (Janzen 2002, fig. 317). One fossil Eupelmidae has been described previously from Baltic amber, *Propelma rohdendorfi* Trjapitzin (1963), which Gibson (1995) transferred to the extant genus *Eupelmus* Dalman (Eupelminae). There are also three fossil Encyrtidae, including *Eocencnemus sugonjaevi* Simutnik (2002) from Late Eocene Rovno Russian amber, but there are no described fossil Tanaostigmatidae. The purpose of this paper is to describe the new fossil taxon with putative affinities to Tanaostigmatidae and analyze its relationships relative to *Cynipencyrtus*, other Tanaostigmatidae, Encyrtidae and Eupelmidae. The fossil Neanastatinae will be described separately with an analysis of their classification and relationships relative to the four extant genera of the subfamily, *Lambdobregma*, *Metapelma*, *Neanastatus* Girault and *Eopelma* Gibson.

Material and methods

The seven amber pieces containing the specimens were obtained from Jens-Wilhelm Janzen, Seevetal, Germany, but are now the property of the American Museum of Natural History (AMNH), New York, NY, USA. The specimens were examined and photographed using the equipment and techniques described in Gibson *et al.* (2007). Some images were digitally retouched using Adobe Photoshop CS3™ in order to enhance clarity. Original images can be obtained from the author. Morphological terms follow Gibson (1989, 1995, 1997) and abbreviations used on the illustrations for the terms are given in the Appendix. A single description is given for the genus and species because only one species is recognized. It is a composite description based on all the specimens, which vary in preservation and views available for examination. Tanaostigmatidae *sensu lato* (*s. l.*) is used for the family including *Cynipencyrtus*, whereas Tanaostigmatidae *sensu stricto* (*s. s.*) is used for the family excluding *Cynipencyrtus*.

Systematics

Leptoomus Gibson, n. gen.

Type species: *Leptoomus janzeni*, **n. sp.**

Leptoomus janzeni, **n. sp.**
(Figs 1–19, 21)

Type material. *Holotype* (female, AMNH BaJWJ-400): near the end of a somewhat wedge-shaped block of clear, yellowish Baltic amber of unknown origin. The block is about 12 mm in length and is enlarged toward the end with the specimen. The specimen is complete except that the right leg projects out of one side of the block so that the mesotarsus lacks the apical four tarsomeres. A thin sliver of amber is also missing from the

block next to the frontal surface of the head so that the right antenna is missing beyond the third flagellar segment, but an impression of the flagellum remains in the amber (Fig. 3); internally a crack from the damaged area extends on the right side of the specimen to about the posterior margin of the prepectus. The wings are flat over the body (Fig. 1) so that the propodeum and metasoma are not visible from dorsal view and because of the shape of the block the body is not clearly visible from a direct ventral view.

Paratypes: 4 females (AMNH BaJWJ-401–404), 2 males (AMNH BaJWJ-405 and 406) in separate amber pieces.

Etymology. The genus name is formed from the Greek words *leptos*, meaning "thin" or "small" and *omos*, meaning "shoulder", in reference to the structure of the prepectus. The species name is in honour of Jens-Wilhem Janzen, who acquired the type series as part of his long interest in Baltic amber.

Description. Body length 2.4–2.75 mm. Head and body dark brown, but appearing silvery where surrounded by thin layer of air (e.g., Figs 4, 13, 16).

Head. In frontal view (Fig. 3) broadly rounded, slightly wider than high, not vaulted above eyes; reticulate to coriaceous-reticulate ventrally and uniformly setose except scrobal depression bare. Clypeus delimited laterally by small anterior tentorial pit near oral margin at level of inner margin of torulus (Fig. 3: atp), smooth, shiny, and bare except for 2 long setae laterally, one more basal than other; apical margin straight-transverse (Fig. 3). Scrobal depression comparatively broad, distinct but smoothly merged with parascrobal region and vertex, and scrobes separated ventrally by convex, dorsally tapered interantennal region (Figs 3, 5). Toruli distinctly below lower margin of eyes (Figs 3, 5); distance between toruli equal to distance between lower margin of torulus and oral margin, about 1.25 times width of torulus, and about 0.5 length of malar space. Malar space with complete malar sulcus (Figs 3, 5, 10). Eye with very short, inconspicuous, sparse microtrichia; in dorsal view (Figs 1, 2) minimum distance between eyes about 5–6 times diameter of anterior ocellus and about 0.36 times head width. OOL slightly greater to slightly less than diameter of posterior ocellar diameter (Figs 1, 7); OOL:POL:LOL about 1:3:2.5 (Figs 1, 2). Mandible with acute ventral tooth and very slightly concave dorsal truncation (Fig. 3, *cf.* Tachikawa 1973, fig. 2C). Antenna (Figs 3, 5) 12-segmented (1:1:7:3); scape compressed but thick, length excluding radicle about 4 times maximum width; funicle with all segments slightly transverse to subquadrate, the basal segment not distinctly ringlike or conspicuously differentiated from subsequent segments; clava compact, about as long as combined length of apical 3 funicular segments, subdivided by fine sutures and in lateral view with apex strongly, obliquely truncate (Fig. 5), the truncate region consisting of oval micropilose sensory region (Fig. 3).

Mesosoma. Pronotum in dorsal view (Figs 4, 7, 8) with short, coriaceous-reticulate collar, anteriorly the collar evenly rounded into vertical surface without distinct neck and laterally extending to mesothoracic spiracle and inner margin of prepectus, with dorsolateral margin obliquely angled relative to concave posterodorsal margin so as to form a short, posteriorly projecting lobe overlaying shallow anterolateral depression of mesoscutum (*cf.* Figs 4, 6, 8); in lateral view posterior margin of pronotum arcuate so as to partly surround anterior margin of prepectus (Figs 10–13), but usually with narrow inflexed band (Figs 3, 10–12: ppi) abutting anteroventral margin of prepectus (one female with normally inflexed portion extending posteriorly exterior to prepectus as flat, lobelike surface, Fig. 13: ppi). Prepectus visible in dorsal view (Fig. 4), moderately thick rather than flaplike, but appressed to mesoscutum and not conspicuously protuberant; in lateral view (Figs 10–13) comprising about one-third combined length of prepectus and acropleuron, isodiametric-coriaceous, with posterior margin at almost right angle to dorsal margin (Fig. 11) and appressed to acropleuron, and with anterior angle rounded and projecting under spiracle very slightly anterior to level of spiracle (Figs 11–13: sp1); in ventral view (Fig. 3: pp) keel-like, with inner and outer surfaces forming a pouch external to ventrolateral margin of pronotum (Fig. 3: ppi) and projecting conspicuously beyond anterior margin of mesosternum (Figs 5, 10: ams) so sternum and prepectus form a deep U-shape when prothorax slightly displaced from sternum (Figs 5, 10). Mesonotum, when not flexed, with posterior margin of mesoscutum overlapping anterior margin of scutellar-axillar complex slightly so as to separate inner angles of axillae mesally (Figs 1, 4, 7: arrows), but

when flexed with mesoscutum and scutellar-axillar complex separated by linear membranous band and inner angles of axillae contiguous (Fig. 8: arrow). Mesoscutum quadrangular, wider than long (Figs 1, 2, 4, 8) except in BaJWJ-403 (Fig. 7) (probably an artefact of preservation), reticulate, uniformly setose and without evident parapsidal lines or linear notauli, but with shallow longitudinal depression extending between posteriorly projecting lobe of pronotum and lateral margin of axilla (cf. Figs 6, 7: not); posterior margin almost straight-transverse, curved slightly posteriorly when mesonotum unflexed (Figs 4, 7) and slightly emarginate when mesonotum flexed (Fig. 8); scutellar-axillar complex similarly sculptured and setose as mesoscutum; axillae transverse-triangular with dorsal surface in same plane as scutellum and distinguished from scutellum by very shallow, linear furrow (Figs 4, 6–8). Acropleuron (Figs 10, 11, 13) convexly enlarged, extending posteriorly to metacoxa between metapleuron and mesocoxa, but separated from base of mesocoxa by slender, ventral portion of mesepimeron (Fig. 14: epm); acropleural sulcus horizontal, extending straight forward to near posteroventral angle of prepectus where arched dorsally as more obscure, obliquely angled furrow (Figs 10, 11: acs); finely, obliquely strigose-coriaceous over about anterior half, but minutely netlike coriaceous mesally and shiny and almost smooth posteriorly. Mesosternum quadrangular, without distinct discrimen but apparently slightly convex on either side of mediolongitudinal furrow; posterior margin differentiated as slender rim (Figs 10, 13, 15: msr) posterior to mesofurcal pit (Figs 10, 14, 15: mfp), the margin straight-transverse but separated from each mesocoxa by wide membranous region (Figs 9, 14: mb) along anterior margin of coxa lateral to basomedial lobe. Mesotrochantinal plate (Figs 14, 15: mtp) inflected internally at abrupt angle to mesosternum, comparatively narrow mesally in region under basomedial lobes of mesocoxae (Fig. 15: bml), but laterally with slender, transverse region between posterior margin of mesosternum and membranous region anterior to each coxa (Figs 14, 15: mb). Metanotum not clearly visible in any specimen, but apparently bandlike below scutellum (Gibson 1989, cf. fig. 49); metapleuron (Fig. 11: pl₃) triangular, very finely isodiametric coriaceous and appearing bare in most specimens but with 2 setae above carinate ventral margin in BaJWJ-402. Propodeum not clearly visible in any specimen but transverse without distinctly differentiated plical and callar regions, surface low convex with linear postspiracular sulcus; possibly with short median carina, but at least with large spiracle within anterior half (Fig. 11: sp2), and setose lateral to spiracle.

Appendages. Fore wing (Figs 1, 2, 16) hyaline; marginal and stigmal veins separated by distinct though short hyaline break and stigmal vein with distinct uncus (Fig. 16); female with mv about 1.3–1.4x length of stv, 1.0–1.2x length of pmv, and 0.3–0.4x length of smv (n=3), and male with mv about 1.2x length of stv, 0.85x length of pmv, and 0.3x length of smv (n=1); basal and mediocubital folds setose and basal cell almost completely setose except narrowly along mediocubital fold; disc with broad speculum (Fig. 16: spc) contiguous with parastigma extending between basal fold and base of marginal vein (cf. Tachikawa 1973, fig. 2A). Mesocoxa in lateral view (Figs 10, 11, 13) inserted ventral to metacoxa near posterior margin of acropleuron, lateral surface with oblique ridge extending between posteroventral and anterodorsal angles, the surface concave ventral to, and convex dorsal to ridge such that concave region narrowed toward base. Metacoxa in lateral view about twice as high as wide and almost vertical, inserted high on mesosoma with broad, almost vertical anterodorsal attachment (Fig. 11). Protibia with curved, apically bifurcate tibial spur (Fig. 21: pts); inner apical margin with secondary fine comb (Fig. 21: sec) consisting of about 6 flattened setae in oblique row; inner dorsoapical margin above secondary fine comb with peglike (female, Fig. 21: pas) or more spinelike (male, Fig. 21 insert: pas), apparently articulated spicule; outer surface with 2 strong spines subapically, at least in female (Fig. 21: pls). Mesotibia with about 12 short pegs (female, Fig. 19 insert: map) or spines (male, Fig. 18) arranged in 1 or 2 irregular rows along inner apical margin and with strong, microsetose tibial spur extending for distance about equal to length of basitarsus (Fig. 19); metatibia with two spinelike tibial spurs. Tarsi 5-segmented (Fig. 19); female mesotarsus with straight line of peglike setae along anterior and posterior ventral margins of basal 4 tarsomeres, distally the pegs not extending along anteroapical margin of each tarsomere, and at least basitarsus appearing to have more pegs along anterior than posterior margin (Fig. 19); male mesotarsus with more spinelike setae ventrally (Fig. 18).
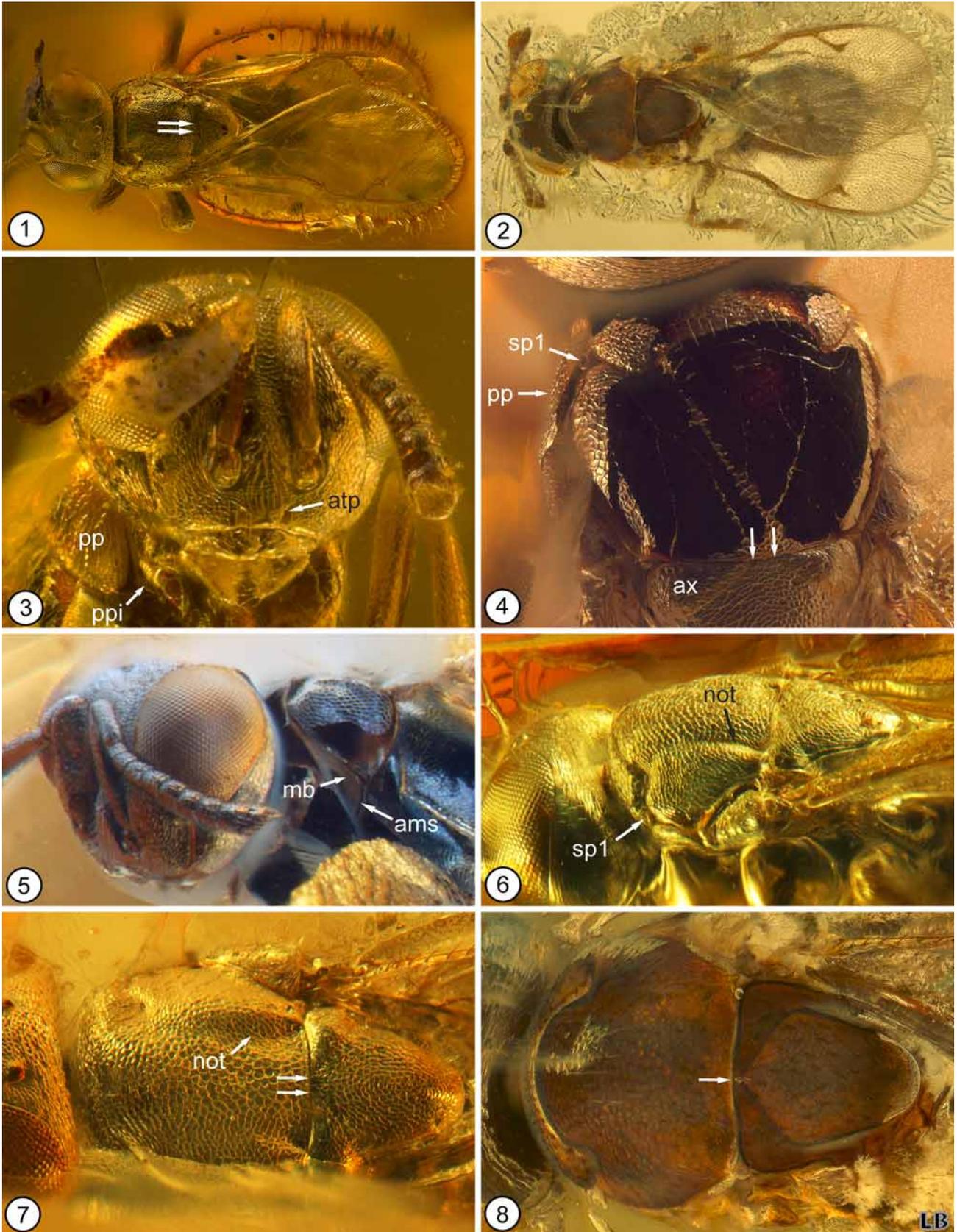
FIGURES 1–8. *Leptoomus janzeni*. 1 and 2, habitus dorsal: 1, ♀ holotype; 2, ♂ 405. 3, head, antenna and prepectus (holotype). 4, mesonotum dorsal (♀ 401). 5, head, antenna and prepectus (♀ 401). 6–10, mesonotum: 6, dorsolateral (♀ 402); 7, dorsal (♀ 404); 8, dorsal (♂ 405) [arrows point to inner angle of axillae on Figs 1, 4, 7, 8].
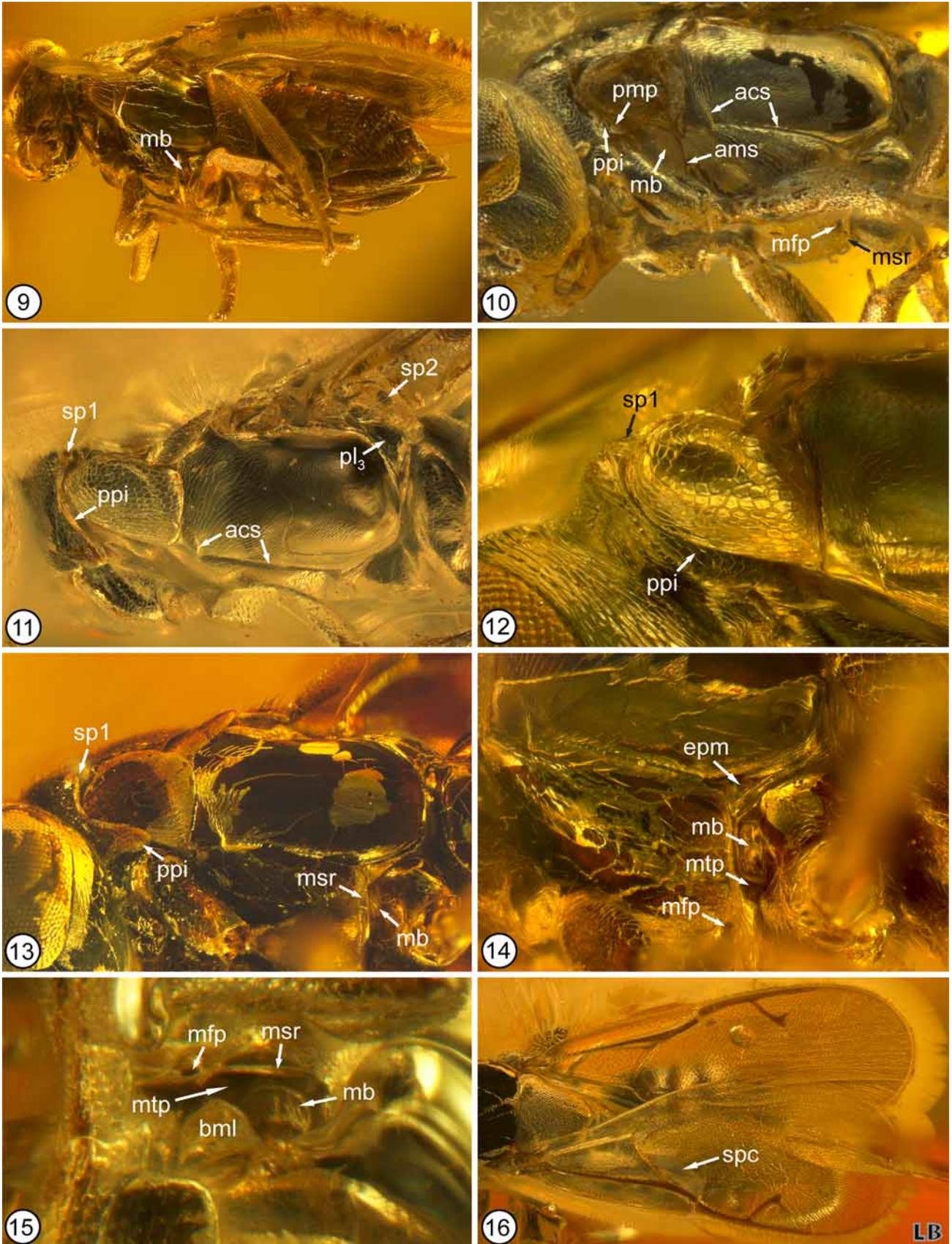
FIGURES 9–16. *Leptoomus janzeni*. 9, habitus lateral (holotype). 10 and 11, mesosoma lateral: 10, ♂ 406; 11, ♀ 401. 12, pronotum-prepectus lateral (♀ 402). 13, mesosoma lateral (♀ 404). 14 and 15, mesocoxal articulation: 14, ventrolateral (holotype); 15, posteroventral (♀ 402). 16, fore wings (♀ 401).
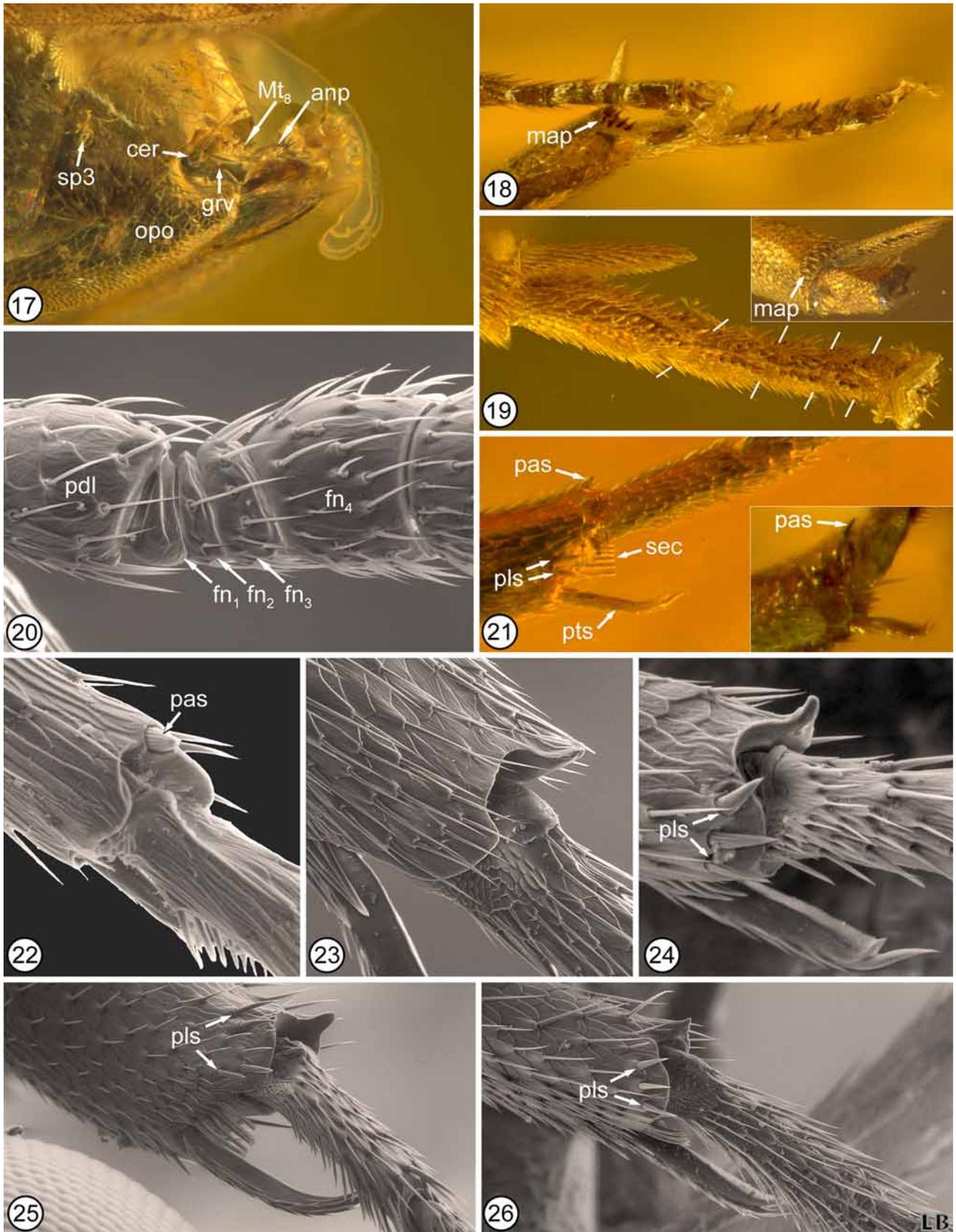
FIGURES 17–26. 17–19, *Leptoomus janzeni*: 17, apex of gaster (♀ 402); 18, mesotarsus and apex of mesotibia (♂ 406); 19, mesotarsus [lines indicate separation between tarsomeres] and [insert] mesotibial apical pegs (holotype). 20, *Cynipencyrtus flavus*, apex of pedicel to fourth funicular segment. 21–26, apex of protibia: 21, *L. janzeni* (♀ 401) and [insert: ♂ 406]; 22, *Eopelma* **n. sp.**; 23, *Lambdobregma* **n. sp.**; 24, *C. flavus*; 25, *Tanaoneura hirticoxa* LaSalle; 26, *Aenasius* sp.
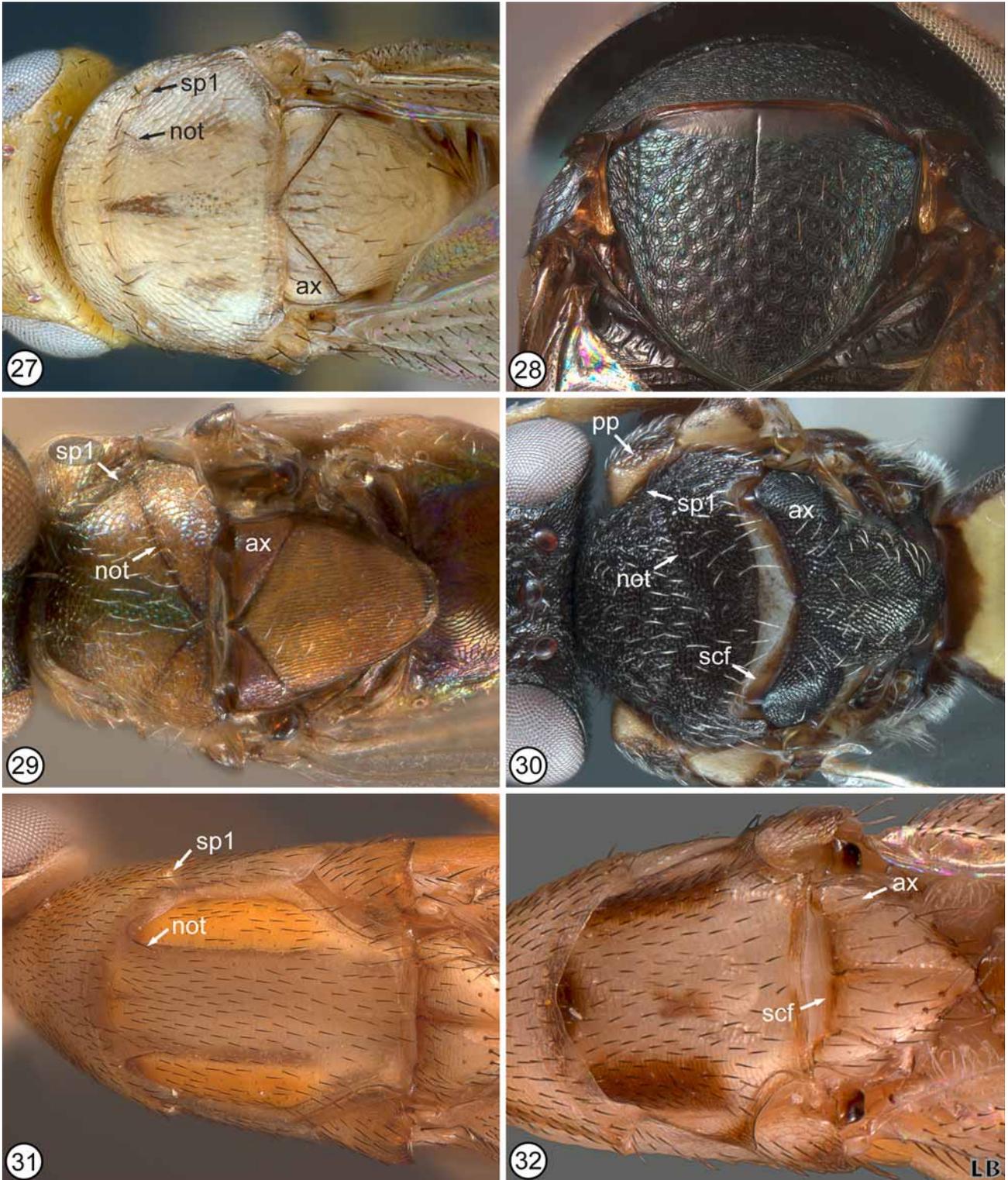
FIGURES 27–32. 27, *Cynipencyrtus flavus*, mesosoma dorsal [mesonotum unflexed]. 28, *Aenasius* sp., mesonotum dorsal [flexed]. 29 and 30, mesosoma dorsal [mesonotum flexed]: 29, *Charitopus cuprifrons* (Motschulsky); 30, *Tanaoneura hirticoxa*. 31 and 32, *Neanastatus* sp., mesosoma dorsal: 31, mesonotum unflexed; 32, mesonotum flexed.

Metasoma. Metasoma of female with 8 tergites and with small anal plate (Fig. 17: anp) over ovipositor sheaths; broadly sessile with Mt_1 (petiole) transverse, striplike; Mt_2-Mt_7 of similar length, transverse-rectangular, finely coriaceous with transverse rows of setae (Fig. 9); Mt_7 with spiracle (Fig. 17: sp3); Mt_8 (syntergum)

short dorsally, setose, with dorsal surface (Fig. 17: Mt$_8$) differentiated from outer plate of ovipositor (Fig. 17: opo) by longitudinal groove (Fig. 17: grv) posterior to cercus (Fig. 17: cer). Cercus at anterolateral angle of Mt$_8$ but not conspicuously advanced, with 2 short and 2 long setae, the setae not kinked. Hypopygium extending about half length of gaster. Ovipositor sheaths protruding only slightly beyond apex of metasoma (Fig. 17).
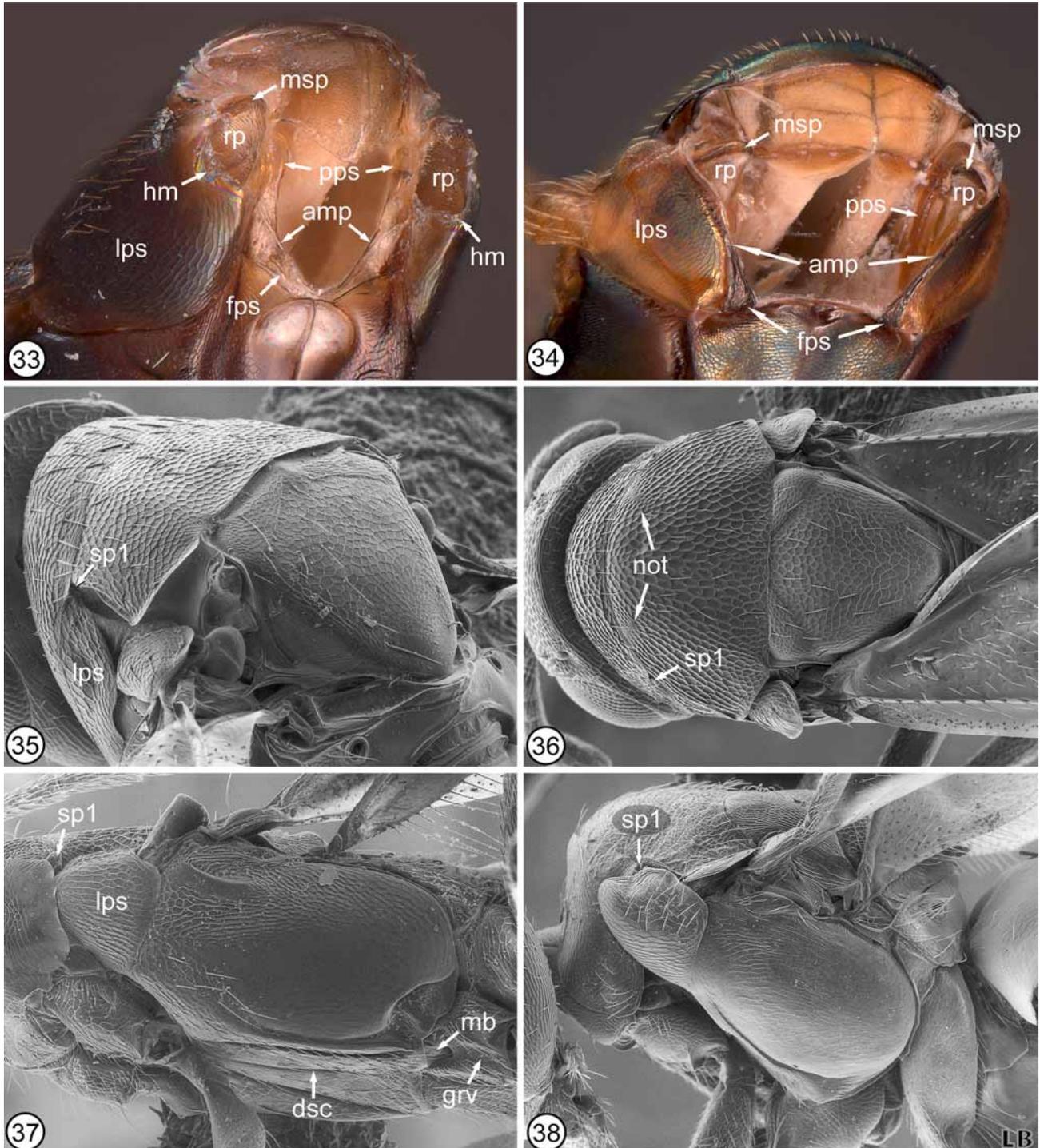
FIGURES 33–38. 33 and 34, prepectus [prothorax removed]: 33, *Neanastatus* sp.; 34, *Ericydnus* sp. 35, *Cynipencyrtus* sp., mesosoma dorsolateral [mesonotum flexed]. 36, *C. flavus*, mesosoma dorsal [mesonotum unflexed]. 37 and 38, mesosoma lateral: 37, *Eopelma* **n. sp.**; 38, *Tanaostigmodes* sp.
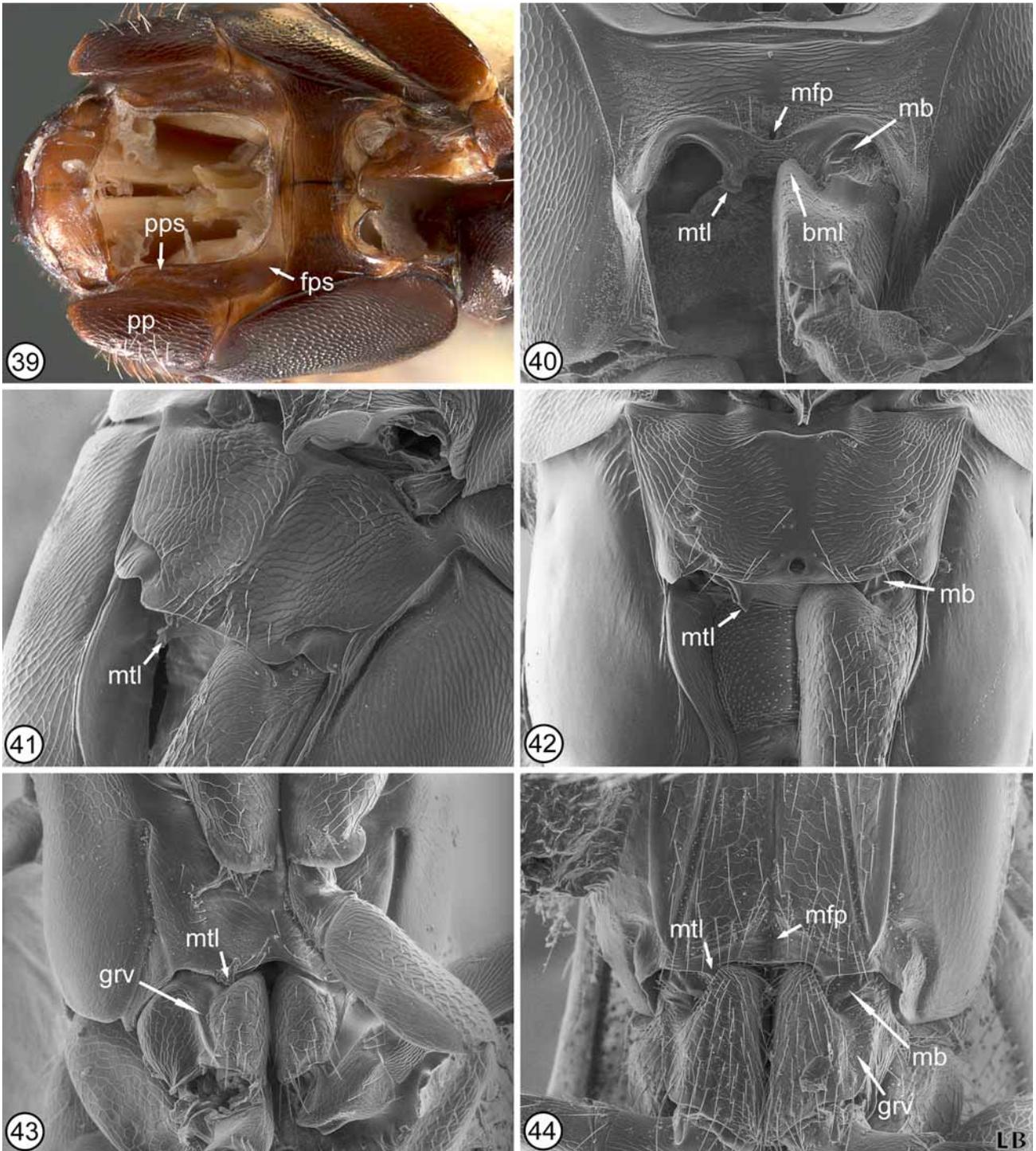
FIGURES 39–44. 39 and 40, *Tanaostigmodes* sp. [left leg removed]: 39, mesosoma ventral [prothorax removed]; 40, mesocoxal articulation ventral. 41 and 42, mesocoxal articulation [left leg removed]: 41, *Ericydnus* sp., ventrolateral; 42, *Bothriothorax noveboracensis* Howard, ventral. 43 and 44, mesocoxal articulation ventral: 43, *Cynipencyrtus flavus*; 44, *Eopelma* **n. sp.**

Discussion

Analysis of structural features. Structural features of *L. janzeni*, *Cynipencyrtus*, Tanaostigmatidae *s. s.*, Encyrtidae, and Eupelmidae are evaluated below to investigate the monophyly of Tanaostigmatidae and to determine familial classification of *L. janzeni*. Features are discussed by body region.

1. Apical margin of clypeus. LaSalle (1987) described the clypeus of Tanaostigmatidae *s. s.* as bilobed (narrowly emarginate and longitudinally depressed medioapically). In the other taxa included in this analysis the apical margin of the clypeus is either straight-transverse, slightly incurved or, in Eupelminae, very rarely protuberant (Gibson 1995, figs 31, 32).

Analysis. A bilobed clypeus is unique for Tanaostigmatidae *s. s.* among the taxa treated and might represent an autapomorphy of the group, but distribution and polarity of such a clypeus is incompletely known throughout Chalcidoidea. Dzhanokmen (2000) recorded a bilobed clypeus for at least some Miscogasterinae and Pteromalinae (Pteromalidae), but there has been no comprehensive survey of clypeal structure throughout the 31 recognized subfamilies of this family. A bilobed clypeus is possessed by members of at least some genera of Epichrysomallinae, Otitesellinae and Sycophaginae (Agaonidae). Phylogenetic relationships and familial classification of the latter three subfamilies are incompletely resolved, but members are gall makers or parasitoids within fig (*Ficus*) galls (Rasplus *et al*. 1998). Consequently, comprehensive survey of clypeal structure throughout Chalcidoidea combined with an analysis of other features and biology is necessary to determine when a bilobed clypeus might indicate common ancestry or convergence resulting from adaptation to a similar ecological niche such as plant galls.

2. Number and structure of funicular segments. Within Eupelmidae, all 8 genera of Calosotinae and 33 genera of Eupelminae have eight funicular segments, of which the first segment is almost always shorter than the subsequent segments though only sometimes strongly transverse and ringlike. Within Neanastatinae, *Metapelma* and *Lambdobregma* have eight funicular segments and a variably long first segment, whereas *Eopelma* has seven funicular segments with the basal two segments shorter than the third segment, which is the longest segment, and *Neanastatus* has six funicular segments with the basal segment ringlike (Gibson 1989). Tanaostigmatidae *s. s.* has eight funicular segments including two basal segments that are strongly shortened to ring segments (LaSalle 1987, figs 54–84) or, very rarely, with the third segment similarly reduced (LaSalle 1987, fig. 53). Individuals of *Cynipencyrtus* have seven funicular segments including three basal segments that are strongly shortened to ring segments (Fig. 20; Tachikawa 1978, figs B, D), as first correctly described by Tachikawa (1963). LaSalle and Noyes (1985, fig. 1) subsequently described and illustrated the funicle of *Cynipencyrtus* as 8-segmented with the basal four segments ringlike, but this likely was based on the photograph of the slide-mounted female antenna of *C. flavus* given in Tachikawa (1978, fig. B), in which the lateral, vertical ridge on the basal funicular segment (Fig. 20) superficially appears as a division between two segments. Although this ridge may represent a line of fusion between two segments, the female antenna of *C. flavus* definitely has only three ring segments (Fig. 20), as is also apparent for the male antenna illustrated by Tachikawa (1978, fig. D). Most Encyrtidae have six or extremely rarely seven funicular segments. *Leptoomus janzeni* also has seven visible funicular segments, with the basal segment not shortened or otherwise conspicuously modified relative to the more distal segments (Figs 3, 5).

Analysis. An 8-segmented funicle is undoubtedly the groundplan structure for Chalcidoidea as well as for all three subfamilies of Eupelmidae and Tanaostigmatidae *s. s.* Consequently, loss of a single funicular segment could be a synapomorphy for *L. janzeni* + *Cynipencyrtus* + Encyrtidae, with further loss of segments occurring for almost all Encyrtidae. However, funicular segments have been lost independently in other chalcid taxa and therefore the presence of only seven segments is not strong evidence for the monophyly of *L. janzeni* + *Cynipencyrtus* + Encyrtidae or of any sister-group relationship with *Eopelma* or *Neanastatus*. The 7-segmented funicle of *Eopelma* may have resulted from fusion of the third and fourth funicular segments, but the 6-segmented funicle of *Neanastatus* likely evolved through loss of the basal two segments and strong shortening of the third segment.

3. Relative structure of pronotum, prepectus and mesothoracic spiracle. LaSalle and Noyes (1985) observed that the prepectus is large and distinctly swollen anteriorly in *Cynipencyrtus* as well as in Tanaostigmatidae *s. s.* This is because in both taxa the prepectus forms a pouch around an anteriorly projecting process of the lateral margin of the mesoscutum, the mesoscutal process *sensu* Gibson (1989, fig. 50: msp). The ante-

riorly protuberant prepectus is conspicuous in Tanaostigmatidae *s. s.* because each mesoscutal process and surrounding cuticle (Figs 30, 38, 39: pp) project exterior to the pronotum below the mesothoracic spiracle (Fig. 38; Gibson 1989, figs 49, 63, 63). The vertical pronotum extends posteriorly on the inner side of the protuberant prepectus to the level of the mesothoracic spiracle near the anterior margin of the notaulus (Fig. 30: not). Furthermore, in ventral view the anterior margin of the mesosternum and protuberant prepecti form a deep U- shape (Fig. 39; Gibson 1989, fig. 95). The prepectus is also anteriorly protuberant in *Cynipencyrtus*, but this is not visible externally because the regions are covered by the lateral panels of the pronotum anterior to the level of the mesothoracic spiracle (Fig. 35; Gibson 1989, *cf.* figs 47, 48). Consequently, the prepectus is not protuberant in dorsal view (Figs 27, 36; Gibson 1989, fig. 65), in lateral view it appears as a flat, flaplike sclerite behind the pronotum (Gibson 1989, fig. 47), and in ventral view there is no conspicuous U- shape (Gibson 1989, fig. 96). When the pronotum is removed, the protuberant prepectus of *Cynipencyrtus* is evident, the concealed cuticle being more membranous than the externally exposed cuticle (Gibson 1989, fig. 48). In both Tanaostigmatidae *s. s.* and *Cynipencyrtus*, the more or less truncate posterior margin of the lateral prepectal surface is appressed to and not freely moveable relative to the acropleuron (Fig. 38) because the prepectus forms a single cuticular surface around the mesoscutal process (Fig. 39; Gibson 1989, figs 47, 49).

The prepectal structure of *L. janzeni* is similar to Tanaostigmatidae *s. s.* because the prepectus has a distinct width in both dorsal (Fig. 4) and ventral (Fig. 3) view, with the posterior margin being truncate and apparently immoveable relative to the acropleuron (Figs 10–13), and in ventral view forming a deep U-shape with the anterior margin of the mesosternum (Figs 5, 10). In lateral view the prepectus of *L. janzeni* is about as large as that of Tanaostigmatidae *s. s.*, comprising about one third the combined length of the prepectus and acropleuron and having about the same amount anterior to the anterior margin of the tegula (*cf.* Figs 11, 38). However, the prepectus does not appear to project as much anteriorly in *L. janzeni* as in Tanaostigmatidae *s. s.* because the mesothoracic spiracle is virtually at its anterior margin (Figs 11–13) rather than distinctly posterior to the anterior margin on its inner side (Fig. 38). Furthermore, because the prepectal pouches of *L. janzeni* are not as wide as in Tanaostigmatidae *s. s.*, particularly in dorsal view (*cf.* Figs 3, 4, 30, 39; Gibson 1989, figs 63, 95), they are not as conspicuous. Finally, the pronotum of *L. janzeni* has a transverse collar similar to *Cynipencyrtus* (*cf.* Figs 4, 27), though the lateral surface is unique relative to Tanaostigmatidae *s. s.* or *Cynipencyrtus*. Unlike in Tanaostigmatidae *s. s.* (Gibson 1989, fig. 48), the lateral pronotal surface does not extend posteriorly between the prepectal pouch and mesoscutum, but rather it is emarginate around the anterior margin of the prepectal pouch (Figs 10–12). Furthermore, in most specimens the lateral surface is inflexed posteriorly (Figs 10–12: ppi) so that a narrow band abuts the anteroventral surface of the prepectal pouch, though in one female the normally inflexed region lies flat exterior to the prepectus (Fig. 13: ppi).

Encyrtidae have an anteriorly projecting mesoscutal process (Fig. 34: msp) similar to Tanaostigmatidae *s. l.* (Gibson 1989, *cf.* figs 50, 52) that, like in *Cynipencyrtus*, projects anteriorly interior (Gibson 1989, *cf.* figs 51, 52) to a usually strongly transverse pronotal collar (Gibson 1989, figs 66, 75; Noyes 1997, figs 14–16, 18). Unlike in *Cynipencyrtus*, the mesoscutal process is not entirely surrounded by cuticle so that there is no prepectal pouch, but in addition to the flat lateral surface of the prepectus (Fig. 34: lps) there is a small, triangular, ventral region (Fig. 34: fps) (= frontal surface of the prepectus *sensu* Gibson 1986, figs 37, 38) and internally a cuticular rod (Fig. 34: pps) (= prepectal strut *sensu* Gibson 1989, fig. 52) that extends between the anteroventral margin of the prepectus and the lateral margin of the mesoscutum interior to the mesoscutal process. Based on position, the internal prepectal strut of Encyrtidae is undoubtedly homologous with the inner margin of the prepectal pouch on the inner side of the mesoscutal process in Tanaostigmatidae *s. s.* (Fig. 39: pps) and in *Cynipencyrtus*. In Encyrtidae, loss of most of the cuticle between the inner margin of the frontal prepectal surface and the lateral surface of the prepectus not only resulted in the prepectal strut, but also in a secondary "anterior" margin of the prepectus laterally at its juncture with the pronotum (Fig. 34: amp). This margin acts as a line of articulation around which the lateral surface of the prepectus pivots so that it is a moveable flap (Gibson 1989, fig. 51), unlike in *Cynipencyrtus* or Tanaostigmatidae *s. s.*

The prepectus is never conspicuously protuberant in Eupelmidae, but in some Calosotinae it projects anteriorly under the spiracle (Gibson 1989, figs 29–31), appearing in ventral view as a small pouch on either side of the pronotum (Gibson 1989, fig. 91). Within Calosotinae, small prepectal pouches are characteristic only of *Eusandalum* Ratzeburg and closely related taxa (Gibson 1989). All Calosotinae differ conspicuously from *Cynipencyrtus* and Tanaostigmatidae *s. s.* in pronotal structure, in dorsal view the pronotum being more or less pentagonal and narrower than the mesonotum so that the mesoscutum appears to have "shoulders" (Gibson 1989, figs 67–69, 73, 74). The pronotum of Neanastatinae is much more similar to that of *Cynipencyrtus* and most Encyrtidae, except that in dorsal view it is more elongate-triangular (Fig. 31; Gibson 1989, figs 39, 41) rather than strongly transverse. Furthermore, individuals of *Neanastatus* have a mesoscutal process (Fig. 33: msp) that is lengthened interior to the pronotum anterior to the level of the mesothoracic spiracle, and that projects through a hole in the apically more hyaline (Fig. 33: hm) covered portion of the frontal surface of the prepectus (Gibson 1989, *cf.* figs, 44, 46). Because of this, a prepectal strut (Fig. 33: pps) is partly differentiated dorsally from the ventromedially contiguous frontal prepectal surfaces (Fig. 33: fps) interior to the mesoscutal process, and the posterolateral margin of the pronotum broadly covers the externally visible anterolateral margin of the prepectus (Gibson 1989, *cf.* figs 44, 46). Consequently, pronotal-prepectal structure of *Neanastatus* is most similar to Encyrtidae. The pronotal-prepectal structure of *L. janzeni* (Fig. 11) is more similar to that of *Eopelma* (Fig. 37), in which the prepectus narrows anteriorly to the level of the mesothoracic spiracle, does not extend interior to the pronotum, and has a truncate posterior margin. However, the prepectus of *Eopelma* is not bulbous and its lateral surface, as for other eupelmids, is a flat moveable flap that during mesonotal flexing rotates relative to the frontal surface so as to override the acropleuron anteriorly (Gibson 1986, *cf.* figs 29, 30; Gibson 1989, *cf.* figs 30, 32 and 33, 34).

Analysis. Hypotheses of generic relationships of Calosotinae in Gibson (1989, fig. 1) indicate that the small prepectal pouches of some members were derived secondarily in the subfamily and therefore are convergent to similar structures in Tanaostigmatidae *s. s.* and *Cynipencyrtus*. An externally visible, though comparatively thin prepectal pouch could therefore be a synapomorphy for *L. janzeni* + Tanaostigmatidae *s. s.* However, this structure could also be symplesiomorphic at that level. Although most specimens of *L. janzeni* have the posterior margin of the pronotum narrowly inflexed and abutting the anterior surface of the prepectal pouch, one female shows that the inflexed portion could also project posteriorly exterior to the prepectus (Fig. 13). A structure similar to that of *L. janzeni* could be ancestral to one lineage in which the lateral surface of the pronotum and the spiracle were extended posteriorly between the protuberant prepectus and mesoscutum concurrently with loss of the pronotal collar (Tanaostigmatidae *s. s.*), and one lineage in which the lateral surface of the pronotum was extended posteriorly over the prepectal pouch prior to reduction (*Cynipencyrtus*) and loss (Encyrtidae) of most of the secondarily concealed prepectal cuticle. Regardless, combined pronotal-prepectal structure indicates *Cynipencyrtus* is more closely related to Encyrtidae and is incorrectly classified in Tanaostigmatidae. Furthermore, the combination of a vertical pronotum and anteriorly protuberant prepectal pouches that extend exterior to the lateral surface of the pronotum is autapomorphic for Tanaostigmatidae *s. s.* A vertical pronotum itself, although unique among the taxa treated, is not necessarily apomorphic for Tanaostigmatidae *s. s.* Some other Chalcidoidea, including many Melanosomellini (Pteromalidae: Ormocerinae) have a vertical pronotum very similar to Tanaostigmatidae *s. s.* The similar pronotal-prepectal structures of *Neanastatus* (Fig. 33) and Encyrtidae (Fig. 34) must also be convergent if *L. janzeni* + Tanaostigmatidae *s. s.* + *Cynipencyrtus* + Encyrtidae form a monophyletic group. The pronotal-prepectal structure of *L. janzeni* could, however, be derived from one similar to that of *Eopelma* by reducing the length of the pronotum in combination with elongating the mesoscutal process into the frontal surface of the prepectus so that it formed a pouch around the process, with this abutting the posterior margin of the pronotum at the level of the mesothoracic spiracle (*cf.* Figs 11, 37).

The presence of small prepectal pouches in some Calosotinae and the pronotal-prepectal structures of *L. janzeni*, Tanaostigmatidae *s. s.*, *Cynipencyrtus* and Encyrtidae suggest that there is a functional advantage for

an elongate mesoscutal process in taxa with a greatly enlarged acropleuron. The mesoscutal process is the site of insertion of the pl_2-t_2c muscle (Figs 33, 34: rp). This muscle originates from the acropleuron (Gibson 1986, fig. 31: 5) and upon contraction flexes the mesonotum as part of the jumping mechanism (Gibson 1986). The longer the mesoscutal process the longer the pl_2-t_2c muscle and greater functional efficiency. Eupelmidae are characterized by a long mesosoma compared to the shorter, more robust mesosoma of *L. janzeni*, Tanaostigmatidae *s. s.*, *Cynipencyrtus* and most Encyrtidae. Elongation of the mesoscutal process in the latter taxa may have allowed the mesosoma to be shortened while still maintaining functional efficiency of the pl_2-t_2c muscle. If so, an elongate mesoscutal process and short mesosoma could be synapomorphic for the taxa. Alternatively, if *L. janzeni*, Tanaostigmatidae *s. s.*, *Cynipencyrtus* and Encyrtidae evolved from some ancestor with a short mesosoma and small subalar acropleuron, their elongate mesoscutal processes may have evolved concurrently with enlargement of the pl_2-t_2c muscle and acropleuron to produce the functional equivalent of the long mesosoma of Eupelmidae.

4. Notauli. LaSalle (1987) proposed posteriorly convergent, sinuate notauli that meet at or near the posterior margin of the mesoscutum, when complete, as one of two postulated synapomorphies for Tanaostigmatidae *s. s.* (Fig. 30) + Encyrtidae (Fig. 29). LaSalle and Noyes (1985) differentiated *Cynipencyrtus* from other Tanaostigmatidae in part by the absence of notauli. A critical-point dried female of *C. flavus* from Japan (Canadian National Collection, Ottawa) with an unflexed mesonotum has short, straight, posteriorly convergent, linear notauli behind the pronotum (Fig. 27), with an overlying band of punctulate-reticulate sculpture (Figs 27, 36). Each notaulus appears to be distinctly mesal of the respective mesothoracic spiracle (Fig. 27), unlike in Encyrtidae (Fig. 29) and Tanaostigmatidae *s. s.* (Fig. 30), in which the notaulus, when present, originates anteriorly adjacent to the spiracle. Despite this difference, the mesoscutum is uniformly convex in *Cynipencyrtus*, Tanaostigmatidae *s. s.* and Encyrtidae. *Leptoomus janzeni* lacks linear notauli and most specimens in dorsolateral (Fig. 6) or dorsal view (Fig. 7) have a variably distinct furrow extending the length of the mesoscutum from the posterodorsal angle of the pronotum to near the outer edge of the axilla. The two furrows differentiate convex median and lateral mesoscutal lobes similar to many male Eupelminae or the longitudinally differentiated mesoscutum of some female Eupelminae (see figs in Gibson 1995) and Neanastatinae (Gibson 1989, figs 39, 41, 42). Within Eupelmidae, linear, V-shaped notauli that originate anteriorly near the mesothoracic spiracles and that meet anterior to the posterior margin of the mesoscutum are possessed only by some Calosotinae (Gibson 1989, figs 59, 69, 73). Gibson (1989) stated that notauli were missing from Neanastatinae, but short, straight, linear notauli are visible in light-colored individuals of *Neanastatus* (Fig. 31), although usually they are partly or entirely concealed by the overhanging pronotum (*cf*. Figs 31, 32). The posteriorly projecting notaulus is distinctly mesal of the spiracle, but the exposed portion is a continuation of a ∩-shaped line that extends laterally to the spiracle (Fig. 31). It is unknown whether the notauli of *C. flavus* extend to the spiracles beneath the pronotum as in *Neanastatus* (*cf*. Figs 27, 31).

Analysis. The similarity between the mesoscutal structure of *L. janzeni* and Eupelminae or Neanastatinae is, at most, a retained symplesiomorphy because complete, furrow-like notauli that differentiate median and lateral mesoscutal lobes are characteristic of many Pteromalidae and other Chalcidoidea. A uniformly convex mesoscutum could be a synapomorphy for Tanaostigmatidae *s. s.* + *Cynipencyrtus* + Encyrtidae, but notaular structure of *Cynipencyrtus* is aberrant if the taxa constitute a monophyletic lineage. Most Encyrtidae either lack or have incomplete notauli, but these structures likely represent secondary reduction because when incomplete they originate widely apart adjacent to the mesothoracic spiracles as in Tanaostigmatidae *s. s.* The notauli are also incomplete in *Cynipencyrtus*, but they apparently originate about midway between each spiracle and the midline (Fig. 27). Simple reduction is insufficient to explain this difference in structure from the notauli of Tanaostigmatidae *s. s.* and Encyrtidae. It also needs to be clarified whether the similar notauli of *Neanastatus* and *Cynipencyrtus* represent convergence or indicate the notaular structure of *Cynipencyrtus* is symplesiomorphic relative to that of Tanaostigmatidae *s. s.* and Encyrtidae.

5. Mesonotal flexing mechanism. Most Eupelmidae have a straight-transverse transscutal articulation with the posterior margin of the mesoscutum and anterior margin of the scutellar-axillar complex hingelike articulating mesally for mesonotal flexing (Gibson 1989, fig. 59). The only exception is *Neanastatus*, in which the transscutal articulation is straight-transverse but the posterior margin of the mesoscutum is free from the anterior margin of the scutellar-axillar complex. When the mesonotum is flexed, a distinct membranous region separates the two margins (*cf.* Figs 31, 32; Gibson 1989, fig. 62). The scutellar-axillar complex has a very slender depressed flange along its anterior margin (Fig. 32: scf) that is overlain by the posterior margin of the mesoscutum when the mesonotum is not flexed (Fig. 31). The mesonotal articulatory structures of *Cynipencyrtus* and Encyrtidae resemble that of *Neanastatus*. In *Cynipencyrtus*, the slightly curved posterior margin of the mesoscutum overlies the anterior margin of the scutellar-axillar complex so that the inner angles of the axillae appear to be separated when the mesonotum is not flexed (Fig. 36), though they are seen to be contiguous beneath the transparent cuticle of the mesoscutum (Fig. 27) and when the mesonotum is flexed (Fig. 35). There is no distinct membranous region between the mesoscutum and scutellar-axillar complex when the mesonotum is flexed (Fig. 35) because the posterior margin of the mesoscutum still overhangs the anterior margin of the scutellar-axillar complex slightly, though from posterior view the two are seen to be separated by a membranous line that allows flexing (Fig. 35). Many Encyrtidae have a mesonotal flexing mechanism similar to that of *Cynipencyrtus* because the mesoscutum and scutellar-axillar complex are closely associated when the mesonotum is flexed (Fig. 28), though the posterior margin of the mesoscutum usually is more distinctly curved or angulate mesally (Noyes 1997, figs 13–18) and the scutellar-axillar complex usually has a more distinct depressed or smooth band anteriorly (Fig. 28). As in *Cynipencyrtus*, the depressed region is concealed by the posterior of the mesoscutum when the mesonotum is not flexed (Gibson 1989, fig. 66; Noyes 1997, *cf.* figs 21, 22). However, the extent to which the mesoscutum and scutellar-axillar complex are separated when the mesonotum is flexed is quite variable in Encyrtidae, some having a distinct band of membrane between the two sclerites (Fig. 29; Gibson 1989, fig. 76) similar to *Neanastatus* (Fig. 32) and Tanaostigmatidae *s. s.* (Fig. 30). All Tanaostigmatidae *s. s.* have the mesoscutum and scutellar-axillar complex separated comparatively widely by membrane when the mesonotum is flexed (Fig. 30) and, similar to those encyrtids with a distinct membranous region separating the sclerites, there is a depressed, laterally widened flangelike region along its anterior margin (Fig. 30: scf). Unlike in Encyrtidae, the anterolateral angles of the axillae project anteriorly into the posterior margin of the mesoscutum so that this is somewhat M-like rather than transverse (*cf.* Figs 29, 30).

Four of five females and both males of *L. janzeni* have the mesonotum visible in dorsal view. The mesonotum is not conspicuously flexed in any specimen and the posterior margin of the mesoscutum is almost straight without any conspicuous separation between it and the anterior margin of the scutellar-axillar complex (Figs 4, 6–8). The inner angles of the axillae appear to be separated mesally behind the mesoscutum (Figs 1, 4, 7) except for one male (BaJWJ-406), in which the inner angles of the axillae are contiguous a short distance behind the posterior margin of the mesoscutum (Fig. 8).

Analysis. The different appearance of the axillae in specimens of *Cynipencyrtus* with a flexed (Fig. 35) or unflexed (Fig. 36) mesonotum suggest that the mesonotum is flexed in BaJWJ-406 (Fig.8) and unflexed in the other specimens of *L. janzeni* (Figs 4, 7). The absence of any distinct separation between the sclerites or an evident rim along the anterior margin of the scutellar-axillar complex of BaJWJ-406 (Fig. 8) further indicates the mesonotal flexing mechanism of *L. janzeni* is very similar to that of *Cynipencyrtus* (Fig. 35). The presence of a depressed rim along the anterior margin of the scutellar-axillar complex, but with this still closely associated with the posterior margin of the mesoscutum when the mesonotum is flexed (Fig. 28), likely is the groundplan structure for Encyrtidae. A distinct separation between the sclerites is characteristic of only some encyrtids (Fig. 29), suggesting that this structure evolved secondarily within the family. Although the distinct membranous bands of *Neanastatus* (Fig. 32), Tanaostigmatidae *s. s.* (Fig. 30) and some Encyrtidae (Fig. 29) likely are convergent, the similar mesonotal flexing mechanisms could indicate a common ancestor having a

structure similar to that of *L. janzeni*, *Cynipencyrtus* or the hypothesized groundplan structure of Encyrtidae. The extreme mesonotal flexing mechanism of Tanaostigmatidae *s. s.*, with the anterolateral angles of the axillae projecting into the mesoscutum (Fig. 30), is autapomorphic for the group.

6. Shape of axillae. Size and shape of the axillae are variable in Eupelmidae, even in the same subfamily (see figs in Gibson 1989), though in Calosotinae and Eupelminae the axillae are always longer than wide, even when triangular with contiguous inner angles (see figs in Gibson 1989, 1995). Within Neanastatinae, *Eopelma* and *Neanastatus* (Fig. 32: ax; Gibson 1989, fig. 62) have elongate axillae that are widely separated by the base of the scutellum, whereas *Lambdobregma* has more transverse-triangular axillae, though they are separated from the scutellum by a variably crenulate furrow (Gibson 1989, fig. 39). *Leptoomus janzeni* (Figs 4, 6–8), *Cynipencyrtus* (Figs 27, 35, 36) and most Encyrtidae (Fig. 29: ax; Noyes 1997, figs 13–18, 21, 22) have distinctly transverse-triangular axillae with contiguous inner angles (unless superficially separated by the posterior margin of the mesoscutum) that are flat and in the same plane as the scutellum. Tanaostigmatidae *s. s.* also have triangular axillae with contiguous inner angles (Fig. 30: ax), but they are more elongate-triangular and much larger than the axillae of the previous taxa.

Analysis. Transverse-triangular axillae likely are apomorphic relative to more elongate-triangular axillae and represent a possible synapomorphy for *L. janzeni* + *Cynipencyrtus* + Encyrtidae. Relative scutellar-axillar structure of Tanaostigmatidae *s. s.* is more similar to many Melanosomellini, particularly some genera that have the anterolateral angles of the medially contiguous or subcontiguous axillae anteriorly angulate so that the transscutal articulation is more or less M-like.

7. Relative structure of acropleuron and metacoxa. Not only is the acropleuron completely enlarged in *L. janzeni*, but its posterior margin is broadly rounded, the metapleuron is reduced to a small triangular region dorsally, and the comparatively long metacoxa is inserted high on the mesosoma with an anterodorsal line of attachment so that it projects almost vertically behind the acropleuron (Fig. 11). *Cynipencyrtus* (Gibson 1989, fig. 48) and Tanaostigmatidae *s. s.* (Fig. 38; Gibson 1989, fig. 49; LaSalle 1987, fig. 5) have very similar structures. Encyrtidae also have a completely enlarged acropleuron, which is broadly rounded to variably angulate posteriorly, but the metacoxa is comparatively short and has a dorsal line of attachment so that it projects obliquely in a posteroventral direction, and usually it inserts more ventrally (Gibson 1989, fig. 51; Noyes 1997, figs 7, 8). Size of the acropleuron is variable in Eupelmidae, but when completely enlarged its posterior margin is more or less angulate and the metacoxa has a dorsal line of attachment so that it projects obliquely in a posteroventral direction (Fig. 37; Gibson 1989, figs 29, 38, 40, 43).

Analysis. Monophyly of *L. janzeni* + *Cynipencyrtus* + Tanaostigmatidae *s. s.* could be supported by combined acropleural-metacoxal structure, though different chalcidoids without an enlarged acropleuron also exhibit the two different metacoxal attachment structures. Many Melanosomellini and Agaonidae also have a comparatively high metacoxal attachment and vertical orientation, which may indicate some functional advantage of this structure for taxa associated with galls.

8. Mesocoxal articulatory structure. Structure of the mesocoxal articulatory mechanism is variable in Eupelmidae, particularly within Eupelminae. Male Eupelminae have the posterior margin of the mesosternum differentiated as a slender, transverse rim that abuts the anterior margin of the mesocoxae (Gibson 1986, figs 11, 12). Furthermore, the mesotrochantinal plate, which is quite broad and bears the mesotrochantinal lobes laterally, projects internally at a right angle to the mesosternum (Gibson 1986, fig. 13) so that it is concealed by the mesocoxae (see figs in Gibson 1995). This structure is similar to most other Chalcidoidea and is considered plesiomorphic (Gibson 1989). Female Eupelminae have an apomorphic structure in which a narrow mesotrochantinal plate, terminated by the mesotrochantinal lobes, projects posteriorly in the same plane as the mesosternum, and there is a conspicuous membranous region between the incurved posterior margin of the mesosternum and base of each mesocoxa (Gibson 1986, fig. 17; Gibson 1989, figs 102, 103). These modifications allow the mesocoxae of female Eupelminae to rotate anteriorly out of the combined mesocoxal fossae (Gibson 1986, fig. 18; Gibson 1989, fig. 38) so that they and the middle legs can extend straight forward (Gib-

son 1986, fig. 22). Both sexes of Calosotinae have mesocoxal articulatory structures similar to female Eupelminae, though size of the membranous region anterior to each mesocoxa varies among the genera (Gibson 1989, figs 99–101), with the putative most basal genus having the smallest membranous regions (Gibson 1989, fig.99). The mesocoxal articulatory structure of Tanaostigmatidae *s. s.* is also similar to Calosotinae and female Eupelminae because the mesocoxae can rotate entirely out of the fossae and there is a comparatively large membranous region anterior to each coxa (Figs 39, 40: mb). However, unlike in Calosotinae and female Eupelminae, the mesotrochantinal lobes do not project into the anteroventral margin of the mesocoxa and they are not visible externally (Gibson 1989, fig. 95). Rather, the comparatively broad mesotrochantinal plate of Tanaostigmatidae *s. s.* is inflected internally (Gibson 1989, fig. 118) and each quite widely separated mesotrochantinal lobe (Figs 39, 40: mtl) articulates with the respective mesocoxa under an overlying basomedial lobe of the coxa (Figs 39, 40: bml). Also unique to Tanaostigmatidae *s. s.* is that the mesosternum is quite deeply depressed posteromedially so that in ventral view the mesofurcal pit (Fig. 40: mfp) is at a lower level than the mesosternum, anteromesal to arcuate bands of shiny cuticle between the mesosternum and each mesocoxa (Fig. 39).

In Neanastatinae, the mesotrochantinal plate is inflected internally (Gibson 1989, figs 112–114) and the mesocoxae cannot rotate out of the fossae. However, all genera except *Lambdobregma* have a basally widened groove on the lateral surface of the mesocoxa so that there is a variably distinct cavity between it and the pleurosternum laterally (Gibson 1989, figs 45, 46). This lateral cavity is much wider in *Eopelma* (Fig. 37: mb) than in other Neanastatinae and in ventral view each mesocoxa has a distinct transverse membranous region over about the outer half of its anteroventral margin (Fig. 44: mb), which differentiates a narrower and therefore more distinct basomedial lobe than in *Neanastatus* or *Metapelma* (*cf.* Fig. 44 with Gibson 1989, figs 93, 94). The mesocoxal articulatory structure of *Cynipencyrtus* (Fig. 43) is comparatively plesiomorphic because the mesotrochantinal plate is inflected internally (Gibson 1989, fig. 119) and the posterior margin of the mesosternum abuts the base of the mesocoxae without a membranous region ventrally or a well differentiated mesocoxal basomedial lobe (Gibson 1989, fig. 96). However, similar to *Neanastatus* and *Metapelma*, the mesocoxa has a basally widened groove and a small cavity laterally between it and the pleurosternum (Fig. 43: grv; Gibson 1989, fig. 47). Mesocoxal articulatory structure is variable in Encyrtidae. Most encyrtids have the posterior margin of the mesosternum transverse with a differentiated rim behind the mesofurcal pit (Figs 41, 42) and only quite a small cavity in the anterior margin of the mesocoxa laterally (Fig. 41). However, some encyrtids have a more distinct, transverse membranous region along the anterolateral margin of the coxa (Fig. 42) or even quite a large, subcircular ventral membranous region (Gibson 1989, figs 97, 98). Increased size of the membranous region in Encyrtidae correlates with a narrower and more distinctly differentiated mesocoxal basomedial lobe (Gibson 1989, figs 97, 98). The mesotrochantinal plate is inflected internally in all encyrtids and the quite widely spaced mesotrochantinal lobes are overlain by the respective basomedial lobe of each mesocoxa (Figs 41, 42). The mesotrochantinal plate is also inflected internally in *L. janzeni* (Fig. 15: mtp) and the posterior margin of the mesosternum is straight-transverse with a differentiated rim behind the mesofurcal pit (Figs 10, 13, 15). The mesocoxa lacks a basally widened groove laterally (Figs 13, 14), but each has a transverse membranous region along the anterolateral ventral margin (Figs 9, 13, 14), which differentiates quite a distinct mesocoxal basomedial lobe (Fig. 14).

Analysis. The only common name associated with Eupelmidae, back-rolling wonders, was originated by Clausen (1927) to describe how *Anastatus mirabilis* (Walsh and Riley) (Eupelminae) contorts into a U-shape during jumping (see Gibson 1986) and usually tumbles upon landing. Gibson (1986) postulated that the ability to rotate the mesocoxae forward in some taxa with an enlarged acropleuron evolved so that the middle legs could be directed straight forward to protect the head and antennae on landing. The different mesocoxal articulatory structures described above suggest several similar transformation series from plesiomorphic "male eupelmine-like" to apomorphic "female eupelmine-like" articulatory structures. Calosotinae (Gibson 1989, figs 99–101), female Eupelminae (Gibson 1989, figs 102, 103), Tanaostigmatidae *s. s.* (Gibson 1989, fig. 95)

and some Encyrtidae (Gibson 1989, fig. 97) have apomorphic structures with distinct membranous regions ventrally anterior to the mesocoxae that allow the mesocoxae to be rotated from the combined mesocoxal fossa. Except in Encyrtidae, the membranous regions appear to be more a part of the mesosternum than the mesocoxae because the posterior margin of the mesosternum is distinctly incurved (Gibson 1989, figs 99–103). Noyes and Hayat (1984, p. 248) stated that Charitopodini (Encyrtidae: Tetracneminae) "probably contains some of the most primitive encyrtids known ... and most genera have membranous areas surrounding the mid coxae which allow the mid legs to be flexed forward ... characteristic of the Tanaostigmatidae and some Eupelmidae". However, most Encyrtidae have only a small cavity between the mesocoxa and mesosternum laterally (Fig. 41) similar to *Cynipencyrtus* (Fig. 43) or a transverse membranous region laterally along the anteroventral margin of the mesocoxa (Fig. 42) similar to *L. janzeni* (Fig. 14) or *Eopelma* (Fig. 44). This suggests that the structures of Encyrtidae comprise a transformation series in which a small lateral cavity (Fig. 41) is the likely groundplan structure from which secondarily evolved a wider (Fig. 42) or quite large ventral membranous region (Gibson 1989, fig. 97). If so, the latter structure is convergent to Tanaostigmatidae *s. s.*, Calosotinae and female Eupelminae. The mesocoxal articulatory structure of Tanaostigmatidae *s. s.* (Figs 38, 39) is also very likely convergent to those of Calosotinae and female Eupelminae based on several differences in structure described above. Furthermore, the transverse membranous region along the anterolateral ventral margin of the mesocoxa in *Eopelma* (Fig. 44) undoubtedly was derived from a structure similar to that possessed by *Neanastatus* (Gibson 1989, fig. 46) and *Metapelma* (Gibson 1989, fig. 45) through widening of the cavity between the mesocoxal groove and pleurosternum in a transformation similar to that described for Encyrtidae. The similar structures of *Cynipencyrtus* (Fig. 43), *Neanastatus* and *Metapelma* could indicate a common ancestor between Neanastatinae and *Cynipencyrtus* if absence of a coxal groove is a secondary feature of *Lambdobregma*. The mesocoxa of *L. janzeni* lacks a lateral, basally widened groove (Figs 13, 14), but the ventral membranous region along its anterior margin could have been derived from a lateral cavity that was secondarily widened, thereby differentiating a more distinct basomedial lobe similar to some Encyrtidae and *Eopelma*. The mesocoxae of *L. janzeni* appear to have at least some ability to rotate anteriorly. The internally inflected mesotrochantinal plate consists of a comparatively narrow median portion that bears the trochantinal lobes and is overlain by the mesocoxal basomedial lobes, plus a slender region between the mesosternum and internal subcircular membranous regions anterior to each coxal base (Fig. 15). Secondary exposure of the slender ventral portion of the mesotrochantinal plate and the internal membranous regions would result in a structure similar to that of Tanaostigmatidae *s. s.* (*cf*. Figs 15, 39, 40). If so, the mesocoxal articulatory structure of *L. janzeni* could indicate it is more closely related to Tanaostigmatidae *s. s.* than to *Cynipencyrtus* or Encyrtidae.

9. Position of mesocoxae and structure of mesosternum. One feature that LaSalle and Noyes (1985, p. 1261) used to differentiate Encyrtidae from Tanaostigmatidae *s. l.* was "articulation of middle coxa usually anterior to midline of mesosternum" versus "posterior to midline of mesosternum". However, in ventral view the anterior margin of the secondarily exposed mesocoxal fossa in Tanaostigmatidae *s. s.* is very near or even anterior to the midline of the mesosternum (Fig. 39; Gibson 1989, fig. 95) similar to Encyrtidae (Gibson 1989, figs 97, 98). As a result, the mesosternum is strongly transverse in both taxa (Figs 39–42). In lateral view, position of the mesocoxal articulation relative to the midline of the mesopleuron is much less obvious in Tanaostigmatidae *s. s.* because the membranous region anterior to the mesocoxa is not visible and the anteriorly protuberant prepectus adds visually to the length of the pleuron (Fig. 38; Gibson 1989, *cf*. figs 49, 95). The mesocoxae are attached obviously posterior to the midline in *Cynipencyrtus* (Gibson 1989, fig. 96), *L. janzeni* (Figs 9–11, 13) and Eupelmidae (Fig. 37; Gibson 1989, figs 91–94). The mesosternum is quadrate or slightly transverse in *Cynipencyrtus* (Fig. 43) and *L. janzeni*, whereas in Eupelmidae it is obviously longer than wide. Furthermore, a sulcate discrimen is characteristic of all Neanastatinae (Fig. 37: dsc; Gibson 1989, figs 45, 46, 92–94) and most Calosotinae (Gibson 1989, figs 32, 91) and Eupelminae, including the hypothesized basal lineages of the latter two subfamilies. A median darker line on the mesosternum indicates the dis-

crimen of most Tanaostigmatidae *s. s.*, but this is not sulcate (*cf.* Figs 39, 40), as for *Cynipencyrtus* (Fig. 43; Gibson 1989, figs 47, 96). Most Encyrtidae also appear to have the discrimen indicated only by a darker line rather than a sulcus (Gibson 1989, figs 97, 98, 115, 116), though some have at least a partial, shallow, median groove (Fig. 41).

Analysis. The posterior position of the mesocoxae in *L. janzeni*, *Cynipencyrtus* and Eupelmidae is symplesiomorphic and therefore largely uninformative. In Tanaostigmatidae *s. s.* the more anterior insertion of the mesocoxae and transverse mesosternum apparently result from secondary partial exposure of the mesotrochantinal plate and ventral membranous regions (Figs 39, 40), whereas in Encyrtidae they result from anterior displacement of the mesocoxae (Figs 41, 42). This difference indicates "advanced mesocoxae" are convergent in Encyrtidae and Tanaostigmatidae *s. s.*, and the two different structures are autapomorphic for the respective taxa. Most Encyrtidae lack the ability to rotate their mesocoxae from the combined fossa (see above). The distinctly more anterior position of the mesocoxae in Encyrtidae compared to other taxa may have evolved so that during a jump their middle legs could be directed forward sufficiently to protect the head and antennae or control tumbling during landing. If so, advanced mesocoxae in Encyrtidae is a functional adaptation equivalent to mesocoxal rotation in Tanaostigmatidae *s. s.*, female Eupelminae and Calosotinae. Except for *Eopelma*, members of Neanastatinae have unusually long middle legs compared to the other taxa and this may be a third adaptive method for protecting the head or controlling tumbling. The polarity of a sulcate discrimen is uncertain, but presence or absence of a sulcus appears to be correlated largely with length of the mesosternum in the taxa studied.

10. Speculum/linea calva. The fore wing of *L. janzeni* has a speculum, a broad bare region contiguous with the parastigma (Fig. 16: spc), similar to *Cynipencyrtus*, Tanaostigmatidae *s. s.* and most Eupelmidae. Encyrtidae as well as a very few Calosotinae, very few female Eupelmidae and three of the four genera of Neanastatinae have a linea calva, a very slender, oblique bare band separated from the parastigma. The absence of a linea calva from *Eopelma* is because the fore wing is completely setose and this undoubtedly is derived in Neanastatinae.

Analysis. The speculum of *L. janzeni* is a symplesiomorphic feature and therefore largely uninformative for inferring sister-group relationships. A linea calva likely is a groundplan feature of Neanastatinae, but the linea calva characteristic of Aphelinidae and the few Calosotinae and female Eupelminae with a similar bare band indicates multiple origins for this feature.

11. Protibial dorsoapical spicules. Gibson (1989, character 18) recorded presence of protibial dorsoapical spicules in Eupelmidae (Gibson 1989, figs 134, 135: pas) and absence in Tanaostigmatidae *s. s.* and Encyrtidae. Presence of spicules was undetermined for *Cynipencyrtus*. All Eupelmidae were stated to have one or more spicules (presence and absence coded for *Eusandalum* in the matrix is erroneous because the coding for characters 18 and 20 is reversed). Furthermore, Tanaostigmatidae *s. s.* was described as having a unique feature, an apical "cuticular denticle". Further study shows that all genera of Neanastatinae except *Lambdobregma* have a single protibial spicule dorsoapically towards the inner side (Fig. 22: pas). Species of *Lambdobregma* lack the spicule but have a cuticular denticle apically on the outer side (Fig. 23) similar to Tanaostigmatidae *s. s.* (Fig. 25), but also to *Cynipencyrtus* (Fig. 24) and at least some Encyrtidae (Fig. 26). The apical protibial structure of *Lambdobregma* differs from these latter taxa only in having uniform setae on the inner side (Fig. 23) rather than some stronger spinelike setae apically (Figs 24–26: pls). Individuals of *L. janzeni* have a dorsoapical projection (Fig. 21: pas), which appears to be articulated and therefore a dorsoapical spicule rather than a denticle, plus two strong spines apicolaterally (Fig. 21: pls).

Analysis. Absence of protibial dorsoapical spicules is hypothesized as plesiomorphic, but presence of spicules is not reliable for phylogenetic inference because they are present in many groups that parasitize wood-boring insects (Gibson 1989). The apparent presence of a spicule in *L. janzeni* could indicate it was a parasitoid of a wood-boring beetle or, similar to most Eupelminae, represent a retained symplesiomorphy. If the latter, *L. janzeni* is indicated as basal to Tanaostigmatidae *s. s.* + *Cynipencyrtus* + Encyrtidae. However, common

possession of a protibial apical denticle by the latter taxa likely is not evidence of their monophyly. Distribution of a protibial denticle is not known accurately throughout Chalcidoidea, but at least some other chalcidoids have a denticle, including many Ormocerinae and Agaonidae. Further study is necessary is to accurately determine the distribution of protibial apical denticles and spicules in Chalcidoidea and any functional differences or ecological correlations for the two structures. The absence of strong apicolateral spines in *Lambdobregma* (Fig. 23) and other Neanastatinae (Fig. 22) may be phylogenetically informative relative to their presence in *L. janzeni* (Fig. 21), *Cynipencyrtus* (Fig. 24), Tanaostigmatidae *s. s.* (Fig. 25) and Encyrtidae (Fig. 26). However, this feature has not been studied previously and accurate distribution data is required before phylogenetic inference.

12. Mesotibial apical pegs. The inner surface of the mesotibia of *L. janzeni* has stronger, spine- or peg-like setae apically (Figs 18, 19 insert: map) similar to *Cynipencyrtus* (Gibson 1989, fig. 144), Encyrtidae, most female Eupelminae and all Neanastatinae (*cf.* figs in Gibson 1989) except *Eopelma*. Mesotibial apical pegs are lacking from Tanaostigmatidae *s. s.* and Calosotinae except for some species of *Calosota* Curtis (Gibson 1989).

Analysis. Mesotibial apical pegs are part of the functional complex correlated with an enlarged acropleuron and jumping; therefore, convergent evolution of pegs correlated with independent enlargements of the acropleuron is likely (Gibson 1986). The absence of mesotibial pegs in *Eopelma* likely reflects secondary loss within Neanastatinae. Absence from Tanaostigmatidae *s. s.* could be symplesiomorphic or synapomorphic through secondary loss.

13. Mesotarsal pegs. Gibson (1989) described the varied mesotarsal peg patterns of *Cynipencyrtus*, Tanaostigmatidae *s. s.* and Eupelmidae. Tanaostigmatidae *s. s.* were stated to either have setalike spines ventrally (Gibson 1989, state 1) or more peglike spines along only the posterior margin (Gibson 1989, state 2, fig. 143), whereas *Cynipencyrtus* was described as having peglike spines along both margins, but with a greater number of pegs along the anterior margin (Gibson 1989, state 4, fig. 144). Mesotarsal peg pattern is highly variable in Eupelmidae, but Neanastatinae is unique in having pegs only along the anterior ventral margin and with these extending distally along the apical margin of each tarsomere (Gibson 1989, state 3, fig. 142). Encyrtidae also have variable mesotarsal peg patterns, with some encyrtids having pegs along the anterior margin that continue distally along the apical margin or that form one or more oblique rows on the shorter tarsomeres, and often also with pegs on the posterior and outer surfaces. The mesotarsal peg pattern of *L. janzeni* appears to be most similar to *Cynipencyrtus* (*cf.* Fig. 19 with Gibson 1989, fig. 144), but I am uncertain of the exact number and arrangement of pegs other than they definitely do not extend distally along the anteroapical margin of each tarsomere (Figs 18, 19).

Analysis. The different patterns of mesotarsal pegs in Eupelmidae as well as in other taxa with an enlarged acropleuron indicate these evolved more than once as part of the functional complex correlated with increased jumping ability (Gibson 1989). Phylogenetic inferences involving *L. janzeni* are also unreliable because of uncertainty concerning its true mesotarsal peg pattern, but at least the pattern does not support a relationship with Neanastatinae.

14. Cerci. Bouček (1988) proposed that presence of at least one strongly kinked and unusually long cercal seta is an autapomorphy of Tanaostigmatidae *s. s.* Noyes (2000) also stated that cerci that are advanced anteriorly on the metasoma is characteristic of all Encyrtidae except for two genera.

Analysis. *Leptoomus janzeni* (Fig. 17: cer) appears to lack a kinked cercal seta and definitely does not have the cerci advanced on the metasoma, but both of these features are plesiomorphies and therefore phylogenetically uninformative.

Relationships and classification of *L. janzeni*. Among the 19 families of Chalcidoidea, an acropleuron that is convexly enlarged so as to extend to the metapleuron at least dorsally is characteristic of female Eupelminae, three of four genera of Neanastatinae, six of eight genera of Calosotinae, Tanaostigmatidae *s. s.*, *Cynipencyrtus*, Encyrtidae, a very few Aphelinidae (Gibson 1989, character 3) and *L. janzeni*. Because the

mesopleura of these taxa are so conspicuously different from other Chalcidoidea, it has long been proposed as evidence that Tanaostigmatidae *s. l.*, Encyrtidae and Eupelmidae comprise a monophyletic group. The completely enlarged acropleuron of some Aphelinidae (e.g., *Coccobius* Ratzeburg, *Eutrichosomella* Girault) is certainly convergent to the other taxa (Gibson 1989), but the different mesopleural structures of Calosotinae and Neanastatinae (see figs in Gibson 1989) also indicate separate transformation series in enlargement of the acropleuron within these two subfamilies. Furthermore, the lack of an enlarged acropleuron in male Eupelminae suggests another independent origin of a completely enlarged acropleuron for females of this subfamily (Gibson 1989). In all instances, an enlarged acropleuron is just one of several skeletomusculature features that are variously modified in the different taxa and that together function to improve jumping ability (Gibson 1986). Trjapitzin (1977) suggested that the selection pressure for the modifications and increased jumping ability in Encyrtidae was to escape predators such as ants and some neuropterans while searching for homopteran hosts on vegetation. Gibson (1986) suggested a similar reason for the modifications and increased jumping ability in Eupelmidae, that is, for rapid escape from predators while exposed on dead trees searching for woodboring hosts. An acropleuron enlarged completely to the metapleuron is a postulated groundplan feature of only *L. janzeni*, *Cynipencyrtus*, Tanaostigmatidae *s. s.* and Encyrtidae, and therefore could support monophyly of these taxa. However, the other skeletomuscular features correlated with an enlarged acropleuron and increased jumping ability differ among the taxa, which may indicate that the functional complexes evolved convergently in at least some of the taxa.

Of Eupelmidae, Tanaostigmatidae and Encyrtidae, Encyrtidae is the most strongly supported as monophyletic (see Gibson *et al.* 1999) though most of their differentiating features either are not shared by all members (e.g., cerci almost always advanced on metasoma, marginal vein usually very short) or rarely are possessed by other chalcidoids (e.g., outer plates of ovipositor connected to eighth metasomal tergite by paratergites or completely separated, prepectus with a prepectal strut, and fore wing with linea calva). The anteriorly advanced position of the mesocoxae is autapomorphic for Encyrtidae (analysis 9). Two other proposed autapomorphies of Encyrtidae cannot be evaluated for fossil taxa. Heraty *et al.* (1997, fig. 19) proposed that the interfurcal muscle attaching to the lateral arm of the mesofurca underneath the laterophragmal muscle was autapomorphic and Noyes (2000) proposed that tentorial arms reaching the frontovertex between the inner eye margin and torulus is another autapomorphy. This latter hypothesis requires further study. Dzhanokmen (1994) hypothesized that the dorsal arm of the tentorium ending near the inner eye margin is a groundplan feature of Pteromalidae, but also reported that the arm reached the head surface "at a distance" from the inner eye margin in Spalangiinae and Eunotinae and "near the antennal toruli" in four other subfamilies. Regardless, because *L. janzeni* exhibits none of the observable features that differentiate Encyrtidae there is no evidence to support its classification in this family.

Classification of *L. janzeni* in Eupelmidae is more difficult to evaluate because no unequivocal autapomorphies determine membership of this family. Membership is based primarily on absence of the apomorphic features that distinguish Encyrtidae and Tanaostigmatidae, and classification of Calosotinae, Eupelminae and Neanastatinae as one family may represent a paraphyletic or even polyphyletic grade-level taxon (Gibson 1989). Male Eupelminae and both sexes of some genera of Calosotinae, particularly *Archaeopelma* Gibson, are similar in structure to Cleonyminae (Pteromalidae). This suggests that the former two subfamilies are closely related to Cleonyminae or some lineage(s) of Cleonyminae, but relationships of Neanastatinae to Calosotinae, Eupelminae and other Chalcidoidea are obscure (Gibson 1989). Despite these uncertainties, classification of *L. janzeni* in Eupelminae is excluded because Eupelminae is characterized by strongly dimorphic sexes (Gibson 1989). Different combinations of features define Calosotinae and Neanastatinae, none of which are unique to the respective subfamily (Gibson 1989), but *L. janzeni* is excluded from Calosotinae based on the absence of external mesotrochantinal lobes (analysis 8) and a very different pronotal structure (analysis 3), and is excluded from Neanastatinae based on absence of mesotarsal pegs from along the anteroapical margin of the tarsomeres (analysis 13), presence of a speculum (analysis 10), and a quadrate mesosternum without a

sulcate discrimen (analysis 9). Two features are shared by *L. janzeni* and some or most Eupelmidae–complete, broadly separated furrows that differentiate median and lateral mesoscutal lobes (analysis 4), and apparently a protibial dorsoapical spicule (analysis 11). However, these two features are almost certainly symplesiomorphic and therefore not evidence that *L. janzeni* is most closely related to Eupelmidae.

Tanaostigmatids were classified initially as part of Eupelmidae until Peck (1951) segregated them as their own family in a catalog. He did not provide any justification for this new classification, but when LaSalle and Noyes (1985, p. 1261) transferred *Cynipencyrtus* from Encyrtidae to Tanaostigmatidae they stated the essential feature that distinguishes tanaostigmatids from eupelmids and encyrtids, "the presence of a large prepectus, which is distinctly swollen anteriorly". Gibson (1989) suggested that the prepectal structure of *Cynipencyrtus* represents an intermediate stage in the evolution of the prepectal structure of Encyrtidae (analysis 3), and thus questioned the monophyly of Tanaostigmatidae *s. l.* Monophyly of Tanaostigmatidae excluding *Cynipencyrtus* appears to be strongly supported by several features, including a unique pronotal-prepectal structure (analysis 3), extreme mesonotal flexing (analysis 5), unique mesocoxal articulation structure (analyses 8, 9), unique presence of at least one strongly kinked cercal setae (analysis 14), and possibly by absence of mesotibial apical pegs (analysis 12) and a bilobed clypeus (analysis 1). Although both *Cynipencyrtus* and *L. janzeni* lack these features, *L. janzeni* has an externally exposed, anteriorly protuberant prepectus that has the posterior margin truncate and apparently immoveable relative to the acropleuron, and which in ventral view form a deep U-shape with the anterior margin of the mesosternum. The apomorphic prepectal structure supports a sister-group relationship with Tanaostigmatidae *s. s.* if the similarity is synapomorphic at this level. The mesocoxal articulatory structure of *L. janzeni* could also support a sister-group relationship with Tanaostigmatidae *s. s.*, though there appears to be considerable homoplasy in this feature (analysis 8). However, as discussed under analysis 3, an externally protuberant prepectus could be synapomorphic at the level of *L. janzeni* + Tanaostigmatidae *s. s.* + *Cynipencyrtus* + Encyrtidae. The combined structure of the mesothoracic spiracle, pronotum and prepectus of Tanaostigmatidae *s. s.* and that of *Cynipencyrtus* and Encyrtidae can all be derived from a structure similar to that of *L. janzeni*. Even though the structures of *Cynipencyrtus* and Encyrtidae are superficially quite different from those of *Leptoomus* and Tanaostigmatidae *s. s.*, the differences may result from secondary modification, in which case an externally protuberant prepectus represents a retained symplesiomorphy at the level of *L. janzeni* + Tanaostigmatidae *s. s.* Consequently, relative mesothoracic spiracle-pronotal-prepectal structure may support *L. janzeni* as the sister group of Tanaostigmatidae *s. s.* + (*Cynipencyrtus* + Encyrtidae). The other two postulated uniquely retained symplesiomorphies of *L. janzeni* (analyses 4, 11) further support such a sister-group relationship, with loss of furrowlike notauli and loss of an articulated protibial dorsoapical spicule representing possible synapomorphies for Tanaostigmatidae *s. s.* + *Cynipencyrtus* + Encyrtidae. However, different patterns of shared states of two other characters conflict with this hypothesis. A sister-group relationship of *L. janzeni* with *Cynipencyrtus* + Encyrtidae is supported by transverse-triangular axillae (analysis 6) and a 7-segmented funicle (analysis 2) in *Cynipencyrtus* and the postulated groundplan of Encyrtidae. One studied feature also supports possible monophyly of *L. janzeni* + Tanaostigmatidae *s. s.* + *Cynipencyrtus*–relative acropleural-metacoxal structure (analysis 7). If this relationship is accurate, the single transformation series hypothesized to explain the pronotal-prepectal structures of *Cynipencyrtus* and Encyrtidae is inaccurate, and the two similar structures represent independent transformation series of the mesoscutal process being lengthened interior to the pronotum.

Two other features that have been proposed to support the monophyly of *Cynipencyrtus* + Tanaostigmatidae *s. s.* + Encyrtidae or of just the latter two taxa cannot be examined for *L. janzeni*. Heraty *et al.* (1997, character 3, state 2) showed that the mesofurcae of *Cynipencyrtus*, Tanaostigmatidae *s. s.* and Encyrtidae all have similar "lyre shaped" lateral arms, which in Encyrtidae are somewhat flattened against the venter of the mesosoma. However, Heraty *et al.* (1997) also noted that *Eutrichosomella* has a lyre shaped mesofurca and suggested that this type might distinguish taxa with a short, stocky mesosoma, and likely is convergent. *Cynipencyrtus* and Tanaostigmatidae *s. s.* are additionally similar in having a mesofurcal bridge, but this feature is

symplesiomorphic (Heraty *et al.* 1997). LaSalle and LeBeck (1983, fig. 1) also hypothesized encyrtiform ovarian eggs as a synapomorphy for Tanaostigmatidae *s. s.* + Encyrtidae. The ovarian egg of *Cynipencyrtus* is of a simple, oblong, subcylindrical form (J. Heraty, pers. comm.). Consequently, ovarian egg structure does not support relationships of *Cynipencyrtus* with either Tanaostigmatidae *s. s.* or Encyrtidae. However, Clausen (1940) stated that Encyrtidae have either encyrtiform or stalked eggs, both of which are "two-bodied" in form, and also stated that the eggs of Aphelinidae are "of the two-bodied type such as is found in several other families" and that the eggs of Eupelmidae "bear a stalk of varying length at the anterior end". A more comprehensive survey of ovarian egg structure throughout Chalcidoidea is required, and particularly to determine the groundplan structure for Encyrtidae.

Analysis of character-state transformations involving *L. janzeni* and *Cynipencyrtus*, and of the likely groundplan states of Tanaostigmatidae and Encyrtidae is complicated by some members of Neanastatinae exhibiting similar features to one or more of the taxa. Gibson (1989) noted that the convex, triangular pronotum of Neanastatinae could be ancestral to the strongly transverse pronotum of Encyrtidae and *Cynipencyrtus* and the even more reduced pronotum of Tanaostigmatidae *s. s.* Furthermore, the fore wing linea calva of most Neanastatinae and the characteristic mesotarsal peg pattern of this subfamily are similar to some Encyrtidae. Some genera of Neanastatinae share other similarities with Tanaostigmatidae *s. l.* and/or Encyrtidae. Unlike other eupelmids, *Neanastatus* has an internally projected mesoscutal process that projects through the frontal surface of the prepectus, being more or less intermediate in structure between *Cynipencyrtus* and Encyrtidae (analysis 3). Individuals also have a derived mesonotal flexing structure (analysis 5) and, similar to *Cynipencyrtus*, posteriorly directed, linear notauli (analysis 4) and a mesocoxal articulatory structure with a cavity between the anterolateral margin of the mesocoxa and the pleurosternum (analysis 8). *Neanastatus* and *Eopelma* also have reduced numbers of funicular segments (analysis 2) and *Eopelma* has a mesocoxal articulatory structure similar to, and a pronotal-prepectal structure that could be ancestral to that of *L. janzeni*. Furthermore, *Lambdobregma* has a protibial apical denticle rather than a spicule and has more or less transverse-triangular axillae, though these are distinguished by furrowlike scutoscutellar sutures.

Conclusions

Based on current understanding of structure, a completely enlarged acropleuron, a comparatively short mesosoma correlated with a quadrate or transverse mesosternum, and an elongate mesoscutal process, could support monophyly of *L. janzeni* +Tanaostigmatidae *s. s.* + *Cynipencyrtus* + Encyrtidae. Structural evidence also indicates that *L. janzeni* is most likely the sister group of Tanaostigmatidae *s. s.* + (*Cynipencyrtus* + Encyrtidae) or possibly of just *Cynipencyrtus* + Encyrtidae. If either of these two hypotheses of relationships are accurate then classifying *Leptoomus* or *Cynipencyrtus* in Tanaostigmatidae renders this family paraphyletic relative to Encyrtidae. From a phylogenetic perspective, it would be more accurate to classify *Leptoomus* as its own family (if the first hypothesis is accurate) or to classify it along with *Cynipencyrtus* in Encyrtidae (if the second hypothesis is accurate). However, classifying either *Leptoomus* or *Cynipencyrtus* in Encyrtidae would render what is one of the more recognizable and demonstrably monophyletic families of Chalcidoidea as almost undefinable. Furthermore, skeletomusculature features that are modified somewhat differently in the three subfamilies of Eupelmidae, *Leptoomus*, *Cynipencyrtus*, Tanaostigmatidae *s. s.*, Encyrtidae and Aphelinidae to increase jumping ability suggest at least some convergent evolution. If, for example, the conspicuous modifications correlated with jumping in Tanaostigmatidae *s. s.* are hypothesized as convergently evolved to other taxa with an enlarged acropleuron, then such features as its vertical pronotum, scutellar-axillar structure, metacoxal attachment, protibial apical denticle, and bidentate clypeus might reflect possible relationships with Melanosomellini or Epichrysomallinae, two other taxa of gall makers or parasitoids of gall makers. Molecular techniques provide evidence of evolutionary relationships independent of morphology and should

help resolve questions whether similar features shared among the different taxa result from symplesiomorphy, synapomorphy or homoplasy. Further morphological studies are also necessary, particularly to better establish the groundplan features of Encyrtidae and to evaluate the monophyly of Neanastatinae and possible relationships with Tanaostigmatidae *s. l.* and Encyrtidae. Until evolutionary relationships of the treated taxa are established more confidently by such studies it seems prudent to classify *L. janzeni* along with *Cynipencyrtus* in Tanaostigmatidae.

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Appendix. Abbreviations used for terms on plates of illustrations

acs   acropleural sulcus
amp   secondary anterior margin of prepectus
ams   anterior margin of mesosternum
anp   anal plate
atp   anterior tentorial pit
ax   axilla
bml   basomedial lobe of mesocoxa
cer   cercus
dsc   discrimen
epm   mesepimeron
fn_x funicular segment 1–4
fps   frontal prepectal surface
grv   groove
hm   hyaline membrane
lps   lateral prepectal surface
map   mesotibial apical pegs
mb   membrane
mfp   mesofurcal pit
msp   mesoscutal process
msr   mesosternal rim
Mt_8 syntergum
mtl   mesotrochantinal lobe
mtp   mesotrochantinal plate
not   notaulus
opo   outer plate of ovipositor
pas   protibial dorsoapical spicule
pdl   pedicel
pls   protibial apicolateral spines
pl_3 metapleuron
pmp   posterior margin of pronotum
pp   prepectal pouch
ppi   posterolateral inflection of pronotum
pps   prepectal strut
pts   protibial spur
rp   resilin pad of pl_2-t_2c muscle
scf   scutellar flange
sec   secondary fine comb
sp1   mesothoracic spiracle
sp2   propodeal spiracle
sp3   metasomal spiracle
spc   speculum