First record of *Polymerurus* (Gastrotricha, Chaetonotida) from Australia with the description of a new species from Queensland and of cuticular ultrastructure in *P. nodicaudus*

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Abstract. Identification of specimens in the genus *Polymerurus* (Gastrotricha, Chaetonotida) is reported for the first time from Australia. The genus includes 3 species from a freshwater lake in southern Queensland. Two species, *Polymerurus rhomboides* and *P. nodicaudus,* are well-known cosmopolitans: *P. rhomboides* is now known from every continent except Antarctica, and *P. nodicaudus* from all continents except Africa and Antarctica. An ultrastructural description of the cuticle in *P. nodicaudus* is provided and confirms earlier observations on the structure of spined scales in other species of Chaetonotida, suborder Paucitubulatina. The utility of cuticle ultrastructure is discussed in reference to the search for characters defining higher-level taxa in the Paucitubulatina. A new species, *P. andreae,* also cohabits the Queensland lake and is distinguished by the following combination of characters: wide mouth ring; pharynx with terminal bulb; simple spineless scales on the dorsal, lateral, and ventrolateral body surfaces; and a column of ventral interciliary scales in rectangular, ovoid, and intermediate shapes.

Additional key words: gastrotrich, meiofauna, Paucitubulatina, electron microscopy

Gastrotrichs are a small but diverse group of microscopic worms living in marine, brackish, and fresh-water habitats, and may constitute an abundant part of the meiobenthos in both marine intertidal (Hochberg 1999) and fresh-water lentic systems (Strayer & Hummon 2001). Schwank (1990) estimates ~360 species of Gastrotricha within the order Chaetonotida, most of which are fresh-water species from lentic habitats, with fewer lotic, marine, and brackish water representatives. Chaetonotidan gastrotrichs are renowned to be among the smallest known metazoans, generally <1 mm in total body length, and some as small as 80 μm. Despite this miniscule size, many chaetonotidans are recognized to have both a complex anatomy and lifecycle (see Ruppert 1991; Weiss 2001). Their anatomical complexity is reflected partly in the ornamentation of the cuticle, wherein various spines and scales cover much of the body and may aid in defense and/or flotation. Some of this complexity has been characterized at the ultrastructural level, but to date the fine structure of only 3 species has been examined despite the vast array of cuticular elaborations that exist among species (Rieger & Rieger 1977).

The Chaetonotida is traditionally divided into two monophyletic suborders: the Multitubulatina contains a single family and genus, and the Paucitubulatina includes 6 families and >20 genera. The most speciose family of Paucitubulatina is the Chaetonotidae, containing 13 genera and nearly half of all known species of Gastrotricha. A recent cladistic analysis identified the Chaetonotidae as potentially paraphyletic (Hochberg & Litvaitis 2000), while molecular results using SSU rDNA have hypothesized both polyphyly (Zrzavy 2002) and monophyly (Todaro et al. 2003); the latter molecular studies included few genera and species. To date, no convincing morphological synapomorphies that define the Chaetonotidae have been identified; however, it may be reasonable to hypothesize that such characters may be found in the complexity of the cuticle. Still, such synapomorphies are unlikely to be found in cuticle ornamentation because variation in ornamentation appears to be highly pervasive, as noted in a family diagnosis by Kisielewski (1991): "Body covered, at least partly, with simple scales, spined scales,

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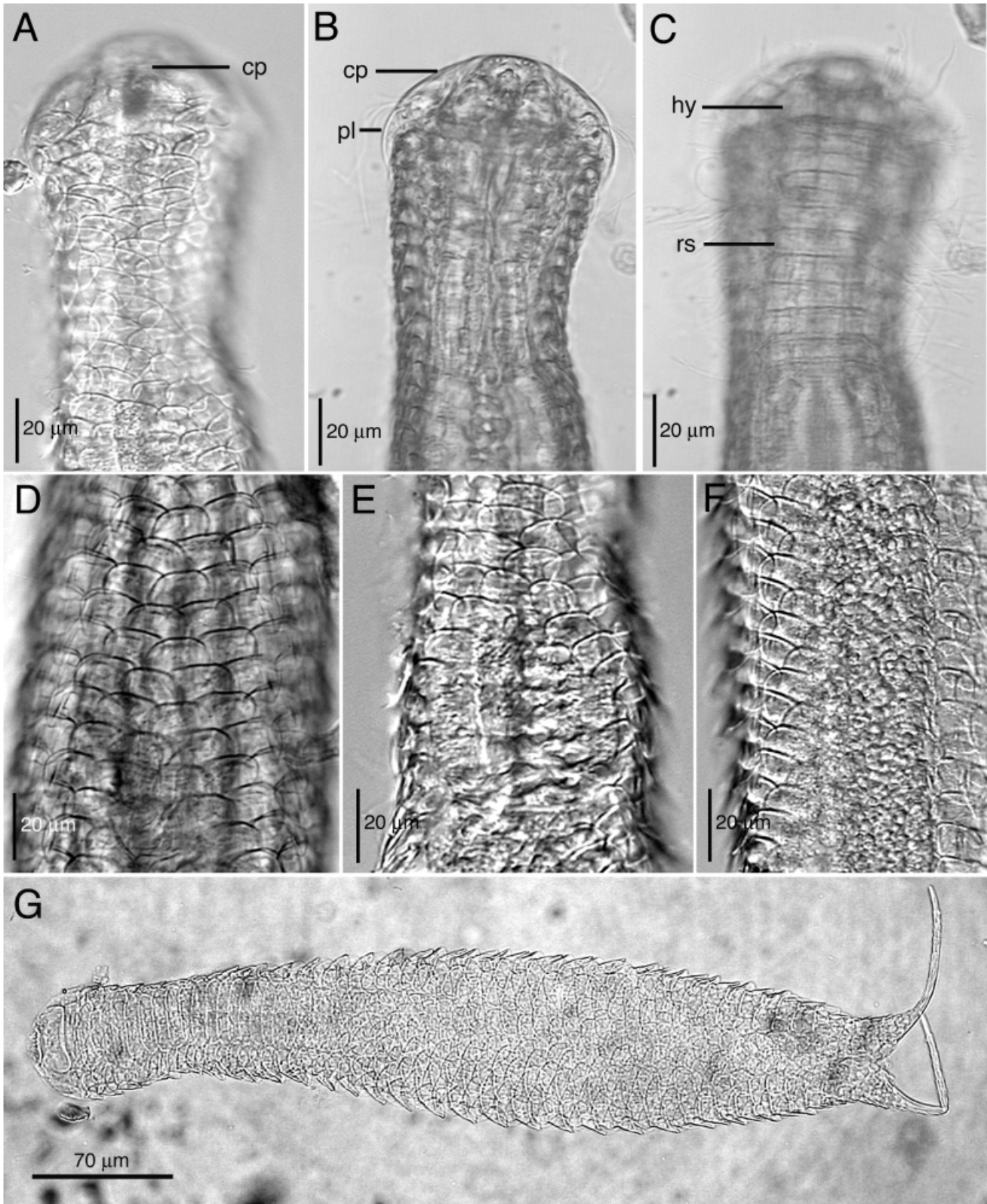
pedunculated scales or scales bearing lamellae, or, occasionally, with a layer of soft and uniform cuticle."

The genus *Polymerurus* includes the species with the largest described individuals within both Paucitubulatina and Chaetonotidae, ranging 260–770 μm long, and is well represented in fresh-water systems worldwide (Kisielewski 1991). Members of this genus are recognized by their elongate body and long, superficially segmented posterior furca. The cuticular covering of the body is highly diverse, consisting of simple flat scales, simple spined scales, stalked scales, and stalked spined scales, all with various geometric shapes. Estimates by Ruppert (1988) and Kisielewski (1991) place ~16–17 species in the genus, most of which possess spined scales. *Polymerurus nodicaudus* (VOIGT 1901) and *P. rhomboides* (STOKES 1887) are the 2 most commonly occurring species in fresh-water systems and are hypothesized to be the most geographically widespread cosmopolitan species. Both species have been described from Asia, Europe, and North and South America (e.g., Schwank 1990; Kisielewski 1991; Lee & Chang 2000), with *P. rhomboides* also known from parts of Africa (unpubl. data). Prior to this study, neither species has been reported from Australia or Antarctica.

During an investigation of Australian fresh-water meiofauna, 3 species of *Polymerurus* were encountered in an artificial lake in southern Queensland, on the campus of the University of Queensland in Brisbane. Based on morphological characteristics, 2 of these species are cosmopolitans and the third is as yet undescribed. The objectives of the present paper are twofold: to provide the first description of *Polymerurus,* including a new species, from Australia and to provide the first ultrastructural account of the cuticle in the genus, with the intention of identifying potential synapomorphies for the Chaetonotidae.

Methods

Specimens of *Polymerurus nodicaudus, P. rhomboides,* and the new species were collected from water and vegetation along the shore of a fresh-water lake on the campus of the University of Queensland, St. Lucia, Brisbane (~27°30′S, 153°0′E). Live gastrotrichs were sorted using a dissecting microscope.

Voucher specimens for the Queensland Museum were fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer for 24 h, transferred to glycerine on a glass slide, sealed with nail polish, and deposited in the Invertebrate Zoology section of the Queensland Museum. Photographs of live and fixed specimens were taken with an Olympus BH2 compound microscope equipped with DIC/Nomarski optics and a Panasonic CP610 digital camera. Measurements of gastrotrichs were obtained with an ocular micrometer. For analysis of ultrastructure, gastrotrichs were fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.2) for 24 h, followed by a buffer rinse (15 min × 4) and postfixation in 1% OsO_4 in 0.1 M cacodylate buffer for 1 h. Specimens were rinsed in buffer (15 min × 4), dehydrated in a graded ethanol series, transferred to propylene oxide, and embedded in an Araldite/Epon mixture (Procure 812 substituted for Epon; Proscitech, Australia). Resin blocks for transmission electron microscopy (TEM) were sectioned at 60 nm with a Diatome diamond knife on a Reichert or Sorvall ultramicrotome, collected on coated grids, and stained with uranyl acetate and lead citrate. Grids were examined with a JEOL 1010 TEM at the Centre for Microscopy and Microanalysis, University of Queensland, and digital photographs were obtained with a Megaview III color CCD camera and processed with analySIS® (Soft Imaging System). Additional grids were examined with a JEOL 100 CX II TEM at the Smithsonian Marine Station at Fort Pierce, Florida. For light microscopy observations, 1 specimen of *P. nodicaudus* was sectioned longitudinally at 1.5 μm and the sections were stained with Richardson's stain. Digital photographs were taken with a Nikon CoolPix 995 on a Zeiss compound microscope.

Results

Taxonomic account

Order Chaetonotida REMANE 1924
Suborder Paucitubulatina D'HONDT 1971
Family Chaetonotidae GOSSE 1864
Genus *Polymerurus* REMANE 1927

Polymerurus andreae nov. sp. (Figs. 1, 2)

Material. Five specimens examined alive as whole mounts. Two mature whole-mount specimens

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Fig. 1. Specimens of *Polymerurus andreae* nov. sp. viewed with light microscopy. A–F are optical sections of the dorsal, medial, and ventral regions of the body. **A.** Dorsal view of head region. **B.** Medial view. **C.** Ventral view showing interciliary, rectangular scales. **D.** Dorsal view of mid-trunk region showing overlapping simple scales. **E.** Medial view of pharyngeointestinal region. **F.** Medial view of trunk region. **G.** Holotype mounted in glycerine. Cephalion (cp); hypostomion (hy); pleurion (pl); rectangular scale of interciliary region (rs).
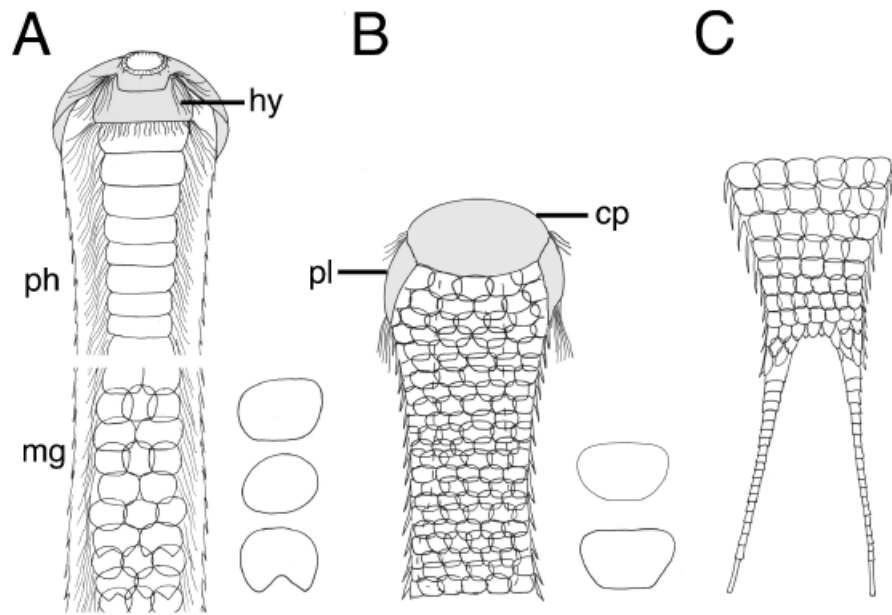
Fig. 2. Illustrations of features visible in type specimens of *Polymerurus andreae* nov. sp. **A.** Ventral view of anterior body region. Scale shapes present on ventral midgut region (mg) are also shown. **B.** Dorsal head view. Scale shapes present on dorsal body surface are shown. **C.** Dorsal view of posterior caudal furca. Cephalion (cp); hypostomion (hy); pleurion (pl); pharyngeal region (ph).

prepared as types (QM G218781, QM G219324) and deposited in the Queensland Museum, South Brisbane, Australia.

Etymology. The species is named in honor of Ms. Andrea Crowther, Research Assistant at the Queensland Museum, who provided invaluable assistance with this research.

Diagnosis. *Polymerurus* with total body length 500–710 μm. Head well defined with wide mouth rim and head plates in the form of cephalion, paired pleuria, and ventral hypostomion. Caudal furca with 19–21 segments per side. Body covered with simple scales without spines; dorsal scales are rhomboid, ≤15 μm wide and with rounded edges. Ventral field of pharyngeal region with single longitudinal series of rectangular scales. Midgut region with alternating rows of 2 and 3 scales each; scales are ovoid, rectangular, or of an intermediate shape.

Description. Slender body, 500–710 μm long, of which the caudal furca makes up 80–125 μm of the total body length. The head is only slightly trilobed and contains 4 head plates; a single, large, dorsal cephalion to 60 μm wide and 23 μm long; paired lateral pleuria; and a hypostomion (Figs. 1A–C, 2). Paired tufts of cilia emerge from a region between the cephalion and pleuria. A row of cilia emerges from the base of the hypostomion. The mouth is 17 μm wide and rigid. Pharynx to 163 μm long and 30 μm wide at midlength, increasing to 38 μm wide at a slight, bulb-like swelling (Fig. 1B,E). Width of body at pharyngeointestinal junction to 45 μm and reaching a maximum width of 80 μm around 50% body length. Width of intestine to 33 μm. In a 610-μm-long

specimen, the caudal furca is 115 μm long. The segmented portion of the furca is ≤90 μm long and composed of 19–21 segments; the terminal segment is the longest, 15 μm. Two columns of ventral locomotory cilia begin just beyond the hypostomial ridge and extend down the length of the body.

The body is covered by simple spineless scales of varying shape (Fig. 1). The dorsal and lateral cuticular covering is composed of flat, rhomboid scales with rounded edges (Figs. 1, 2). All scales lack a stalk (peduncle). On the dorsal side, there are 41 rows and 6 columns of scales from the head to the top of the caudal furca. Scales in anterior and midbody region are ~15 μm wide and overlapping. Scales decrease in size toward the posterior body region, ranging in width 5–10 μm. The smallest scales are present on the lateral margins of the caudal furca and are slightly pointed at the posterior end. Ventral interciliary field covered with scales (Fig. 1C). A single specimen, 610 μm long, was measured for interciliary scales. A single column of 22 rectangular scales lines the interciliary region of the pharynx and anterior midgut. Individual scales are ~38–41 μm wide. The single column is followed by 29 rows of scales that alternate between 2 and 3 scales each (Fig. 2). Scales of adjacent rows slightly overlap. The two-scale rows consist of two similarly shaped rectangular scales each 20–25 μm wide. Scales become more irregular in size and shape toward the posterior end of the body. The three-scale rows consist of 3 oval-shaped scales all of similar size, ~17–18 μm wide. A pair of terminal rectangular scales surround the anus.
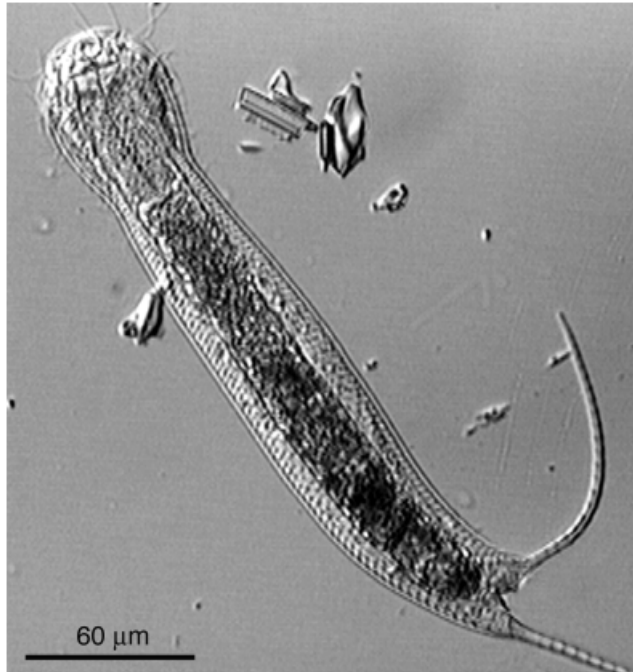
Fig. 3. Light micrograph of specimen of *Polymerurus rhomboides,* showing the characteristic elongate and segmented furca.

Sperm were not observed using bright-field optics or DIC. A single specimen possessed a developing oocyte (unmeasured) and no accessory reproductive organs (e.g., x-organ) were evident.

Polymerurus rhomboides (STOKES 1887) (Fig. 3)

Material. Sixteen specimens examined alive as whole mounts. Three mature whole-mount specimens prepared as vouchers and deposited in the Queensland Museum, South Brisbane, Australia (QM G218776–78).

Description. Dimensions of Australian specimens agree with specimens recorded from Europe and Brazil (see Kisielewski 1991), although total body length was often larger in Australian specimens. Body length from tip of head to tip of adhesive tubes, 480–550 μm long. Body width at midpoint to 50 μm wide. Pharynx to 80 μm long and 23 μm wide with no bulb. Mouth to 9 μm wide. Cephalion to 50 μm wide and pleuria to 23 μm long. Hypostomial ridge is 10 μm posterior of mouth rim. Oval, pedunculated scales cover dorsal and lateral body wall. Caudal furca to 127 μm long, composed of ~22 segments.

Polymerurus nodicaudus (VOIGT 1901) (Figs. 4–8)

Material. Eleven specimens examined alive as whole mounts. Two whole-mount specimens pre-pared as vouchers and deposited in the Queensland Museum, South Brisbane, Australia (QM G218779–80). Three specimens processed for TEM. One specimen sectioned longitudinally at 1.5 μm and stained for light microscopy.

Description. Specimens fit well within the range of variation reported in the literature (see Schwank 1990; Kisielewski 1991). Body 300–470 μm long and to 40 μm wide at midpoint. Pharynx to 99 μm long and 24 μm wide with only a slight posterior swelling. Mouth to 11 μm wide. Ventral head cilia to 16 μm long. Head plates present as a cephalion, paired pleuria, and a ventral hypostomion (Fig. 4A,B). Cephalion to 52 μm wide and 30 μm long. Body covered in spined scales; dorsal and lateral spines were longer than interciliary spines. Spines of head region are ~6 μm long and gradually increase in length along the body, reaching a maximum of 27 μm length. Interciliary spines in midtrunk region 4–8 μm long, with largest spines 10–16 μm long at posterior end (Fig. 4C). Caudal furca is 128–160 μm long and composed of 22–23 segments.

Cuticle structure in *P. nodicaudus*

In *Polymerurus nodicaudus,* a cuticle covers the entire body (Fig. 5). The head region bears 4 cephalic plates that represent thickened areas of the cuticle: a dorsal cephalion, paired lateral pleuria, and a ventral hypostomion (Figs. 4, 5). TEM revealed that the cuticle was composed of 2 layers: (1) a basal layer (i.e., endocuticle) composed of an inner fibrous region and an outer electron-dense region (Figs. 6, 8), and (2) an outer exocuticle (i.e., lamellar layer) composed of a single bilayer (Fig. 6D,E). These 2 layers were continuous around the periphery of the animal. The inner region of the basal layer was electron lucent and contained very fine striations indicative of fibrous material (Fig. 6). The thickness of the fibrous region varied slightly between specimens and/or body regions (e.g., dorsal scaled areas versus ventral ciliary region), generally ranging 313–436 nm, with the upper limits present on the dorsal and dorsolateral body surface. The outer region of the basal layer ("thin surface zone of the basal layer," Rieger & Rieger 1977) that gives rise to simple scales was electron dense and varied 105–120 nm thick (Fig. 6C–E). The only region where there appeared to be a substantial change in cuticle thickness was in the segmented portion of the caudal furca. In this region, the cuticle artificially peeled away from the epidermis, so measurements of the inner fibrous region of the basal layer could not be made. However, the surface zone of the basal layer was 122–160 nm thick along its length and
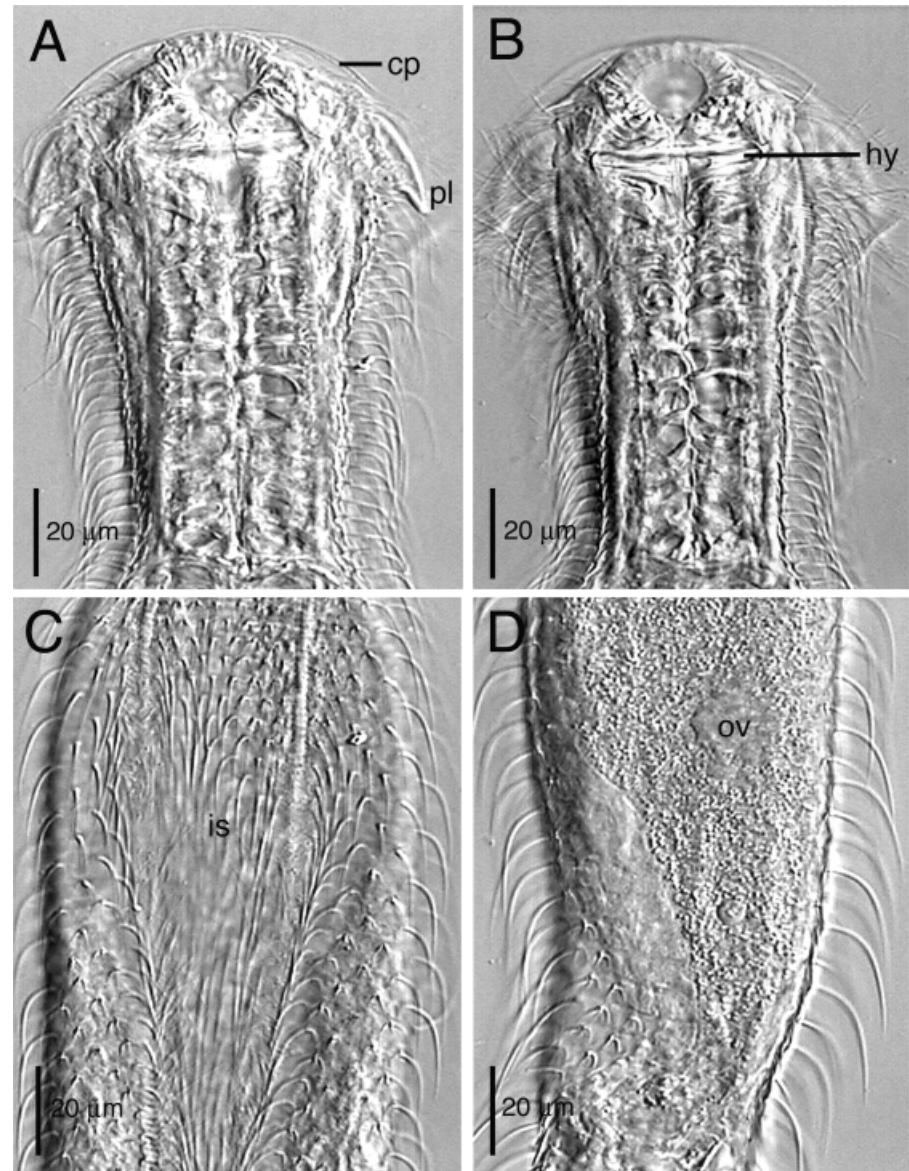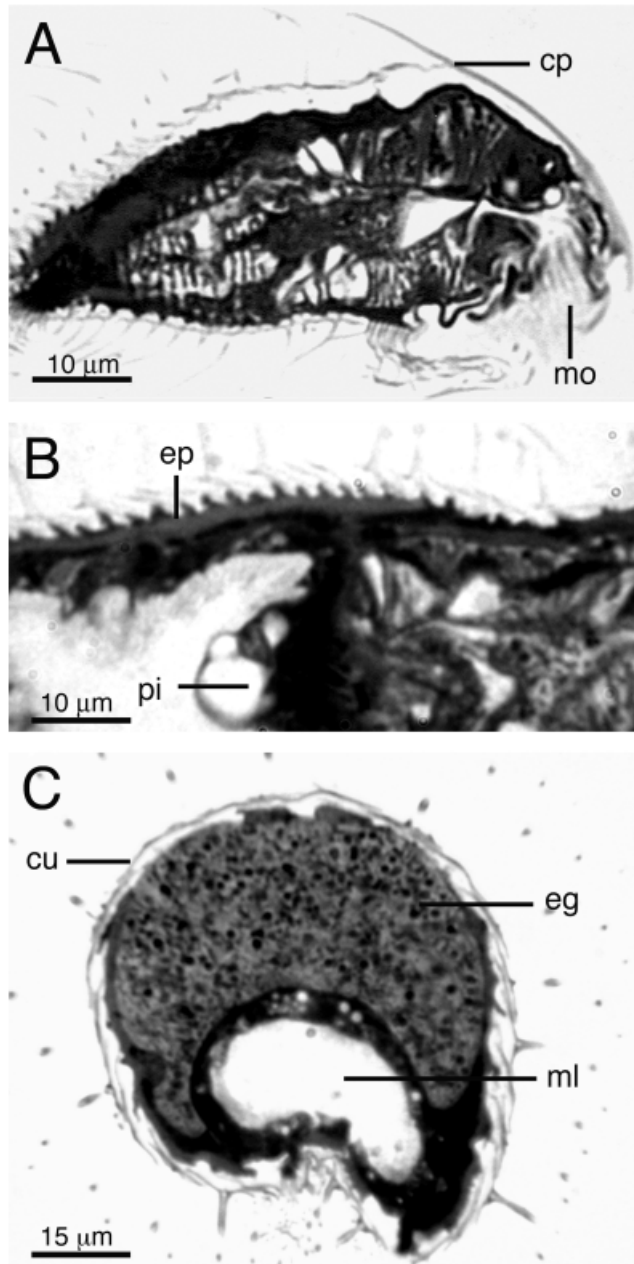
Fig. 4. Light micrographs of specimens of *Polymerurus nodicaudus*. **A.** Medial view of head region. **B.** Ventral view of head region. **C.** Ventral view of midgut region. **D.** Medial view through lower midgut region. Cephalion (cp); hypostomion (hy); ventral interciliary spines (is); ovum (ov); pleurion (pl).

increased to 340 nm thick in regions that appear segmented using bright-field optics.

Along most of the body, the surface zone was differentiated into distinct scales, each of which gives rise to a single spine (Figs. 4, 6A,B). The caudal region of each scale projected freely (Fig. 6B). All scales were slightly convex on either side of the midline (Figs. 6D,E, 7); the midline was a slightly thickened region in the form of a central ridge that produced a spine around mid-scale length (Figs. 6C, 7). The posterior region of the spine was biconvex with a slight ridge (Fig. 6E). Scales on the dorsal and lateral body wall were $\leq 6\,\mu m$ in width (edge to edge) and thickness ranged 86–98 nm. All dorsal and lateral scales bear spines; sectioned material only revealed spines with lengths of 1.18–1.55 μm because of their pronounced curvature; hence TEM-based length measurements are underestimates. Bright-field optics revealed spines that varied in size from the tip of the head to the caudal furca. Also, spines differed in size from dorsal to ventral, with smaller spines always present on the ventrolateral and ventral body wall (Fig. 8B). All spines were hollow, had a base ~ 760–890 nm wide, and a cuticle thickness ~ 46 nm. The cuticle composing the spine base was 90–99 nm thick. Smaller scales and spines were present on either side of the ventral ciliary rows. The basal fibrous zone in the ventral body region was 222–300 nm thick. A single exocuticular layer of ~ 10–14 nm thickness surrounded all spines and scales (Fig. 6D,E).

Fig. 5. Photographs of semi-thick sections of specimens of *Polymerurus nodicaudus,* showing that a cuticle completely encases the body. **A.** Longitudinal section through the head. **B.** Longitudinal section through the pharyngeointestinal junction showing wavy epidermis (ep) on dorsal body wall. **C.** Cross section through midgut region. Cuticle (cu); cephalion (cp); egg (eg); midgut lumen (ml); mouth (mo); pharyngeointestinal junction (pi).

Epidermis ultrastructure

Beneath the basal cuticular layer or endocuticle was a thin sheet of epidermis that may be syncytial, at least in the dorsal and lateral regions of the body. The epidermis varied in thickness around the periphery of the body and no cell membranes were evident in any of the sectioned material. In several regions of the body (based on cross sections only), thin extensions of the epidermis were present below the cuticle, and cellular extensions appeared to interdigitate with muscle cells (Fig. 8). Underlying longitudinal muscles were joined to epithelial cells by way of adhaerens junctions (Fig. 8D). Other regions had thicker epidermal layers that varied 345–525 nm thick. Microvilli were rare (observed only on cells in the trunk region) and only penetrated the fibrous region of the basal cuticular layer when present (Fig. 8D). Few organelles were observed in the epidermis. Ventrally, two columns of bilateral, multiciliated epidermal cells were present and extended the length of the body (Fig. 8). The multiciliated cells appeared separate (i.e., not extensions) from the general body epithelium (Fig. 8A); however, a complete series of serial sections was not examined. The multiciliated cells generally stained darker than the rest of the epidermis in both semi-thick (1.5-μm) and ultrathin (60-nm) sections. In cross section, ∼10 cilia emerged from each cell (Fig. 8). All cilia were covered by a single layer of exocuticle.

Discussion

Taxonomy

Prior to the current study, only 6 species of Gastrotricha were described from Australia, all members of the Macrodasyida (Hochberg 2002a,b, 2003). The present report of fresh-water chaetonotidan gastrotrichs in Queensland, especially in the form of potentially cosmopolitan species, reveals that the Australian fauna shares similarities with more distant geographic regions, and our current understanding of the degree of Australian endemism is likely to change with increased sampling here and in the surrounding regions, especially the IndoPacific. However, unlike the case for marine species, the occurrence of geographically isolated fresh-water gastrotrichs cannot be explained by long-shore dispersal or the Pangaea hypothesis (see Ruppert 1977 for review). Rather, the presence of chaetonotidans such as *Polymerurus rhomboides* and *P. nodicaudus* in isolated inland water bodies is more likely a testament to their primary mode of parthenogenic reproduction and the airborne dispersal capabilities of their eggs.

Three species of *Polymerurus* were identified in the current study, 2 of which fit descriptions of previously described animals, *P. nodicaudus* and *P. rhomboides.*
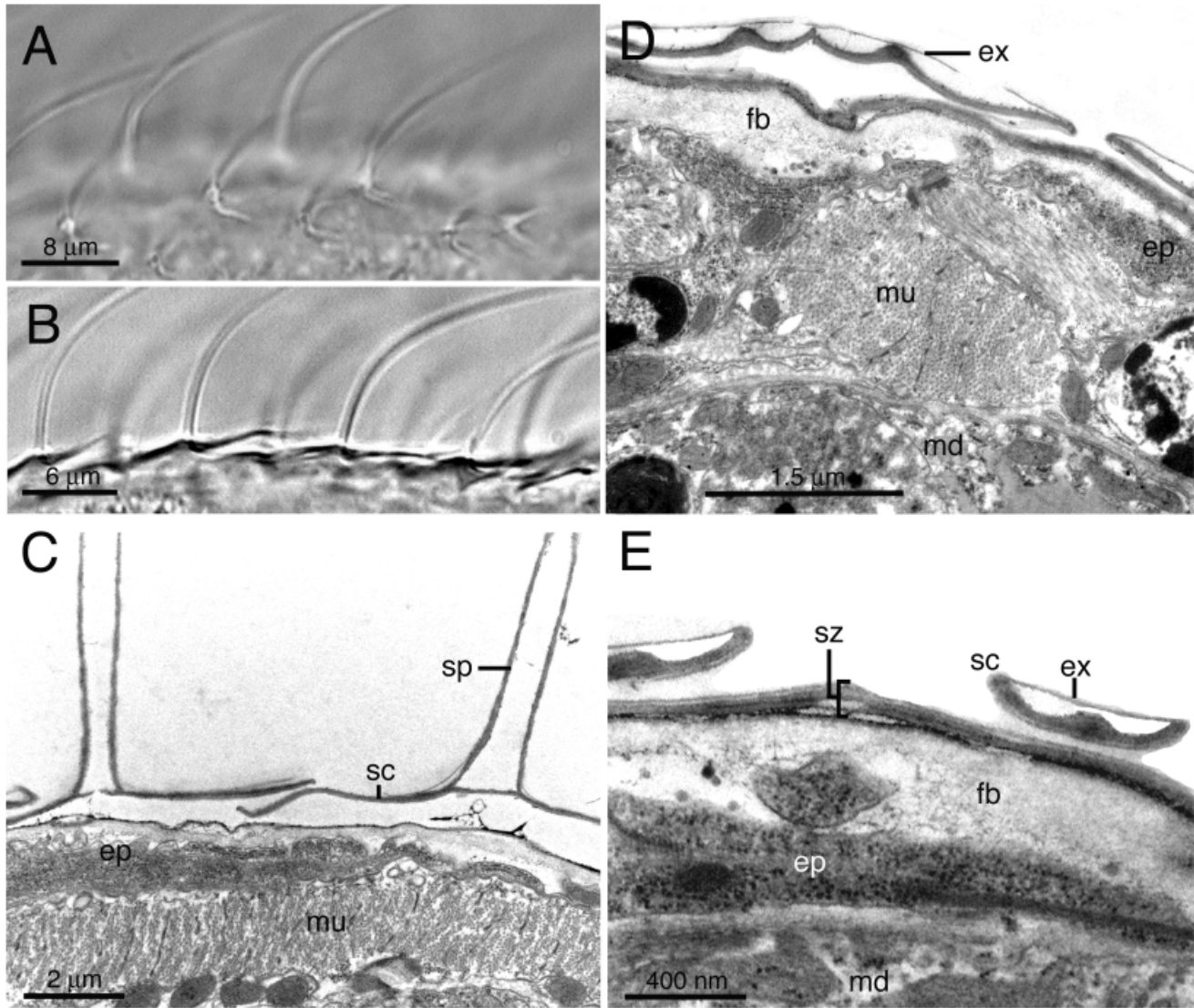
Fig. 6. Cuticle structure of specimens of *Polymerurus nodicaudus*. **A, B.** Light micrographs of spines in dorsolateral view and lateral view, respectively. **C.** TEM micrographs of spines and scales. **D.** Cross section through posterior region of scales. **E.** Cross section through anterior region of scales. Compare cross sections to illustrations in Fig. 7. Epidermis (ep); exocuticule (ex); electron lucent fibrous region of endocuticle (fb); midgut (md); subepidermal muscle (mu); scale (sc); spine (sp); electron-dense surface zone of endocuticle (sz).

This attests to the apparent cosmopolitanism (or complexes of sibling species?) that is common to fresh-water and marine Gastrotricha (Todaro et al. 1995, 1996; Strayer & Hummon 2001; Todaro & Rocha 2004). To date, *P. rhomboides* is the most geographically dispersed species in the genus, known from all continents except Antarctica, followed by *P. nodicaudus,* known from all continents except
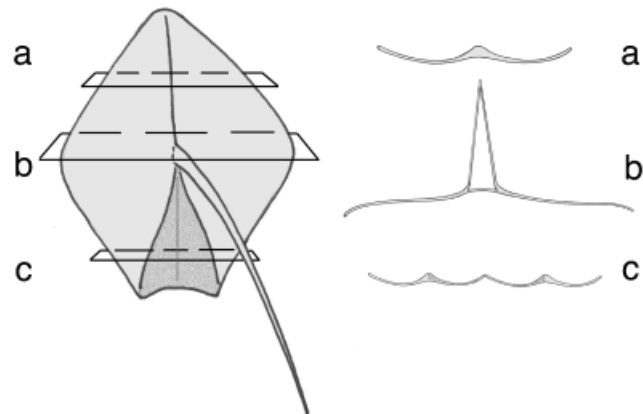
Fig. 7. Schematic of typical dorsal scale of a specimen of *Polymerurus nodicaudus,* with illustrations of cross sections through the different regions (a–c) of the scale.
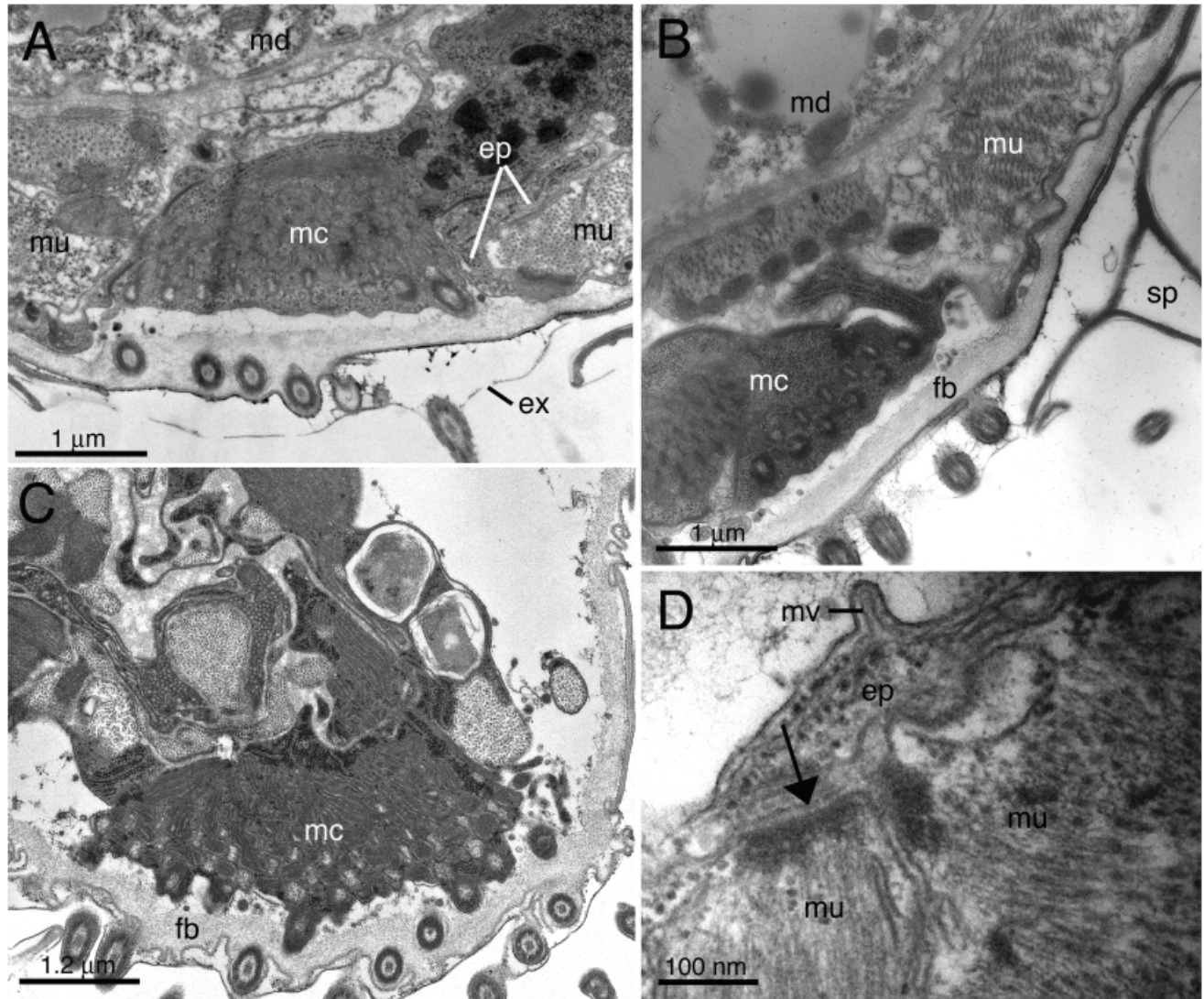
Fig. 8. Transmission electron micrographs of ventral multiciliated epidermal cells in specimens of *Polymerurus nodicaudus*. In several sections, the general body epidermis is only present as filamentous strands and difficult to visualize, hence, the subepidermal musculature appears to be directly beneath the cuticle. **A.** Section from the midgut region of the body, ~20 μm posterior of the pharyngeointestinal junction. Note the thin strand of general body epithelium (ep) next to the subepidermal musculature. **B.** Multiciliated epidermal cell and ventrolateral spined scale. Same body region as (A). **C.** Multiciliated epidermal cell from pharyngeal region of body, 30 μm from mouth. **D.** Microvillus of dorsal epithelium projecting into the endocuticle. Arrow points to myo-epithelium junction. Exocuticle (ex); electron-lucent fibrous region of endocuticle (fb); multiciliated epidermal cell (mc); midgut tissue (md); subepidermal muscle (mu); microvillus (mv); spine (sp).

Antarctica and Africa. Ruppert (1988) places 16 species in the genus, but several species have subsequently been synonymized by various researchers (see Schwank 1990; Kisielewski 1991), so the exact number of species remains questionable. Moreover, as stated by Strayer & Hummon (2001), taxonomic descriptions of conspecifics from different continents should be regarded as dubious unless sufficient details are provided, e.g., extent of morphological variation,

museum quality specimens, high-resolution photographic analysis, etc. Based on these criteria, the specimens collected in Australia are putatively considered conspecifics of their European counterparts.

The third species of *Polymerurus* appears to be new to science based on the available material, although knowledge of morphological variation is regrettably absent because of the paucity of specimens. In addition, the measurements (e.g., length of body and

caudal furca, etc.) should be considered the lower end of metric variation within the species; a partial specimen was found and, based on a few measurements of the anterior body region (e.g., pharynx length of 186 μm), can be expected to reach greater than the recorded 710 μm body length of the species. While body length appears equal to or slightly exceeding that of other species in the genus, details of cuticular sculpture appear unique to the Australian specimens.

Specimens of *P. andreae* nov. sp. possess a dorsal covering of simple spineless scales and a ventral interciliary column of spineless rectangular and ovoid scales. Spineless scales are only known from 4 species of *Polymerurus*: *P. biroi* (DADAY 1905), *P. callosus* (BRUNSON 1950), *P. elongatus* (DADAY 1905), and *P. rhomboides*. Among these, *P. rhomboides* is known to have stalked (pedunculated) spineless scales, *P. elongatus* bears terminal spines on posterior scales only, and *P. biroi* and *P. callosus* remain insufficiently described. The cuticular ornamentation of the ventral interciliary field of specimens of *P. andreae* is also highly unusual for members of the genus: a longitudinal series of rectangular plates are present in the pharyngeal region followed by alternating rows of ovoid, rectangular, and intermediate-shaped scales in the midgut region. The only other species of *Polymerurus* with a similar field of ventral scales is a subspecies of *P. squammofurcatus* PREOBRAZENSKAJA 1926 from Brazil (Kisielewski 1991), *P. squammofurcatus matogrossensis.* Unfortunately, the scales were not illustrated, so the precise differences remain unknown. However, the latter species has spined scales on its dorsal cuticle, among other differences in general morphology that distinguish it from *P. andreae* nov. sp.

Cuticle structure in *Polymerurus*

The structure of the gastrotrich cuticle has received much attention over the past century because of its complexity in ornamentation and ultrastructure, and its unique association with locomotory and sensory cilia as an exocuticular cover (see Rieger & Rieger 1977; Teuchert 1977; Hochberg 2001). Zelinka (1889) and Remane (1926, 1936) were the first to document a range of complex cuticular sculptures characteristic of gastrotrichs such as *Chaetonotus* (Chaetonotida) and *Tetranchyroderma* (Macrodasyida), and paved the way for later research that would capitalize on cuticular sculpture as a tool in taxonomy and phylogenetic inference (e.g., Rieger & Rieger 1977). Since then, the structure of the body cuticle has figured prominently in discussions of animal phylogeny (e.g., Travis 1983; Schmidt-Rhaesa et al. 1998).

The seminal research of Rieger & Rieger (1977) documented the ultrastructure of the cuticle in both macrodasyidan and chaetonotidan gastrotrichs. In their work, 30 species of Gastrotricha were studied: 16 species with smooth cuticles and 14 species with sculptured cuticles. In general, the cuticle of all gastrotrichs is highly similar and always composed of an inner basal layer or endocuticle, and an outer surface layer or exocuticle (also known as the "lamellar layer"). The basal layer is further subdivided into 2 homogeneous regions: a thick, inner electron-lucent zone composed of fibers, and a thinner, outer electron-dense zone. Differences in the number of exocuticular sheets and the thickness of the endocuticular layer are common among species within Macrodasyida, and may form the basis for future systematic revisions (Rieger & Rieger 1977). Moreover, species with elaborate cuticles exhibit differences beyond the general geometry of their sculptures (e.g., hooks, scales, spines, etc.) and in the layer of the cuticle from which they originate. For example, in most species of Macrodasyida with sculptured cuticles, scales and hooks are differentiations of the fibrous, electron-lucent zone of the endocuticle, whereas in the few chaetonotidans that have been examined, scales and spines are differentiations of the electron-dense zone of the endocuticle. These differences, along with others among species of Macrodasyida, support an earlier hypothesis of Remane (1936) that suggested a polyphyletic origin of cuticular sculptures in Gastrotricha. In general, the present work on *Polymerurus nodicaudus* agrees with these findings.

The cuticular sculptures present in species of *Polymerurus* fall into two broad categories: scales borne on peduncles (stalked scales) and scales that lack peduncles (simple scales). In both cases, the scales may bear a more or less centrally located spine. *Polymerurus rhomboides* is a well-known chaetonotidan with stalked, spineless scales while specimens of *P. nodicaudus* bear simple (non-stalked), spined scales. The ultrastructure of stalked scales in species of *Polymerurus* is unknown, but based on evidence from other species (e.g., Rieger & Rieger 1977), stalked scales are likely to represent regional thickenings of the column-like peduncles, and therefore are derivatives of the surface zone of the basal layer in all chaetonotidans. Simple scales, such as those of *P. nodicaudus,* are also derivatives of the surface zone of the basal layer but lack a peduncle. In no case were scales observed to emerge from the fibrous, electron-lucent zone of the basal layer anywhere along the body, as in macrodasyidans. The ultrastructure of the scales is also broadly similar along the length of the body,

although slight differences in size and shape may vary among individuals and among conspecifics from around the world (see Schwank 1990; Kisielewski 1991).

Based on earlier observations of other species (Rieger & Rieger 1977) and observations of *P. nodicaudus,* we might expect minimal ultrastructural variation to be present in the cuticle among species of Chaetonotida–Paucitubulatina and, when present, restricted to two regions: the basal layer and the substructure of scales. Variations in the basal layer are limited to differences in thickness of both the fibrous and surface zones. Whether such differences reflect adaptive responses to different habitats (e.g., related to granulometry of different intersitital biotopes) or are correlated with surface ornamentation (e.g., scales vs. spines) remain to be determined. Scale substructure appears to be similar among species of Chaetonotidae (*Chaetonotus, Heterolepidoderma, Polymerurus*), with a typical homogeneous appearance, but the scales of *Xenotrichula* sp. examined by Rieger & Rieger (1977) have an unusual striated substructure. This substructure differs from the surface zone that makes up the stalk and basal plates, which have a more homogeneous appearance, and probably reflect the plesiomorphic condition of the cuticle. Determining whether this striated substructure is characteristic of other species of Xenotrichulidae will depend on additional observations.

Further research on the ultrastructure of the cuticle in chaetonotidan gastrotrichs should focus on gathering data from species in all 6 families of Paucitubulatina. In particular, species within the Chaetonotidae exhibit the widest range of cuticular ornamentation within the suborder, and may therefore demonstrate the range of variability to be expected throughout the Paucitubulatina. Of special interest are species of *Ichthydium* that have secondarily lost much of their ornamentation, and species of *Musellifer,* which may occupy a basal position within the Paucitubulatina (Hochberg & Litvaitis 2000).

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