

Redescription of the genus *Apalonia* CASEY, description of immature stages and reevaluation of its tribal placement (Coleoptera: Staphylinidae: Aleocharinae)

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Abstract

Apalonia CASEY, 1906 (Coleoptera: Staphylinidae: Aleocharinae) is redescribed based on the type species, *A. seticornis* CASEY. Immature stages are described for the first time and new bionomic data are presented. Morphological resemblance between *Apalonia seticornis* and *Meronera venestula* (ERICHSON, 1839) is discussed. The larvae of the two species have the labrum fused to the clypeus, which is unique among the larvae of Aleocharinae and exhibit virtually identical chaetotaxy. Adults of both species share similarities in the morphology of head appendages – in particular those of the mandibles, maxilla and labium; form of the mesointercoxae; a microphagous diet with a strong mycophagous component where unique mouthpart morphology may represent adaptations to fungivory. *Apalonia* is transferred from the tribe Lomechusini to Athetini, based on the derived similarities that *Apalonia* share with the athetine species *Meronera venestula*.

Key words: Coleoptera, Staphylinidae, Aleocharinae, Athetini, larvae, Lomechusini, *Apalonia*, *Meronera*, taxonomy.

Introduction

The genus *Apalonia* was erected by CASEY (1906) to contain a single species *A. seticornis* from Florida. CASEY (1906) hypothesized a close relationship between *Apalonia* and *Myrmedonia* ERICHSON, 1837 (= *Drusilla* LEECH, 1819), primarily due to morphological similarities of the mesointercoxae (see redescription). CASEY (1911) added another species to the genus, *A. divisa* CASEY, and refined his hypothesis on *Apalonia*'s relationship with *Myrmedonia* by noting that *Apalonia* resembled the *fauveli*-type (Casey never elaborated on what constitutes as a member of the “*fauveli*-type” except that it includes *Pella fauveli* (CASEY) [= *M. fauveli*] of *Myrmedonia*, due to the lack of an occipital suture (“infra-lateral cephalic carinae” of Casey). CASEY (1911) further suggested that *fauveli*-type *Myrmedonia* species might not belong in *Myrmedonia*, but within *Apalonia* as a novel subgenus.

Subsequently FENYES (1918–1921) in his aleocharine catalogue treated *Apalonia* as a subgenus of *Zyras* STEPHENS, 1835 and expanded *Apalonia* to include other species of *Myrmedonia*, including *M. fauveli*, but did so with no justification. BERNHAUER & SCHEERPELTZ (1926), as well as MOORE & LEGNER (1975) follow this tradition of treating *Apalonia* as a subgenus of *Zyras*. SEEVERS (1978), in his revision of North American Aleocharinae, re-elevated *Apalonia* to generic status to include only two species, *A. seticornis* and *A. divisa*, retaining species that previous authors periodically treated as *Zyras* (*Apalonia*) within *Zyras*.

After SEEVERS (1978), *Apalonia* did not appear in the literature until PACE (1997, 2008a, b, 2009) in a series of papers described 39 new species, transferred an additional six species that Pace originally described under *Macrogerodonia* (BERNHAEUER, 1941) and two species described

by Sharp from *Myrmedonia*. KLIMASZEWSKI et al. (2005) treated *Apalonia* as part of the “Zyras group of genera” and synonymized *A. divisa* under *A. seticornis*.

Historically *Apalonia* has either been directly placed within or allied with genera that belong to the Lomechusini. This treatment has been a consequence of *Apalonia seticornis* expressing meso-metaventral morphology that resembles what is considered typical for lomechusines. Similarity between *A. seticornis* and lomechusine meso-metaventral morphology may be due to convergence. Other characters must be explored in order to test the placement of *A. seticornis* within the tribe Lomechusini.

Apalonia is redescribed and immature stages are described for the first time along with bionomic data. Similarity between *Apalonia* and *Meronera* SHARP, 1887 is introduced, illustrated and discussed. Tribal assignment of *Apalonia* is reconsidered based on comparative morphology and phylogenetic evidence based on molecular data drawn from a study by ELVEN et al. (2010). *Apalonia* is transferred from the tribe Lomechusini to the Athetini. Reevaluation of Pace’s species based on original descriptions leads my hypothesis that these species belong outside of *Apalonia* and many belong in the genus *Myrmedonota* CAMERON, 1920.

Methods

Dry specimens were observed using an Olympus SZX7 stereomicroscope. Dissected structures were observed with the stereomicroscope and an Olympus BX51 compound microscope. Illustrations were made using a camera lucida, Olympus U-DA, mounted on the compound scope. Scale bars were drawn using an Olympus slide micrometer. Body measurements were made using a stereomicroscope ocular micrometer. Images were taken with a Microoptics imaging system and combined using CombineZM.

Dissections were made using pins in water or euparal (see HANLEY & ASHE 2003 for details). Dissected parts or entire specimens were cleared in 10% KOH at ambient temperature overnight; specimens were then washed in distilled water and further cleared in glacial lactic acid for a variable amount of time, and again washed in distilled water. Some larvae were also stained using chlorazol black solution and washed in distilled water.

Cleared specimens were then placed in dilute glycerin (25% EtOH, 25% distilled H₂O, 50% glycerin) and the solution was allowed to evaporate, leaving the glycerin and specimens. Once observations were complete, glycerin immersed specimens were washed in 70% EtOH and mounted permanently as described below.

For permanent mounts, cleared specimens or parts were brought successively to an ethanol concentration of 100% and then placed into Euparal on a glass substrate. Full body dissections were made and preserved on microscope slides. Dissected genitalia and mouthparts were preserved on bisected cover slips, subsequently glued onto a bisected glue board and mounted under the respective specimen (see MARUYAMA 2004 for details).

All specimens collected and reared were mounted using water-soluble fish glue. Larvae were quickly passed through boiling water to kill and fix the specimens. Larval specimens were preserved either as permanent slide mounts or in 70% EtOH.

Apalonia seticornis were kept in plaster rearing blocks with a glass top for observations (STEEL 1970). Rearing blocks were initially thoroughly moistened and kept in plastic containers on top of a paper towel, which was periodically moistened to maintain plaster moisture (ideas provided by M.K. Thayer).

Terminology follows the work of ASHE & WATROUS (1984; larval chaetotaxy), GUSAROV (2002; aedeagal orientation), MARUYAMA (2006; epipharyngeal surface), SAWADA (1970, 1972;

chaetotaxy, mouthpart and median lobe morphology) and SEEVERS (1978; parameral morphology). For brevity, figure captions pertaining to larval and adult labial morphology (Figs. 1–15, 43, 45) have abbreviations omitted when they are the same as those in their original publications (ASHE & WATROUS 1984; SAWADA 1970, 1972).

Abbreviations applied in the text of this manuscript are as follows: HW = mean head width; HL = mean head length; HW/HL = ratio between mean head width and length; OL = mean ocular length; OLHL = ratio between mean ocular length and mean head length; PW = mean pronotal width; PL = mean pronotal length; PW/PL = ratio between mean pronotal width and length; HL/PL = ratio between mean head length and mean pronotal length; HW/PW = ratio between mean elytral width and mean elytral length; EW = mean elytral width; EL = mean elytral length; EW/EL = ratio between mean elytral width and length; EL/PL = mean ratio between mean elytral length and pronotal length; AL = antennal length; HL/AL = ratio between head length and antennal length; MsW = mesonotum width; MsL = mesonotum length; MsW/MsL = ratio between mesonotum width and length; MtW = metanotum width; MtL = metanotum length; MtW/MtL = ratio between metanotum width and length; T9W = tergite VIII width; T9L = tergite VIII length; T9W/T9L = ratio between tergite VIII width and length; CKTE = collection of the author; FMNH = Field Museum of Natural History, USA; NMNH = National Museum of Natural History, Smithsonian Institute, USA; SEMC = Snow Entomological Museum Collection, University of Kansas, USA.

Material Examined

IMMATURES (3): KANSAS: “USA: Kansas: Douglas/Co., Lawrence, April/reared from adults/leg. K.T. Eldredge” (SEMC: 1 first instar on permanent slide, 1 second instar on permanent slide, 1 third instar in glycerin, 1 pupa in ethanol).

ADULTS (25): FLORIDA: “Okeechobee VII.36./A. Bierig coll./Fla. / USA/Field Mus. Nat. Hist./1966/A. Bierig Colln./Acc. Z-13812” (FMNH: 5); “Jacksonville/III.37./Fla. / USA//Apalonia/cinca Bier/don. C. Koch//cinesa Bier/Apalonia/ex. auctore//Chicago NHMus/M. Bernhauer/Collection” (FMNH: 1); “Tampa/31.3 Fla//Coll Hubbard/&Shwarz” (NMNH: 1); same collectors with differing dates and localities as follows: “Crescent/City Fla” (NMNH: 1); “Enterprise/20.5 Fla” (NMNH: 4). KANSAS: “USA: KANSAS: Douglas Co./Lawrence, N38.95546/W95.26632, 16.ii.2010/Berlese sifted leaf litter/leg. K.T. Eldredge”; “USA: Kansas: Douglas/Co., Lawrence, April/col. Adult’s 1st brood/leg. K.T. Eldredge” (CKTE: 3 with pupal chamber, 1 without pupal chamber, 1 permanent slide mounted); “USA KANSAS Douglas Co./Lawrence, 7.2 km S/38°51.78’ N.95°16.08’W/1 July 2001, J.S.Ashe/ex: under stone” (SEMC: 1); “Douglas Co. Kan/VIII-6-50/C. D. Michner” (SEMC: 1); “USA: KANSAS: Anderson Co./Anderson Co. Prairie Pres./N38.17021°, W95.24283°/2.ii.2010, leg. Z.H. Falin./ex. Under rocks, abandoned/quarry KAN1F10 001” (SEMC: 1). OKLAHOMA: “OKLAHOMA: LATIMIER Co./5MI. W. RED OAK/5-VII-76/K. STEPHAN” (SEMC: 1); same locality with differing dates as follows: “15-X-76” (SEMC: 1); “25-XII-76” (SEMC: 1); “III-80” (SEMC: 1). TEXAS: “Columbia/Tex//Coll Hubbard/&Shwarz” (NMNH: 1).

Tribe Athetini CASEY, 1910

To date, *Apalonia* had been treated as a member of the tribe Lomechusini FLEMING, 1821. Although lomechusines have never been satisfactorily defined, the following characters are often applied to the group: 1) galea elongate (SEEVERS 1978, NEWTON et al. 2000, MARUYAMA 2006); 2) mesocoxae broadly separated (SEEVERS 1978, NEWTON et al. 2000); 3) metaventral process much longer than mesoventral process, which extends little between mesocoxae (SEEVERS 1978, NEWTON et al. 2000); 4) athetine bridge of median lobe present (MARUYAMA 2006); proximal separation of median lobe that receives compressor plate deeply divided, appearing as if almost reaching parameral proximal costa in lateral view (SEEVERS 1978, MARUYAMA 2006); tarsal formula 4-5-5 (SEEVERS 1978, MARUYAMA 2006, NEWTON et al. 2000).

Apalonia was placed within the Lomechusini due to their shared tarsal formula and mesointercoxal morphology (Fig. 41). Unlike other lomechusines, *Apalonia* does not possess an elongate galea (Fig. 48) and a median lobe with a deeply divided base (Fig. 24). In addition to these traditionally valued characters, *Apalonia* also possesses a broad fused glossa (Fig. 43), marginal dilation of the lacinia, dorsal molar region (Fig. 54) with rows of small denticles, and a prostheca (Fig. 53–54) with multiple types of teeth forming a complex differentiated margin. These additional characters are not diagnostic for any tribe, but are a combination of states that are not present among lomechusines.

ELVEN et al. (2010) demonstrated that another lomechusine, *Meronera venestula* (ERICHSON, 1839) belonged to the tribe Athetini based on molecular data. *Apalonia seticornis* strongly resembles *Meronera venestula* and a comparison of the morphology yielded the following similarities: 1) labrum (Figs. 49–50) shape and submembranous area; 2) epipharyngeal surface structure (Figs. 51–52); 3) epipharynx proximal sclerite structure; 4) mandibular mola (Figs. 53–57) surface with denticulate rows and prostheca with multiple types of teeth forming a complex differentiated margin; 5) galea and lacinia (Figs. 47–48) short; 6) galea with distal lobe and apical spine which appears to be an apical extension of the proximal sclerite; 7) lacinia with a marginal dilation that differentiates the distal comb and isolated spines, of which the isolated spines are composed of teeth of two different types; 8) labial (Figs. 43, 45) palpal chaetotaxy identical; 9) labial palpal segment II with membranous zone; 10) glossa fused with a pair of setae on dorsal surface; 11) hypopharynx (Figs. 44, 46) morphology; 12) female sternite VIII (Figs. 35–36) with rounded emargination and microtrichae adorning apex (Figs. 37–38); 13) spermatheca (Figs. 39–40) with proximal portion with a simple loop, distal portion divided into a bulbous and smooth section that gives rise to a second chamber at an oblique angle with circumventral sculpturing towards an apical umbilicus; 14) median lobe (Figs. 23–26) shape; 15) parameral costal morphology; 16) part of apical lobe of median lobe similarly divided; 17) divide of median lobe base shallow; 18) arcuation of apical lobe to athetine bridge of median lobe in lateral perspective; 19) internal sac (Figs. 27–28) copulatory piece; 20) paramere (Figs. 29–32) of similar morphology; 21) mesointercoxae (Figs. 41–42) broadly separated, metaventral process longer than mesoventral process, mesocoxal cavity marginal bead incomplete posteriorly; 22) body (Figs. 19–22) with nearly identical macrochaetotaxy, despite *Apalonia seticornis* having macrosetae much longer and thicker.

In addition to the characters that place *Apalonia seticornis* outside of the Lomechusini, many characters suggest a close relationship to the athetine species *Meronera venestula*. I take this to be sufficient evidence to transfer *A. seticornis* from the Lomechusini to the Athetini.

Apalonia CASEY, 1906

TYPE LOCALITY: Florida, USA.

TYPE SPECIES: *Apalonia seticornis* CASEY, fixed by original designation.

DIAGNOSIS: Larvae are distinctive from known aleocharine larvae by the following characters: 1) labrum fused to head (Figs. 1–2); 2) scale-like sculpturing on labrum and clypeal area of head (Fig. 1); 3) broad ligula transverse and apically broadly rounded (Fig. 6); antennal sensory appendage broad and conical with base parallel sided (Fig. 3).

Adults may be separated from all or most other genera of Aleocharinae by the following combination of characters: 1) 4-5-5 tarsal formula; 2) broadly separated mesocoxal cavity with mesoventral process much longer than metaventral process and mesocoxal marginal bead incomplete posteriorly (Fig. 41); 3) head with distinct neck; 4) body glabrous, except for macrosetae and some inconspicuous and sparse microsetae (Fig. 19); 5) macrosetae very strong

and long (Figs. 19–20); 6) mandibles with well developed of denticulate dorsal molar regions (Fig. 54); 7) four segmented maxillary palpi; 8) lacinia with marginal dilation, thus with a distinct distal comb; 9) galea with distal lobe developed; (Fig. 48); 10) three segmented labial palpi; 11) glossa broad and fused; (Fig. 43); 12) median lobe with a complete athetine bridge and differentiated apical lobe (Figs. 23–24).

Apalonia seticornis CASEY, 1906

Apalonia divisa CASEY, 1911; synonymy, KLIMASZEWSKI et al. (2005).

LARVA – INSTAR III: Larval taxonomy has received relatively little attention among the Aleocharinae. Subsequently, descriptions suffer from a lack of comparative morphological data that would, in its presence, elucidate diagnostic characters. Therefore, in light of limited larval data, the description is presented in relation to the third and final larval instar of *Atheta cortaria* (KRAATZ, 1856), which ASHE & WATROUS (1984) utilized in developing a nomenclatural system for aleocharine larval chaetotaxy.

Overall habitus generalized and not markedly distinct. Body colors with sclerites light grey and membrane pale whitish.

Head, in dorsal view, sub-circular (Fig. 1); width slightly greater than length ($HW/HL = 1.12$, $HW = 0.29$ mm, $HL = 0.26$; $n = 1$); clypeus fused to labrum; labral-clypeal region with two rows of denticle-like surface texture, beginning near anterior margin of antennal fossae and extending further anteriorly to labrum, paired rows of surface texture converging apically but never coming into contact; campaniform sensilla with Ed1, Em1, Ec3 and P4–5 absent; laterally (Fig. 2) with clypeal region inflated; campaniform sensilla with L3, V1 and Lc3 absent. Antennal (Fig. 3) length slightly greater than half head length ($HL/AL = 1.89$, $AL = 0.14$ mm; $n = 1$); solenidia IIS3 and IIS2 absent. Epipharynx (Fig. 14) occupying area ventral of labrum and extending posterior to clypeal region; labral region simple with two pairs of setulae at anterior margin and a pair on the lateral margin; two pairs of pores at anterior margin and a pair at middle; clypeal region of epipharynx with a bifurcated patch of scale like surface texture; posterior margin with a single row of texture that consists of scale like structures that are slightly more elongate and parallel sided than majority of patch; patch of surface texture converged just posterior of labral margin and divergent posteriorly, harboring three sets of pores at the base of patch bifurcation; lateral area of patch with a pair of large pores with two to three additional smaller pores apically. Mandible (Fig. 4) proximally quadrate and distally incurved slightly; pair similar in morphology with a single subapical dorsal tooth with a serrate inner margin; region apical of subapical tooth also with a dorsal row of serration. Maxilla (Fig. 5) mala with inner apical region with a compact multi-rowed area of spinose setae. Labial complex (Fig. 6) with submentum and mentum divided by a suture; palpomere I without pores; ligula transverse and apically broadly rounded and adorned with three sub-equally spaced pores.

Pronotum (Fig. 7) hemicircular with anterior margin slightly truncate; transverse ($PW/PL = 1.67$, $PW = 0.38$ mm, $PL = 0.23$ mm; $n = 1$); campaniform sensilla with P5, Da1, Da3, Db1–3, Dc1, Dc3, Dd1–2, and C5 absent. Prosternal region (Fig. 14) Pr2–3, Eu2, Ls1–2, St4, and Pohy1 absent. Mesonotum (Fig. 8) transverse ($MsW/MsL = 2.60$, $MsW = 0.39$ mm, $MsL = 0.15$; $n = 1$); chaetotaxy with Da3, Db3, Dc2, and Dd2 absent. Metanotum transverse ($MtW/MtL = 3.38$, $MtW = 0.41$ mm, $MtL = 0.12$ mm; $n = 1$).

Abdomen: Tergite I (Fig. 9) transverse; chaetotaxy and campaniform sensilla morphology with A5, Da2, Db2–3, Dc2, Dd2, C1, and C5 absent. Sternite II (Fig. 10) transverse; chaetotaxy with D2–3 and P5–6 absent. Tergite VIII (Fig. 11) transverse; chaetotaxy with A4–5, Da2, Dc2, and Dd2 absent and an additional seta Pa1 present; gland opening at apex present as an

inconspicuous horizontal slit; glandular sac was not observed in prepared third instar specimen, but observed in a prepared first and second instar specimens and exhibited structures that might represent ASHE & WATROUS's (1984) gland duct attachment sclerite, which in form was acutely sagittate. Tergite XI (Fig. 12) quadrate ($T9W/T9L = 1.00$, $T9W = T9L = 0.17$ mm; $n = 1$). Tergite X anal hooks absent.

Foreleg (Fig. 13) chaetotaxy and campaniform sensilla morphology: coxa with A13–4, P12–3, V1, and C1–3 absent and Ad3 migrated ventrally; trochanter with A11–2, Av1–2 and C5 absent; tarsungulus with two ventral setae.

PUPA (Figs. 16–17): length 1.12 mm ($n = 1$); body with pale cream color with darker eye spots and base of mandibles (whether pupae darken with age is not known); exarate and adecticate; body surface entirely microtrichous; head and legs folded ventrally with antennae tucked between mid and hind legs, antennae folded against body along lateral sides; abdominal segment IX with what appears to be remnants of larval urogomphi; head with two, pronotum with three pairs of prominent setae; numerous other, less apparent pairs of setae covering most of body.

ADULT: Body (Figs. 19–20) length on average 2.12 mm ($n = 19$); overall color yellowish to orange with some segments black. Head, pronotum, elytra and most of abdomen ranging from yellow to orange; head usually a darker shade than rest of body and can sometimes reach a light brown; elytra usually concolorous with pronotum and abdomen, but may be slightly infuscate; abdominal tergite VI black and sternite VI light to dark brown; tergite V sometimes black to brown in darker colored specimens, and may be bicolorous with the anterior half yellow to orange and posterior half black to brown; antennae yellow to orange with segments IX–XI black, segment VIII sometimes dark brown; legs yellow to orange.

Head subcircular in dorsal view ($HW/HL = 1.04$, $HW = 0.38$ mm, $HL = 0.37$ mm; $n = 19$); eyes occupy one third of head length ($OL/HL = 0.35$, $OL = 0.13$ mm; $n = 19$) and are coarsely faceted; neck distinct and in lateral view vertex rapidly, and almost vertically, sloping posteriorly towards neck; setae pale in color and directed posteriomediaally. Antennae clavate; segment I–III elongate, I ovular and III subulate in overall shape; IV–V globular and subequal in length; VI–VIII subquadrate; IX–X transverse; XI conical, apex slightly deflected ventrally and overall somewhat compressed laterally. Labrum (Fig. 49) transverse; apicomedial surface with submembranous area; seta d2 migrated to epipharyngeal surface and posterior to m2. Epipharynx (Fig. 51) with setula b absent and two lateral pairs of setulae; medial pore field with numerous pores and a pair of larger pores anterior of midline; regions lateral to medial pore field with scale-like processes that demonstrate transformations into more longitudinal brick-like processes, and amidst with one to two (numbers variable and sometimes unequal, as illustrated) pairs of larger pores; basolateral region with three to four (numbers variable and sometimes unequal, as illustrated) approximately longitudinal rows of pores; basal transverse row absent; proximally with a pair of lateral sclerites, each with a medial transverse band of fringe-like sculptures, and anterior (left proximal sclerite flipped over, appearing as if anterior group is posterior of transverse fringe) to is a group of subrectangular tile-like sculpture and a pair of pores lateral of them. Mandibles (Figs. 53–54) triangular with a broad base; dorsal and ventral surface covered in roughly circularly clustered elongate pores (Fig. 57); right mandible with a small medial tooth accompanied by a distal serration; left mandible also with subapical serration, but lacking a tooth; four pairs of scrobal setae present; dorsal molar region well developed with multiple transverse rows of denticulate texture and margin with trichiate to teeth-like processes; protheca divided into two approximate sections and a medial buffer region (a region that is difficult to assign a definite prothecal homologous unit), section I mostly composed of a dorsal row of filamentous trichae and a ventral row of small teeth grading in from section II, section II mostly composed of a dorsal row asymmetrically acute-ended blades and a ventral row of large teeth grading into section I. Maxilla (Fig. 48) with palpi four segmented; palpal segment IV with

filamentous sensillae; galea short and stout; distal lobe present on section I with an apical spine that demarcates the inner limit of section I and II, section II with adorally directed row of trichae; lacinia with a marginal dilation that differentiates section I (distal comb) and section II (isolated spines), of which section II is composed of stouter teeth that are laterally inserted on medial dilation and a dorsal row of setae proximal to more distal teeth-like isolated spines. Labium (Fig. 43) with three segmented palpi; palpal segment II the shortest and with a membranous zone; segment I slightly longer than III setula β and δ absent; glossa undivided with a pair of long setae on dorsal surface.

Pronotum (Figs. 19–20) trapeziform and convex in cross section; as wide as long (PW/PL = 1.07, PW = 0.39 mm, PL = 0.37 mm; n = 19) and as long and wide as head (HL/PL = 1.01, HW/PW = 0.97; n = 19); widest at subapical angles and anterior margin arcuate, extending anteriorly past subapical angles; basal margin also arcuate and extending posterior to subposterior angles; marginal bead pronounced and visible throughout pronotal margin, even visible dorsally at anterior and posterior edge; hypomerion fully visible in lateral view, and terminating at subapical pronotal angles, appearing as if incomplete in lateral view; lateral margin with three pairs of macrosetae; basal margin with a pair of macrosetae; disk with three pairs of macrosetae; very few isolated inconspicuous pale microsetae present. Prosternum smooth, not carinate.

Elytra (Figs. 19–20) transverse (EW/EL = 1.37, EW = 0.50 mm, EL = 0.37 mm; n = 19) and as long as pronotum (EL/PL = 1.01; n = 19); each elytron with a faint marginal bead running from anterolateral corner to anteromedial corner along suture; lateral margin with two pairs of macrosetae; disk with two pairs of macrosetae; inconspicuous pale microsetae present, but more dense and thus more obvious compared with pronotum. Mesocoxae (Fig. 41) broadly separated; mesoventral process, compared with metaventral process, extending little between mesocoxae; isthmus subequal in length to mesoventral process; mesocoxal cavity bead incomplete, disappearing near posterior limit.

Abdomen (Figs. 19–20) with tergal gland present at the base of segment VII, occupying roughly half of tergal width; an additional gland present on sternite IV, of similar morphology to the tergal gland, but occupying less surface area of posterior margin; base of tergal and sternal segments II–VIII (sternite II absent) costate, and additionally tergites III–V basally impressed; tergite VIII (Fig. 33) bisinuate with apicomedial area bluntly and apicolateral margin acutely produced; sternite VIII (Figs. 35, 37) apically evenly arcuate in males and with a small rounded emargination adorned with fringing trichae in females; tergite II with a pair of marginal macrosetae; tergites III–VII each with two pairs of marginal macrosetae; tergite VIII with two pairs of marginal and two pairs of submarginal macrosetae; sternite III with a pair of marginal and a pair of near-dorsal apicolateral macrosetae; sternites IV–VI with a pair of discal, two pairs of marginal and a pair of near-dorsal apicolateral macrosetae; sternite VII with two pairs of discal, three pairs of marginal and a pair of near-dorsal apicolateral macrosetae; sternite VIII with four pairs of marginal and two pairs of submarginal macrosetae.

FEMALE: spermatheca (Fig. 39) with proximal portion with a simple loop; distal portion divided into a bulbous and smooth section that gives rise to a second chamber at an oblique angle with circumventral sculpturing towards an apical umbilicus.

MALE: Median lobe (Figs. 23–24) oblong and with a complete aethetine bridge; paramerally with a horizontally elongate foramen, proximal costa short and inconspicuous, median and arcuate costa short and well sclerotized, and distal portion of apical lobe conspicuously differentiated from rest of median lobe by a suture; laterally with the apical lobe deflected paramerally; compressor plate partially covered by basal portion of median lobe, and the split to receive the compressor plate overlapping proximal end of compressor plate. Internal sac (Fig. 27) with

copulatory piece with a broad and rounded basal process and a gently sinuate apical process with apex deflected apamerally, suspensoria lightly sclerotized and composed of many overlapping acute spines, median apophyses U-shaped and oriented horizontally to median lobe, paramedian apophyses rectangular with a proximal articulation with the median apophyses; relative positions of internal sac structures when extruded will most likely reflect observations made with *M. venestula* (Fig. 28), with the copulatory piece-suspensoria complex surpassing the median-paramedian apophyses complex distally (copulatory piece-suspensoria complex proximal to median-paramedian apophyses complex when internal sac is not extruded, as is the case observable in Fig. 27, where the internal sac is partially distended). Paramere (Fig. 29) elongate with apical lobe extending past velum; apical lobe (Fig. 30) with setulae a, b and d approximated at apex, setula c migrated to middle.

Bionomics

Adults were collected in April and May and kept in plaster rearing containers (see Materials and Methods). Adults were collected from grass clippings (see Collecting for details).

Meronera venestula has been recorded to feed on fungal mycelia (ASHE 1985), and a well-developed dorsal molar region was observed in dissected specimens, similar to those found in spore feeding Aleocharinae (e.g. subtribe Gyrophaenina KRAATZ, 1856). In *M. venestula* the well-developed dorsal molar region is thought to be correlated with fungivory (ASHE 1993) and may represent an adaptation to triturating fungal particulates against the proximal sclerites of the epipharynx (LAWRENCE 1989, LESCHEN 1993). Given morphological correlates, it was hypothesized that moistened baker's yeast would be an adequate food source for generalist mycophagous staphylinids, since the author had previously successfully reared spore feeding *Sepedophilus* GISTEL, 1856 larvae on yeast (idea of substituting baker's yeast was provided during discussions with M.K. Thayer). Since *Meronera* and *Apalonia* are thought to be closely related at the time and share a similarly well-developed molar region, it was hypothesized that *Apalonia* would also readily feed on baker's yeast.

The pellet-shaped yeast was therefore fed to the *Apalonia* adults. Specimens immediately began to feed on the yeast in an almost grazing fashion. The head was extended and slowly drawn back while the maxilla scraped the surface of a yeast pellet. This was repeated in the same area of the pellet, to the point that enough yeast was removed that a trench was visible on the pellet surface.

Although yeast does not form mycelia, fungi will nonetheless infest the moist yeast and mycelia will form. Although direct feeding was not observed as in *M. venestula* (ASHE 1985), subsequent gut content analyses revealed some individuals to have also fed on the infesting fungal mycelia.

Copulation was never observed, but courtship-like chasing behavior was observed for the first time, and another form of chasing behavior, identical to those described by ASHE (1985) for *M. venestula*, was often observed. The first type of chasing behavior began with an individual, presumably a male, reaching out towards another individual, thought to be a female, and tried to palpate the other. Soon after, a chase will assume where the supposed male chases the female. Copulation is assumed to occur after such a ritual chase, but was never observed. The second form of chasing behavior takes place when two individuals simultaneously try to palpate each other. As the two individuals begin to circle a chase will begin where the two run in circles. This soon ends with both individuals dashing off in separate directions. The second chasing behavior may represent a male-to-male confrontation of some sort, but there are no observations to support this theory and ASHE (1985) had observed this behavior to take place amongst both sexes.

Eggs are laid individually, directly on the substrate with no apparent oviposition site preference. Larvae experience three instars and similarly feed on yeast. Cannibalism was never observed. Three larval instars were completed within a week. Pupation occurred in a silken chamber, and although pupal chamber construction was not observed, it is assumed to be excreted from a gland at the abdominal apex (ASHE 1981) (The author has observed a larva of *Homalota* sp. secrete a droplet from the abdominal apex, place the drop of liquid on a substrate, and withdraw the droplet back into the body as the abdomen was brought away from the substrate, generating a strand of silk. It is likely that other aleocharines generate silk and construct pupal chambers in a similar manner). Curiously, ASHE (1985) was not able to observe this silk pupal chamber construction in *M. venestula*. Pupal chambers often incorporated debris provided for them. Sand, sawdust and moss were provided and all three substrates were accepted for pupal chamber construction. When no substrate was provided, larvae either spun a naked cocoon up against a surface, or chewed plaster in order to incorporate these particulates into the pupal chamber. Pupation took approximately four to five days. Teneral adults, upon emergence, will immediately begin feeding in a teneral state, which itself lasts two to three days.

Collecting Specimens

Apalonia seticornis have been collected in various habitats, ranging from forest leaf litter (Fig. 59), grass clippings at the edge of woods (Fig. 58), to under stones of a prairie. Until this study, *A. seticornis* was most commonly collected individually under stones and rarely in leaf litter samples.

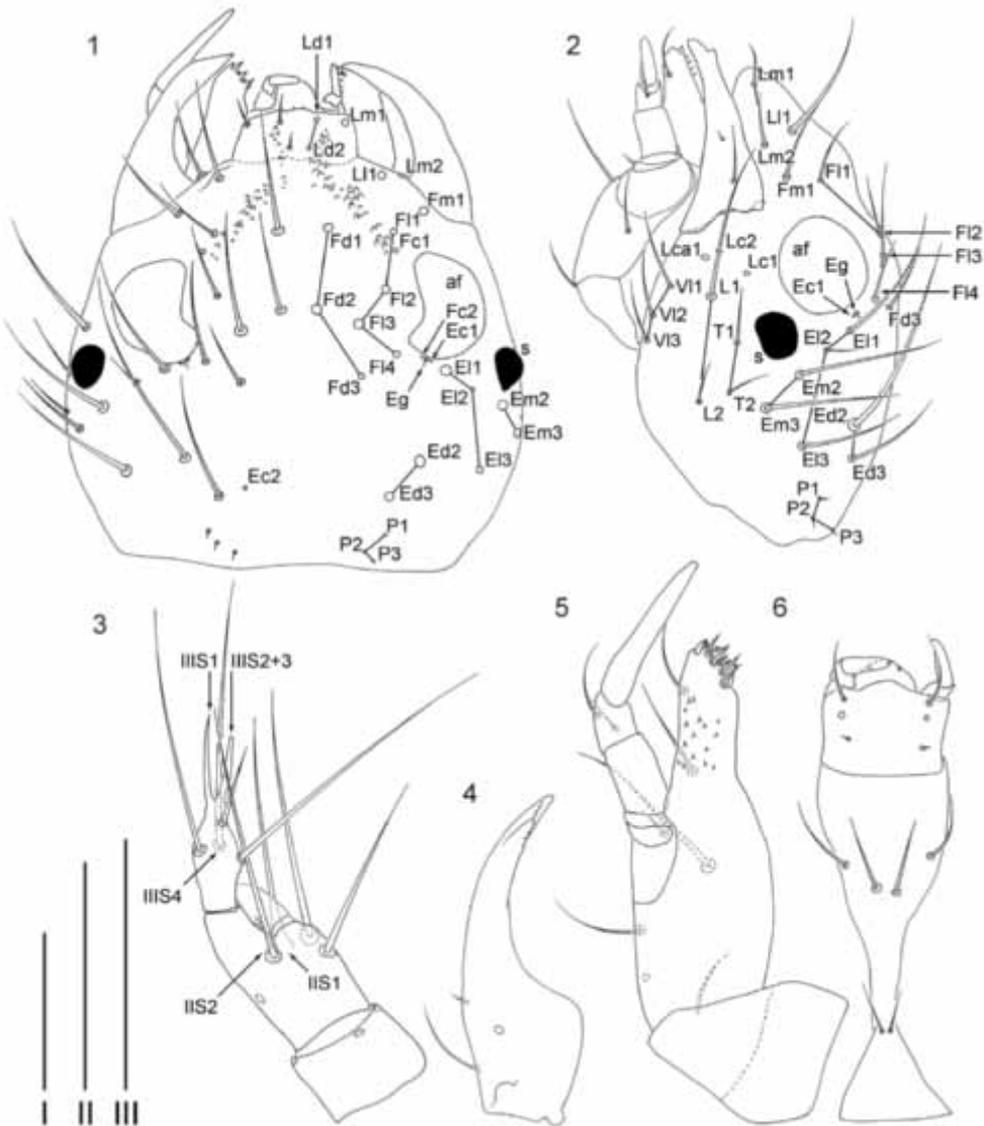
Specimens collected for this study were taken in April and May by sifting and sorting grass clippings in a plastic pan. Large numbers were never collected at once, and one to two individuals were obtained per sifting event. *Apalonia seticornis* was collected together with *M. venestula*, which were far more abundant. Adults may be differentiated in the field by differing coloration and by their behavior: *A. seticornis* is slow moving when undisturbed and will settle under cover, while *M. venestula* is fast moving and will actively move around without necessarily seeking out cover.

Discussion

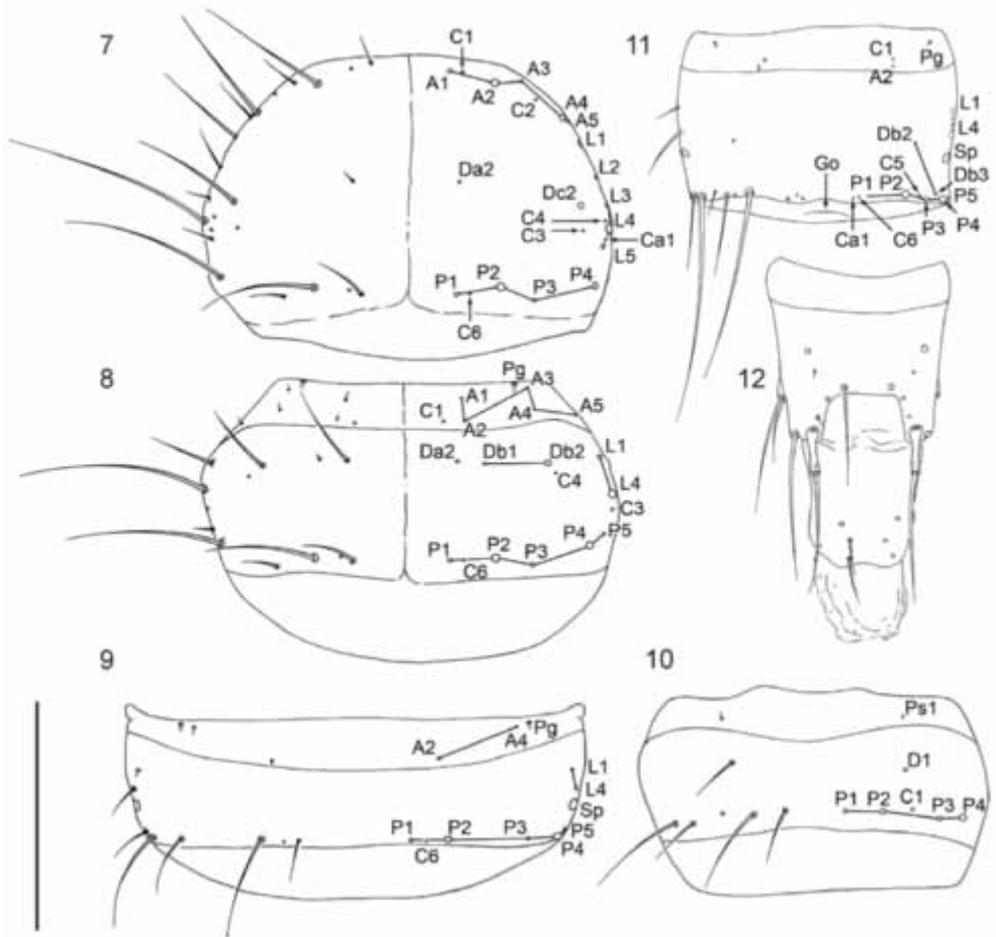
A survey of the literature has shown that most, if not all described *Apalonia* belong to other genera. A subset of these species most likely belong to the genus *Myrmedonota* CAMERON: *A. ancilla* PACE, 1997; *A. ancilloides* PACE, 2008b; *A. archidonensis* PACE, 2008b; *A. circumflexa* PACE, 1997; *A. globulifera* PACE, 2008a; *A. hemisphaerica* PACE, 2008a; *A. inca* PACE, 2001; *A. izzoi* PACE, 2008a; *A. laboriosa* PACE, 2009; *A. latissima* PACE, 2008; *A. margaritae* PACE, 2008b; *A. minor* PACE, 2008b; *A. myrmecobia* PACE, 2008a; *A. myrmecophila* PACE, 2008b; *A. osellaorum* PACE 2008b; *A. pampeana* PACE, 1997; *A. pernambucoensis* PACE, 2009; *A. sigchosensis* PACE, 2008b; *A. stilifera* PACE, 1997; *A. terminalis* PACE, 2008a; *A. vicina* PACE, 2008b; *A. westerduijni* PACE, 2008b; *A. zaparos* PACE, 2008b.

Acknowledgements

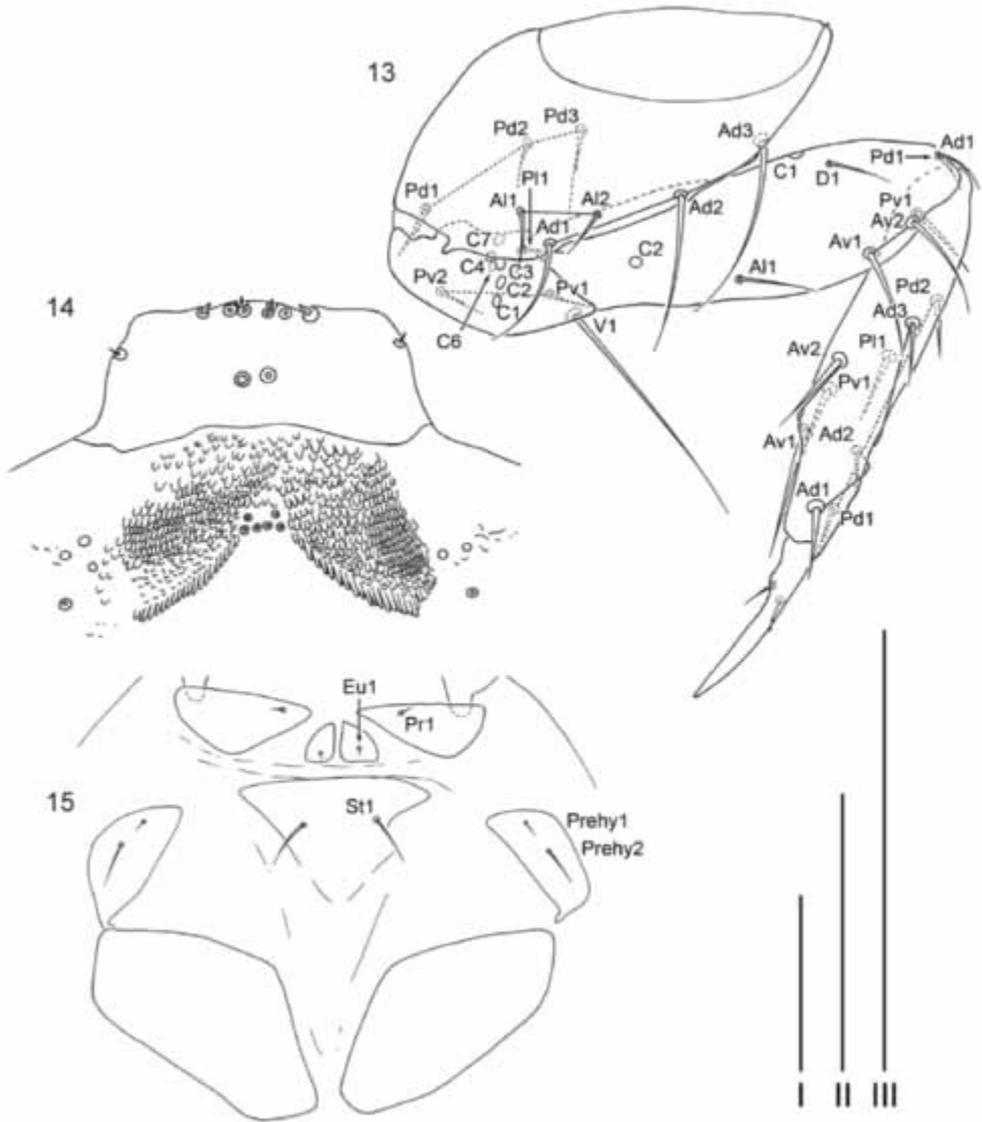
I would like to thank: A.E.Z. Short, C. Chaboo and C. Maier for their assistance in preparing the manuscript; S. Davis for looking after the *Apalonia seticornis* colony during my absence.



Figs. 1–6: *Apalonia seticornis* larval instar III structures. 1) head, dorsal; 2) head, lateral; 3) left antenna, dorsal; 4) left mandible, dorsal; 5) left maxilla, dorsal; 6) labium, ventral. Scale: 0.1 mm: I) Figs. 1–2; II) Figs. 4–6; III) Fig. 3. Abbreviations: af = antennal fossae; eg = epicranial gland; s = stemmata.



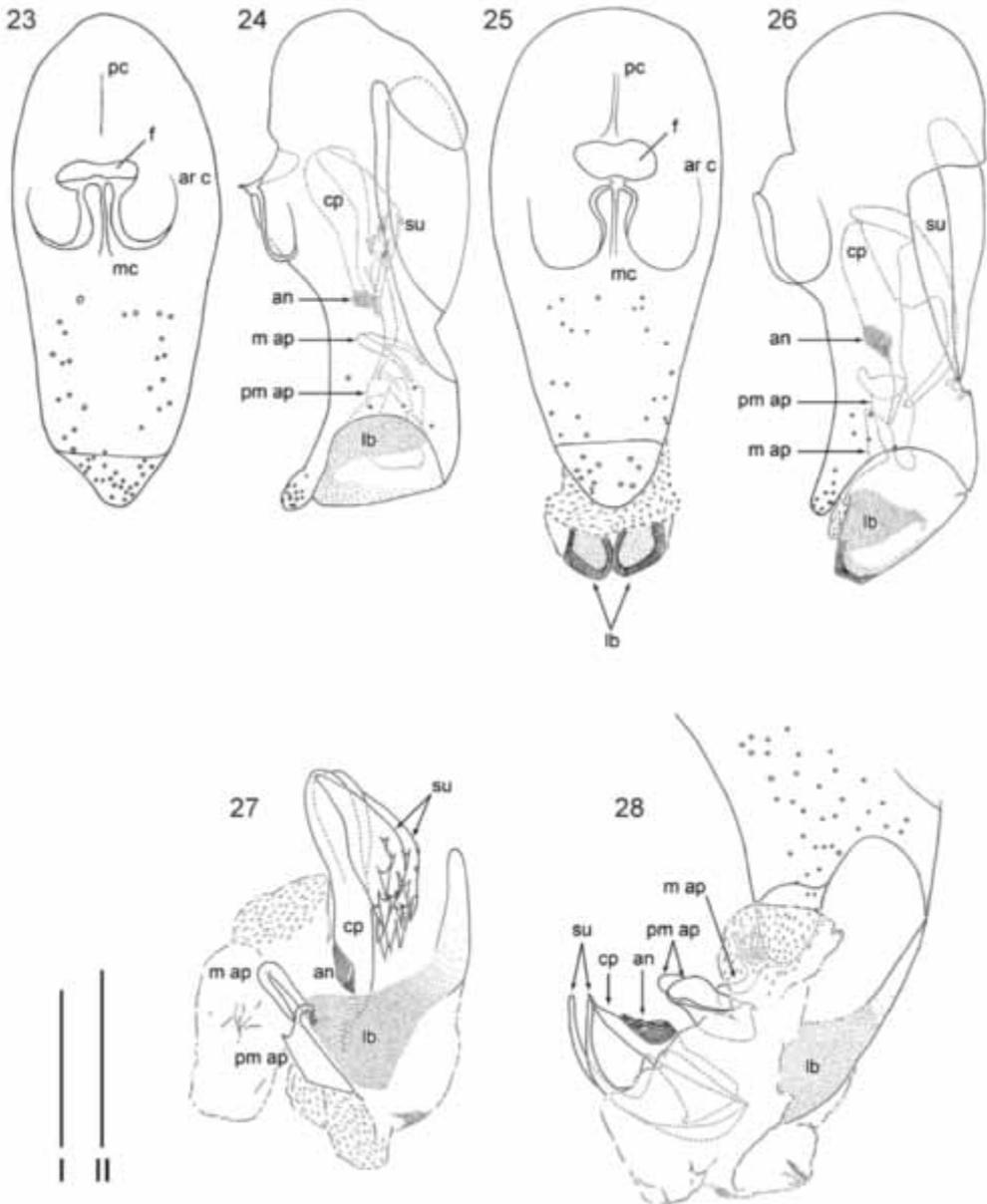
Figs. 7–12: *Apalonia seticornis* larval instar III structures. 7) pronotum; 8) mesonotum; 9) tergite I; 10) sternite II; 11) tergite VIII; 12) tergite IX+X. Scale: 0.1 mm. Abbreviations: Go = gland opening; Pg = pretergal gland; Sp = spiracle.



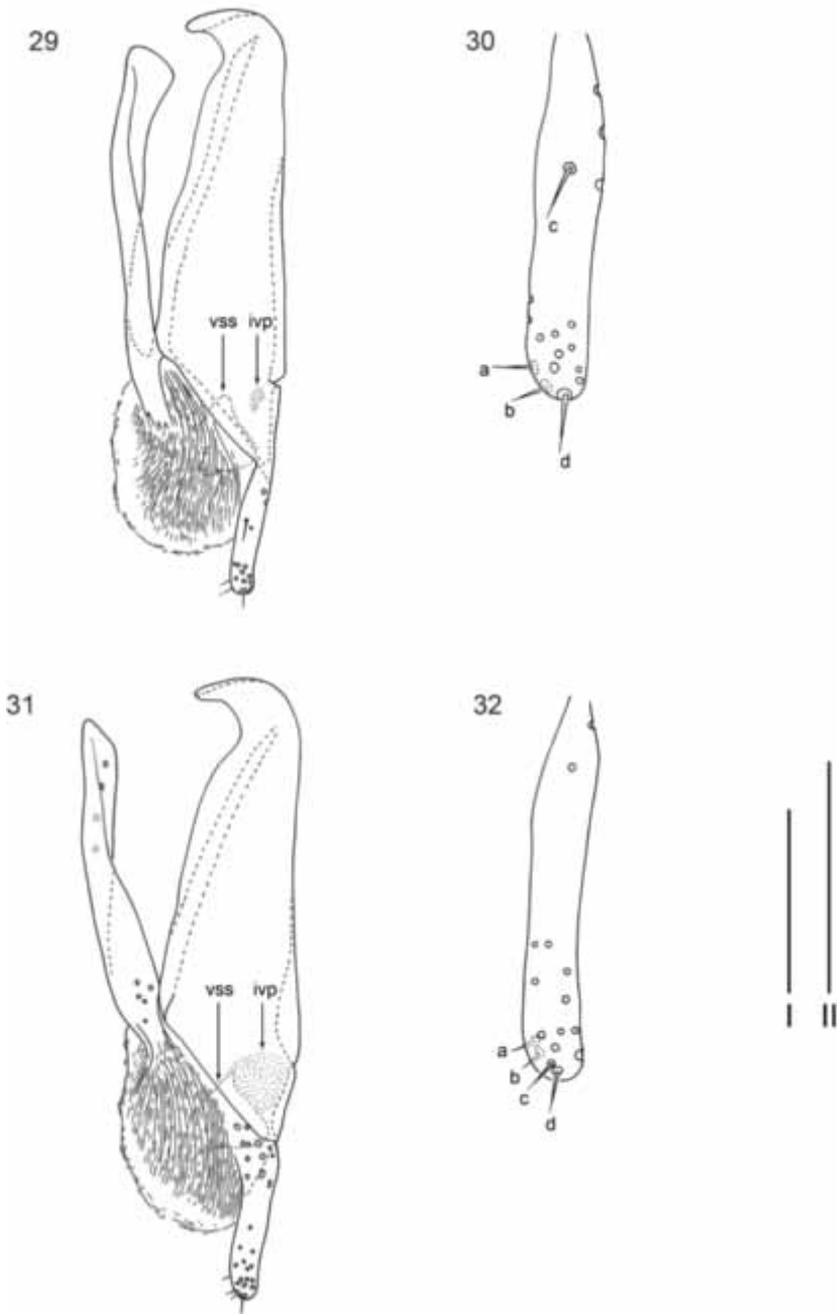
Figs. 13–15: *Apalonia seticornis* larval instar III structures. 13) left foreleg, anterior; 14) epipharynx; 15) prosternal region. Scale: 0.1 mm: I) Fig. 15; II) Fig. 13; III) Fig. 14.



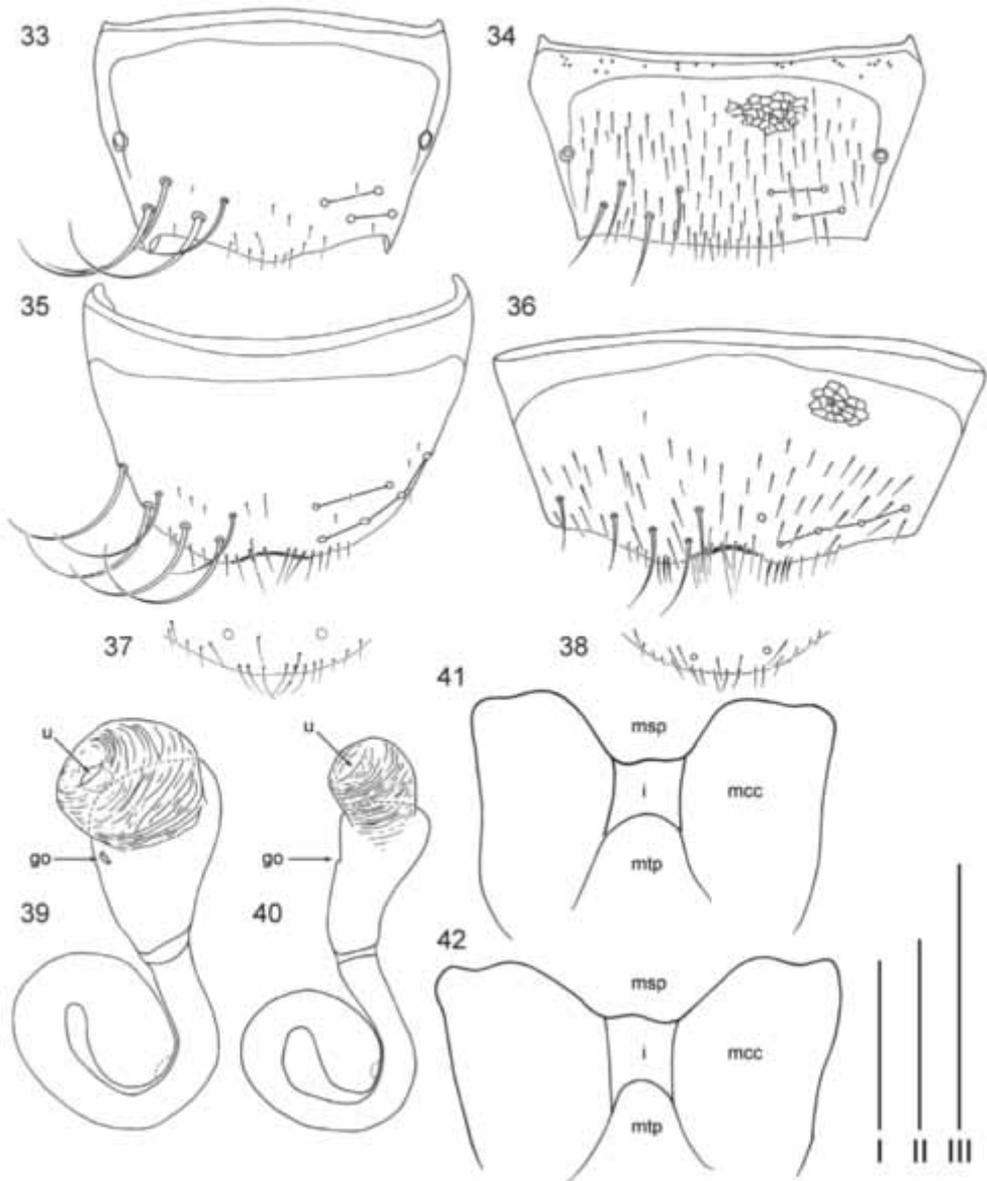
Figs. 16–22: Habitus images. 16–20: *Apalonia seticornis*: 16) pupa, ventral; 17) pupa, dorsal; 18) third instar larva feeding on yeast pellet; 19) adult, dorsal; 20) adult, lateral. 21–22: *Meronera venestula*: 21) adult, dorsal; 22) adult, lateral. Scale: larva and pupae, 0.5 mm; adults, 1.0 mm.



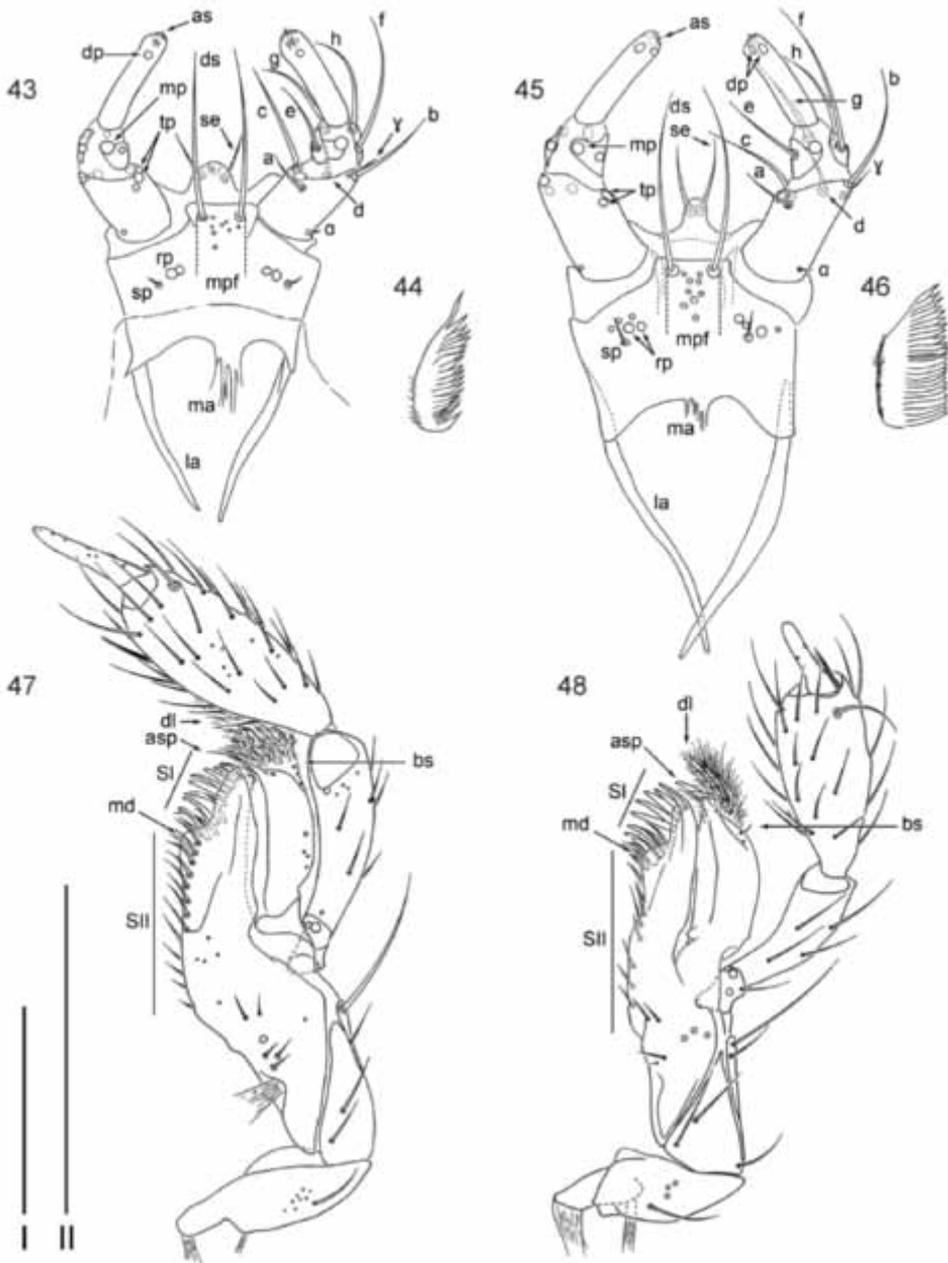
Figs. 23–28: Median lobe structures. 23–24, 27: *Apalonia seticornis*: 23) median lobe, parameral; 24) median lobe, lateral; 28) partially everted internal sac, lateral. 25–26, 28: *Meronera venestula*: 25) median lobe, parameral; 26) median lobe, lateral; 28) everted internal sac, lateral. Scale: I) Figs. 23–26, 0.1 mm; II) Figs. 27–28, 0.1 mm. Abbreviations: ac = arcuate costa; an = annulus; cp = copulatory piece; f = foramen; m ap = median apophyses; mc = median costa; pm ap = paramedian apophyses; pc = proximal costa; su = suspensorium.



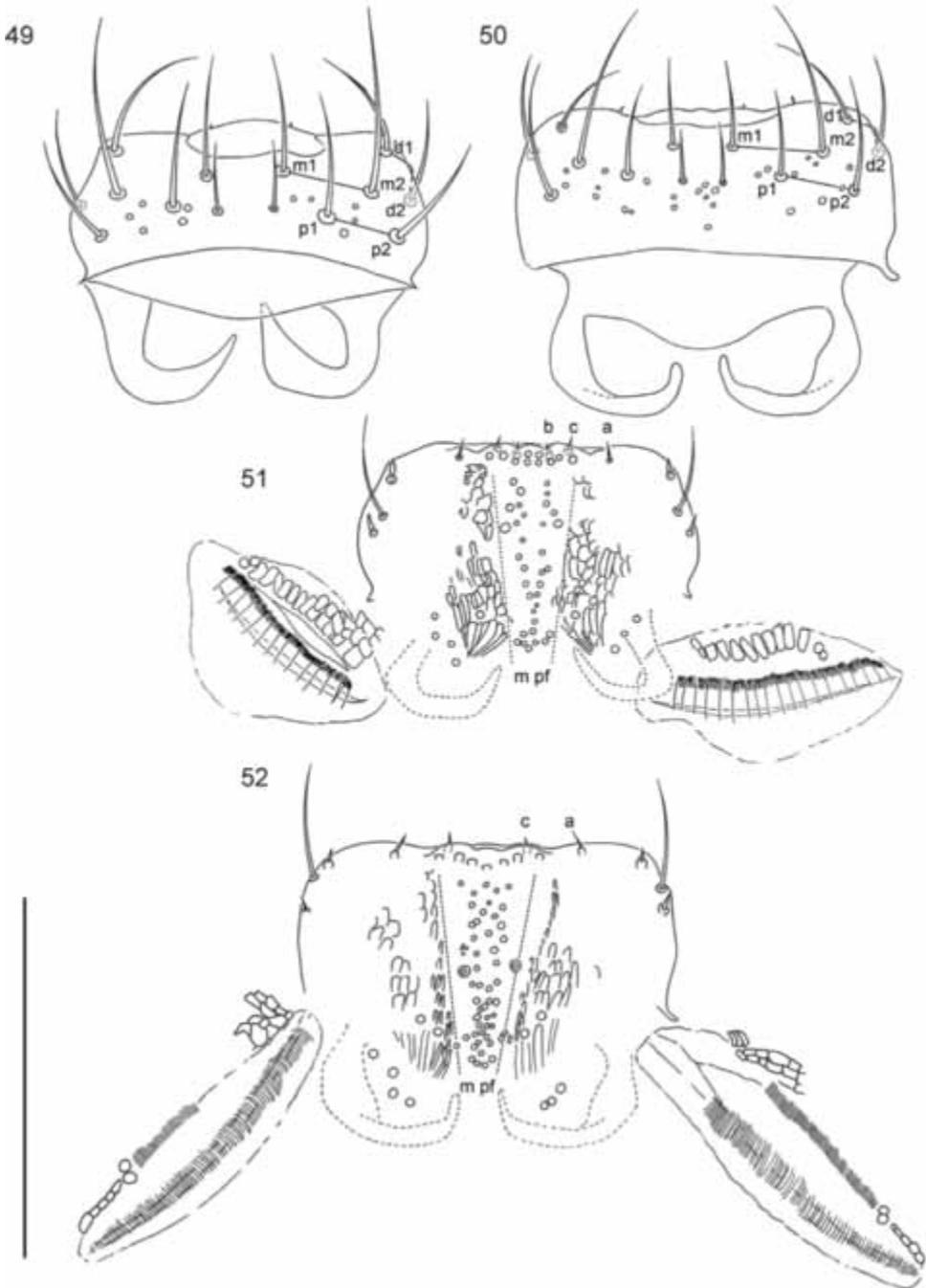
Figs. 29–32: Parameral structures. 29–30: *Apalonia seticornis*: 29) paramere, outer lateral; 30) apical lobe, outer lateral. 31–32: *Meronera venestula*: 31) paramere, outer lateral; 32) apical lobe, outer lateral. Scale: I) Figs. 19, 31, 0.1 mm; II) Figs. 30, 32, 0.05 mm. Abbreviations: ivp = internal velar pad; vss = velar sac sclerite.



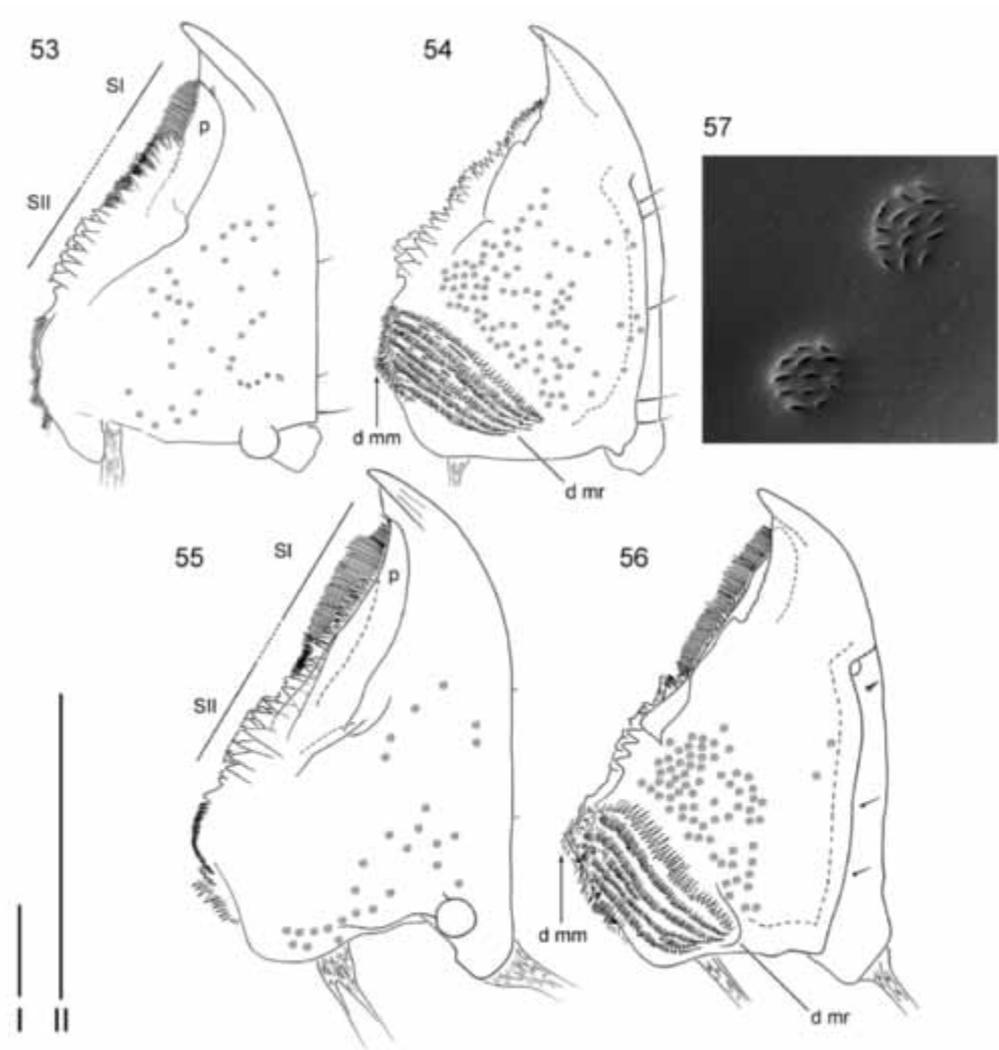
Figs. 33–42: Abdominal segment VIII, spermathecae and mesointercoxae. 33, 35, 37, 39, 41: *Apalonia seticornis*: 33) tergite VIII; 35) sternite VIII, female; 37) apex of sternite VIII, male; 39) spermatheca; 41) mesointercoxae. 34, 36, 38, 40, 42: *Meronera venestula*: 34) tergite VIII; 36) sternite VIII, female; 38) apex of sternite VIII, male; 40) spermatheca; 42) mesointercoxae. Scale: I) Figs. 39–40, 0.1 mm; II) Figs. 33–38, 0.1 mm; III) Figs. 41–42, 0.2 mm. Abbreviations: go = gland opening; i = isthmus; mcc = mesocoxal cavity; msp = mesoventral process; mtp = metaventral process; u = umbilicus.



Figs. 43–48: Labial complex and maxilla. 43–44, 48: *Apalonia seticornis*: 43) labial complex, ventral; 44) right hypopharyngeal lobe; 48) left maxilla, ventral. 45–47: *Meronea venestula*: 45) labial complex, ventral; 46) right hypopharyngeal lobe; 47) left maxilla, ventral. Scale: 0.1 mm: I) Figs. 47–48; II) Figs. 42–46. Abbreviations: asp = apical spine; bs = basal seta; dl = distal lobe; la = lateral apodeme; ma = median apodeme; md = marginal dilation; mpf = medial pore field; se = sensillate elements; S = section.



Figs. 49–52: Labrum and epipharynx. 49, 51: *Apalonia seticornis*: 49) labrum; 51) epipharynx. 50, 52: *Meronera venestula*: 50) labrum; 52) epipharynx. Scale: 0.1 mm. Abbreviation: m pf = median pore field.



Figs. 53–57: Mandibles. 53–54: *Apalonia seticornis*: 53) left mandible, ventral; 54) right mandible, dorsal. 55–57: *Meronera venestula*: 55) left mandible, ventral; 56) right mandible, dorsal; 57) porous cuticular structures of mandibular surface. Scale: I) Fig. 57, 2 μm ; II) Figs. 53–56, 0.1 mm. Abbreviations: d mm = dorsal molar margin; d mr = dorsal molar region; p = prostheca; S = section.



Figs. 58–59: Habitat of *Apalonia seticornis*. 58) edge of grass lawn and woods where most specimens were collected from this study; 59) secondary growth forest where *A. seticornis* are occasionally sifted from leaf litter.

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