

Review of the family Rotoitidae (Hymenoptera: Chalcidoidea), with description of a new genus and species from Chile

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A new genus and species of Rotoitidae, *Chiloe micropteron* Gibson and Huber, is described from females and one male from Chile. The taxon is the second known genus and species, and the male is the only one known for the family. Scanning electron micrographs illustrate external and internal structure of *C. micropteron* females, and external structure of *Rotoita basalis* Bouček and Noyes, the other described genus and species. The original description of the axillae, prepectus and fore wing venation given for *R. basalis* is amended and additional features are described based on re-examination of three specimens studied by Bouček and Noyes and study of one additional female. The family diagnosis is modified to include features of *Chiloe* and some previously undescribed characters that are used to infer relationships within Chalcidoidea. A six-segmented clava in females and possibly a five-segmented clava in males support monophyly of Rotoitidae. A 14-segmented antenna in females, structure of the prepectus, and a single site of origin from the axillar phragma for the mesotergal–mesotrochanteral muscle could indicate Rotoitidae as the basal lineage of Chalcidoidea, whereas ovipositor structure indicates Rotoitidae as the second-most basal lineage, with Mymaridae being the basal lineage.

KEYWORDS: Chalcidoidea, Rotoitidae, *Rotoita*, *Chiloe*, taxonomy, morphology, phylogenetic relationships, Chile.

Introduction

Rotoitidae is the most recently described of the 20 currently recognized families of Chalcidoidea (Bouček, 1988a, 1988b). The family was established for the new genus and species, *Rotoita basalis* Bouček and Noyes (1987), which was based on three fully winged females from New Zealand. The authors stated that they also

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had two other females from the North and South Islands of New Zealand that might represent two additional species.

Rotoitidae was assigned to Chalcidoidea based on the mesothoracic spiracle being at the external edge of the mesoscutum, level with the tegula, and the flagellum having apically free, longitudinal (multiporous plate) sensilla. Both these features are autapomorphies of Chalcidoidea. The family was diagnosed by a combination of features, among which a six-segmented clava in females is unique within Chalcidoidea. Other features that have been stated as differentiating Rotoitidae from other Chalcidoidea include the combination of 14-segmented antennae, four-segmented tarsi, apparent absence of a prepectus, absence of notauli, peculiar wing venation, and strongly transverse scutellum (Bouček and Noyes, 1987; Bouček, 1988a; Noyes and Valentine, 1989; Gibson *et al.*, 1999).

Since the description of Rotoitidae several new structural, behavioural, and molecular features have been found to be informative for inferring relationships among Chalcidoidea. These include features of the ovipositor (Quicke *et al.*, 1994), mesofurca and mesofurcal muscle structure (Heraty *et al.*, 1997), fore leg (Basibuyuk and Quicke, 1995), hind wing (Basibuyuk and Quicke, 1997), grooming behaviour (Basibuyuk and Quicke, 1999), and sequence information from the mitochondrial 16S rRNA gene (Dowton and Austin, 1994; Dowton *et al.*, 1997) and the D2 region of the 28S rDNA gene (Campbell and Heraty unpublished, as cited in Gibson *et al.*, 1999).

In this paper we describe a second genus and species of Rotoitidae, *C. micropteron* Gibson and Huber, from Chile based on females and the first known male for the family. Placement of *Chiloe* in Rotoitidae is substantiated by a 14-segmented antenna with a six-segmented clava in females, and four-segmented tarsi in combination with a bifurcate protibial spur in both sexes. Individuals of both sexes are micropterous and differ significantly in structure from *Rotoita*. We supplement the family diagnosis of Rotoitidae based on features of *Chiloe* and on reinterpretation of some features described originally for *Rotoita* by Bouček and Noyes (1987). We also describe some previously unstudied features important for inferring phylogenetic relationships of Rotoitidae based on states possessed by one or both of *Rotoita* and *Chiloe*. *Chiloe micropteron* and *R. basalis* are illustrated for the first time with scanning electron micrographs.

Material and methods

According to the locality labels, specimens of the new genus were collected in yellow pan traps placed in secondary growth forest. The collector, Dr L. Masner, provided more detailed information on the collection site, as discussed under Biology. Most specimens were critical-point dried and point mounted, but three were chemically dried with hexamethyldisilazane (HMDS) and three more have been kept in 70% ethanol. Eleven critical-point dried specimens were later cleared in 10% KOH, dehydrated, and mounted in Canada balsam on slides; four specimens were mounted on stubs and gold coated to obtain scanning electron micrographs. A brief diagnosis of *Chiloe* is given and the genus and species are characterized within a single description. The description is based on critical-point dried, point-mounted specimens of both sexes and, for antennal measurements, on slide-mounted specimens. Internal structure is based on slide-mounted specimens or scanning electron microscopy of females that were first used to illustrate external structure and were subsequently dissected.

The modified description of *Rotoita* is based on examination of the two paratypes of *R. basalis*, one unassigned female from New Zealand cited in Bouček and Noyes (1987) (North Island, AK, Huia, September 1980, B. M. May, Malaise trap in bush), and one newly collected, critical-point dried female that we identify as *R. basalis*. This specimen is in the Canadian National Collection of Insects (CNCI), Ottawa, was used for the SEM illustrations of *Rotoita*, and has the following label data: NEW ZEALAND: Bullock Creek, 26.II–1.III.1993, MT [Malaise trap] edge *Nothofagus* forest, L. LeSage. The specimen was gold coated for SEM but the gold was subsequently removed by soaking in a dilute solution of potassium cyanide. Figures 47 and 48 were drawn from the slide-mounted paratype from St Arnaud.

Micrograph negatives were scanned into a computer with a 35 mm scanner, digitized, enhanced, and the final plates compiled and labelled using Adobe Photoshop™. The original unretouched negatives are available from the senior author.

***Chiloe* Gibson and Huber, gen. nov.**

Rotoitidae; Gibson, 1993: 651 (figure 227).

Rotoita sp.; Heraty *et al.*, 1997.

Type species. Chiloe micropteron Gibson and Huber, sp. nov. Gender: neuter.

Etymology. Named after the coastal island in southern Chile where most of the specimens were collected.

Diagnosis. Fore wing lanceolate (figure 19) and extending at most to apex of second gastral tergum (figures 20a, 45); hind wing absent; ocelli absent (figures 1, 2, 7); prepectus independent, not fused ventrally with mesepisternum (figure 45); notauli present but indistinct (figures 8, 10); transscutal articulation present (figure 7); axillae obliquely subquadrate (figure 11) and separated by a broad furrow along anterior margin of scutellum (figures 7, 8, 10, 11); gaster without spiracles on tergum 6 (figures 24–26).

The above features differentiate *Chiloe* from *Rotoita*; further details are given in the description. Females of *Chiloe* have a 14-segmented antenna (figures 13, 45) with a subcompact six-segmented clava (figure 15) similar to females of *Rotoita* (figure 39, 40). Males of *Chiloe* have a 13-segmented antenna with a rather loose five-segmented clava. It remains to be shown whether this is a generic feature of *Chiloe* or a family characteristic because males of *Rotoita* are unknown.

***Chiloe micropteron* Gibson and Huber, sp. nov.**
(figures 1–32, 45)

Type material. HOLOTYPE ♀ (CNCI) on card point, labelled: 'CHILE: Chiloe Is., 50 m Terao nr Chonchi; Feb. 21, 23, 1988; P.T. [pan trap], 2nd growth forest; L. Masner, Chile Exp.'; 'Holotype *Chiloe micropteron* ♀ Gibson and Huber CNC No. 22425'. ALLOTYPE ♂ (CNCI) on card point, with same data as holotype but collection date 18–21 February 1988. PARATYPES: 24 females on points and 11 females on slides, with same data as holotype but some with collection dates 21–24 February 1988; 1 female, 'CHILE: Osorno Puyehue N.P. [National Park], Antillanca, 1200 m, 16.II.1988, *Nothofagus* tree line, L. Masner, Chile Exp.'; 1 female, 'Osorno, 250 m, Puyehue Nat. Park, ca Anticura; 12–14.II.1988, *Nothofagus* for., P.T., L. Masner, Chile Exp.'

Specimens are deposited in the CNCI, The Natural History Museum, London, and the National Museum of Natural History, Washington, DC.

Etymology. The species name refers to the short fore wings.

Female. Body length 940 μm (holotype), mean = 829 (691–973, $ssd=84$, $n=21$). Body brown to yellowish with dark setal sockets; face below toruli, lateral surface of mesosoma, and legs at least apically often slightly to distinctly lighter than mesosomal dorsum and metasoma; antenna with scape usually brownish and pedicel and flagellum yellowish white to white; mouthparts except mandibles, and intersegmental membrane white.

Head except occiput and postgenae uniformly, densely setose with short, straight, bristle-like setae originating from dark setal sockets (figures 1–3, 7); in frontal view broadly circular, about 1.2 times wider than high and 1.6–1.9 times wider than long (figure 1); in lateral view flattened hemispherical, with frons evenly and indistinguishably merging into vertex (figure 2); in dorsal view crescent-like with occiput concave (figure 7) and separated dorsally and laterally from gena by abrupt angle. Eye small, with about 32 ommatidia, and as setose as head capsule (figures 1, 2); in lateral view eye length about 0.88 malar space, 0.38 head width, and 1.4 eye width. Gena with distinct malar sulcus (figures 2, 45). Ocelli absent. Torulus slightly below middle of head, with ventral margin slightly below ventral margin of eye (figures 1, 2, 45); distance between toruli equal to distance between a torulus and eye. Clypeus semicircular, flat and sloping toward oral margin, but with apically reflexed rim (figure 5). Labrum flap-like with row of setae subapically (figures 4, 5). Mandibles well developed, crossing medially, each with a dorsobasal lobe articulating with oral margin (figure 4) and with two teeth, the ventral tooth small and pointed apically, the dorsal tooth very broad and apically serrate (figures 4, 5). Maxillary palpus two-segmented (figure 6); labial palpus one-segmented with three long apical setae (figure 6).

Antenna not distinctly geniculate, with straight to slightly curved, moderately clavate flagellum (figures 13, 45); antennal measurements given in table 1. Scape with short but distinct radicle about 0.15 times scape length, and distinctly broadened toward apex, as setose as head capsule (figure 14). Pedicel as setose as scape (figure 14). Flagellum with slightly shorter and denser setae ventrally on apical one or two funicular segments and clava (figure 15); funicle and clava each six-segmented; clava with distinct sutures between segments, the sutures with contiguous, elliptical pustules (figure 16).

Mesosoma box-like, with anterior, posterior and lateral faces almost vertical (figure 9), about 1.2 times as long as wide and 1.2 times as long as high. Pronotum in dorsal view not visible medially (figure 7); in lateral view glabrous except for two or three inconspicuous setae anterodorsally, and with its posterolateral margin almost straight and connected by membrane to anterior margin of mesepisternum (figure 9); mesothoracic spiracle at dorsal margin of pronotum distinctly anterior to tegula (figures 8, 9, 45). Prepectus an independent slender sclerite in membrane between pronotum and mesepisternum, as long as pronotal height (figure 45); concealed when pronotum extended to mesepisternum but not fused with anterior margin of mesepisternum or to corresponding prepectus ventrally. Prosternum vertical, diamond shaped. Mesoscutum short, about 1.5 times broader than long, slightly less densely setose than head (figure 7); notauli widely separate and inconspicuous (figures 8, 10), extending almost to posterior margin of mesoscutum under some angles of light; transscutal articulation shallowly arcuate (figure 7); scutellar–axillar

Table 1. Measurements in μm of ♀ antennae of *Chiloe micropteron*, from slide-mounted specimens ($n=9$).

Character	Mean	Range	<i>ssd</i>
Scape + radicle L	116	109–124	4.7
Scape + radicle W	40	36–44	2.5
Scape + radicle L/W	2.9	—	—
Pedicel L	48	46–50	1.5
Pedicel W	38	37–41	0.9
Pedicel L/W	1.26	—	—
F1 L	30	28–32	1.1
F1 W	24	23–25	0.7
F1 L/W	1.0	—	—
F2 L	35	33–38	2.3
F2 W	32	31–32	0.6
F2 L/W	1.09	—	—
F3 L	36	35–38	1.4
F3 W	33	32–34	0.8
F3 L/W	1.09	—	—
F4 L	38	37–39	1.0
F4 W	35	34–37	1.1
F4 L/W	1.09	—	—
F5 L	40	39–41	0.7
F5 W	38	35–39	1.1
F5 L/W	1.05	—	—
F6 L	39	38–40	0.8
F6 W	39	38–41	1.1
F6 L/W	1.0	—	—
Clava 1 L	37	33–40	2.4
Clava 1 W	45	39–49	3.4
Clava 1 L/W	0.82	—	—
Clava 2 L	32	27–35	2.8
Clava 2 W	48	47–50	1.5
Clava 2 L/W	0.67	—	—
Clava 3 L	35	32–38	2.2
Clava 3 W	50	46–53	2.5
Clava 3 L/W	0.7	—	—
Clava 4 L	34	30–38	2.4
Clava 4 W	51	46–55	3.5
Clava 4 L/W	0.67	—	—
Clava 5 L	34	32–36	1.9
Clava 5 W	47	42–54	5.8
Clava 5 L/W	0.60	—	—
Clava 6 L	36	33–39	1.7
Clava 6 W	39	31–45	5.0
Clava 6 L/W	0.92	—	—

complex subequal in length to mesoscutum, with distinct transverse furrow along anterior margin ending laterally in pit at inner angle of each axilla (figures 7, 8, 10); axillae widely separated, with dorsal surface of axilla obliquely subquadrate, and with two setae anterolaterally (figures 7, 11); scutellum in dorsal view transverse-oval to trapezoidal, with five to nine setae on each side and bare centrally or at least medially (figures 7, 11), in posterior view with transverse marginal depression (figure 11), and in lateral view apex abruptly recurved and overhanging metanotum (figure 9). Metanotum vertical, visible laterally below axilla but concealed between

scutellum and propodeum (figures 8–11). Mesopleuron subrectangular and almost vertical, about twice as high as long and about as long as lateral panel of pronotum, with slightly depressed femoral groove but without distinctly differentiated episternum and epimeron (figure 9). Metapleuron distinguished from propodeum by oblique suture extending from near posterior margin of metacoxa toward dorsal notch on posterior margin of mesopleuron (figure 45); metathoracic spiracle in notch along posterior margin of mesopleuron (figure 9). Propodeum almost vertical (figures 9, 45), slightly convex, its surface extensively covered with minute, flat, triangular, denticulate microsculpture (figure 20b), except smooth sublaterally and lateral to spiracle (figures 11, 20a), and with row of three or four setae below spiracle (figure 20a); spiracle small and circular (figure 20a).

Fore wing (figures 19, 20a, 45) greatly reduced, slightly curved, without apparent venation; about basal third (humeral plate) dark brown, and slightly narrowed apically or differentiated by slight constriction (figure 19) from paler elongate-lanceolate, dorsally densely setose, apical two-thirds (figures 19, 20a). Hind wing absent.

Legs with tarsi four-segmented. Protibia with patch of spatulate setae antero-apically, the setal patch narrowed toward base of tibia, and with two longer, apical, spatulate setae (protibial comb) adjacent to spur (figure 18); tibial spur bifurcate, slightly sinuate but with outer tine almost straight, and inner tine obliquely angled relative to outer tine and projecting from near midlength of spur (figures 17, 18); basitarsus with comb of about eight long, curved, spatulate setae on anterior surface, the basal four or five setae oriented transversely across base of basitarsus (figure 18). Mesotibia without distinct apical spur. Metatibia with one apical spur.

Metasoma with petiole ring-like, very short and concealed between propodeum and gaster (figure 8). Gaster with seven visible terga (figures 24, 25, 45); tergum 1 almost entirely vertical, uniformly setose dorsally; terga 2–6 transverse-rectangular, subequally long and loosely connected by membrane, bare along anterior margin but uniformly setose over at least posterior half; tergum 6 without spiracle but with large, transverse-oval, sublateral setal patch (figure 26); tergum 7 with large sublateral cercal plate in depressed region near anterior margin; cercal plate with three setae of different lengths, one very long (figures 25, 26, 45). Hypopygium short, extending only to base of ovipositor (figure 25). Ovipositor sheaths projecting very slightly (figure 25).

Internal features: Axillar phragma about as long as width of axilla, narrow, extending from anterior margin of axilla laterally and obliquely angled in same direction as dorsal surface of axilla (figure 21). Mesotergal–mesotrochanteral muscle originating entirely or almost entirely from axillar phragma, band-like, about as long as height of mesoscutum and converging ventrally to tendon-like apodeme extending height of mesopleuron (figures 21, 22). Mesophragma truncate apically, extending to posterior apex of propodeum (cf. *Rotoita*, figure 47). Mesotrochantinal plate extending dorsally to anterior margin of metasternum, the mesocoxal fossae separated by cuticle (figure 12). Mesofurca without mesofurcal bridge or interfurcal processes (figure 23). Metasternum with metafurcal pits widely separated, each pit at anterior margin of metasternum posterior to mesocoxal fossa (figure 12); metafurcae consisting of separate apodemes (cf. *Rotoita*, figure 47).

Ovipositor with second (upper) valvulae undivided and uniformly convex basally but distally with median suture from about mid-length differentiating left and right upper valvulae, the left valvula slightly overlapping right valvula (figures 28, 29, 32);

first (lower) valvulae in ventral view enclosed by membranous sheath (figures 30, 32), the left and right lower valvulae clearly visible only near apex (figure 27); in cross-section the lower valvulae composed of subtriangular left and right median lobes (figure 32) and widely overlapping thin lateral walls (figures 28–32), the left and right lateral walls together forming a bilayered sheath around the median lobes (figures 30, 32) except apically (figure 27).

Male. Body length (allotype) 713 μm . Similar to female except antenna 13-segmented, with indistinctly differentiated five-segmented clava; all flagellar segments clearly separated, the six funicular segments submoniliform and the claval segments slightly trapezoidal. Eye smaller, with about 25 ommatidia and about 0.7 length of malar space. Colour generally slightly lighter than in most females. Extruded genitalia about 119 μm long.

Remarks. The total body length given for females is skewed slightly because critical-point dried specimens have the gaster inflated, with the terga well separated by stretched intersegmental membrane. The actual body size of live females is probably closer to 700 μm . Gibson (1993, figure 227) previously illustrated the female as a representative of the family and Heraty *et al.* (1997) described the structure of the mesofurca under the name *Rotoita* sp.

Biology. Unknown, but likely a parasitoid of some soil-dwelling host because both sexes are micropterous and their collection in pan traps indicates a soil or leaf-litter habitat. The type locality is a ravine with semi-open vegetation consisting of second growth native shrubs. It is a fenced area now owned by A. Ugarte, the nephew of the late L. Peña, Chile's foremost field naturalist.

***Rotoita* Bouček and Noyes**
(figures 33–44, 46–48)

Rotoita basalis Bouček and Noyes, 1987: 408–410; Bouček, 1988a: 570; Noyes and Valentine, 1989: 37.

Features of *R. basalis* described by Bouček and Noyes (1987) are newly illustrated by a photograph of the fore wing (figure 46) and scanning electron micrographs of the head (figures 33, 34), mesosoma (figures 35–38), antenna (figures 39, 40), protibia and tarsus (figures 41, 42), hind wing (figure 43) and apical two gastral terga (figure 44). Examination of three *R. basalis* females and a fourth female of what likely is a closely related species enables us to amend three statements in the original description of the genus and species, and figures 1 and 3 in Bouček and Noyes (1987). *Rotoita* was described originally as having the prepectus apparently absent. Although not externally visible in dry-mounted specimens, a slender prepectus is visible along the anterior margin of the mesopleuron in the slide-mounted paratype of *R. basalis*. The prepectus appears to be ventrally narrowed and fused with the mesepisternum (figure 48). Bouček and Noyes (1987) also illustrated and described the axillae as being widely separated and strongly advanced. All point-mounted females have a short, transverse or somewhat obliquely angled sulcus adjacent to the tegula (figures 35, 37, 38). However, the oblique line extending to the anterolateral corner of the scutellum from the transverse sulcus in figure 3 of Bouček and Noyes (1987) does not exist (figures 35, 37, 38). Rather, the line represents the inner margin of an underlying, narrow, elongate structure (axillar phragma) that is visible in the slide-mounted, cleared specimen from which the drawing was made (figure 47). The axillae apparently are indistinguishably fused with the mesoscutum except for

the short sulcus adjacent to the base of each fore wing, which likely are the only remaining indications of the anterior margins of the axillae and of the transscutal articulation (figures 35, 37, 38) (see further under Discussion). Bouček and Noyes (1987) also described the costal cell as being about one-quarter as long as the fore wing, the marginal vein as being slightly shorter than the costal cell, and the stigmal vein as being about one-quarter as long as the marginal vein. The submarginal vein was illustrated as reaching the anterior margin of the wing slightly distal to the basal vein (Bouček and Noyes, 1987, figure 1). However, appearance of the relative lengths of the costal cell and marginal vein depend partly at the angle from which the wing is viewed and back-lit by illumination. All point-mounted specimens actually have the marginal vein only about half as long as illustrated by Bouček and Noyes (1987) because the submarginal vein extends from the basal vein about half the distance to the base of the stigmal vein before attaining the anterior margin of the wing. Although very narrowly attenuate beyond the basal vein the costal cell is longer than was illustrated, with the marginal vein being subequal in length or only slightly longer than the stigmal vein (figure 46).

The original description of *Rotoita* is supplemented with the following: fore wing stigma with cluster of four placoid sensilla divided into two groups of two separated by a distinct gap; hind wing with three hamuli at apex of marginal vein and with four setae in a row on dorsal surface of marginal vein opposite the hamuli (figure 43); protibia with a row of spatulate setae (protibial comb) along anterior apical margin (figure 41); protibial spur with tines of bifurcation long, straight and parallel (figures 41, 42); protarsus with tarsal comb composed of three spatulate setae on basitarsus and two spatulate setae on second tarsomere (figure 41); propodeum sometimes with callus differentiated by a fine, oblique carina extending from anterior margin of propodeum medial to spiracle, behind and lateral to spiracle, where it is abruptly recurved and extended to posterior margin of propodeum as dark sulcus parallel with lateral margin of propodeum; mesofurca with short anterior interfurcal process on each lateral furcal arm (figure 47); metafurcae widely separated (figure 47); mesotergal–mesotrochanteral muscle inserted into golf tee-like pedicel above mesocoxa (figure 47).

Remarks. We agree with Bouček and Noyes (1987) that the female *Rotoita* from Huia probably represents a very similar but separate species from *R. basalis*. In addition to having distinct setiferous punctures on the frontovertex as well as other more subtle differences mentioned by them, its propodeum has a distinct, oblique post-spiracular propodeal carina that posterior and lateral to the spiracle recurves toward the posterior margin of the propodeum as a dark sulcus. Specimens of *R. basalis* have a very fine longitudinal sulcus posterior and lateral to the spiracle (figure 37), but they lack the oblique post-spiracular carina (figures 35, 37). Additional specimens are required to substantiate that the observed differences are interspecific and are not correlated with a larger body size, as remarked by Bouček and Noyes (1987).

Discussion

The six-segmented clava of females and the five-segmented clava of males are unique features within Chalcidoidea that likely indicate monophyly of Rotoitidae. Almost all other extant chalcidoids have a clava composed of three or fewer segments, although some *Diglochis* (Pteromalidae: Pteromalinae) have a very small fourth claval segment and a 14-segmented antenna (Dzhanokmen, 1979), and *Idioporus*

affinis LaSalle and Polaszek (Pteromalidae: Eunotinae) has an 11-segmented antenna with the clava composed of four distinct segments (LaSalle *et al.*, 1997). The extinct subfamilies Baeomorphinae and Bouceklytinae (Tetracampidae) and some extinct Mymarommatoidea (the hypothesized sister group of Chalcidoidea; Gibson, 1986a) also had a four-segmented clava, and 12 and 13 antennal segments, respectively (Yoshimoto, 1975). Some extant Eucharitidae have 14 or more antennal segments (Bouček and Noyes, 1987) and 14-segmented antennae are characteristic of several other families of parasitic Hymenoptera (Naumann and Masner, 1985; Gibson, 1986a). Fourteen antennal segments is considered here to be the groundplan number for rotoitid females, but the discovery of males of *Rotoita* is necessary to make a reliable hypothesis of the groundplan number for males. Polarity of a 14-segmented antenna in rotoitid females is debatable. Bouček and Noyes (1987) suggested 14 segments was a primitive feature for the family within Chalcidoidea. If so, it indicates that Rotoitidae is the basal lineage of Chalcidoidea. It also suggests that a 13-segmented antenna with a three-segmented clava, characteristic of many chalcidoids, was derived through the loss of one claval segment and the transformation of two other claval segments into funicular segments. The 13-segmented antenna with a five-segmented clava possessed by male *Chiloe* results from loss of a single claval segment.

Gibson (1986a) hypothesized three synapomorphies for Chalcidoidea, including the presence of an independent prepectus that is externally visible at least dorsally. The discovery that both *Chiloe* and *Rotoita* have a slender, independent prepectus extending the height of the pronotum supports inclusion of Rotoitidae in Chalcidoidea. Because the prepectus is in the membrane between the pronotum and mesepisternum it is concealed when the posterolateral margin of the pronotum extends to the mesepisternum. This condition could also indicate that Rotoitidae is the sister group of other Chalcidoidea because an elongate, concealed prepectus is the structure from which the dorsally exposed prepectus of most chalcidoids is hypothesized to have evolved secondarily (Gibson, 1999).

Quicke *et al.* (1994) discovered that Chalcidoidea except Mymaridae have a longitudinally cleft, overlapping, asymmetric upper valve (second valvulae), with the two sides joined by membrane so that there is a central lumen (Quicke *et al.*, 1994, figures 53–67, 69, 71–75). The upper valve in Mymaridae is uniformly convex rather than cleft and has a single central lumen (Quicke *et al.*, 1994, figure 52). *Chiloe* appears to have an intermediate structure in which the upper valve is uniformly convex basally but is cleft apically beginning near the middle of the ovipositor (figures 28, 29, 31). In cross-section the slightly overlapping upper valves appear to be single walled, without a central lumen (figure 32). It is likely that the central lumen has collapsed as a result of drying and the upper valves are actually double walled, as occurs in other chalcidoids (Quicke *et al.*, 1994). If the structure of the upper valves of *Chiloe* is intermediate between that of Mymaridae and other Chalcidoidea this supports a relatively basal position for Rotoitidae within Chalcidoidea and perhaps a sister-group relationship with other Chalcidoidea excluding Mymaridae. Quicke *et al.* (1994, figures 68, 70) illustrated dorsally continuous upper valves for *Anastatus* (Eupelmidae) and *Tanaostigmodes* (Tanaostigmatidae), but at least in *Tanaostigmodes* this is because the illustrated section was subapical. Delanoue and Arambourg (1965) showed previously that the upper valves of *Eupelmus* (Eupelmidae) are asymmetric and overlapping. Quicke *et al.* (1994) did not serially section the ovipositor of any chalcidoid to determine variation along its

length so additional study is required prior to making reliable phylogenetic inferences. The structure of the lower valves of *Chiloe* is complex and our interpretation is tentative until their exact structure can be determined by serial sectioning of the ovipositor. Each lower valve appears to be composed of a large subtriangular median (inner) lobe and a thin lateral (outer) wall that curves around under each median lobe to the other side so that the two lateral walls together form a double-layered sheath around the lower valves (figures 30, 32) except apically (figure 27). Apparently, the lateral walls can overlap to differing extents and because of this there may (figure 27) or may not (figure 30) be any external evidence of the median division between the two lower valves.

The structure of the protibial spur has often been considered informative for inferring relationships within Chalcidoidea. Usually, described states of the protibial spur have been limited to 'spur simple and straight' (needle-like) compared with 'spur bifurcate and curved'. However, the Tetracampidae are often considered to have an intermediate structure because the spur is bifurcate but the tines are straight (Gibson *et al.*, 1999). The protibial spur of *R. basalis* (figure 42) is very similar to those known for Tetracampidae (Bouček, 1958, figures 5–7; Domenichini, 1978, figure 13, bottom). The protibial spur of *C. micropteron* is similar but the inner tine is slightly angled relative to the outer tine (figure 17). The groundplan structure of the protibial spur is uncertain for Chalcidoidea. A curved and only apically bifid protibial spur has generally been thought to be the groundplan structure for Chalcidoidea because this is possessed by almost all Apocrita other than Chalcidoidea (Basibuyuk and Quicke, 1995) and is characteristic of those chalcidoid taxa with five-segmented tarsi (Gibson *et al.*, 1999). However, some Mymarommatoidea and Mymaridae have bifurcate spurs with relatively long and straight tines, and with the inner tine angled relative to the outer tine (Gibson *et al.*, 1999), much like that of *C. micropteron* (figure 17). This structure may therefore be the groundplan state for Chalcidoidea because of its distribution in Mymarommatoidea and Chalcidoidea. More extensive survey of protibial spur structure throughout Chalcidoidea is required prior to making confident phylogenetic inferences.

The presence of a comb ('fine comb' or 'basitarsal comb' *sensu* Basibuyuk and Quicke, 1995) of spatulate setae ('paddle-shaped' setae *sensu* Basibuyuk and Quicke, 1995) on the ventral surface of the basitarsus in Rotoitidae (figures 18, 41) is characteristic of most Chalcidoidea. Basibuyuk and Quicke (1995) stated that the orientation of the basitarsal comb varies considerably among chalcidoid families and might be phylogenetically informative. The basitarsal comb is oriented longitudinally in many chalcidoids and in most Hymenoptera, but in some chalcidoids it is oblique or even nearly transverse (Basibuyuk and Quicke, 1995, figure 7H). The basitarsal comb of *C. micropteron* is unusual because the basal four or five spatulate setae originate transversely near the base of the basitarsus (figure 18), but in lateral view the comb appears to be longitudinal (figures 17, 18) because the setae are long and curved (figure 18). The basitarsal comb of *R. basalis* has only three spatulate setae (figure 41). A more extensive survey throughout Chalcidoidea is required to determine the exact structure of the basitarsal setae in different groups. It is necessary to differentiate between lines of 'paddle-shaped' setae *sensu* Basibuyuk and Quicke (1995) and similar-looking setae that constitute the basitarsal comb, and to determine whether the basitarsal comb is along the anteroventral margin of the basitarsus (figures 18, 41; Basibuyuk and Quicke, 1995, figure 8B) or along the posteroventral margin (Basibuyuk and Quicke, 1995, figures 7G, 8C).

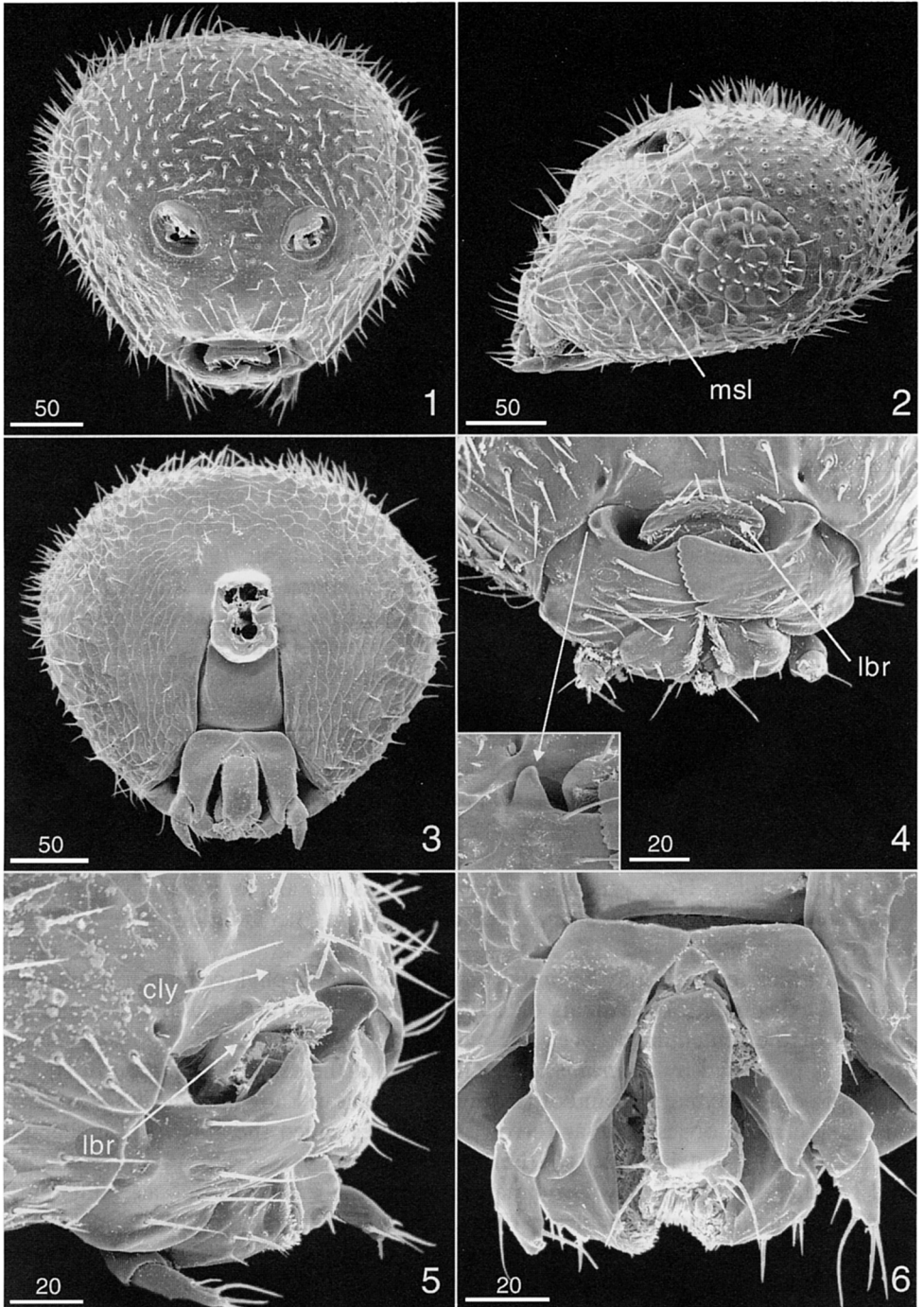
A row of setae on the dorsal surface of the marginal vein opposite the hamuli on the hind wing of *R. basalis* (figure 43) is characteristic for Chalcidoidea plus some other Apocrita as listed by Basibuyuk and Quicke (1997).

Chiloe micropteron has a unique structure of the mesotergal–mesotrochanteral (t_2 – tr_2) muscle for Chalcidoidea. Most chalcidoids (for exceptions see Gibson, 1986b, 1989) have t_2 – tr_2 extending through the mesothorax as a tubular muscle, originating partly from the dorsal surface of the axilla (t_2 – tr_{2a}) and partly from an anteriorly projecting axillar phragma (t_2 – tr_{2b}), and inserting into a golf tee-like pedicel just above the mesocoxa (Gibson, 1985, figure 37; Gibson, 1986a, figures 34, 35). In *C. micropteron*, t_2 – tr_2 extends only the height of the mesoscutum, is band-like rather than tubular, and tapers ventrally to a tendon-like ligament (figures 21, 22) rather than having a golf tee-like insertion (cf. figure 47). Furthermore, the muscle originates entirely or almost entirely from a very slender axillar phragma that projects anteriorly and somewhat ventrally from the anterior margin of the axilla near its lateral margin (figures 21, 22). A single site of origin from the axillar phragma is also possessed by the hypothesized sister group of the Chalcidoidea, the Mymarommatoidea (Gibson 1986a). We have been unable to confirm from specimens at hand whether the band-like muscle is actually composed of an anterior and posterior set of muscle fibres (t_2 – tr_{2a} and t_2 – tr_{2b} ; see Gibson, 1999) and thus likely is secondarily reduced. The mesotergal–mesotrochanteral muscle was destroyed as part of the process of slide-mounting the paratype of *R. basalis*; however, there is a golf tee-like pedicel immediately above each mesocoxa (figure 47), which indicates presence of a tubular muscle extending through the mesothorax. Presence of a narrow axillar phragma (figure 47) indicates site of origin of the muscle, but complicates interpretation of the fate of the axilla in *Rotoita*. We interpret the short, transverse sulcus adjacent to each tegula (figures 35, 37, 38) as a remnant of the transscutal articulation, which remained after fusion of the axillae with the mesoscutum. The sulcus would therefore be the anterior margin of the axilla, from which the axillar phragma originates in other chalcidoids (Gibson, 1986a, figure 35) and mymarommatooids. However, what we interpret as the axillar phragma in *Rotoita* originates posterior to the sulcus, apparently from the anterior margin of the scutellum (figure 47).

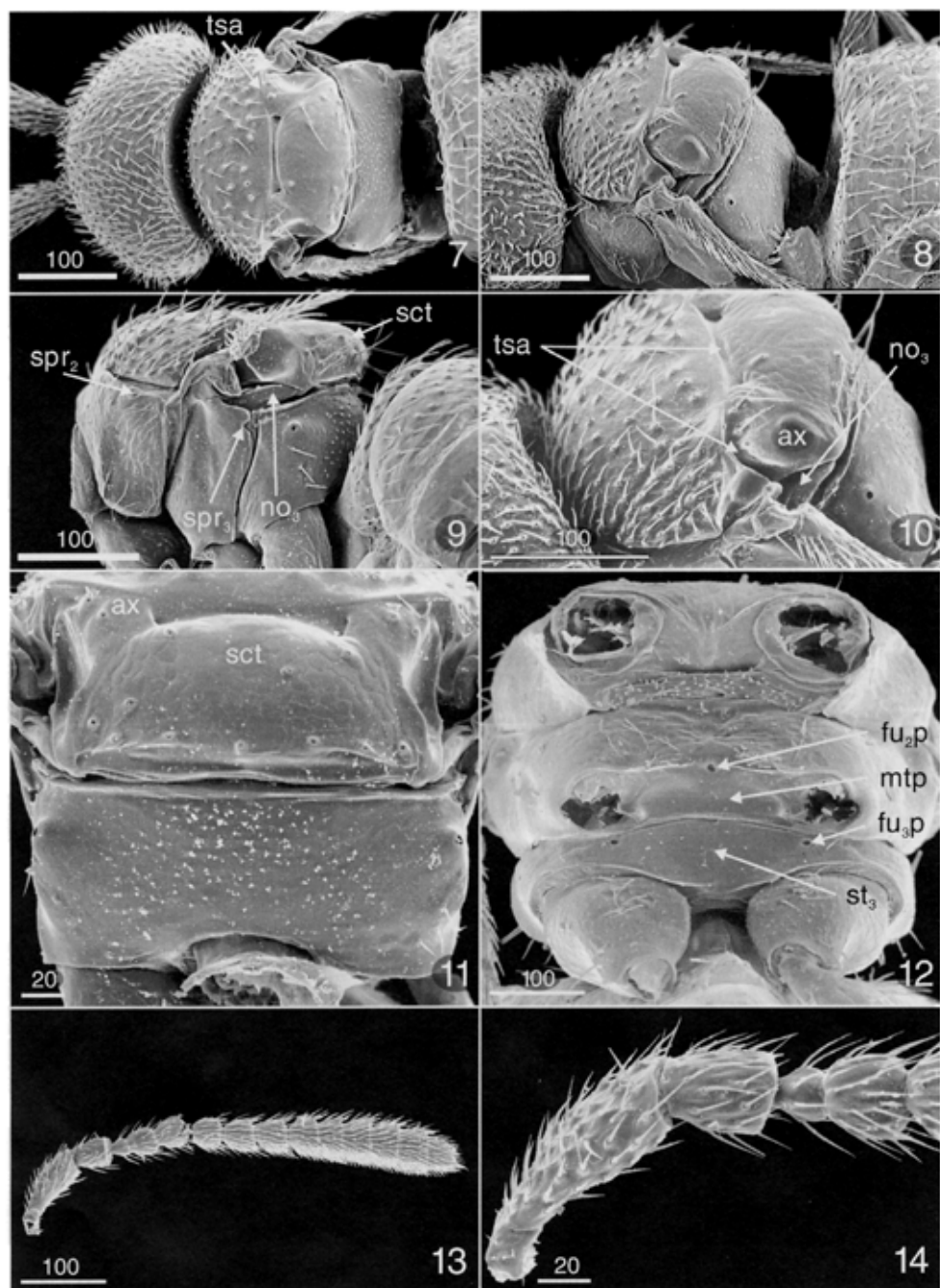
Two other features may be important for resolving phylogenetic relationships within Chalcidoidea. Individuals of *Chiloe* have a deep furrow along the anterior margin of the scutellum between the axillae (figures 7, 8, 10, 11). A very similar furrow is possessed by *Australomymar* Girault, but the exact distribution of such a furrow in other Mymaridae and other Chalcidoidea is unknown. Some other apocritans have a more or less similar furrow, sometimes called the anterior scutellar pit (Masner, 1991), scutellar sulcus (Wharton *et al.*, 1997) or scutellar furrow (Ronquist and Nordlander, 1989). Mymarommatoidea lack the furrow as well as a differentiated dorsal axillar surface (Gibson 1986a, figure 11). Presence of an exposed meta-thoracic spiracle (figure 9) might also be informative but distribution of this state throughout Hymenoptera is also unknown.

Conclusions

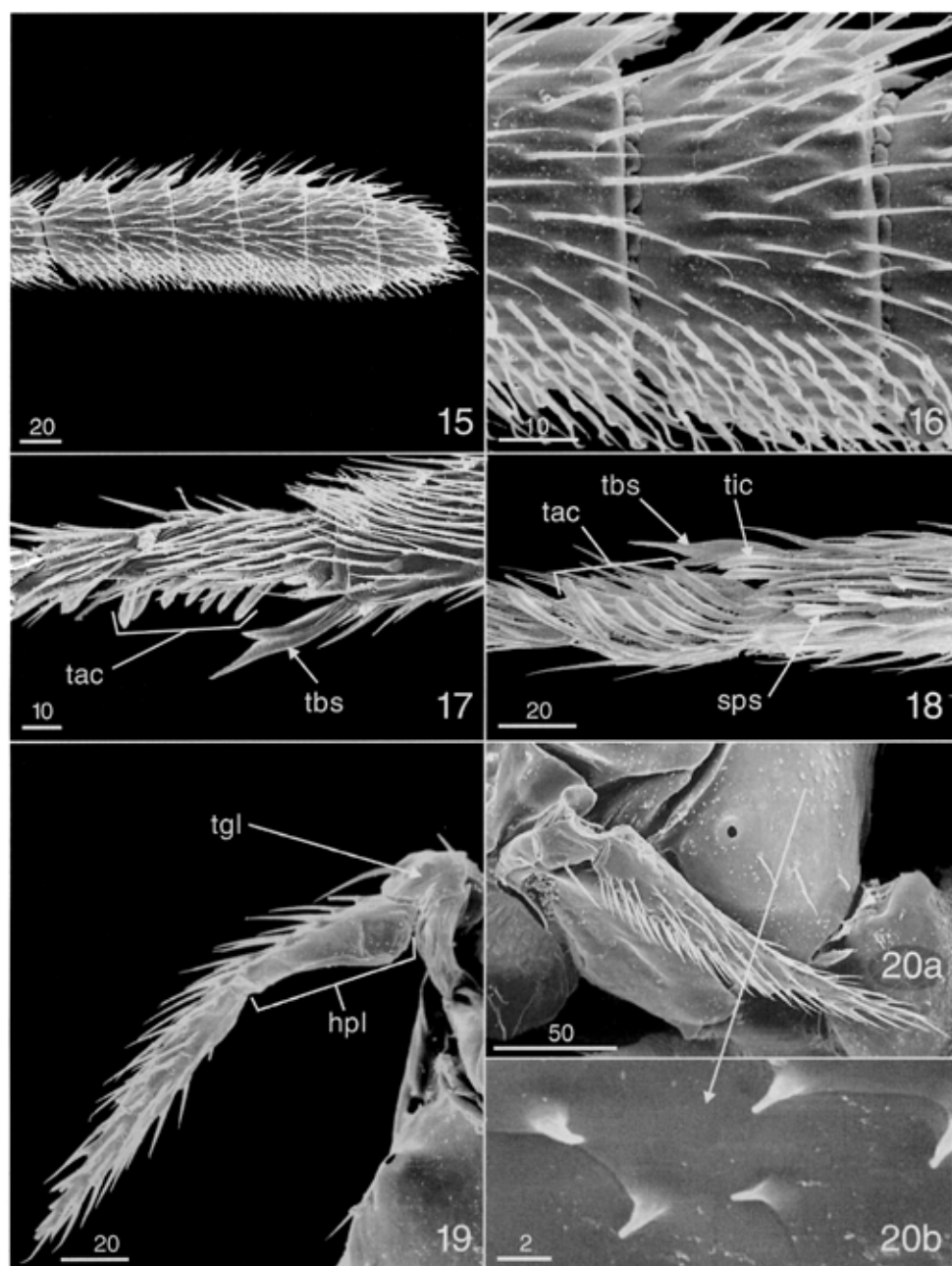
The occurrence of *Rotoita* in New Zealand and *Chiloe* in southern Chile is a classical Gondwanan distribution, which suggests that Rotoitidae is an ancient lineage of Chalcidoidea. The very divergent morphology of the two genera, beyond



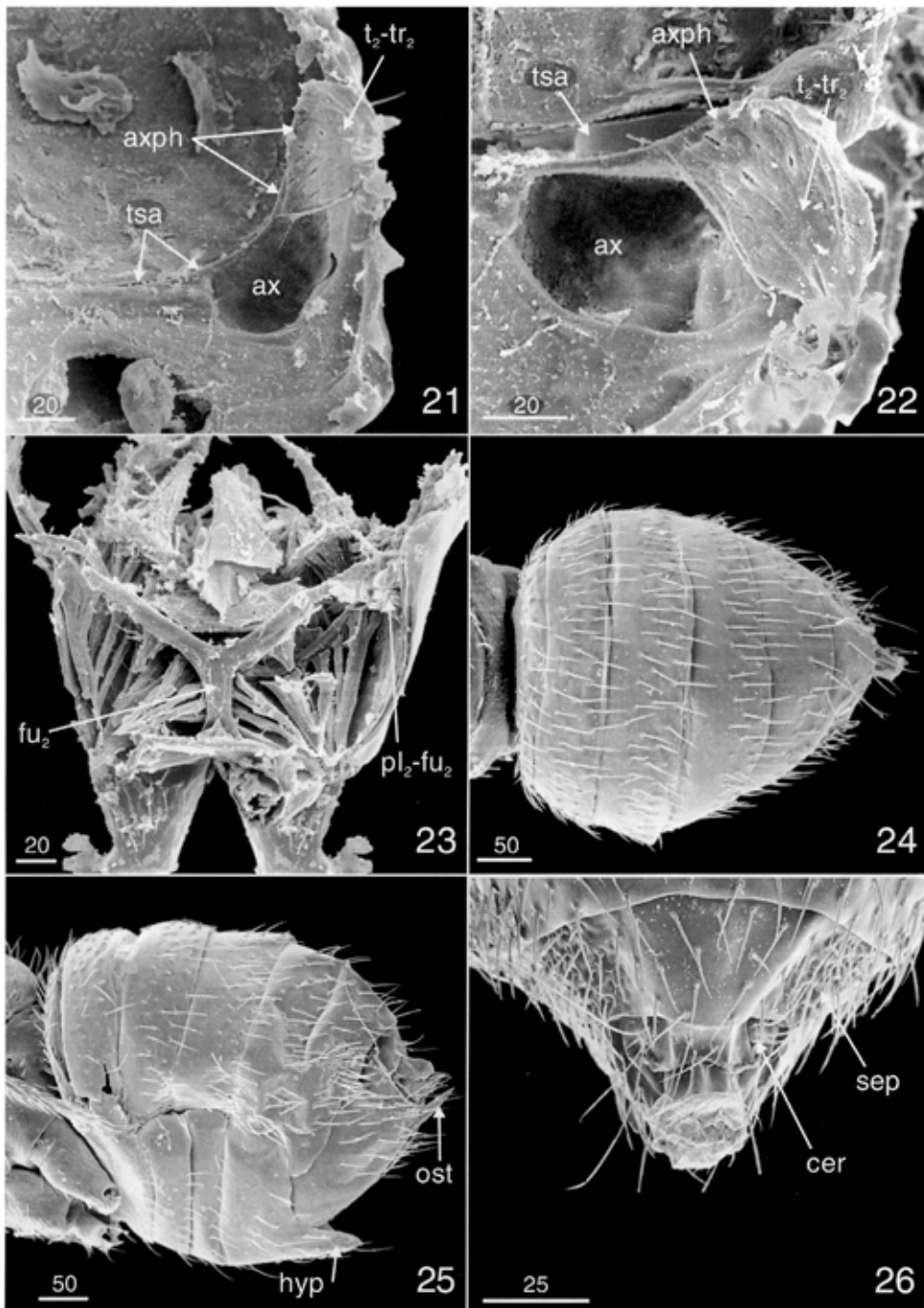
FIGS 1–6. *Chiloë micropteron* Gibson and Huber, ♀. (1–3) Head: (1) anterior view; (2) lateral view; (3) posterior view. (4, 5) Labrum and mouthparts: (4) anterior view (magnified area of mandibular denticle); (5) anterolateral view. (6) Labiomaxillary complex, posterior view. Scale bars = μm ; abbreviations: cly, clypeus; lbr, labrum; msl, malar sulcus.



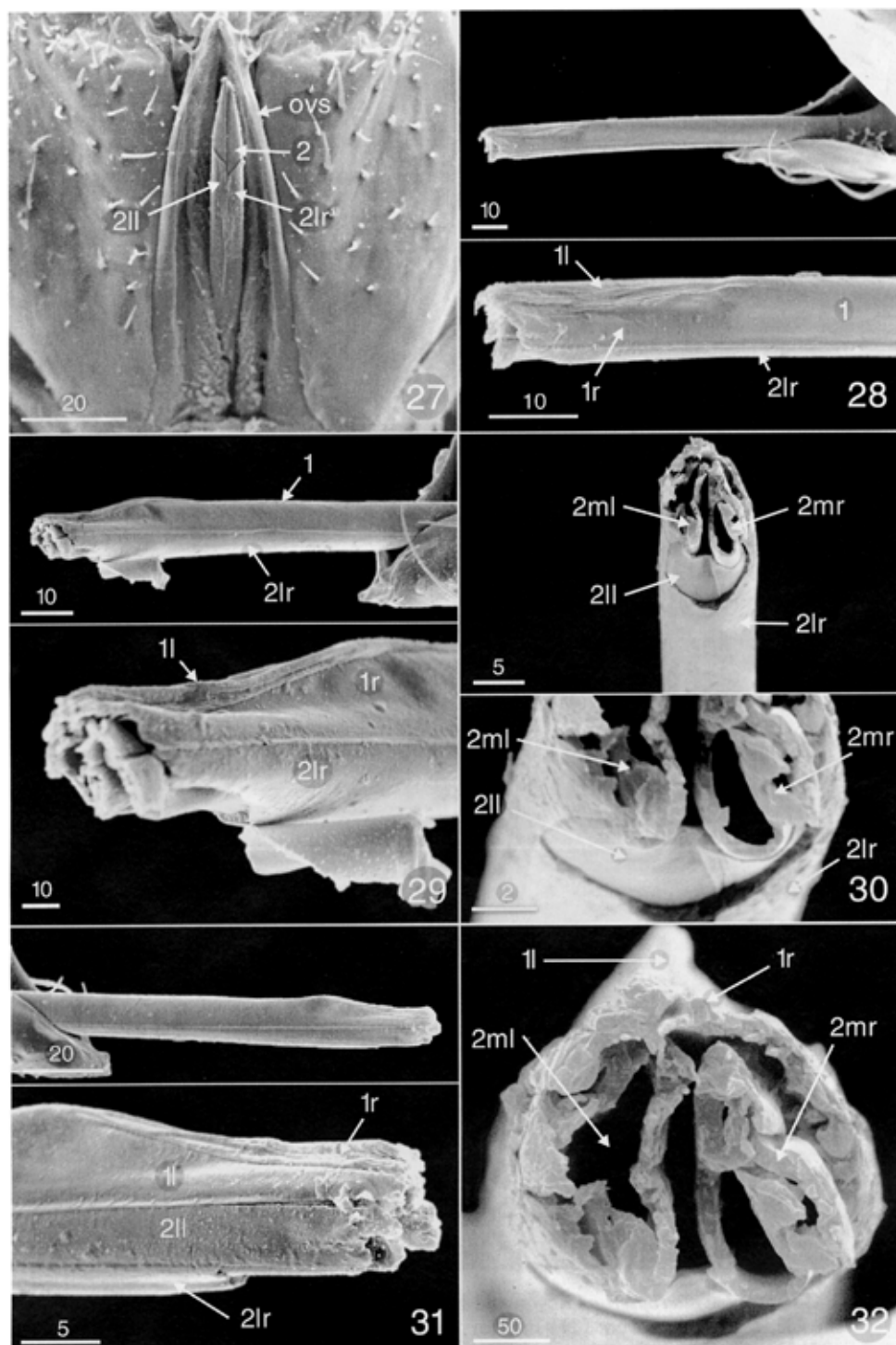
FIGS 7–14. *Chiloë micropteron* Gibson and Huber, ♀. (7) Head and mesosoma, dorsal view; (8) mesosoma, dorsolateral view; (9) mesosoma, lateral view; (10) mesonotum, dorsolateral view; (11) scutellar-axillar complex—petiole, posterior view; (12) mesosoma, ventral view, pro- and mesocoxae removed; (13) antenna; (14) scape—second funicular segment. Scale bars = μm ; abbreviations: ax, axilla; fu_2p , mesofurcal pit; fu_3p , metafurcal pit; mtp, mesotrochantinal plate; no_3 , metanotum; sct, scutellum; spr_2 , mesothoracic spiracle; spr_3 , metathoracic spiracle; st_3 , metasternum; tsa, transscutal articulation.



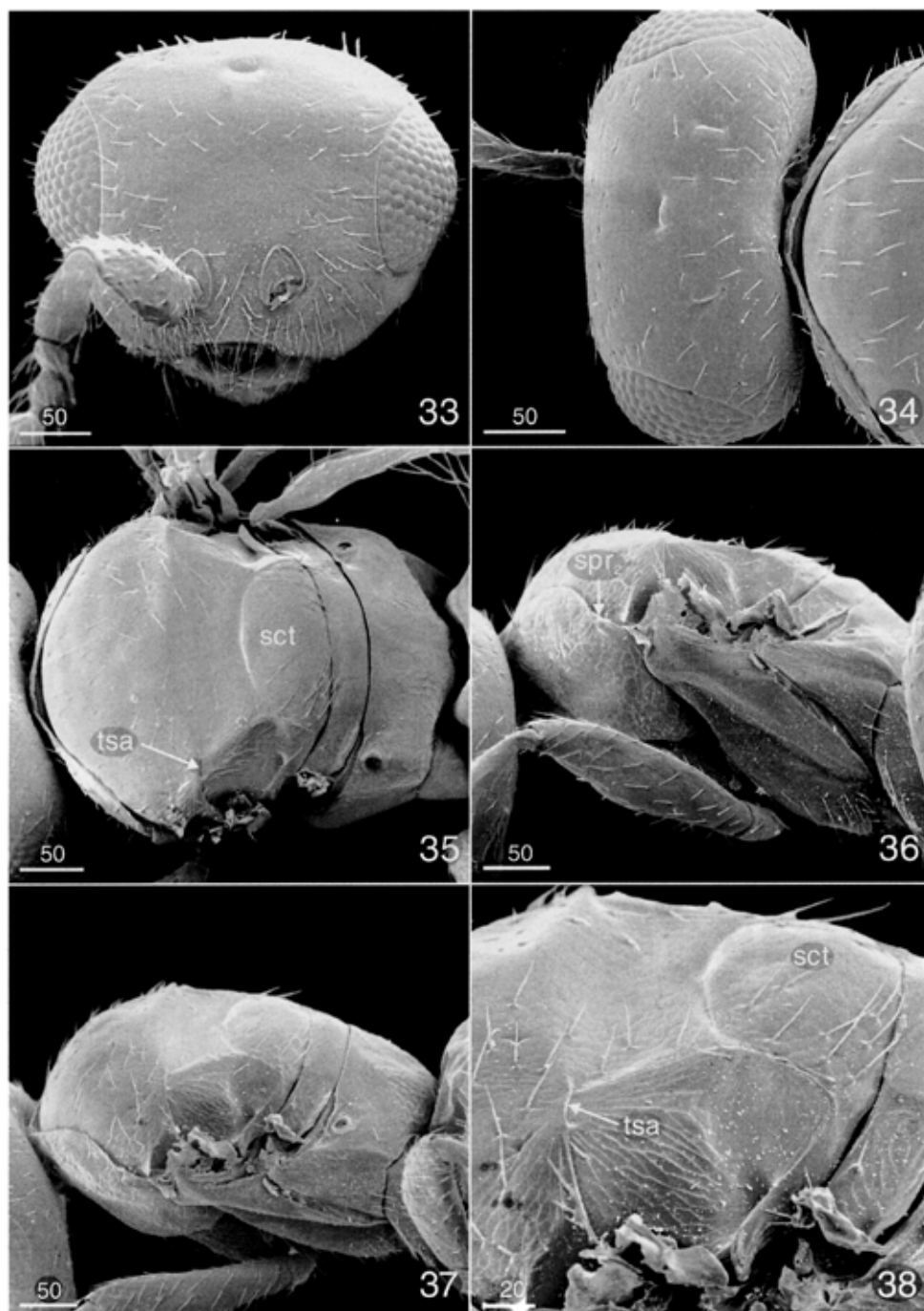
FIGS 15–20. *Chiloë micropteron* Gibson and Huber, ♀. (15) Antennal clava; (16) claval segments with intersegmental pustules; (17) apex of protibia and basitarsus, posterior view; (18) apex of protibia and basitarsus, anterior view; (19) fore wing; (20a) propodeum and fore wing, lateral view; (20b) propodeal microsculpture. Scale bars = μm ; abbreviations: hpl, humeral plate; sps, spatulate setae; tac, tarsal comb; tbs, tibial spur; tic, tibial comb; tgl, tegula.



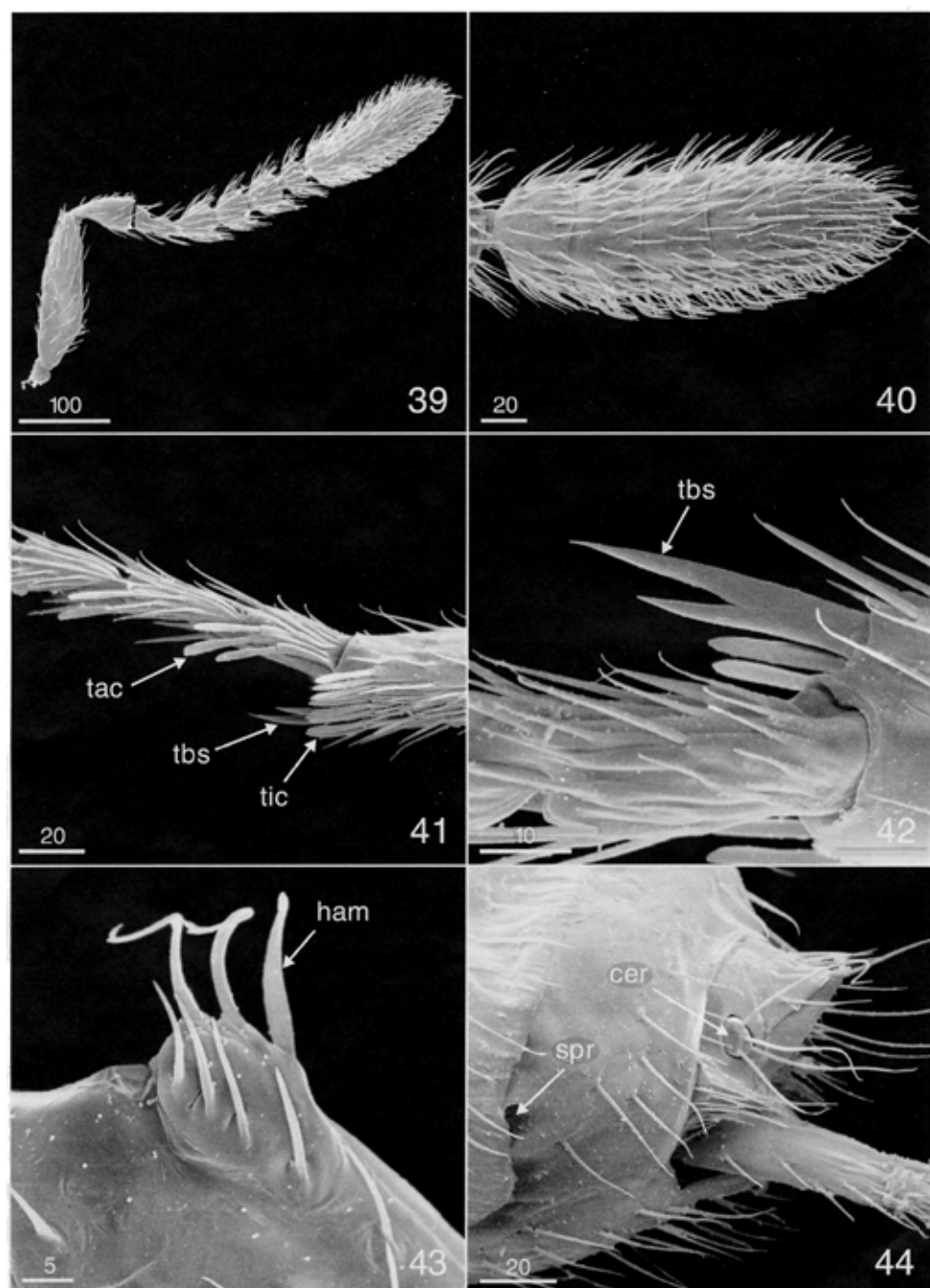
FIGS 21–26. *Chiloë micropteron* Gibson and Huber, ♀. (21, 22) Mesotergal–mesotrochanteral muscle, tendon removed: (21) interior, ventral view; (22) interior, anterolateral view. (23) Dissected mesofurca, posterior view. (24–26) Gaster: (24) dorsal view; (25) lateral view; (26) apex, dorsal view. Scale bars = μm ; abbreviations: ax, axilla; axph, axillar phragma; cer, cercus; fu_2 , mesofurca; hyp, hypopygium; ost, ovipositor stylet; $\text{pl}_2\text{-fu}_2$, mesopleural–mesofurcal muscle; sep, setal patch; $\text{t}_2\text{-tr}_2$, mesotergal–mesotrochanteral muscle; tsa, transscutal articulation.



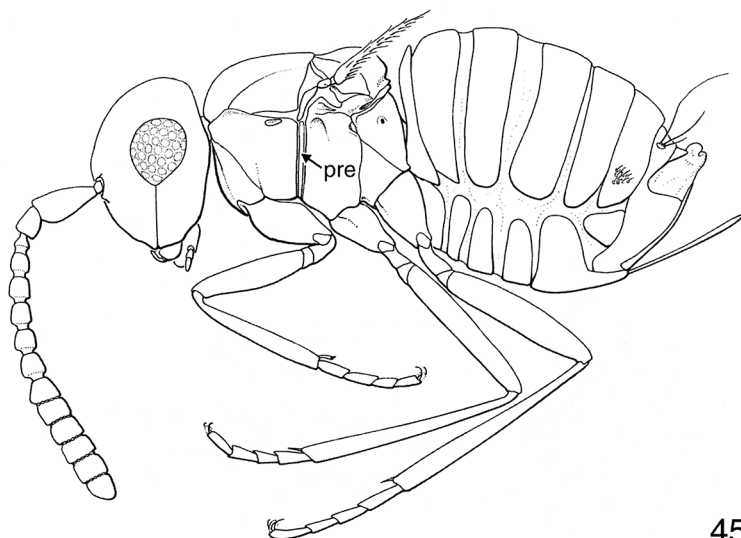
FIGS 27–32. *Chiloë micropteron* Gibson and Huber, ♀. (27) Ovipositor, ventral view. (28–32) Ovipositor valvulae, cut crosswise near middle: (28) dorsolateral view; (29) lateral view of right side; (30) apex of cut section, posteroventral view; (31) lateral view of left side; (32) apex of cut section. Scale bars = μm ; abbreviations: 1, upper valvula; 1l, left upper valvula; 1r, right upper valvula; 2, lower valvula; 2ll, left lateral wall of lower valvula; 2lr, right lateral wall of lower valvula; 2ml, left median lobe of lower valvula; 2mr, right median lobe of lower valvula; ovs, ovipositor sheath.



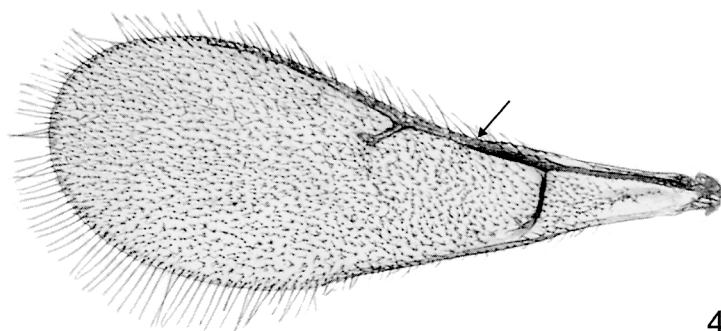
FIGS 33–38. *Rotoita basalis* Bouček and Noyes, ♀. (33, 34) Head: (33) frontal view; (34) dorsal view. (35–37) Mesosoma: (35) dorsal view; (36) lateral view; (37) dorsolateral view. (38) Posterior mesonotum, dorsolateral view. Scale bars = μm ; abbreviations: sct, scutellum; spr_2 , mesothoracic spiracle; tsa, transscutal articulation.



FIGS 39–44. *Rotoita basalis* Bouček and Noyes, ♀. (39) Antenna; (40) clava; (41) apex of protibia and basal three tarsal segments, anterior view; (42) protibial spur and basitarsus, posterior view; (43) hamuli and marginal setae on hind wing; (44) apical two gastral terga, lateral view. Scale bars = μm ; abbreviations: cer, cercus; ham, hamulus; spr, spiracle; tac, tarsal comb; tbs, tibial spur; tic, tibial comb.



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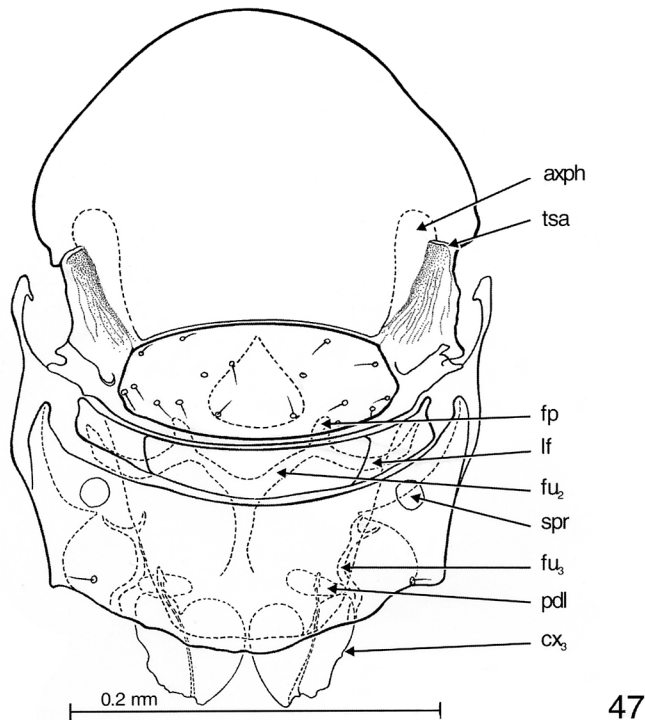


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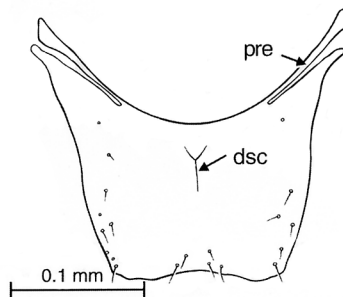
FIGS 45, 46. (45) *Chiloë micropteron* Gibson and Huber, ♀: lateral habitus. (46) *Rotoita basalis* Bouček and Noyes, ♀: fore wing (arrow points to apex of costal cell). Abbreviation: pre, prepectus.

features correlated with presence or absence of wings, also suggests a long period of separation.

Based on current knowledge of character-state distribution, a sister-group relationship of Mymaridae with other Chalcidoidea appears to be supported by our study of the ovipositor structure of *Chiloë*. If the upper valve is found to be uniformly convex along its entire length in all mymarids and if the valve is found to be cleft right to the base in all other chalcidoids, then the intermediate structure of *Chiloë* indicates Rotoitidae are the second oldest lineage in the Chalcidoidea. However, the 14-segmented antenna of female rotoitids, structure of the prepectus, and single site of origin of the mesotergal–mesotrochanteral muscle from the axillar phragma could conflict with this conclusion. It is necessary to determine not only the exact ovipositor structure of *Rotoita*, but also that of a greater representation of Mymaridae and other Chalcidoidea to help resolve the apparent conflict. Not enough is known about the distribution of states of such characters as the prepectus, skeletomusculature,



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FIGS 47, 48. *Rotoita basalis* Bouček and Noyes, ♀: (47) dorsal view of mesosoma showing internal structures; (48) ventral view of mesopleurosternum and prepectus. Abbreviations: axph, axillar phragma; cx_3 , metacoxa; dsc, discrimen; fp, anterior interfurcal process of the mesofurca; fu_2 , mesofurca; fu_3 , metafurca; lf, lateral furcal arm; pdl, pedicel; pre, prepectus; spr, spiracle; tsa, transscutal articulation.

protibial spur, basitarsal comb and metathoracic spiracle to support or refute the relative placement of Mymaridae and Rotoitidae within Chalcidoidea based on ovipositor structure. There is serious need for such comprehensive morphological studies.

Mymaridae are exclusively egg parasitoids, and some Tetracampidae, another family that has been considered as a basal group of Chalcidoidea, are also egg parasitoids (Bouček, 1988a). Biology is yet unknown for Mymarommatoidae, the presumed sister-group of Chalcidoidea, and for Rotoitidae. Because of the small size of mymarommatoids and rotoitids it has been suggested that these also are egg

parasitoids (Bouček and Noyes, 1987). Although this biological association needs to be determined, if proven correct this would suggest that egg parasitism is the groundplan biology of Chalcidoidea.

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