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The contribution of preoral chamber and foregut morphology to the phylogenetics of Scolopendromorpha (Chilopoda)

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Abstract

Recent morphology-based cladistic analyses of Scolopendromorpha have contributed suites of characters from the epipharynx and hypopharynx (peristomatic structures) and the foregut/gizzard that have been analysed together with traditional characters. Cladistic relationships in the Scolopocryptopidae and Scolopendridae and their implications for deep branchings in Scolopendromorpha as a whole are appraised in light of a new analysis of 84 morphological characters that adds and illustrates taxa not available for previous studies, notably the Neotropical scolopocryptopid *Tidops* Chamberlin, 1915, and the Australian scolopendrid *Notiasemus* Koch, 1985. Analysis with implied weights resolves the basal nodes of Scolopendridae in a pattern compatible with the traditional classification of Attems, including *Edentistoma* [Arrhabdotini] as sister to Otostigmini, and Asanadini as sister to *Notiasemus* + Scolopendrini; Plutoniuminae is sister to a 23-segmented scolopocryptopid clade. With equal character weights, the monophyly or paraphyly of blind Scolopendromorpha (Cryptopidae and Scolopocryptopidae) have equal cost, and a basal position of Arrhabdotini in the Scolopendridae emerges as an alternative.

Keywords: Scolopocryptopidae, epipharynx, hypopharynx, gizzard, cladistics

1. Introduction

The cladistic relationships of major groups of Scolopendromorpha were first analysed by Schileyko & Pavlinov (1997) using a small character sample that included all the recognised genera in the order as terminal taxa. To increase the amount of character evidence applied to morphology-based phylogenetics of Scolopendromorpha, new characters from the preoral chamber and the foregut were added to a matrix that includes other, mostly traditional morphological characters (Edgecombe & Koch 2008, Koch et al. 2009). The details of the so-called peristomatic structures (the epipharynx and hypopharynx according to Verhoeff 1902–1925; see also Koch & Edgecombe 2006, 2008) contributed 16 new characters, and the gizzard that is elaborated at the posterior end of the foregut in scolopendromorphs (Balbiani 1890) was the source of 13 new characters. In total, the 29 characters from these newly studied character systems represent more than one-third of the character suite used in the most

recent analysis. The present study expands on prior work on the peristomatic structures and the gizzard by considering these organ systems and other morphological character data for lineages that were previously unavailable for study. Foremost among these are two geographically restricted genera, *Tidops* Chamberlin, 1915, and *Notiasemus* Koch, 1985, whose inclusion in the dataset brings the number of genera sampled to 22 of 35 currently recognised scolopendromorph genera (Minelli 2006). Additionally we include a second species of *Asanada* Meinert, 1886, a genus resolved basally within the Scolopendridae in prior analyses that used a single species.

2. Materials and methods

Taxon sampling

Edgecombe & Koch (2008) and Koch et al. (2009) sampled members of 20 scolopendromorph genera, including 26 and 30 species, respectively, together with three outgroup species to sample Geophilomorpha, Lithobiomorpha and Scutigeromorpha. Here we present new data for three additional scolopendromorph species, which extends our sampling for cladistic analysis to 37 terminal taxa. The monotypic genus *Notiasemus* Koch, 1985, is added based on its type species, *N. glauerti* Koch, 1985. In its original description, *Notiasemus* was referred to Scolopendrinae but various phenetic and phylogenetic analyses by Koch & Colless (1986) tended to ally it with a 'cluster of 'primitive' species' (Koch & Colless 1986: 100) that included members of *Asanada* Meinert, 1886, *Cormocephalus* Newport, 1844, and *Arthrorhabdus* Pocock, 1891. The Neotropical *Tidops* Chamberlin, 1915, is coded based on *T. collaris* (Kraepelin, 1903), using paratypes of *T. echinopus* Chamberlin, 1921, a junior subjective synonym of *T. collaris* fide Schileyko & Minelli (1998). Because *Asanada* was resolved as topologically basal in the Scolopendridae when analysed with a single species, *A. socotrana* Pocock, 1899, we explore the generality of its characters in a second species, *A. brevicornis* Meinert, 1886.

Voucher specimens and their geographical data were listed in previous works (Edgecombe & Koch 2008: Tab. 1, Koch et al. 2009: Tab. 1). Voucher details for newly added taxa are as follow: *Notiasemus glauerti* Koch, 1985, WAM 97/2921, Australia: Western Australia, Talbot Road Reserve, 31°52'24''S 116°02'52''E, leg. J. Dell, 18–31.x.1993; *Tidops collaris* (Kraepelin, 1903), MCZ 32933, Guyana: Labba Creek, leg. F. M. Gaige, Bryant Walker Expedition, 27.vii.1914; *Asanada brevicornis* Meinert, 1886, BMNH 1889.7.15.21–23, Andamans, leg. E. W. Oates.

Dissection

Methods for dissection of the preoral chamber to expose the epipharynx and hypopharynx are 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).

Light microscopy

Light microscopic studies of the epipharynx, hypopharynx, and gizzard were performed with a Leica MZ16 stereomicroscope equipped with a Leica IM 50 digital camera. Images were taken to document the sclerotised and/or pigmented parts of the preoral chamber and cuticular surface of the foregut. All images and plates were edited with the Adobe Photoshop CS3 and Adobe Illustrator CS3 software.

Scanning electron microscopy

After cleaning in an ultrasonic bath, dissected head pieces and gizzards were dehydrated in a graded ethanol series and critical point dried using a Bal-Tec CPD 030. The dried materials were then mounted on stainless steel stubs with double sticky tabs, coated with gold in a Bal-Tec SCD 040 sputter coater, and examined with a Fei Quanta 200 scanning electron microscope (Philips).

Terminology

Descriptive terminology applied to the epipharynx and hypopharynx, including kinds of cuticular projections and sensilla, follows Edgecombe & Koch (2008). Terminology used for the gizzard follows Koch et al. (2009).

Cladistic analysis

The data matrix in Tab. 1 codes for the 80 characters used by Koch et al. (2009); characters 1–65 were described by Edgecombe & Koch (2008) and characters 66–80 by Koch et al. (2009). Four new characters (characters 81–84) are added here. The complete list of characters is given in Appendix 1. Parsimony analyses were performed with TNT (Goloboff et al. 2008a) using heuristic searches involving 1000 random addition sequences and TBR branch swapping saving up to 100 trees per replicate. Character optimisation was explored with TNT and WINCLADA (Nixon 2002). Multistate characters 3 and 44 were ordered, the remainder unordered. Jackknife resampling (Farris et al. 1996) and Bremer support (Bremer 1994) were used as measures of nodal support. 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. 2008b) was implemented in TNT.

Scolopendromorpha was rooted using exemplars of three other chilopod orders as outgroups, following arguments by Edgecombe & Koch (2008) for the choice of specific scutigeromorph, lithobiomorph and geophilomorph taxa.

Tab. 1 Data matrix for 84 morphological characters coded for the relationships of scolopendromorphs and outgroups (Appendix 1). Question marks (?) indicate missing data; dashes (–) indicate inapplicable character states.

Taxa	Characters								
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	8888 1234
Scutigera coleoptrata	0000000000	00-0000000	600-000?00	0000000000	00000?0000	0000-0000-	0000-0-00-	---00-----	0010
Lithobius forficatus	1111110000	0000000000	1000000000	0000000000	0000100100	0000-00-0-	0100-0-00-	---00-----	0000
Mecistocephalus tahitiensis	1121110000	2320010000	0010101-00	0000010000	0000--1?21	??03-00-0-	-????0-00-	---00-----	0000
Plutonium zwierleini	1121111111	2120111100	?110401101	1000111100	1000000220	1013-00100	10??01-120	-010100001	0000
Theatops erythrocephalus	1121111111	2100011100	5110311101	1000111110	1100000220	1013-00100	?00?010120	-010100001	0000
Theatops posticus	1121111111	2100011100	5110401101	1000111100	1000000220	1013-00100	10???1-120	-010100001	0000
Cryptops australis	1121111111	1100010000	4200101110	0101010000	0010100120	0014-01001	21???0-120	-010100110	0000
Cryptops hortensis	1121111111	2100010000	4200001110	0101010000	0010100120	0014-01001	211000-120	-010100010	0000
Cryptops spinipes	1121111111	2100010000	4200101110	0101010000	0010100120	0014-01001	21???0-120	-010110110	0000
Paracryptops weberi	1121111111	2100010000	4300201110	0101010000	0010100120	1014-01001	20???0-120	-010100010	0000
Kethops utahensis	1121111111	2200010000	3200100100	0001011110	0010000120	10?3-00100	10???00120	-010111100	0000
Newportia longitarsis stechowi	1121111111	2210010000	3201201110	0001010110	0100000220	0013-00100	10?0000120	-010111100	0011
Tidops collaris	1121111111	2210010000	3300201110	0001010110	0100000220	1003-00???	20???00120	-010111100	0011
Scolopocryptops ferrugineus	1121111111	2200010110	3211300000	0000111110	0101000220	1013-00100	10?0000120	-010111100	0000
Scolopocryptops spinicaudus	1121111111	2200010110	3211310000	0000111110	0101000220	1013-00100	10???00120	-010111100	0000
Dinocryptops miersii	1121111111	2210010110	3211310000	0000111110	0101000220	1013-00100	10???00120	-010111100	0000
Scolopendra canidens	1121111111	2101000100	2110300000	1010101011	0101000111	0012110000	03?1?01121	11100-----	0000
Scolopendra cingulata	1121111111	2101000100	2110300000	1010101011	0101000111	0012110000	0311000121	11100-----	0000
Scolopendra laeta	1121111111	2101000100	2110300000	1010101011	0101000111	0012010000	03???00121	11100-----	0000
Scolopendra morsitans	1121111111	2101000100	2110300000	1010101011	0101000111	0012010000	0311000121	11110-----	0000
Scolopendra oraniensis	1121111111	2101000100	2110300000	1010101011	0101000111	0012110000	03???01121	11100-----	0000
Scolopendra pinguis	1121111111	2101000100	2110300000	0000101011	0101000111	0012010000	03???00121	11110-----	0000

Tab. 1 cont.

Taxa	Characters								
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	8888 1234
Cormocephalus aurantiipes	1121111111	2101000101	2111300000	1010100011	0101000111	0012010000	031?000121	11100-----	0000
Cormocephalus hartmeyeri	1121111111	2101000101	2111300000	0010100011	0101000111	0012010000	03???00121	11000-----	0000
Cormocephalus rubriceps	1121111111	2101000101	2111300000	0010100011	0101000111	0012010000	03???00121	?1100-----	0000
Akymnopellis chilensis	1121111111	2101000100	2110300000	0010100011	0101000111	0012010000	03?1001121	01100-----	0000
Arthrorhabdus formosus	1121111111	2101000100	2110400000	1010101011	1101000111	0012010000	03???00121	00100-----	0000
Campylostigmus orientalis	1121111111	2101000101	?111300000	0010100011	0102011111	0012000000	03???00???	??????????	0000
Scolopendropsis bahiensis	1121111111	2101000101	2110300100	1010101001	1101000111	0012110000	03???0-121	01100-----	0000
Notiasemus glauerti	1121111111	2101000100	2110300100	0010100010	0101000120	0014-00000	02???00121	11000-----	0000
Asanada brevicornis	1121101111	2101000100	0110401100	0010100000	1001000121	0014-10000	02???0-121	00000-----	1100
Asanada socotrana	1121101111	2101000100	0110401100	0010100000	1000000121	0014-10000	02???0-121	00000-----	1100
Otostigmus astenus	1121111111	2100100100	2110300000	0000101110	0101000111	0111-10010	02?1100120	-1100-----	0000
Alipes crotalus	1121111111	2100100100	2110300000	0000101110	0001000111	0111-10000	02???00120	-1100-----	0000
Ethmostigmus rubripes	1121111111	2110100100	2100300000	0000101110	0101000111	0111-10010	0211100120	-1100-----	0000
Rhysida nuda	1121111111	2110100100	2110300000	0000101110	0101000111	0111-10000	02?1100120	-1100-----	0000
Edentistoma octosulcatus	1121111111	2110100100	0210300000	0000100010	1002011111	0011-10010	02???00110	-0000-----	0200

3. Results

Comparative Morphology

Tidops collaris (Scolopocryptopidae: Newportiinae). – Peristomatic structures of *Tidops collaris* are typical for Scolopocryptopidae, and most details closely resemble the states in *Kethops utahensis* (see Edgecombe & Koch 2008 and Figs 1A, B). This particularly concerns the border between labral and clypeal parts of the epipharynx (Fig. 1B), which shows an elongate transverse bulge followed by a similarly elongate median spine field (whereas in *Newportia longitarsis*, both bulge and median spine field are confined to the medial region; see Edgecombe & Koch 2008: Fig. 15f). The proximal labral part anterior to the bulge is covered by node-like scales, which are confined to the lateral labral parts as in *Kethops* (Fig. 1B), but are more spine-like and medially confluent in plutoniumines and scolopocryptopines (absent in *Newportia*). In contrast to the state in *Kethops*, no sclerotised connection exists between the median labral tooth and the border to the clypeal part of the epipharynx. In *Tidops*, this median sclerotisation of the labral part fades out immediately proximal to the median labral tooth as in *Newportia*, Scolopocryptopinae, and Plutoniuminae. A row of bullet-shaped sensilla proximal to the median spine field is absent in *Tidops* (Fig. 1D); we did not recognise these sensilla in *Kethops* either but are still uncertain about their true absence. A medial cluster of epipharyngeal sensilla on the clypeal part is arranged as a transverse band immediately proximal to the median spine field as in all scolopocryptopids, with each sensillum being positioned in a rounded to bell-shaped depression (Fig. 1D). Further characters of the clypeal part of the epipharynx remain unknown in *Tidops* as this part was damaged in the single specimen available for our studies. The hypopharynx of *Tidops collaris* corresponds to the state in scolopocryptopids in lacking a tuft of bristles on the lateral flaps flanking the hypopharyngeal 'Schlundplatte'. It uniquely differs from all other scolopocryptopids in the absence of nipple-shaped sensilla on the 'Schlundplatte' (Fig. 1C).

The gizzard of *Tidops collaris* (Fig. 2) corresponds to the sieve-type documented throughout Cryptopidae and Scolopocryptopidae (Koch et al. 2009). Its posterior, sieve-bearing part was found in the 16th trunk segment. The sieve's composition is identical to the state in *Newportia* in showing four different types of projections entirely filling the intestinal lumen. The anteriormost transverse rows are composed of conical, pineapple-shaped outgrowths of the gizzard wall bearing a distal crown of thickened spines (Fig. 2B). These projections are posteriorly followed by a single row of pineapple-shaped projections bearing a kinked, anteriorly directed tapering tip that is densely covered by filiform trichomes (Fig. 2C). The main sieve projections are clusters of elongate, hollow outgrowths of the gizzard wall that bear similarly kinked, tapering distal halves as the pineapple-shaped projections immediately in front of the main projections. Whereas the proximal conical part of the pineapple-shaped projections are equipped with thick cuticular spikes, the elongate proximal halves of the main sieve projections are covered by longitudinal bands of short, filiform trichomes that are either arranged in longitudinal, parallel rows or delimit ovoid fields (Fig. 2D). The posteriormost projections are also elongate and tapering, but shorter than the main sieve projections, evenly curved and only sparsely covered by short filiform trichomes (Fig. 2E).

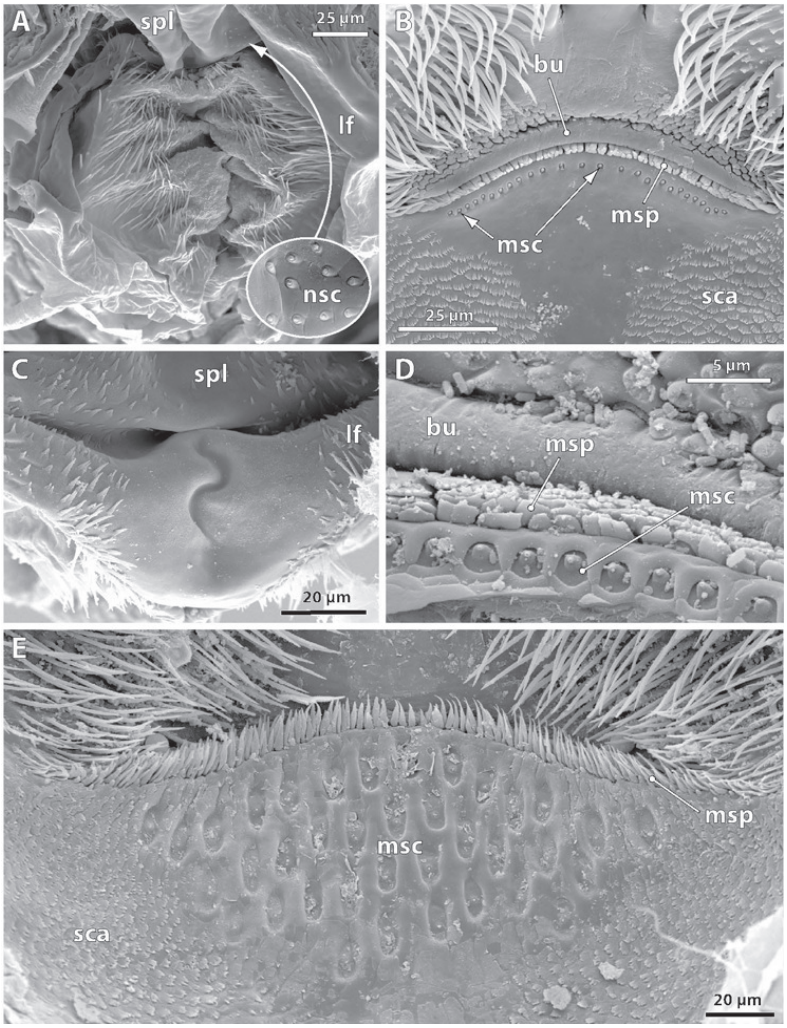

Fig. 1 **A, B**: *Kethops utahensis* (Chamberlin, 1909) (Scolopocryptopidae). **A**: hypopharynx (slightly collapsed in between its lateral flaps (lf)), frontal view, with detail of nipple-shaped sensilla (nsc; inset) on 'Schlundplatte' (spl); **B**: epipharynx, border between labral and clypeal parts made up of convex bulge (bu) and median spine field (msp); median sensilla cluster (msc) of the clypeal part forms a convex row immediately proximal to the median spine field, while lateral bands of scales (sca) are expanded towards the midline. **C, D**: *Tidops collaris* (Kraepelin, 1903) (Scolopocryptopidae). **C**: Proximal part of hypopharynx with 'Schlundplatte' (spl) devoid of sensilla and of bristle tuft; **D**: lateral part of border between labral and clypeal parts of epipharynx, showing bulge (bu), median field of spines (msp), and band of sensilla (msc) on clypeal part. **E**: *Asanada brevicornis* Meinert, 1886 (Scolopendridae). Border between labral and clypeal parts of epipharynx, with lenticular field of sensilla on median clypeal part.

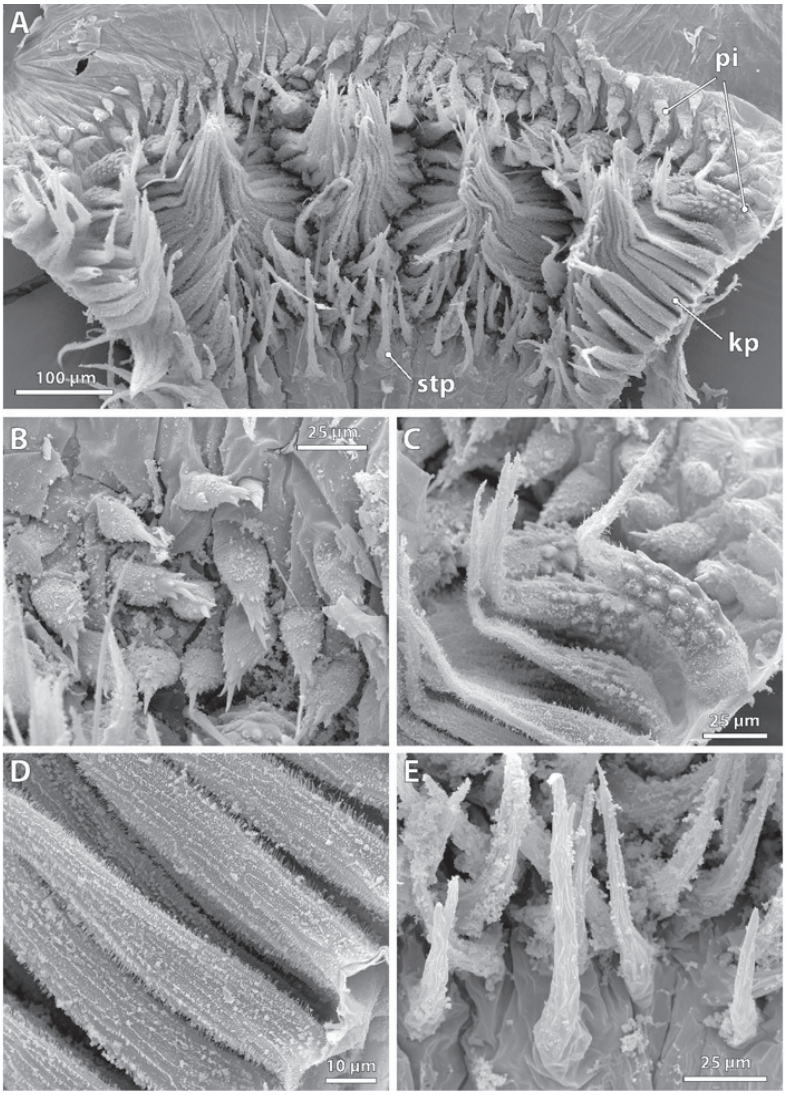

Fig. 2 Gizzard of *Tidops collaris* (Kraepelin, 1903) (Scolopocryptopidae), opened along dorsal midline and fanned out in one plane (anterior is top). **A**: Sieve-like gizzard projections differentiated into four zones detailed in B–E; **B**: Pineapple-shaped anterior gizzard projections ('pi' in A) with distal crown of spines, arranged in three to four rows; **C**: Single row of pineapple-shaped gizzard projection with kinked tips anterior to kinked projections ('kp' in A) from main zone of sieve; **D**: Longitudinally patterned bands of trichomes on basal part of main sieve projections; **E**: Straight projections ('stp' in A) from posteriormost zone of sieve.

Notiasemus glauerti (Scolopendrinae, incertae sedis). – The peristomatic structures of *Notiasemus glauerti* show a unique combination of characteristics of blind and ocellate scolopendromorphs. The epipharynx of *Notiasemus* is unique among Scolopendridae in showing narrow longitudinal bands of bristles flanking the labral teeth (Fig. 3A, C). This state is only shared by blind scolopendromorphs (Cryptopidae and Scolopocryptopidae), whereas scolopendrids usually show wide bristle fields that entirely cover the distal sclerotisation of the submarginal armature on the labral part of the epipharynx. Neither are the bristles of the labral part differentiated into two differently shaped bands in *Notiasemus*, but rather are uniformly long and simple, which is a common trait of blind scolopendromorphs and only shared by *Asanada* (Asanadini) among Scolopendridae. Another state shared only by *Asanada* among scolopendrids is the median sensilla cluster of the clypeal part of the epipharynx (Figs 1C, 3D), which is lenticular and positioned immediately proximal to the median spine field at the border to the labral part, as in Cryptopidae. The shape of these median sensilla on the clypeal part also differs from the usual scolopendrid state in that they are not arranged in figure 8-shaped depressions (Fig. 3D, inset), which *Notiasemus* shares only with *Campylostigmus* among Scolopendridae. Common scolopendrid traits of the epipharynx in *Notiasemus* include the smooth surface of the labral part, which is devoid of node- or spine-like scales (Fig. 3A, C); a continuous, sclerotised connection between median labral tooth and the border to the clypeal part, which in *Notiasemus* is slightly convex as in other scolopendrids but scarcely indicated by an inconspicuous transverse bulge (Fig. 3D); and lateral bands of scales that widely separate paired lateral clusters of sensilla on the clypeal part. As in most scolopendromorphs, a transverse row of bullet-shaped sensilla is also present in *Notiasemus* immediately proximal to the median spine field.

A distinctive feature of the hypopharynx in Scolopendridae that is observed in *Notiasemus* is the presence of a single median grouping of nipple-shaped sensilla on the 'Schlundplatte' in front of the mouth opening (Fig. 3B). Bristles of the lateral flaps flanking the 'Schlundplatte' in *Notiasemus* form a confluent tuft across the midline (Fig. 3B). Among scolopendrids, this unpaired median tuft of bristles is shared by *Asanada*, *Edentistoma* (Arrhabdotini), and Otostigmini, but not by Scolopendrini.

The gizzard of *Notiasemus glauerti* was found in the 15th trunk segment. It shows the typical spine-type of gizzard of the Scolopendridae (Koch et al. 2009) in being composed of spine-bearing scales and strongly sclerotised, posteriorly directed larger spines as the main cuticular armature (Fig. 4A). Among scolopendrids, however, *Notiasemus* is exceptional in having a very short gizzard. It closely resembles the gizzard of *Cormocephalus hartmeyeri* (Scolopendrini; see Koch et al. 2009: Fig. 4D) in that all larger spines of a plica are grouped on a single short plate, and that on the 15 plicae larger plates almost regularly alternate with smaller plates. *Notiasemus* differs from *C. hartmeyeri* in that towards the cardiac valve between the foregut and midgut all spinous plates continue into elongate fields of spine-bearing scales converging into the valve (Fig. 4B, C). Transverse rows of posterior lobes in front of the cardiac valve are absent in *Notiasemus*, which among scolopendrids is shared by *C. hartmeyeri*, but also by *Asanada* (Asanadini) and *Edentistoma* (Arrhabdotini).

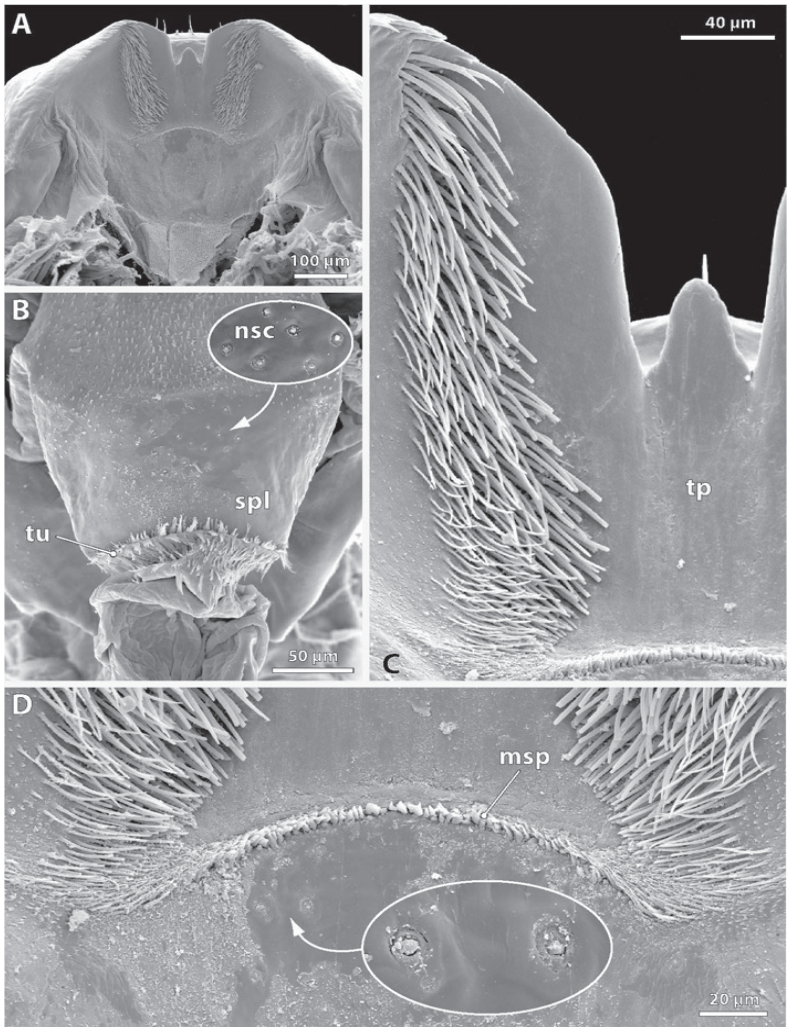

Fig. 3 Peristomatic structures of *Notiasemus glauerti* Koch, 1985 (Scolopendridae). **A**: Overview of epipharynx; **B**: Proximal part of hypopharynx with 'Schlundplatte' (spl), median cluster of nipple-shaped sensilla (nsc; inset), and tuft of bristles (tu) on lateral flaps continuous across midline; **C**: Labral part of epipharynx, showing narrow band of simple bristles and tooth plate (tp); **D**: Border between labral and clypeal parts of epipharynx, with median field of spines (msp), field of sensilla on median clypeal part, and detail of two sensilla (inset).

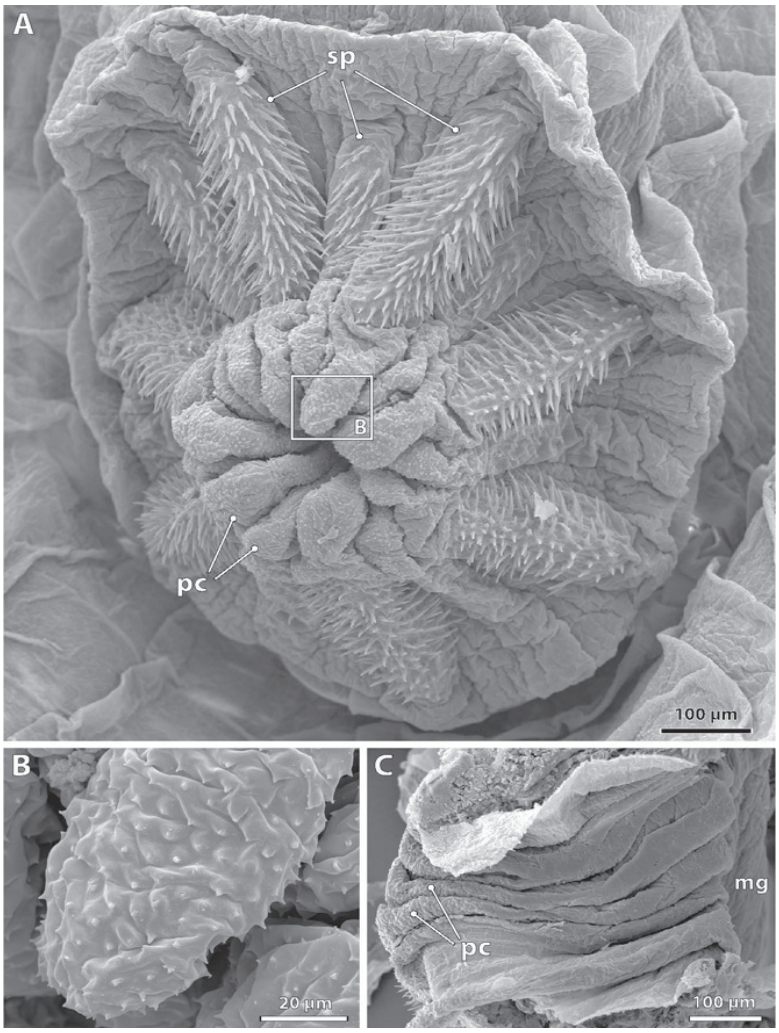

Fig. 4 Gizzard of *Notiasemus glauerti* Koch, 1985 (Scolopendridae). **A**: Oblique frontal view into the posterior end of the foregut, showing spine-bearing plates (sp) on the gizzard's plicae (pc) converging to a constriction, the cardiac valve, that leads into the midgut; **B**: Detail of plica posterior to a spiniferous plate (inset in A), showing scales that bear single small spines; **C**: Longitudinal section through the cardiac valve (right half) at the foregut-midgut (mg) transition (anterior is left), showing absence of posterior lobes in front of cardiac valve.

Asanada brevicornis (Scolopendridae, Asanadini). – Character states of the peristomatic structures and gizzard of *Asanda brevicornis* are identical to the states of *A. socotrana* (see Edgecombe & Koch 2008), including a corresponding position of the gizzard in the 12th trunk segment. Peculiar correspondences exist with *Notiasemus* as outlined above, but *Asanada* in addition shows some typical scolopendrid characters that are not shared by *Notiasemus*, particularly the expansion of the labral bristles on the entire distal sclerotisation of the epipharyngeal submarginal armature, and the position of the median sensilla on the clypeal part of the epipharynx in figure 8-shaped depressions (Fig. 1C). Unusual states of the spine-type of gizzard in *Asanada* concern the arrangement of abundant single spines on a high number of narrow plicae (about 35 plicae in *A. brevicornis*) (Fig. 5A), and the entire absence of spine-bearing scales (Fig. 5B), which is only shared by *Arthrorhabdus formosus* (Scolopendrini) and *Edentistoma* (Arrhabdotini).

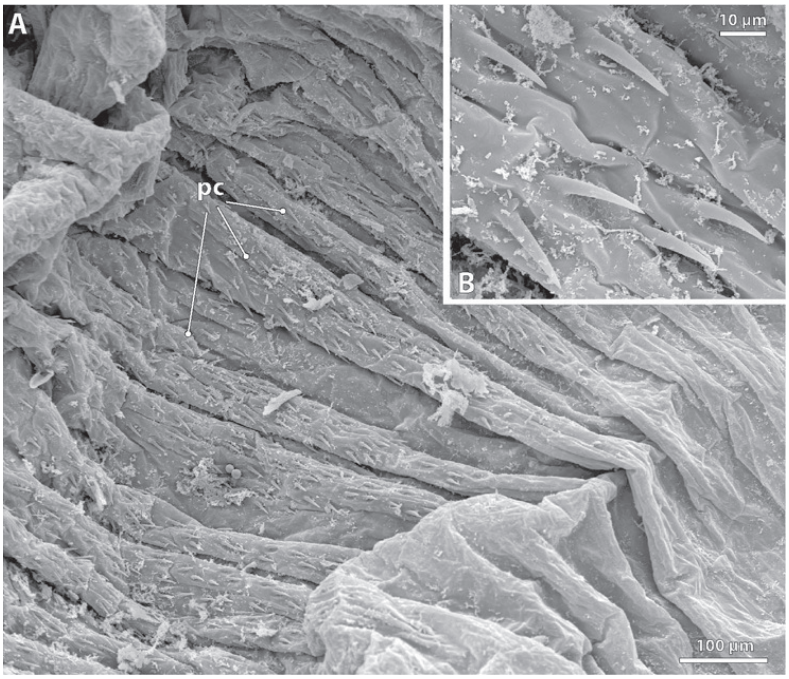

Fig. 5 Gizzard of *Asanada brevicornis* Meinert, 1886 (Scolopendridae). A: Gizzard plicae (pc), showing absence of posterior lobes (lower right corner of image); B: Higher magnification of posteriorly-directed spines on plicae.

Cladograms

Analysis of the 84 character matrix (Tab. 1) with the search options described above yields 42 shortest cladograms of 200 steps under equal weights (Consistency Index 0.55, Retention Index 0.83, Rescaled Consistency Index 0.46), the strict consensus of which is shown in Fig. 6A.

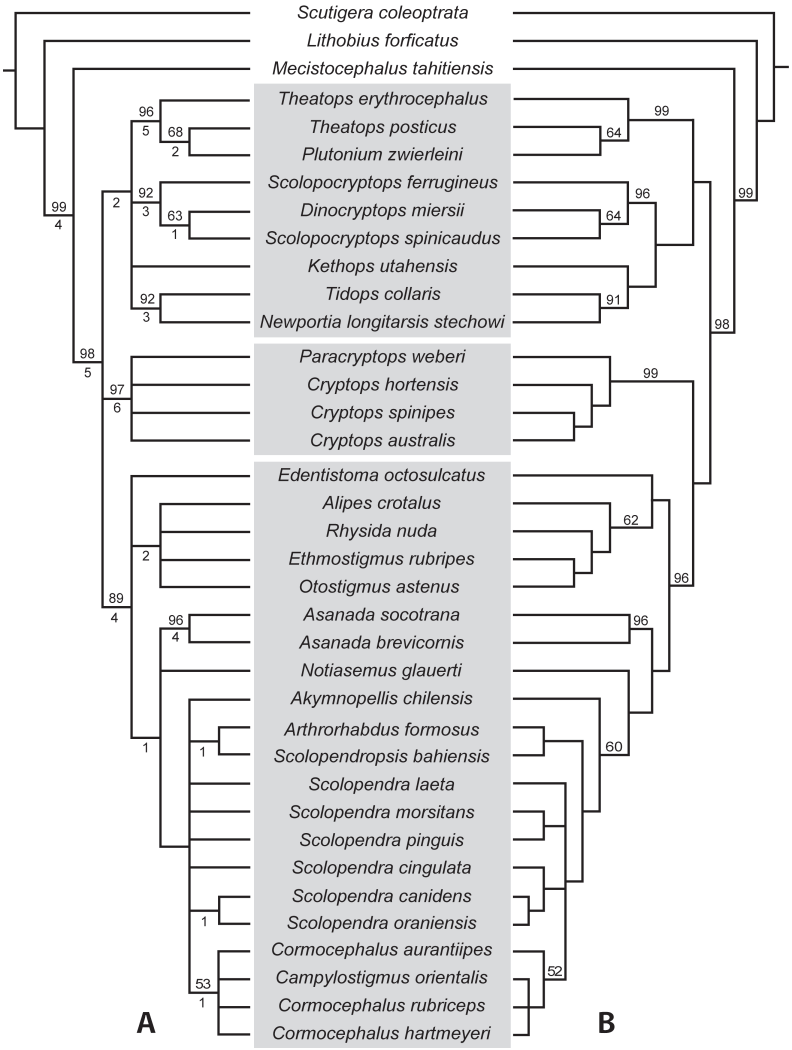

Fig. 6 **A**: Strict consensus of 42 cladograms for characters in Tab. 1 based on equal weights. **B**: Single optimal cladogram with implied weights ($k = 4$), with unsupported nodes shown as collapsed. Numbers above nodes are jackknife frequencies above 50 %; numbers below nodes are Bremer support values. Families Scolopocryptopidae, Cryptopidae, and Scolopendridae (from top to bottom) highlighted in grey boxes.

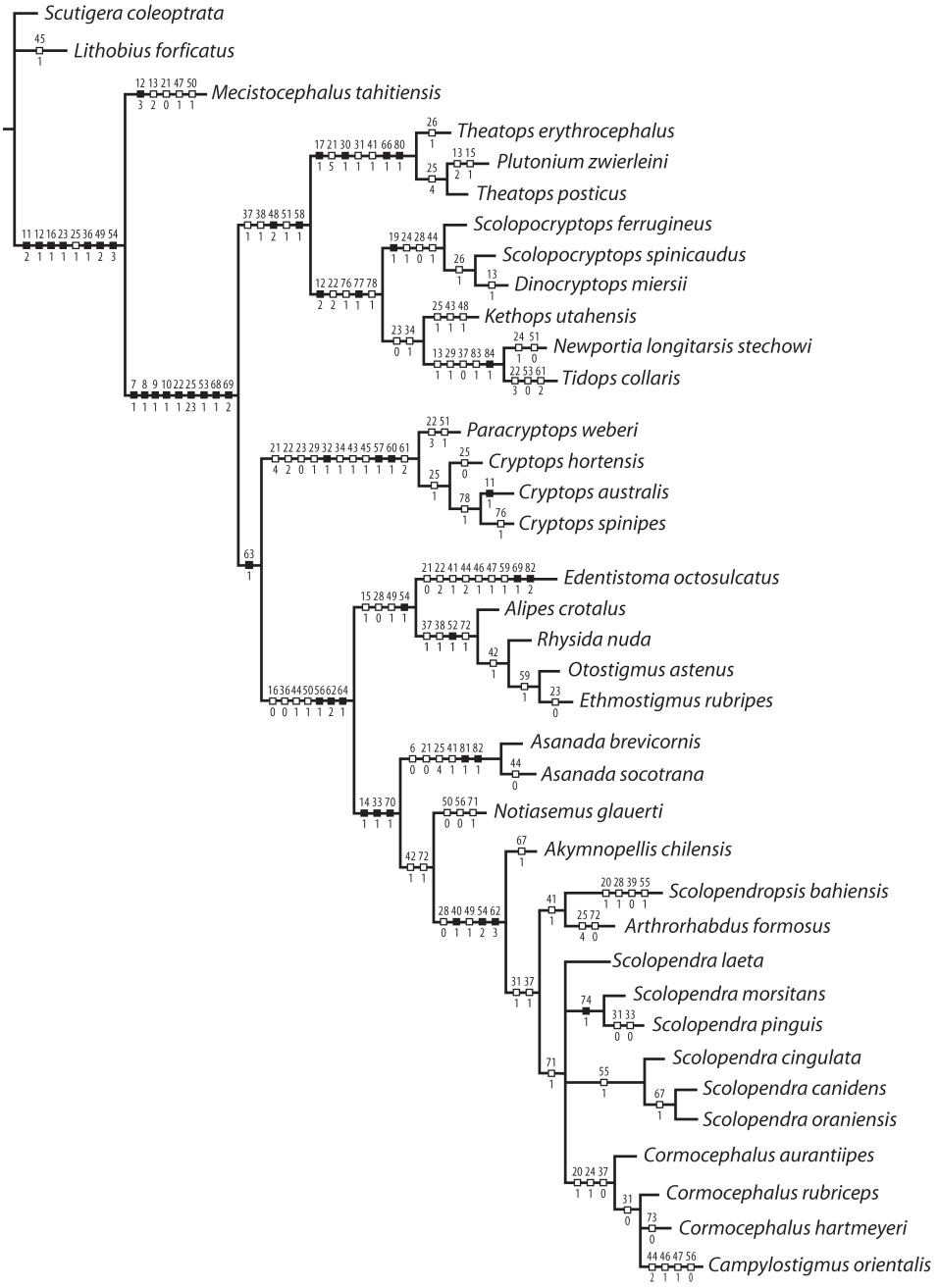

Fig. 7 Characters in Tab. 1 optimised on the single optimal cladogram with implied weights ($k = 4$). Only unambiguous changes are depicted; non-homoplastic changes are black, homoplastic changes white. Branches lacking strict support were collapsed.

To explore clade sensitivity, the characters were reweighted with implied weights using alternative concavity functions. Analysis with a concavity constant (*k*) of 4 selects a single tree as optimal, shown in Fig. 6B. We depict this tree because it is a more explicit hypothesis than those found under higher weights (see below). Its topology is among the cladograms found under equal weights except for one node that alters the position of Cryptopinae relative to other scolopendromorphs, as discussed below. Lower weighting strengths ($k = 5$ and more) also retrieve a single optimal cladogram, but these favour Cryptopinae as sister to a unit of Scolopocryptopidae and Scolopendridae, resolve *Edentistoma* as sister to remaining Scolopendridae, and place *Notiasemus* as sister to *Asanada*.

Relationships in Figure 6B are stable for implied weights with $k = 2$ and $k = 3$ apart from within Scolopendrini. Both $k = 2$ and $k = 3$ yield 10 trees, the strict consensus of which is largely unresolved for relationships between species of *Scolopendra*. The sister group relationship between *Arthrorhabdus* and *Scolopendropsis* depicted in Fig. 6 is not retrieved under implied weights with $k = 2$ or 3, which include trees in which *Scolopendropsis* is instead sister to *Cormocephalus* + *Campylostigmus*. The cladogram retrieved for $k = 4$ unites *Scolopendra* with *Cormocephalus* + *Campylostigmus* based on the spines on the plicae of the gizzard being grouped on plates (character 71), this group being found among the set of equally weighted cladograms as well.

Scolopocryptopidae

Under equal weights, blind Scolopendromorpha are variably monophyletic or paraphyletic. In the resolutions with monophyly of blind taxa, a relationship reinforced by the gizzard uniquely being organised as a sieve with stiff, anterior directed projections (character 75: Fig. 2A), Cryptopinae is sister to Scolopocryptopidae sensu Edgecombe & Koch (2008). Within the latter, the 21-segmented Plutoniuminae (= *Theatops* + *Plutonium*) is nested within a 23-segmented grade of Kethopinae, Newportiinae and Scolopocryptopinae. In equal weighted trees depicting paraphyly of blind taxa, Cryptopinae is sister to all remaining scolopendromorphs, i.e., Scolopocryptopidae is sister to Scolopendridae. In those latter trees, Plutoniuminae is invariably sister group to a clade of 23-segmented Scolopocryptopinae (Kethopinae + Newportiinae). Monophyly of the 23-segmented scolopocryptopids (as in Figs. 6B, 7) is strongly reinforced by gizzard characters. Apomorphies shared by Scolopocryptopinae, Kethopinae and Newportiinae include 'pineapple-shaped' anterior gizzard projections (character 76: Fig. 2A–C for *Tidops collaris*), projections of the main zone in the gizzard sieve being kinked near their midlength and more strongly directed forwards in their distal part (character 77: Fig. 2A, C), and longitudinally patterned bands of trichomes on the basal half of the kinked sieve projections (character 78: Fig. 2D). The novel hypothesis that Plutoniuminae is related to Scolopocryptopidae (rather than to Cryptopinae, cf. Shelley 2002) receives much of its support from characters of the preoral chamber, such as sclerotisation of the labral part of the epipharynx being discontinuous from the median tooth to the border with the clypeal part (character 48; see Edgecombe & Koch 2008: Fig. 1), node- or spine-like scales across the proximal labral part of the epipharynx (character 51: Fig. 1B, D for *Kethops utahensis* and *Tidops collaris*), and paired lateral clusters of sensilla on the clypeal part of epipharynx that are positioned medially so that the two clusters are in close proximity medially (character 58; see Edgecombe & Koch 2008: Fig. 14).

The relationships among blind lineages described above are in part sensitive to weighting regime because most analyses with implied weights favour an alternative pattern of paraphyly in which Cryptopinae is sister to Scolopendridae (Figs. 6B, 7). Nodal sensitivity like this is an indicator that the competing alternatives for the relative placement of Cryptopinae lack strong support, further demonstrated by low jackknife and Bremer support values for the conflicting nodes in each topology.

Scolopendridae

Scolopendrid monophyly is strongly supported, with new characters contributed by the epi- and hypopharynx such as figure-eight shaped pairs of smooth depressions surrounding the sensilla on the clypeal part of the epipharynx (character 56: Fig. 1E), and bristles on the lateral flaps of the hypopharynx being confluent across the midline (character 62: Fig. 3B). The basal branching in that family has two equal cost resolutions under equal weights, but one of these is favoured by implied weights under higher weighting strengths (Figs 6B, 7). The latter involves a sister group relationship between *Edentistoma* (tribe Arrhabdotini) and Otostigmini, as in their traditional classification together as Otostigminae (Kraepelin 1903; Attems 1930). The alliance of *Edentistoma* and Otostigmini is supported by traditional characters such as the humped floor of the spiracular atrium (character 14), and is amplified by new characters like a differentiation of the labral bristles into inner and outer bands (character 49), and discrete ovate or lenticular fields of sensilla positioned laterally on the clypeal part of the epipharynx (character 54) (see Edgecombe & Koch 2008: Figs 8, 10, 16). The alternative basal split in the Scolopendridae under equal weights is a set of trees in which *Edentistoma* is sister to all other Scolopendridae. That relationship can be defended by scolopendrids to the exclusion of *Edentistoma* (and *Asanada*) having the plicae of the gizzard being covered by scales that each bear a single spine (character 72: Fig. 4A, B for *Notiasemus glauerti*). Both possible placements of *Edentistoma* recognise Otostigmini as a monophyletic group that receives new support from a strong arching of the border between labral and clypeal parts of the epipharynx (character 52) (see Edgecombe & Koch 2008: Fig. 16A, C).

All trees under equal weights trees unite *Asanada* and *Notiasemus* with Scolopendrini, with those two genera either as each others' sister (and collectively sister group to Scolopendrini), or as favoured by implied weights under higher weighting strengths, *Asanada* being sister to *Notiasemus* + Scolopendrini. These relationships agree with the longstanding classification of Asanadini and Scolopendrini together as the subfamily Scolopendrinae (Kraepelin 1903; Attems 1930), a hypothesis most obviously supported by spiracles having a three-valved flap (character 14) but also by complete sternal paramedian sutures along the trunk (character 33) as well as posteriorly directed spines on the plicae of the gizzard (character 70: Fig. 5 for *Asanada brevicornis*). A character that previously placed Asanadini at the base of the Scolopendridae was a mandibular bristle band that does not extend onto the lamina dentifera in *Asanada socotrana* (character 44), an apparently plesiomorphic character shared by Cryptopinae, Plutoniuminae, and outgroups such as Lithobiomorpha (see Edgecombe & Koch 2008: Figs 11, 12). However, *A. brevicornis* was found to have a Z-shaped offset in the bristle band, with fan bristles expanded onto the lamina dentifera as in other Scolopendridae, and thus weakening the support for a basal placement of Asanadini.

4. Discussion

The status of blind Scolopendromorpha as a grade or clade remains an open question, with the present analyses demonstrating that the alternatives are either equally parsimonious or are sensitive to character weighting or receive low support values. Characters of the gizzard sieve (Fig. 2) in particular provide new support for Cryptopidae and Scolopocryptopidae being each others' closest relatives (Koch et al. 2009), but conflicting signal is provided by other character systems, such as asymmetry of the oviducts (character 63) that appears to unite Cryptopinae with Scolopendridae (Prunescu 1997). An expanded sampling of multi-locus molecular sequence data would be a valuable contribution to evaluating the cryptopid-scolopocryptopid-scolopendrid problem.

Regarding the two genera added to the present analysis for the first time, the affinities of *Tidops* are unambiguous. An alliance between *Tidops* and *Newportia* was recognised as early as the former's original description (Chamberlin 1915), placing special emphasis on the tarsus of the ultimate leg in both genera being antenniform, subdivided into many tarsomeres (character 83). This relationship has been endorsed in subsequent taxonomic (Attems 1930, Schileyko & Minelli 1998) and phylogenetic (Schileyko & Pavlinov 1997) treatments of Newportiinae. *Tidops* and *Newportia* code identically for their gizzard characters, but receive three coding differences for their peristomatic structures, each of these mapping on the cladogram with homoplasy. *Tidops* apparently lacks a row of bullet-shaped sensilla at the border between the labral and clypeal parts of the epipharynx (character 53: Fig. 1D) that is otherwise observed in all Scolopendromorpha apart from *Kethops*, where it may also be absent. Spine-like scales (character 51) are present on the proximal labral part of the epipharynx in *Tidops* but not in *Newportia*. *Tidops* is devoid of sensilla on its hypopharyngeal 'Schlundplatte' (character 61: Fig. 1C), whereas *Newportia* has a pair of sensillar clusters as in other Scolopocryptopidae. Despite these differences, the sister group relationship between *Newportia* and *Tidops* is stable under both equal and implied weights, receives a high jackknife frequency (92 and 91 %, respectively), and has a Bremer support of 4 under equal weights.

Originally classified in Scolopendrinae (Koch 1985), a plethora of phenetic and phylogenetic analyses by Koch & Colless (1986) resolved *Notiasemus* in a 'strong phenetic group' (Koch & Colless 1986: 104) with species of *Asanada* and *Cormocephalus*, and often with species of *Arthrorhabdus*, typically near the base of Scolopendridae. All analyses by Schileyko & Pavlinov (1997: Figs 1–4) alternatively resolved *Notiasemus* in a clade with *Cormocephalus* and *Campylostigmus*. The present study finds two parsimonious placements for *Notiasemus*, being either sister to *Asanada* in a group that is itself sister to Scolopendrini or alone as sister to Scolopendrini with *Asanada* basal to that whole group (Fig. 6B). *Notiasemus* and Scolopendrini share spine rows on the ultimate leg prefemur that are lacking in *Asanada* and basal Otostigmini (character 42) and have the gizzard plicae covered by scales bearing single spines (character 72: Fig. 4B for *Notiasemus*). When *Notiasemus* and *Asanada* alternatively group as sisters, that relationship finds support from long, simple bristles across the width of the labral bristle band (character 49, shared with Cryptopinae and Scolopocryptopidae: Fig. 3A, C), a lenticular field of sensilla on the clypeal part of the

epipharynx that is situated immediately proximal to the spine field (character 54, shared with Cryptopinae: Figs 1E, 3D), and a lack of posterior lobes in front of the cardiac valve on the gizzard (character 73: Fig. 4A, C). With the previous taxonomic sampling, characters 49 and 54 contributed to resolving *Asanada* basally in the Scolopendridae (interpreting the shared states with Cryptopinae as plesiomorphic). With the expanded sample, under equal weights the lenticular shape of the medial clypeal sensillar field is convergent in Cryptopinae and Scolopendrinae.

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Appendix 1 Characters used in phylogenetic analysis. Characters 1–65 described by Edgecombe & Koch (2008: Appendix 2 therein); characters 66–80 described by Koch et al. (2009).

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 antennal articles: (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: (0) mostly normal trichoid sensilla; (1) mostly collared sensilla.

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 chitinised tooth margins; (2) strongly chitinised 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 incompletely defined; (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, pincer-shaped 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. Accessory denticles on mandibular teeth: (0) absent or at most weakly developed on part of dorsalmost tooth; (1) strong, triangular denticles.

46. 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.

47. 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.

48. 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.

49. 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.

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

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

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

53. 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.

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

55. 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.

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

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

58. 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.

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

60. 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.

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

62. 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.

63. Asymmetry of oviducts: (0) left and right oviducts symmetrical; (1) left oviduct rudimentary or absent.

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

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

66. 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.

67. 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.

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

69. 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.

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

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

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

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

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

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

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

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

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

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

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

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

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

83. Tarsomeres in tarsus 2 of ultimate leg: (0) undivided tarsus 2; (1) tarsus 2 with numerous tarsomeres, lacking pretarsal claw.

84. Ventral spinous process(es) on ultimate leg femur: (0) absent; (1) present. – As recognised by Shelley & Mercurio (2005, Fig. 4, their character 3), Newportiinae (here *Newportia* and *Tidops*) and Ectonocryptopinae share an extension of a row of ventral spines ('spinous processes' fide them) on the prefemur onto the femur.