Anatomy of *Ectonocryptoides* (Scolopocryptopidae: Ectonocryptopinae) and the phylogeny of blind Scolopendromorpha (Chilopoda)

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**Abstract**

The chilopod subfamily Ectonocryptopinae (Scolopocryptopidae) comprises rarely-encountered, small-bodied scolopendromorphs known only from Mexico and Belize. Three species have been described, one in *Ectonocryptops* Crabill, 1977, and two in *Ectonocryptoides* Shelley & Mercurio, 2005. External characters ally this clade with the speciose Neotropical subfamily Newportiinae. Scanning electron microscopic documentation of the mouthparts, peristomatic structures and foregut in *Ectonocryptoides quadrimeropus* Shelley and Mercurio, 2005, together with new data for *Newportia*, enable analysis of ectonocryptopine relationships based on the current character set for scolopendromorph phylogeny. A distinctive “pineapple-shaped” gizzard projection strengthens the alliance between Ectonocryptopinae and Newportiinae, which group together as a well-supported clade that is stable under equal and implied weights. In all shortest cladograms across a range of character weights, Ectonocryptopinae nests within Newportiinae. Scolopocryptopidae (sensu Shelley (2002)), which groups species with 23 trunk segments, kinked gizzard projections, and a pectinate second maxillary claw, is monophyletic in most cladograms under equal weights and is consistently monophyletic when homoplastic characters are down-weighted; the alternative set of equally-weighted cladograms resolves the 21-segmented Plutoniuminae within Scolopocryptopidae. *Ectonocryptoides quadrimeropus* displays pore fields on the ventral surfaces of the swollen tibia and first tarsus of the ultimate leg that evidently represent glandular openings. Observations on *Ectonocryptoides quadrimeropus* and *Newportia monticola* suggest that new systematic characters for Scolopocryptopidae can be found in the specialised apical setae on the terminal antennomere.

**Key words**

Ectonocryptopinae; centipedes; gizzard; epipharynx; hypopharynx.

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Introduction

One of the most remarkable centipede discoveries in recent years is the scolopendromorph subfamily Ectonocryptopinae Shelley & Mercurio, 2005, which comprises minute Scolopocryptopidae (blind taxa with 23 leg-bearing segments and distinctive gizzard structures) from Mexico and Belize and is based on five specimens of three species. *Ectonocryptops kraepelini* Crabill, 1977, is known only from its holotype from Colima, Mexico, which was illustrated for the first time by Shelley & Mercurio (2008). *Ectonocryptoides quadrimeropus* Shelley & Mercurio, 2005, was proposed for two syntypes from Jalisco, Mexico, and was subsequently reported from Puebla (Shelley 2009), and a specimen from Belize was described as *Ectonocryptoides sandrops* Schileyko, 2009. For simplicity in citing binomials, we henceforth abbreviate *Ectonocryptoides* as *E.*, except at the beginnings of sentences, and spell out *Ectonocryptops*.

The Puebla specimen of *E. quadrimeropus*, length 17.8 mm, is the largest ectonocryptopine, which otherwise are 10-12 mm long. This diminutive habitus partly accounts for the taxon’s recent discovery, and though rarely encountered (extensive museum collections from the region lack specimens), new material has been discovered. In July 2009, Fabio Cupul-Magaña collected four specimens of *E. quadrimeropus* under rocks on the grounds of the Universidad de Guadalajara, Puerto Vallarta, Jalisco; one was made available for study, and another will be sequenced in a forthcoming analysis of scolopendromorph phylogenetics based on DNA sequence data. Because *E. quadrimeropus* is the only species of the subfamily known from more individuals than the primary types, it provides a unique opportunity to examine internal anatomical characters applicable to scolopendromorph phylogenetics. Recent comparative studies have introduced new characters from the preoral chamber (Edgecombe & Koch 2008) and gizzard (Koch et al. 2009) that are documented by light and scanning electron microscopy. Herein we survey these characters as well as mouthpart and poison calyx anatomy that have not been documented in the subfamily. *Ectonocryptoides quadrimeropus* can be scored for most characters in an updated version of the character set for scolopendromorph phylogenetics (Edgecombe & Koch 2009), and these data are used to test the hypothesis that Ectonocryptopinae and Newportiinae are sister taxa within the Scolopocryptopidae (Shelley & Mercurio 2005). To supplement existing anatomical data for Newportiinae, we examine peristomatic structures, mouthparts, and gizzard anatomy of *Newportia divergens* Chamberlin, 1922, *N. monticola* Pocock, 1890, and *N. stolli* (Pocock, 1896), to compliment the single species (*N. longitarsis stechowi* Verhoeff, 1938) analyzed previously (Edgecombe & Koch 2008; Koch et al. 2009).

Material and methods

The specimen of *E. quadrimeropus* from Puebla, housed at the American Museum of Natural History (AMNH) (Shelley 2009), was examined along with one collected from the Universidad de Guadalajara, now deposited in the Natural History Museum,
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**Dissection.** Exposure of the epipharynx and hypopharynx is as described by Edgecombe & Koch (2008). Dissection of the foregut to prepare the gizzard for light and scanning electron microscopy was documented by Koch et al. (2009). For examining the poison duct, maxillipeds were cleared overnight in Hoyer’s mixture (Kraus 1984).

**Light microscopy.** Light microscopic studies of the epipharynx, hypopharynx, poison calyx and gizzard were performed with a Leica MZ16A stereomicroscope equipped with a Leica DFC 290 digital camera. Images were taken to document the sclerotized and/or pigmented parts of the preoral chamber and cuticular surface of the foregut. Images and plates were edited with the Adobe Photoshop CS3 and Adobe Illustrator CS3 software.

**Scanning electron microscopy.** All materials were cleaned in an ultrasonic bath except for the Puebla individual because of its fragility. Dissected head pieces and gizzards were dehydrated in a graded ethanol series and critical point dried using a Bal-Tec CPD 030. Dried materials were mounted on stainless steel stubs with either double sticky tabs or araldite and coated with a gold/palladium mixture in a Cressington sputter coater. Scanning electron microscopes used for different stubs were a Philips XL30 and a Fei Qanta 200, a LEO 1455VP with backscatter, and a Hitachi S2500.

**Cladistic analysis.** The data matrix including *E. quadrimeropus* and the three newly surveyed *Newportia* species in Table 1 is updated from versions used in previous analyses. Characters 1-64 were described by Edgecombe & Koch (2008), 65-79 by Koch et al. (2009), 80-82 and 84 by Edgecombe & Koch (2009), and 83 and 85-89 are newly added herein. The complete list of characters is in Appendix 1. Parsimony analyses were conducted using TNT (Goloboff et al. 2003). Heuristic searches involved 1000 random addition sequences and TBR branch swapping, saving up to 100 trees per replicate. TNT and WINCLADA (Nixon 2002) were used to examine character optimisations. Multistate characters 3 and 44 were ordered, whereas other multistate characters were left unordered. Nodal support was measured with jackknife resampling (Farris 1997) and Bremer support (Bremer 1994). Jackknifing with TNT used 1000 replicates with 36% deletion, each replicate involving a heuristic search. Bremer support was calculated from collections of suboptimal trees obtained by heuristic searches. Implied weighting (Goloboff 1993; Goloboff et al. 2008) was implemented in TNT, using the same heuristic search protocol as for equal weights. Clade stability under different weighting regimes was assessed by varying the concavity constant used for implied weights.

Cladograms were rooted between Scolopendromorpha and exemplars of three other chilopod orders (Geophilomorpha, Lithobiomorpha and Scutigeromorpha).
Table 1. Data matrix for 89 morphological characters coded for the relationships of scolopendromorphs and outgroups (Appendix). Question marks (?) indicate missing data; dashes (-) indicate inapplicable character states.

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Characters
Results

Anatomy

The following account uses the AMNH Puebla and NHM Jalisco specimens (body length ca. 11 mm) to supplement the description of *E. quadrimeropus* by Shelley & Mercurio (2005).

Antenna: Jalisco specimen with 17-15 articles. Sensilla trichodea relatively long, sparse, scattered on articles 1 and 2, abruptly increasing in density on article 3 and continuing along length of antenna; most sensilla from article 3 shorter than those on basal two articles; article 3 bearing a circlet of longer sensilla on its basal part, articles 4-5 with a few longer sensilla. Terminal article with a cluster of seven apical sensilla having short, slender apices and swollen bases 1.55-1.69 μm in diameter (Fig. 1D, E) and an additional sensillum of the same structure on each lateral side of antenna in subapical position. Swollen base of the apical sensilla nearly entirely set in a circular depression, their slender shaft largely smooth (i.e., devoid of longitudinal, twisted ribs typical of setae) and their tips apparently devoid of a terminal pore.

Epipharynx: Labral bristle fields composed of uniformly simple bristles, those lateral in the field being more slender and somewhat shorter than those mediad (Fig. 3A). Border between labral and clypeal parts showing a transverse bulge that is gently arched towards the median labral tooth (Fig. 2C, *bu*); bulge longer than median spine field at border (Fig. 3B, *msp*). Proximal labral part wholly smooth, without node-or spine-like scales. Sclerotised connection lacking between median labral tooth and border to clypeal part (ch. 47, state 2), median sclerotisation of the labral part fading out immediately proximal to median labral tooth. Row of bullet-shaped sensilla proximal to median spine field (ch. 52, state 1; as defined by Edgecombe and Koch 2008: 899) represented by one or two small sensilla laterally and a pair of sensilla mediad, the latter pair positioned proximal to the border (arrows in Fig. 3B). Median cluster of sensilla on the clypeal part arranged as a transverse band of 19 bottle-shaped sensilla coeloconica at most two-deep (both specimens), situated a short distance proximal to median spine field as in all scolopocryptopids (ch. 53, state 3) (Fig. 2C, *msc*). Each clypeal sensillum of diameter 1.01-1.12 μm, set in a rounded (circular to ovate) depression (Fig. 3B) and equipped with a terminal pore (Fig. 3B, inset). Lateral bands of branching scales on clypeal part prominent but not continuous mediad; each scale branching into a few short spines along its proximal margin (Figs. 2C, 3C, *sca*). Transverse band with a few bottle-shaped sensilla, extending along much of width across proximal edge of bands of branching scales (Fig. 3C, arrows), lateralmost sensilla more elongate than those mediad.

Hypopharynx: Proximal part not clearly exposed in either specimen, preventing definite observations on *Schlundplatte* (Fig. 4D, *spl*). Proximal part of lateral flaps (Fig. 4B, D, *lf*) bearing cluster of flattened spines with a few short branches and simple spines in usual position of tuft (Fig. 4D, *tu*).

Mandible: Eight (Jalisco specimen) or nine (Puebla specimen) pectinate lamellae (Fig. 5C, *pl*). Four and five groups of paired teeth on opposing mandibles; accessory
Figure 1. Apical sensilla on the terminal antennomere in (A-C) Newportia monticola, and (D-E) Ectonocryptoides quadrimeropus (Jalisco specimen). A, overview of apical part, showing cluster of terminal sensilla surrounded mostly by sensilla trichodea; arrowheads point to sensilla types shown in B and C. B, two sensilla basiconica, one in inset showing rows of pores, surrounded by sensilla trichodea. C, two types of bottle-shaped sensilla amidst sensilla trichodea, the former primarily distinguished by the absence (arrows) or presence (arrowhead) of a socket. D, overview of apical part of terminal antennomere. E, cluster of terminal sensilla.
Figure 2. Epipharynx of Newportiinae (A, D), Kethopinae (B), and Ectonocryptopinae (C). A, Newportia monticola. B, Kethops utahensis. C, Ectonocryptoides quadrimeropus (Jalisco specimen). D, N. stolli, border between labral and clypeal part of epipharynx, showing the arrangement of bottle-shaped sensilla (arrows) behind median spine field. Abbreviations: bu, bulge at border between labral and clypeal parts of epipharynx; db, distal bar of submarginal armature; lsc, lateral cluster of sensilla; msc, median cluster of sensilla; msp, median spine field; sca, lateral field of scales; tp, tooth plate.
Figure 3. Epipharynx of *Ectonocryptoides quadrimeropus* (Jalisco specimen). A, overview of labral part. B, detail of border between labral and clypeal parts, showing the arrangement of minute bullet-shaped sensilla (arrows) and details of the sensilla coeloconica of the median cluster (inset). C, posterior area of left scale field on clypeal part, showing the sensilla (arrows) of the lateral cluster. Abbreviations as in Figure 2.

denticles indistinct. Teeth fringed mostly by a single row of branching bristles with flattened bases; those in ventral part of row branching into four or five slender spines at about half lengths; shorter, more dorsal bristles branching closer to bases into three or four spines; a few longer bristles of the same structure forming a second row near middle of the main row (Fig. 5B, *fr*). Hairy pad a small tuft of bristles branching sub-apically (Fig. 5B, *hp*).

Second maxilla: Dorsal brush on tarsus with typical scolopocryptopid compliment of flattened trichomes (Fig. 6D, *kb*), some branching apically into minute spines. Claw pectinate, with a single row of blunt denticles (Fig. 6E, *cl*).

Maxillipede: Poison calyx terminating slightly short of half length of trochantero-prefemur (ch. 25, state 2). Duct evenly curved (not serpentine), calyx elongate and flask-shaped.

Gizzard: Posterior sieve part situated in 12th trunk segment in Puebla specimen, 16th in Jalisco specimen. Anteriormost transverse row of projections into intestinal lu-
Figure 5. Mandibles of Newportiinae (A, D, E) and Ectonocryptopinae (B-C). A, Newportia monticola. B-C, Ectonocryptoides quadrimeropus (Jalisco specimen), lateral (B) and mesial (C) views on gnathal edge. D, Tidops collaris. E, Newportia stolli. Abbreviations: ad, accessory denticles on teeth; fr, fringe of branching bristles; hp, hairy pad (Haarpolster sensu Borucki (1996)); pl, pectinate lamella; to, tooth.
men arranged in single row consisting of short, conical, pineapple-shaped outgrowths covered by robust, spike-like spines, including at their tips (Fig. 7A, B, s-pi). Posterior to “short pineapple” row is single row of projections with robust spines or spinose

Figure 6. Distal parts of telopodite of second maxilla with dorsal brush and pectinate pretarsal claw in Newportiinae (A, B), Kethopinae (C), and Ectonocryptopinae (D, E). A, Newportia monticola. B, Tidops collaris. C, Kethops utahensis. D, E, Ectonocryptoides quadrimeropus (Puebla specimen). Abbreviations: cl, pretarsal claw; kb, dorsal brush (Kapillarbesen sensu Borucki (1996)); ta, tarsus.
Figure 7. Gizzard anatomy in *Ectonocryptoides quadrimeropus* (Jalisco specimen). A, B, anteriormost row of pineapple-shaped projections fanned out in one plane, overview (A) and detail (B). C-E, kinked sieve projections, anterior rows in lateral (C) and frontal (E) views, and posteriormost rows (D) viewed from posterior. Abbreviations: *cv*, cardiac valve; *kp*, kinked projection; *s-pi*, small pineapple-shaped projection.
scales at their bases, changing to longitudinal bands of trichomes around one-third
lengths, then abruptly kinked and tapering to tips (Fig. 7B), latter bearing longitudinal
bands of trichomes as on proximal part. Main sieve projections are clusters of elon-
gate, hollow outgrowths of gizzard wall bearing kinked, tapering distal halves (ch. 76,
state 1) (Fig 7C, kp). Proximal halves covered by longitudinal bands of short, filiform
trichomes arranged either in longitudinal, parallel rows (ch. 77, state 1) or as elongate
ovoid fields, likewise having short trichomes aligned on kinked distal part (Fig. 7E).
Posteriormost projections also elongate, tapering, but shorter than main sieve projec-
tions, more evenly curved, bearing only sparse, scattered filiform trichomes (Fig. 7D)

Spiracles present on segments 3, 5, 7, 8, 10, 12, 14, 16, 18, 20 and 22, as in E.
sandrops and Ectonocryptops kraepelini.

Ultimate leg with three spiniform processes on ventral side of prefemur (Fig. 9C,
ps) and two on ventral surface of femur. Basal two-thirds of each process with polygonal
surface sculpture as on surrounding cuticle, distal third less strongly tapered, lacking
obvious surface sculpture, accompanied by a slender seta of the same length (Fig. 9D).
In light microscopy, small spiniform structures aligned on ventral, median and lateral
sides of prefemur and femur appearing as spines, but SEM shows basal articulations
(Fig. 9D, ss) rather than direct cuticular outgrowths and thus actually spiniform setae.
More slender setae scattered on the dorsal surface of leg.

Tibia and tarsus 1 densely covered with large pores on flattened ventral surfaces
(Fig. 9A, glp). Pores ovoid, their long axis typically 4.7-5.1 μm wide, surrounded by
asymmetrical rims (Fig. 9B), latter not divided into C-shaped structure, as at bases of
trichoid mechanosensory sensilla scattered on lateral, medial and dorsal sides (Fig. 9A).
A few robust conical sensilla scattered amidst large pores on ventral side of tibia and
tarsus I; sensilla surrounded by distinct stop structures. These differences in surround-
ing structures between sensilla and large pores indicate the latter are openings of glands
rather than simply sockets of broken sensilla. Between large pores are a similar number
of small pores that resemble usual openings of epidermal glands (Fig. 9B). In the Jalisco
specimen, the tarsus terminates in short, stout, conical spur (Fig. 9A, sp) situated beside
circular field that is encircled by a suture and bears four trichoid sensilla, single sensil-
um basiconicum, and a few small pore openings of epidermal gland type (Fig. 9A,
ta2). In Puebla specimen, terminal podomere has a slender slit along its distal edge that
has evidently collapsed. Setae previously observed to emanate from tip of leg (Shelley
2009, fig. 3) apparently broken or concealed within terminal slit.

**Discussion**

In addition to confirming the presence of 11 pairs of spiracles, the new specimens
emend some descriptive details compared to the syntypes of E. quadrimeropus (Shelley
& Mercurio 2005). A W-shaped suture is defined on T1 in the Puebla specimen and,
as in many species of Newportia and in Tidops, its apices are the points at which the
paramedian sutures originate. As such, the arrangement of sutures is more similar to
Figure 8. Gizzard anatomy in Newportiinae. A-C, Newportia monticola. A, overview of gizzard fanned out in one plane (anterior is top), showing gradual transformation of sieve projections from pineapple-shaped over elongate and kinked to short and straight. B-C, anteriormost sieve projections, differentiated into (B) single row of larger pineapple-shaped projections with kinked tips, and (C) several rows of smaller pineapple-shaped projections devoid of kinked tips. D, Newportia stolli, anteriormost rows of small pineapple-shaped projections. E, N. monticola, main sieve projections (lateral view). F-G, N. stolli, larger pineapple-shaped projection with bifid apex and short, conical tip. G, bifid apex of larger pineapple-shaped projection in higher magnification. Abbreviations: l-pi, large pineapple-shaped projection; kp, kinked projection; s-pi, small pineapple-shaped projection; stp, straight projection.
Figure 9. Ultimate leg of *Ectonocryptoides quadrimeropus* (A, B: Jalisco specimen; C, D: Puebla specimen). A, frontal view of apex of terminal article of left leg (dorsal is top). B, section of the glandular pore field on mesial side of tarsus 1. C, prefemur of right leg, ventral view (proximal is top). D, higher magnification of distalmost spiniform process and adjacent spiniform setae on prefemur. Abbreviations: *glp*, glandular pore field; *ps*, spiniform process; *sp*, spur; *ss*, spiniform seta; *ta1*, tarsus 1; *ta2*, tarsus 2.
that documented in *Ectonocryptops kraepelini* (Shelley & Mercurio 2008, fig. 3), which has W-shaped sutures, than in the types of *E. quadrimeropus*, in which slightly divergent paramedian sutures continue to the anterior transverse suture without a median bifurcation (Shelley & Mercurio 2005, fig. 5). The Jalisco specimen shows the paramedian sutures abruptly converging and meeting at the anterior transverse suture, the convergent anteromedian portion corresponding to the middle part of the typical W. A significant difference from the types of *E. quadrimeropus* is that the coxopleuron of the ultimate leg bears a pore field that was not visible under light microscopy in the types.

The terminal structures on the ultimate leg, best exhibited by the Jalisco specimen, are interpreted as a vestigial tarsus 2 and a spur on tarsus I. The circular setigerous field (Fig. 9A, *ta2*) is regarded as tarsus 2 and its surrounding suture as the articulation with tarsus 1. This is consistent with the fact that a short tarsus 2 is known in *Ectonocryptops kraepelini* and the fact that the surface ornament and setation of this field are similar to those on tarsus 1. Because the spur is displaced from the putative tarsus 2 rather than being situated on its apex, it is not regarded as the pretarsus but rather a structure on tarsus 1. A pretarsus is accordingly regarded as absent; the structure identified as a pretarsus in *E. sandrops* (Schileyko, 2009) may represent the spur in *E. quadrimeropus*. The spur may function in association with the presumed glandular pores on the tibia and tarsus 1 (e.g., if the pore openings correspond to spinning glands). In terms of their similar concentration on podomeres of the ultimate leg and shapes of the opening and rims, the obvious comparison of the glandular pores in ectonocryptopines is with the opening of the telopodal glands in Lithobiomorpha (Keil, 1975), which have a defensive function. Glandular pores on the ultimate leg are now recognised as a general character of Ectonocryptopinae because Crabill (1977) identified the median tibial surface in *Ectonocryptops kraepelini* as being “densely porous, internally densely glandular” (1977, p. 348). The apical slit on the ultimate leg in the Puebla specimen likely represents collapse around the terminal structures, such that a tarsal spur and minute tarsus 2 may be concealed within.

Observations on *E. quadrimeropus* and *N. monticola* suggest that additional systematic characters for Scolecopycropodidae may exist in the sensilla on the distal part of the terminal antennomere (Fig. 1). The antenna in both species terminates with a cluster of 7 (*Ectonocryptoides*: Fig. 1E) or 14 (*Newportia*: Fig. 1A) apical sensilla that are differentiated from the normal sensilla (sensilla trichodea) on all antennomeres in being more slender but expanding basally, are set in a shallower socket, and are surrounded by a simple ring rather than the C-shaped stop that partly surrounds the sensilla trichodea (Fig. 1B, C). The terminal sensilla are curved at a variable distance from their tip, more obviously so in *Newportia* than in *Ectonocryptoides*, and in the former they have distinct longitudinal ribs, most strongly so along their basal half, whereas they appear to be smooth in *Ectonocryptoides*. In *Cryptops hortensis*, 8-11 sensilla brachyconica are clustered apically (terminal sensilla of Ernst et al. 2009, fig. 11). Three other kinds of sensilla are present on the distal part of the terminal article in *Newportia*: sensilla basiconica with finely perforated surfaces (Fig. 1B), and two types of short, bottle-shaped sensilla (Fig. 1C, arrows and arrowhead). The bottle-shaped sensilla are arranged in
an irregular ring more apically than the sensilla basiconica. The sensilla basiconica are apparently widely distributed throughout Scolopendromorpha, given their similarity to sensilla on the apical antennomere of *Scolopendra morsitans* L., 1758 (Lewis 2000, fig. 8) and *Cryptops hortensis* (Ernst et al. 2009, fig. 11). The pore-like depressions on these sensilla in *Newportia* are arranged in ordered rows, and details of the “pore” rows compare closely to those on similarly shaped sensilla that are clustered in two groups on the terminal antennal article in all Geophilomorpha (Ernst 2000, fig. 2b), at the anterior edge of articles and in two groups on the terminal article in *Cryptops hortensis* (Ernst et al. 2009, figs. 16, 17), or even more broadly shared with a basiconic sensillum at the tip of the terminal antennal article in *Craterostigmus* (Ernst et al. 2006, fig. 9).

The bottle-shaped sensilla have two different morphologies. One type is defined by a narrow cuticular rim surrounding the sensillum, absence of a socket at the base of the sensillum, and the basal part of the sensillum being delineated from the slender distal part by a shallow groove (Fig. 1C, arrows). Bottle-shaped sensilla of the second type are surrounded by wider rims. These sensilla emerge from a socket and have smooth surfaces, a more conical shape, with no indication of a groove between their proximal and distal parts (Fig. 1C, arrowhead). In both types, the rim surrounding the sensilla is divided by a single suture that cuts across its width. In *N. monticola*, each of these sensilla types is confined to the distal third of the terminal article. Combined with the diversity of structures documented in *Cryptops* by Ernst et al. (2009), we reiterate Lewis’ (2000) conclusion that a broader survey of antennal sensilla is warranted as a potential source of new characters.

**Phylogenetic analysis**

**Characters**

New observations on *Newportia* and *Ectonocryptoides* have prompted re-evaluation of a few previous character codings. The morphology of the hypopharynx of *N. monticola* in particular allows an alternative interpretation of the proximal part of the hypopharyngeal lateral flaps compared to the interpretation favoured by Edgecombe & Koch (2008) in formulating their character 62. *Newportia monticola* shows branching bristles on the lateral flaps in the same position (Fig. 4A) as seen in Cryptopinae (Edgecombe & Koch 2008, fig. 18a). The proximal part of the lateral flaps is subject to considerable collapse, a factor that confounded its recognition in Scolopocryptopidae. The revised identification of the proximal part of the flap means that a tuft of bristles is consistently present in Scolopocryptopidae (Fig. 4A, D, E, tu) and Plutoniuminae as well as in Cryptopidae, and members of the former two groups are re-coded to share the same character state.

A band of bullet-shaped sensilla at the border between the labral and clypeal parts of the epipharynx has been recognised in most examined scolopendromorphs and has been optimised as an apomorph character for Scolopendromorpha (Edgecombe & Koch 2008). This sensilla row was regarded as lacking in *Tidops collaris* (Edgecombe & Koch 2008).
Koch 2009) and could not be detected in *Kethops utahensis* (and was coded as uncertain). *Newportia monticola* likewise appears to lack these sensilla (Fig. 2A), but they are not consistently lacking in Newportiinae because they are present in *N. stolli*. A row of about 10 pigmented spots visible in light microscopy at the usual position of sensilla in other scolopendromorphs is seen in *N. stolli* to correspond to small conical projections in SEM (Fig. 2D, arrows). In *E. quadrimeropus* (see Description), one or two small bottle-shaped sensilla are seen in each half of the border laterally (Fig. 3B, arrows), and their structure corresponds to small bottle-shaped sensilla proximal to the border in the medial epipharynx, including the presence of a terminal pore. We identify these as a modification of the usual scolopendromorph band of sensilla. Because they are of such minute size in, e.g., *E. quadrimeropus*, and their detection requires a clear view inside the groove at the edge of the median field of branching spines, an uncertain coding is applied to a few scolopocryptopid species in which presence of the sensilla has not been ascertained.

Previous studies (Edgecombe & Koch 2008, ch. 45) coded for pronounced accessory denticles on the mandibular teeth in Cryptopinae and Lithobiomorpha. *Newportia monticola* is one of a few non-cryptopine species to display strong and regularly patterned tooth ridges that are divided into short units approaching a dentiform aspect (Fig. 5A). The distinction between the accessory denticles of Cryptopinae and the structures in *Newportia* is too subtle for an absence/presence character, and strength of expression of the accessory denticles varies considerably across Scolopocryptopidae as a whole (Fig. 5), even between species of *Newportia* (Fig. 5A vs 5E). We currently exclude this character.

New data for *Newportia* and *Ectonocryptoides* highlight more variation in the kinds of pineapple-like projections of the anterior part of the gizzard sieve than was known from a smaller taxonomic sample. Accordingly we have added two new characters (ch. 88-89 in Appendix 1) to describe this variation. Previous coding (ch. 75 herein) identified the presence of pineapple-shaped projections as a putative apomorphy of Scolopocryptopidae that is shared with some cryptopine species. A new character scores for a particular kind of pineapple-shaped projection that lacks a kinked tip but instead terminates as spike-like spines and is arranged as a few rows in the anteriorsmost part of the gizzard sieve. This kind of projection is observed only in Newportiinae (Fig. 8A-D, *s-pi*) and Ectonocryptopinae (Fig. 7A, B). A single row of longer projections with scaly bases and kinked tips that have rows of filiform trichomes occurs between the rows of short pineapple-shaped projections and the main sieve projections in some species, such as *N. monticola* (Fig. 8B, *l-pi*). The projections in this position in *N. stolli* and *N. divergens* exhibit a shared structure that is unique to these two species among the taxa sampled, added here as character 89. In other scolopocryptopids (including newportiines) these projections taper to the position where an elongate, kinked tip emerges; in *N. stolli* and *N. divergens* these projections are bifid with short, conical tips emerging from the notches (Fig. 8G). The surfaces of these projections are complex (Fig. 8F, *l-pi*), with the basal parts bearing robust spine clusters that grade laterally as well as distally into short, dense spines.
Results and discussion

Analysis of the data with the search options described above finds 108 shortest cladograms of 214 steps under equal weights (Consistency Index 0.54, Retention Index 0.85). The strict consensus of these is depicted in Fig. 10. The shortest cladograms include two alternative resolutions of blind scolopendromorphs. In one set of cladograms they are a paraphyletic group in which Cryptopinae is basal within Scolopendromorpha, and Plutoniuminae + Scolopocryptopidae is sister to Scolopendridae. In the other set of cladograms, blind scolopendromorphs unite as a clade. In the latter trees, Cryptopinae is sister to a clade in which the 21-segmented Plutoniuminae nest within a 23-segmented group that corresponds to Scolopocryptopidae sensu Shelley (2002). When Cryptopinae assume a basal position, the shortest trees resolve the 23-segmented group as strictly monophyletic and its internal relationships are stable across all trees. In those trees, Plutoniuminae is sister to (Scolopocryptopinae (Kethopinae (Newportiinae + Ectonocryptopinae))). All equally weighted cladograms resolve Newportiinae as paraphyletic with respect to Ectonocryptopinae. Character evidence that supports this topology is discussed below.

Under implied weights, the interrelationships of Plutoniuminae, Scolopocryptopinae, Kethopinae, and Ectonocryptopinae + Newportiinae are stable across a range of concavity functions ($k = 1$ to $k = 10$). All analyses with implied weights recognise Plutoniuminae as sister to Scolopocryptopidae sensu Shelley (2002), and the latter clade is consistently resolved as (Scolopocryptopinae (Kethopinae (Newportiinae + Ectonocryptopinae))), with species-level relationships as depicted in Fig. 11. These relationships are also found among the set of shortest cladograms under equal weights. The only topological lability among blind Scolopendromorpha in the weighting experiments concerns the resolution of the three sampled members of Plutoniuminae and the position of Cryptopinae. Under lower weighting strengths ($k = 5$ and higher; Fig. 11A), Cryptopinae is sister to all other Scolopendromorpha, as in many trees under equal weights. With higher weighting ($k = 4$ and lower; Fig. 11B), Cryptopinae assumes a position not found under equal weights, being sister to Scolopendridae. None of the analyses under implied weights resolve blind Scolopendromorpha as a monophyletic group.

Because the pattern of relationships among Plutoniuminae and Scolopocryptopinae in Fig. 11 is stable for implied weights and is also found under equal weights, it serves as the most appropriate topology for depicting character optimisation (Fig. 12). Ectonocryptoides / Ectonocryptopinae unites with Newportiinae based on seven unambiguous synapomorphies, among them: crescentic tergal sulci (ch. 29, state 1), absence of tarsal spurs on the locomotory legs (ch. 37, state 0), ventral spinose processes on the ultimate leg femur (ch. 84, state 1), absence of a pretarsal claw on the ultimate leg (ch. 85, state 0), and rows of small pineapple-shaped projections at the anterior extent of the gizzard sieve (ch. 88, state 1). Characters 84 and 88 are unique and unreversed. Two additional synapomorphies, tarsus 2 divided into tarsomeres (ch. 82, state 1) and paired longitudinal sutures on the head plate (ch. 87, state 2), are characters of traditional Newportiinae that are forced to reverse in Ectonocryptoides under the hypothesis...
Figure 10. Strict consensus of 108 shortest cladograms under equal weights. Numbers above nodes are jackknife frequencies; numbers below nodes are Bremer support (where no values are shown, jackknife frequency is <50% and Bremer support is 1).
in Fig. 11. The newportiine-ectonocryptopine grouping is strongly supported in jackknife resampling, being present in 94% of replicates, and has one of the highest Bremer supports within Scolopendromorpha (=5).

A novel finding in our study is the nesting of Ectoncryptopinae within Newportiinae, and indeed within *Newportia*. The basal resolution of *Tidops collaris* (Kraepelin, 1903) relative to *Newportia* and *Ectonocryptoides* is especially indicated by the lack of a spiracle on segment 7 in *T. collaris*, an observation first made by Schileyko & Stagl (2004). Presence of a spiracle on segment 7 (character 13, state 1) optimises as synapomorphic for *Newportia* and Ectoncryptopinae. Paraphyly of *Newportia* with respect to Ectoncryptopinae finds support from variability in the node-like or spine-like scales

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**Figure 11.** Strict consensus cladograms for Scolopendromorpha under implied weights with different concavity constants. A, consensus of cladograms with $k=5$ and higher; B, consensus of cladograms with $k=4$ and lower. The subfamilies of Scolopocryptopidae are highlighted in grey boxes.
Anatomy of Ectonocryptoides across the proximal labral part of the epipharynx (ch. 50). These scales are lacking in E. quadrimeropus (Fig. 3A) and some species of Newportia (Fig. 2A), but are present in N. monticola, as in Kethops (Fig. 2B), Scolopocryptopinae (Edgecombe & Koch 2008, Figs. 10C, 15E), and Plutoniuminae (Edgecombe & Koch 2008, Fig. 15D). The hypothesis that Ectonocryptopinae are modified newportiines implies a transformation series in the form of the ultimate legs from the subdivided tarsi of Tidops and Newportia to the more or less claviform appendages of Ectonocryptopinae. Newportia is represented by 10 species in Mexico (Chagas & Shelley 2003), so no biogeographic arguments exclude the possibility of ectonocryptopines being modified newportiines. However, the weak branch support for the internal relationships of Newportiinae and Ectonocryptopinae (apart from the well supported grouping of N. stolli and N. divergens) cautions against altering the taxonomic status of Newportia or Newportiinae at present. Molecular sequence data should help to elucidate this matter.

Figure 12. Character optimisations shown on one of twelve shortest cladograms with implied weights, concavity constant $k=5$. Only unambiguous changes are shown; non-homoplastic changes are black, homoplastic changes white. Branches lacking strict support were collapsed after optimising characters.
The relationships depicted in Fig. 11 for Kethopinae as sister to Ectonocryptopinae + Newportiinae and the monophyly of Scolopocryptopidae as a 23-segmented clade are, as noted above, not retrieved in all cladograms under equal weights. Although the concept of Scolopocryptopidae (sensu Shelley 2002) has generally been viewed in terms of trunk segmentation alone (e.g., Shelley & Mercurio 2005), some other conserved anatomical characters are synapomorphies at the same node in cladograms where that group is monophyletic. Perhaps the most useful among these are the pectinate claw of the second maxilla (ch. 21, state 3) that is observed throughout the group (Fig. 6A-E) and the kinked gizzard projections (ch. 76, state 1) that are unique to 23-segmented Scolopocryptopidae.

In the original treatment of *Ectonocryptops*, Crabill (1977) recognised the genus as being closely allied to *Newportia*, a relationship substantiated by the absence of a pretarsal claw on the ultimate leg and the “extraordinary departure of their ultimate second tarsi from the norm” (Crabill 1977: 346). The latter is an unconvincing synapomorphy given that tarsus 2 of *Newportia* is elongated and antenniform whereas that of *Ectonocryptops* departs from “the norm” in a different manner, by its reduction to a short, bulbous article (and more extreme reduction in *Ectonocryptoides*). Shelley & Mercurio (2005) resolved Ectonocryptopinae as a whole (=*Ectonocryptops* + *Ectonocryptoides*) as sister to Newportiinae (=*Newportia* + *Tidops*) based on the loss of claws on the ultimate leg and the presence of at least one ventral “spinose process” on each ultimate leg femur (in addition to those on the prefemur that are more broadly shared with Scolopocryptopinae). The absence of pretarsal claws on leg pair 23 optimises on our cladogram as apomorphic for Newportiinae and Ectonocryptopinae, but we note that some homoplasy plagues this character in *Newportia*; a claw-like pretarsus is present in a few species of *Newportia* as the genus is broadly interpreted by Schileyko & Minelli (1998), i.e., in species sometimes assigned to *Newportides* Chamberlin, 1921, on the basis of these claws. Some of the other apomorphies of Ectonocryptopinae and Newportiinae also exhibit homoplasy with other blind Scolopendromorpha, notably the crescentic sulci on the tergites (shared with Cryptopinae) and the spiracle on segment 7 (shared with *Dinocryptops* Crabill, 1953, in the Scolopocryptopinae). One of the new characters in this study, the small pineapple-shaped projections of the gizzard (ch. 88) are strictly unique to Ectonocryptopinae and Newportiinae in the context of the taxonomic sampling employed herein, and optimise as apomorphic for that group, but possibly similar projections have been depicted in *Cryptops anomolans* Newport, 1844, by Balbiani (1890, pl. 1, fig. 4). The separation between Cryptopinae and Ectonocryptopinae + Newportiinae in all cladograms herein makes it most probable that similarities within *Cryptops* are convergent rather than homologous.

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Appendix
Characters used in phylogenetic analysis (see Edgecombe & Koch 2008, 2009; Koch et al. 2009 for descriptions).

1. **Shape of head capsule:** (0) domed; (1) flattened.
2. **Trochanter on second maxilla:** (0) separated from prefemur; (1) fused to prefemur with incomplete articulation.
3. **Coxosternite of maxillipede sclerotised in midline:** (0) coxae separated medially; (1) coxosternal plates meeting medially, hinge flexible; (2) midline sclerotised, inflexible.
4. **Maxillipede tarsungulum:** (0) separate tarsus and pretarsus; (1) tarsus and pretarsus fused.
5. **Position of spiracle:** (0) dorsal; (1) pleural.
6. **Coxal organs:** (0) absent; (1) present.
7. **Four laminae of mandible intersect at cruciform suture:** (0) absent; (1) present.
8. **Dorsal brush on tarsus of second maxilla:** (0) absent; (1) present.
9. **Tergite of maxillipede segment and first pedigerous segment:** (0) separate tergites; (1) single tergite.
10. **Gonopods in female:** (0) present; (1) absent.
11. **Hinge between articles of maxillipede telopodite:** (0) absent (entire femur and tibia); (1) hinge between trochanteroprefemur and tibia; (2) hinge between trochanteroprefemur and tarsungulum.
12. **Number of pedigerous post-maxillipede segments:** (0) 15; (1) 21; (2) 23; (3) 47.
13. **Segmental distribution of spiracles:** (0) on macrosegments, excluding segment 7; (1) on macrosegments, including segment 7; (2) on all trunk segments except maxillipede and ultimate pedigerous segment.
14. **Atrium of spiracle covered by tripartite flap:** (0) absent; (1) present.
15. **Spiracles with floor of atrium raised into humps:** (0) humps absent; (1) humps present.
16. **Eyes:** (0) present; (1) absent.
17. **Depigmented ocular patches:** (0) absent; (1) present.
18. **Setation of basal antennomeres:** (0) basal few articles bear numerous sensilla trichoidea dorsally, grading in density as short sensilla become more numerous on more distal articles; (1) basal few articles glabrous or with few sensilla trichoidea dorsally, with abrupt transition to greater density on more distal articles.
19. **Antennal sensilla (coded along most of length of antenna, i.e., articles 5-penultimate article):** (0) mostly normal trichoid sensilla; (1) most sensilla emerging from a collar or tubercle.
20. **Basal plates at posterolateral corners of head plate:** (0) absent; (1) present.
21. **Structure of claw of second maxillary telopodite:** (0) digitiform claw, without accessory spines; (1) three thick, elongate spines with interspersed thin spines; (2) robust median claw with pair of slender spines on each side; (3) pectinate claw; (4) hook-like claw with ventral flange; (5) two curved processes, one above the other; (6) claw lacking.
22. **Tooth plates of maxillipedes:** (0) plates absent; (1) plates with strongly chitinized tooth margins; (2) strongly chitinized anterior margin of coxosternite without plates; (3) blunt, hyaline plate, bearing no tooth margin.

23. **Trochanteroprefemoral process on maxillipede:** (0) absent; (1) present.

24. **Median embayment in posterior margin of maxillipede coxosternite:** (0) absent; (1) present.

25. **Position of poison calyx:** (0) not extending more deeply than into tibia; (1) extending into distal part of trochanteroprefemur; (2) extending half length of trochanteroprefemur; (3) extending into distal part of trochanteroprefemur or to articulation with coxosternum; (4) extending deeply into coxosternum.

26. **Form of poison calyx:** (0) straight or arcuate; (1) serpentine.

27. **Pre- and metatergites:** (0) pretergite and metatergite merged; (1) strong pretergite set off from metatergite by continuous, transverse suture.

28. **Tergite margination:** (0) margins present on more than last tergite; (1) restricted to last tergite only.

29. **Crescentic sulci on tergites:** (0) absent on all tergites; (1) present on most tergites.

30. **Shape of ultimate tergite:** (0) not substantially longer than penultimate tergite; (1) nearly twice as long as penultimate tergite.

31. **Median suture on ultimate tergite:** (0) absent; (1) present.

32. **Line of skeletal thickening across sternites originating at coxa:** (0) absent; (1) present.

33. **Complete paramedian sutures on sternum:** (0) absent; (1) present.

34. **Endosternite:** (0) absent; (1) present.

35. **Setae on locomotory legs:** (0) strong, numerous; (1) slender, sparse.

36. **Structure of tarsi of locomotory legs:** (0) divided into two articles; (1) undivided, at least internally.

37. **Tarsal spurs of locomotory legs:** (0) absent; (1) present.

38. **Tibial spurs of locomotory legs:** (0) absent; (1) present.

39. **Coxopleural process of ultimate leg:** (0) absent; (1) present.

40. **Dorsomedial prefemoral process on ultimate leg:** (0) absent; (1) present.

41. **Strongly thickened, forcipulate ultimate leg:** (0) absent; (1) present.

42. **Armature of ventral side of prefemur of ultimate leg:** (0) spines and spinous processes absent, as on locomotory legs; (1) spine(s) or spinose process(es) present.

43. **Saw teeth on ventral side of ultimate leg tibia and tarsus I:** (0) absent; (1) present.

44. **Fan bristles expanded onto lamina dentifera of mandible:** (0) absent; (1) present, confined to dorsal part of mandible; (2) covering entire surface of lamina dentifera.

45. **Length of mandibular tooth row:** (0) tooth row much more than half length of gnathal edge; (1) tooth row less than half length of gnathal edge.

46. **Medial labral part of epipharynx:** (0) large median tooth, extensive area between labral bristle bands; (1) small median tooth, area between labral bristle bands a narrow strip.

47. **Medial sclerotisation of labral part of epipharynx:** (0) absent (paired lateral bars); (1) sclerotisation continuous from median tooth to border with clypeal part;
(2) sclerotisation confined to region immediately proximal to median tooth, discontinuous with border with clypeal part.

48. **Differentiation of labral bristles:**
   - (0) narrow band of pectinate bristles laterally, wide band of simple bristles medially;
   - (1) band of short, simple bristles laterally and longer simple bristles medially;
   - (2) long, simple bristles across width of band.

49. **Width of labral bristle field:**
   - (0) restricted medially on distal sclerotisation of submarginal armature;
   - (1) completely covering distal sclerotisation of submarginal armature.

50. **Node- or spine-like scales across proximal labral part of epipharynx:**
   - (0) absent;
   - (1) present.

51. **Curvature of border between labral and clypeal parts of epipharynx:**
   - (0) subtransverse or gently convex distally;
   - (1) strongly convex distally.

52. **Single row of bullet-shaped sensilla at proximal margin of field of branching spines at border between labral and clypeal part of epipharynx:**
   - (0) absent;
   - (1) present.

53. **Sensillar field(s) on clypeal part of epipharynx:**
   - (0) medial cluster of sensilla coeloconica proximally, near mouth opening;
   - (1) crescentic or ovate fields of sensilla coeloconica laterally;
   - (2) large field of sensilla coeloconica across medial clypeal part of epipharynx, separated from spine field by a substantial expanse that bears scattered pores;
   - (3) band of sensilla coeloconica medially, immediately proximal to spine field;
   - (4) lenticular field of sensilla coeloconica immediately proximal to spine field.

54. **Differentiation of a proximomedial cluster of button-shaped sensilla at edge of main sensilla cluster on clypeal part of epipharynx:**
   - (0) absent (sensilla cluster uniform);
   - (1) present.

55. **Elongate / figure-8 shaped group of two smooth scutes surrounding each sensillum on clypeal part of epipharynx:**
   - (0) absent;
   - (1) present.

56. **Lid-like cover along distal edge of sensilla coeloconica on clypeal part of epipharynx:**
   - (0) absent;
   - (1) present.

57. **Paired lateral cluster of sensilla on clypeal part of epipharynx:**
   - (0) both groups positioned laterally, widely separated from each other;
   - (1) positioned medially, with each group closely approximating each other near midline.

58. **Elongate, distally branching spines with apices directed distomedially on clypeal part of epipharynx:**
   - (0) absent;
   - (1) present.

59. **Extent of lateral longitudinal bands of scales on clypeal part of epipharynx:**
   - (0) not confluent across midline;
   - (1) confluent across midline, developed proximomedially as polygonal scales.

60. **Sensilla on Schlundplatte:**
   - (0) single grouping of sensilla, continuous across midline;
   - (1) paired lateral groupings of sensilla;
   - (2) sensilla absent.

61. **Bristles on lateral flap of hypopharynx:**
   - (0) lateral flaps lacking tuft of bristles;
   - (1) discrete tuft of bristles on each lateral flap, median region devoid of bristles, spines or scales;
   - (2) bristles on each lateral flap confluent across midline, with identical bristles developed in median region;
   - (3) tuft of bristles on each lateral flap connected by band of scales or short spines across midline.
62. **Asymmetry of oviducts:** (0) left and right oviducts symmetrical; (1) left oviduct rudimentary or absent.

63. **Ventral invagination in spermatophore:** (0) absent; (1) present.

64. **Orientation of testicular vesicles:** (0) longitudinal, parallel to central deferens duct; (1) oblique to deferens duct.

65. **Longitudinal median suture on anterior part of T1, bifurcating into two oblique sutures posteriorly:** (0) longitudinal median suture and oblique sutures absent; (1) longitudinal median suture and oblique sutures present.

66. **Spinulation of coxopleural process:** (0) spine(s) confined to apex or with few dorsal spines markedly separated from apical cluster; (1) spines scattered along length of long, slender process.

67. **Gizzard with plicate walls differentiated at posterior end of foregut:** (0) absent; (1) present.

68. **Length of foregut:** (0) not extending further than pedigerous trunk segment 2; (1) extending to pedigerous trunk segment 5; (2) extending to pedigerous trunk segments 10-16.

69. **Posteriorly directed spines along plicae of gizzard:** (0) absent; (1) present.

70. **Arrangement of posteriorly directed spines on plicae:** (0) single; (1) grouped.

71. **Plicae covered by scales that each bear a single spine:** (0) scales with spines absent; (1) spine-bearing scales present.

72. **Posterior lobes in front of cardiac valve on gizzard:** (0) absent; (1) present as one to several rows.

73. **Cardiac valve:** (0) entirely enveloped by midgut; (1) extended cardiac valve largely anterior to midgut.

74. **Posterior part of foregut organised as a sieve with stiff, anteriorly directed projections:** (0) absent; (1) present.

75. **Anterior gizzard projections with pigmented conical base bearing spinose scales or spines:** (0) absent; (1) present.

76. **Shape of main sieve projections:** (0) evenly curved; (1) kinked near midlength, with distal part more strongly directed forwards.

77. **Longitudinally patterned bands of trichomes on basal half of sieve projections:** (0) trichomes (if present) not patterned; (1) trichomes with longitudinal patterning.

78. **Distal half of sieve projections twisted, branching into large, irregularly curved spines that bear small subsidiary spines:** (0) absent; (1) present.

79. **Sieve projections covered by multifurcating scales that spirally encircle the projection, branching into slender, needle-like spines:** (0) absent; (1) present.

80. **Antennal shape:** (0) filiform, gently tapering; (1) strongly tapering distally.

81. **Longitudinal groove(s) along dorsal side of femur of ultimate leg:** (0) absent; (1) single median groove; (2) paired grooves.

82. **Tarsomeres in tarsus 2 of ultimate leg:** (0) undivided tarsus 2; (1) tarsus 2 with numerous tarsomeres.

83. **Definition of tarsomeres in tarsus 2 of ultimate leg:** (0) regular; (1) irregular.

84. **Ventral spinous process(es) on ultimate leg femur:** (0) absent; (1) present.
85. Pretarsal claw on ultimate legs: (0) absent; (1) present.
86. W-shaped sutures on T1: (0) absent, paramedian sutures, when present, either continuous to anterior transverse suture or terminating behind latter; (1) present, with paramedian sutures originating at posterior apices of the W.
87. Longitudinal sutures on head plate: (0) absent; (1) median, unpaired; (2) paired.
88. Rows of small pineapple-shaped projections at anteriormost part of gizzard sieve that lack kinked tips, bearing short spines along most of their length, coarse spike-like spines at/near their tip: (0) absent; (1) present.
89. Terminal part of large pineapple-shaped projections of gizzard: (0) projection evenly tapering, tip filamentous; (1) projection bifid, with a short conical tip emerging from the notch.