Phylogeny of scolopendromorph centipedes (Chilopoda): morphological analysis featuring characters from the peristomatic area

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Abstract

Alternative schemes for the higher-level systematics of the centipede order Scolopendromorpha have been established from characters of trunk segmentation, including the segmental position of spiracles, and the presence or absence of eyes. A comparative survey of the preoral chamber by light and scanning electron microscopy contributes 16 new characters of the epipharynx and hypopharynx, sampled from 26 species that represent 20 genera. These new data together with 49 additional morphological characters permit cladistic analysis of the major scolopendromorph groups. The shortest cladograms resolve blind Scolopendromorpha as a basal grade within which a clade now classified as Plutoniuminae + Scolopocryptopidae (supported by unreversed characters from the preoral chamber) is sister to the remaining scolopendromorphs. A unique row of bullet-shaped sensilla between the labral and clypeal parts of the epipharynx provides a new autapomorphy of the Scolopendromorpha. Either 21 or 23 trunk segments optimize at the base of the Scolopendromorpha but in either case homoplasy is forced on the cladogram. New characters from the epipharynx give additional support for the monophyly of several traditional groupings, including Cryptopinae, Scolopendridae, Otostigmini, and Scolopendrini, and a basal resolution of Asanadini within Scolopendridae. Of the two competing hypotheses for the position of the enigmatic Mediterranean Plutonium zwierleini—being either sister to the cryptopid Theatops or sister to all other Scolopendromorpha—the former hypothesis is strongly supported; spiracles on all trunk segments in Plutonium are homoplastic with the state in Geophilomorpha. Observations on feeding behaviour are needed to illuminate convergence in characters of the epipharynx and mandible in Edentistoma (Otostigminae) and Campylostigmus (Scolopendrini).

Scolopendromorpha includes the largest and most fiercely predatory centipedes. Global diversity stands at some 700 species, distributed through the tropical, subtropical and temperate parts of all continents. Adult body length ranges from 1 to 30 cm; at the upper end of the range of body size, these centipedes are capable of taking live vertebrate prey, perhaps most spectacular being predation on bats in flight (Molinari et al., 2005). Because of the toxicity of their venom, scolopendromorphs are the most important centipedes in medical and toxicological research (Bush et al., 2001) and are the focus of most studies on bites to humans (Lewis, 1981a).

The systematics of Scolopendromorpha is a source of considerable disagreement (Verhoeff, 1906, 1941; Attems, 1930; Schileyko, 1992, 1996, 2002, 2006; Prunescu, 1997; Schileyko and Pavlinov, 1997; Shelley, 2002). Controversies surround the phylogenetic and taxonomic significance of variability in characters such as numbers of trunk segments, absence of eyes in hypogean lineages, the segmental distribution of respiratory organs along the trunk, and the structure of the spiracles. Alternative classifications have been based on different hypotheses about the systematic importance of these character systems, but most debate has been framed
non-phylogenetically. The only formal cladistic analysis of Scolopendromorpha with broad taxonomic sampling (Schileyko and Pavlinov, 1997) was limited to a small (17 characters) dataset from external morphology and used an idiosyncratic rooting strategy. A hypothetical ancestor was constructed based on theories about commonality, degree of ecological specialization, and assumptions of an annelid-like ancestor, rather than rooting on explicit outgroups such as the Geophilomorpha, a taxon that is almost invariably identified as the sister group of Scolopendromorpha according to the Epimorpha hypothesis (e.g., Dohle, 1985; Borucki, 1996; Prunescu, 1996; Hilken, 1997; Edgecombe et al., 1999; Wirkner and Pass, 2002). Reanalysis of the Schileyko and Pavlinov (1997) matrix with several codings for the plesiomorphic state inverted resulted in a largely unresolved consensus tree (Minelli et al., 2000; fig. 5).

Scolopendromorph phylogenetics requires not only refined analytical methods, but also an injection of character data. Towards this latter objective, the detailed morphology of the preoral chamber is a promising target. Recent comparative studies of the roof and floor of the preoral chamber—the epipharynx and hypopharynx, respectively—for scutigeromorph (Koch and Edgecombe, 2006) and lithobiomorph centipedes (Koch and Edgecombe, 2008) have been a source of new characters for phylogenetics of those groups. Available descriptions from a few species of Scolopendra (Meinert, 1883; Verhoeff, 1918 in Verhoeff, 1902–25; Shukla, 1963; Jangi, 1966) indicate considerable complexity in the peristomial structures of Scolopendromorpha (especially detailed by Verhoeff for Scolopendra cingulata) but documentation has until now been confined to this single genus. This very restricted taxonomic sampling limits the utility of these data for phylogenetic purposes.

Morphology of the preoral chamber, in combination with characters derived from other morphological character systems, is applied herein to ongoing questions in the systematics of the Scolopendromorpha. Most fundamental is the status of one of the two main subtaxa of the Scolopendromorpha in the classical system of Attems (1930), the Cryptopidae. Attems’ classification of Scolopendromorpha is fundamentally based on the presence (Scolopendridae) or absence (Cryptopidae) of ocelli, a character depicted by Kraepelin (1903, p. 27) as a single loss in the cryptopids. The monophyly of the Cryptopidae s.l. (now generally classified as Cryptopidae and Scolopocryptopidae, e.g. Shelley, 2002) has been disputed in a series of studies that have argued that blindness has multiple origins in the Scolopendromorpha (Schileyko, 1996; Schileyko and Pavlinov, 1997), i.e. rendering cryptopids in the traditional sense polyphyletic. Other analyses of morphological characters, with more restricted taxonomic sampling, have instead resolved the blind scolopendromorphs as a paraphyletic group (Edgecombe et al., 1999; Edgecombe and Giribet, 2004). In contrast, combined analyses of morphological and molecular sequence data have generally corroborated the traditional classification by retrieving both Cryptopidae s.l. and Scolopendridae as clades (Edgecombe and Giribet, 2004), a result that is also found in analyses of nuclear coding genes (Regier et al., 2005). The number of times that eyes have been lost in the Scolopendromorpha and whether “cryptopids” are monophyletic, paraphyletic, or polyphyletic thus remain open questions.

The Mediterranean cryptopid Plutonium zwierleini Cavanna, 1881, is the focus of a debate that extends to the deepest level of scolopendromorph phylogeny. The traditional hypothesis that the monotypic genus Plutonium is most closely related to the cryptopid Theatops (Kraepelin, 1903; Verhoeff, 1906; Attems, 1930) has been endorsed and amplified in some modern studies (Würmli, 1975; Shelley, 1997), but an alternative hypothesis identifies Plutonium as basal within the Scolopendromorpha (Schileyko, 1996) and uses it to construct a hypothetical ancestor for rooting the cladogram for internal phylogeny (Schileyko and Pavlinov, 1997). The basal resolution of Plutonium emphasizes a distribution of the spiracles (on all pedigerous segments of the trunk except the last) that is uniquely shared with the order Geophilomorpha. We present arguments from the morphology of the preoral chamber that amplify closest relationships between Plutonium and Theatops.

The present survey samples 20 of 34 currently recognized genera of Scolopendromorpha (Minelli, 2006), includes the morphological data employed in previous systematic and phylogenetic work on the order, and contributes a substantial injection of morphological character evidence for relationships within Scolopendromorpha by documenting new characters from the preoral chamber. The signal from 19 new characters of the mandibles, epipharynx, and hypopharynx contributes to new higher-level hypotheses, notably for the interrelationships of “cryptopids”, and permits a choice between competing schemes based on explicit parsimony arguments.

Materials and methods

Preparations

Light and scanning electron microscopic investigations of the epipharynx and hypopharynx were performed on 26 scolopendromorph species listed in Table 1. Sampling was designed to cover as many genera as possible given the availability of material for preparation.

After removing the appendages, heads were sliced immediately in front of the mouth with a 2.6-mm Ziegler Iris Knife. Light microscopic studies of the two parts were performed with a Leica MZ16 stereomicroscope
equipped with a Spot Flex digital camera (software version 4.6; Diagnostic Instruments, Sterling Heights, MI). Digital images were taken to document the sclerotized and/or pigmented parts (Fig. 1). For both the epipharynx and the hypopharynx, series of digital light micrographs were merged to a single image with the Synoptics software Auto-Montage Pro (Synoptics, Cambridge, UK). For scanning electron microscopy (SEM) the two halves of the head were cleaned in an ultrasonic bath. After cleaning, the materials were dehydrated in a graded ethanol series and then critical-point dried using a Bal-Tec CPD 030. The dried materials were then mounted on stainless steel stubs with double sticky tabs, and coated with gold in an Emitech K550 ion coater. Most species were studied with a Zeiss Leo 435VP electron microscope (Carl Zeiss, North Ryde, Australia) using a Robinson backscatter detector; a few species were examined with a Hitachi S2500 scanning electron microscope (Hitachi, Wokingham, UK). For examining the poison duct, maxillipedes were cleared in Hoyer/C213 mixture (Kraus, 1984) overnight and examined by Nomarski interference contrast with an Olympus BX 50 light microscope (Olympus, Hamburg, Germany) equipped with a Colorview II digital camera. All images and plates were edited with the Adobe Photoshop CS and Adobe Illustrator CS software (Adobe Systems, München, Germany).

**Histology**

In order to clarify the extent of sclerotization and the shape of sclerites, as well as determining whether

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**Table 1**

Scolopendromorph species examined for morphology of the peristomatic structures and coded for cladistic analysis. Vouchers are held at the Australian Museum, Sydney (prefix AM KS), Museum of Comparative Zoology, Harvard University (MCZ DNA), Natural History Museum, London (BM, BMNH (E)), National Museum of Natural History, Smithsonian Institution (USNM), and Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB).

<table>
<thead>
<tr>
<th>Cryptopidae</th>
<th>Cryptopinae</th>
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<tr>
<td>Cryptops (Cryptops) australis (Newport, 1845): AM KS (Australia: New South Wales: Budawang National Park)</td>
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<tr>
<td>Cryptops (Trigonocephrops) spinipes Pocock, 1891: AM KS (Australia: Lord Howe Island)</td>
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<tr>
<td>Paracryptops weberi Pocock, 1891: MCZ DNA 102459 (Indonesia: Sulawesi: Bantimurung-Bulusaraung National Park)</td>
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<th>Scolopocryptopidae</th>
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<tr>
<td>Scolopocryptops ferrugineus (Linnaeus, 1767): MCZ DNA 102461 (Equatorial Guinea); M. Koch collection (Peru)</td>
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<tr>
<td>Scolopocryptops spinicaudus Wood, 1862: M. Koch collection (USA: California: Angelo Coast Nature Reserve)</td>
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<tr>
<td>Dinocryptops miersii (Newport, 1845): BM1889.4.13.3-5 (Brazil: Santa Lucia: Fort de Jacques)</td>
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<th>Kethopinae</th>
<th>Portugilusinae</th>
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<tr>
<td>Kethops utahensis (Chamberlin, 1909): USNM (USA: Utah: Mill Creek)</td>
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<th>Newportiinae</th>
<th>Ploutonioinae</th>
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<tr>
<td>Newportia longitarsis stehowi Verhoeff, 1938: MCZ DNA 102460 (Colombia: Reserva de Común, Chachagüí)</td>
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<tr>
<th>Plutoniuminae</th>
<th>Plutonium zwierleinai</th>
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<tr>
<td>Plutonium zwierleinai Cavanna, 1881: ZMB 1135 (Italy: Sardinia: Sassari)</td>
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| Theatops erythrocephalus (C.L. Koch, 1847): ZMB 3393 (Croatia: Dalmatia) |
| Theatops posticus (Say, 1821): BMNH(E) (USA: Texas: Houston) |

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<tr>
<th>Scolopendridae</th>
<th>Scolopendrinia</th>
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<tr>
<td>Scolopendra canidens Newport, 1844: MCZ DNA 102462 (Uzbekistan: Surkhandarya area: Uzun district: E. slopes Babatag Mountain Range)</td>
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<tr>
<td>Scolopendra cingulata Latreille, 1829: M. Koch collection (Greece)</td>
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<tr>
<td>Arthroperlas formosus Pocock, 1891: ZMB 4942 (Namibia)</td>
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<tr>
<td>Campylostigus orientalis Ribaut, 1923: BMNH(E) (New Caledonia: Province Nord: Mt Panie refuge)</td>
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<tr>
<td>Cormeophalus aurantipennis (Newport, 1843): BM1893.7.4.9-10 (Australia: Western Australia: Perth)</td>
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<tr>
<td>Cormeophalus hartmeyeri Koch, 1893: AM KS 15334 (Australia: Western Australia: Nannup-Pemberton area)</td>
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<tr>
<td>Cormeophalus rubiceps (Newport, 1843): BMNH(E) (New Zealand: North Island: Tiritangi)</td>
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<tr>
<td>Hemiscelopendra chilensis (Gervais, 1847): BM1904.10.29.1-3 (Chile)</td>
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<tr>
<th>Arrhabdotini</th>
<th>Edentistoma octosulcatus Tömösáviray, 1882: ZMB 3618 (Borneo)</th>
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<tr>
<td>Otostigmini</td>
<td>Otostigmus astenus (Kohlrausch, 1881): MCZ DNA 102463 (Fiji: Mt Victoria)</td>
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<td>Ethmostigmus rubipes (Brandt, 1840): AM KS 89384 (Australia: New South Wales: Boonoo State Forest), AM KS 89472 (Australia: New South Wales: Red Cedar Flora Reserve)</td>
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<tr>
<td>Rhysida nuda (Newport, 1845): AM KS 14736 (Australia: New South Wales: Gladensville)</td>
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<tr>
<td>Alipes crotalus (Gerstaecker, 1845): MCZ DNA100454 (Swaziland: Siphiso Valley, Mlawula Nature Reserve)</td>
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epi- and hypopharyngeal clusters are glandular (Verhoeff, 1918, in Verhoeff, 1902–25) or sensory (Meinert, 1883), histological studies were performed for the scolopendrid *Scolopendra oraniensis* Lucas, 1846 collected in Sardinia (Italy). The structures (sensilla or glandular openings) are sufficiently similar in external morphology across the Scolopendromorpha for a single species to inform on general interpretations, and the choice of an exemplar taxon was made considering the quality of fixation. Heads were fixed in Bouin’s solution (modified according to Dubosq-Brazil) at room temperature for 24 h. They were then dehydrated in a graded ethanol series, transferred into 100% acetone and embedded via propylene oxide into Araldite. Series of semithin sections (1 µm) were made with a Jumbo-Diatome diamond knife on an Ultracut E microtome (Fa. Reichert) and transferred onto slides. The sections were then stained with 1% Toluidine, embedded into DepeX and examined with an Olympus BX 50 light microscope equipped with a Colorview II digital camera.

**Morphological data**

Morphological characters used in phylogenetic inference (matrix in Appendix 1) are listed and described in Appendix 2. The 17-character dataset of Schileyko and Pavlinov (1997) for relationships between scolopendromorph genera was modified as discussed under individual characters in Appendix 2 and scored for the species examined herein for the peristomatic structures,
14 characters being extracted or derived from their matrix. Additional ingroup characters were sourced from other literature and original observations, all external morphological characters being scored from direct observation of voucher specimens. Characters bearing on outgroup relationships and ingroup monophyly are represented by characters 1–11, all of which have been extensively discussed in the literature (e.g. Dohle, 1985; Borucki, 1996; Edgecombe et al., 1999; Edgecombe and Giribet, 2004). New characters from the peristomatic structures (Fig. 2) are represented by characters 47–62. These are more extensively discussed and illustrated in Appendix 2.

Characters from the genital system (Demange and Richard, 1969; Prunescu, 1997) and spermatophore structure (Demange and Richard, 1969) have been used in scolopendromorph systematics but have been thus far surveyed in few species. A lack of accessory ventral glands of the ovary, a reduction of the left ejaculatory duct, and a bean-shaped spermatophore with a multilayered wall are shared by all scolopendromorphs documented to date (Demange and Richard, 1969; Prunescu, 1997), including members of both Cryptopidae and Scolopendridae, and probably serve as autapomorphies of Scolopendromorpha. Despite considerable missing data, some characters of the genital system and spermatophores that vary within Scolopendromorpha are included, although using congeneric proxies in several cases. These proxies are cited explicitly in discussion of characters 63–65 in Appendix 2.

Analysis

The most parsimonious cladograms for the 65-character dataset were computed with TNT (Goloboff et al., 2003) using implicit enumeration. Character optimization was explored with TNT and WINCLADA (Nixon, 2002). Multistate characters 3 and 44 were ordered, the remainder unordered. Jackknife resampling (Farris, 1997) and Bremer support (Bremer, 1994) were used as a measure of nodal support. Jackknifing with TNT used 1000 replicates with 36% deletion, each replicate using implicit enumeration. Bremer support was calculated from collections of suboptimal trees obtained by heuristic searches.

Cladograms were rooted between Scolopendromorpha and outgroup exemplars that sample the Scutigeromorpha (Scutigera coleoptrata), Lithobiomorpha (Lithobius forficatus), and Geophilomorpha (Mecistocephalus tahitiensis). These species were selected because they have been surveyed for their peristomatic structures (Koch and Edgecombe, 2006, 2008), and the first two are the most comprehensively documented members of their orders from a morphological as well as a molecular perspective. A meciistocephalid is an appropriate geophilomorph exemplar because this group is strongly supported as sister to all other Geophilomorpha (Edgecombe et al., 1999; Foddai and Minelli, 2000; Bonato and Minelli, 2002; Edgecombe and Giribet, 2004) and retains some plesiomorphic states of the peristomatic area relative to other Geophilomorpha (e.g. a single labral tooth versus a row of denticles in most remaining Geophilomorpha). Several characters for the peristomatic structures are coded as uncertainties in Mecistocephalus because the border between the labral and clypeal parts of the epipharynx, a fundamental landmark that can be recognized in other chilopods, is not clearly delimited in geophilomorphs.

Results

Peristomatic structures of Scolopendromorpha

The main structures of the epipharynx and hypopharynx are depicted in Figs 1 and 2, emphasizing the relationships between sclerotized and unsclerotized parts as well as the position of sensilla clusters, which are generally pigmented in scolopendromorphs. Labelling follows terminology applied to Lithobiomorpha (Koch
and Edgecombe, 2008); all major components of the peristomatic structures are readily homologized between the two groups. An overview of the peristomatic structures by SEM and histological sectioning is shown in Figs 3–5, respectively. A brief summary of morphology is provided in the following section, and ingroup variation in morphology is catalogued in a block of characters in Appendix 2. The epipharynx proved to be more variable than the hypopharynx within Scolopendromorpha, this variation serving as a source for 14 characters (characters 47–60 in Appendix 2). The hypopharynx is conservative to a degree that only two characters (characters 61 and 62) were identified as phylogenetically informative for ingroup relationships.

The epipharynx consists of distinct, non-overlapping labral and clypeal parts (Fig. 1d). As in Lithobiomorpha, the border between these parts is mostly indicated by a median transverse bulge situated in front of a spine field on the distalmost area of the clypeal part (Figs 3b,c and 5a,d,g). The shape of this bulge in Cryptops closely resembles the lithobiomorph state, but in other scolopendromorphs it shows continuous variation, including complete or partial reduction of either its lateral or its medial parts. Generally the bulge forms the proximal margin of a medial, more or less darkly pigmented sclerotization called a tooth plate on the labral part of the epipharynx. When interconnected, the shape and length of the tooth plate determine the shape of the bulge as well (see Fig. 1d–g; Appendix 2, character 48). The transition zone between tooth plate and transverse bulge is generally smooth, but may be characterized by a rugose or scaly surface, particularly in those taxa that lack an obvious, pigmented sclerotized interconnection (see Appendix 2, character 51).

Adjacent to the tooth plate, the labral part of the epipharynx is broadly strengthened by the paired distal bar of the submarginal armature. The distal bar corresponds to the state in lithobiomorphs in forming a subtriangular, faintly pigmented plate that is variably covered by bristle bands (Fig. 3a; see also Appendix 2,

![Fig. 3. Epipharynx of Scolopendromorpha. SEM images. (a,c) Scolopendra canidens: (a) labral part of epipharynx; scale bar = 50 μm; (c) clypeal part of epipharynx; scale bar = 50 μm. (b,d) Cormocephalus hartmeyeri: (b) lateral part of border between labral and clypeal parts of epipharynx; scale bar = 10 μm; (d) median sensilla cluster on clypeal part of epipharynx; scale bar = 30 μm. (e) Cryptops spinipes: lateral cluster of sensilla on clypeal part of epipharynx; scale bar = 15 μm. (f) Scolopendra cingulata: sensilla in median cluster on clypeal part of epipharynx; scale bar = 5 μm. Abbreviations: bu, bulge; db, distal bar of submarginal armature; lsc, lateral sensilla cluster; msc, median sensilla cluster; msp, median spine field; rbs, transverse row of bullet-shaped sensilla; sca, scales; tp, tooth plate; tsp, field of triangular spines.](image-url)
characters 49 and 50) and shows no connection to the proximal bar of the submarginal armature. Mesially, the distal bar continues into the strongly sclerotized margin of the labral side-pieces. The proximal bars laterally border the clypeal part of the epipharynx, which otherwise shows no sclerotized areas. The shape of the proximal bars is conservative; these bars in scolopendromorphs differ from the lithobiomorph state mainly in being broader and in showing mesially a pronounced, darkly pigmented point of articulation with the mandibular condyle.

Apart from the median spine field, pigmented areas within the clypeal part of the epipharynx are restricted to fields of sensilla (Fig. 1d: rbs, lsc, msc). A transverse row of bullet-shaped sensilla is consistently arranged proximal to the median spine field at the border to the labral part (Fig. 3b: rbs). Additional sensilla are consistently distributed in a paired lateral cluster (Fig. 3e: lsc) next to a field of short triangular spines (tsp). Another more medially positioned sensilla cluster (msc) shows significant variation in its arrangement and fine structure (see Appendix 2, characters 54–57). In scolopendrids this cluster may be paired or unpaired (Fig 3c,d), but the special arrangement of each sensillum of this cluster in figure-of-eight-shaped depressions (Fig. 3f) readily permits their homologization. Lateral and medial sensilla clusters are consistently separated by longitudinal bands of spiny scales (Fig. 3e: sca) extending to variable degrees from the border of the labral part of the epipharynx towards the proximomedial area of the clypeal part (see Appendix 2, character 60). The pigmentation of the sensilla clusters is based on the exocuticular lining of the channels through which underlying epidermal cells protrude towards the cuticular surface (Fig. 5a, b–e, g). The histology of these cells, including comparisons with scutigeromorphs and lithobiomorphs (Koch and Edgecombe, 2006, 2008), permits considering their protrusions through the cuticle as dendrites. Verhoeff’s assumption (1918, in Verhoeff, 1902—25: 508) that the sensilla clusters represent fields of glandular openings (ldr, dr, and ebr in his figures 42, 44–46) is not supported by our histological studies. All cells penetrating the cuticle in each sensilla cluster have the same appearance in histological section and differ from epidermal glandular cells in forming an only slightly heightened epithelium with strongly enlarged nuclei instead of large numbers of vesicles (Fig. 5b,e). Definitive evidence for the sensorial nature of these cells, however, needs to be based on forthcoming ultrastructural studies. Comparison of the sensilla clusters of scolopendromorphs and externally similar epi- and hypopharyngeal “organs” in insects (Moulins, 1971; fig. 3) renders it probable that the sensilla in chilopods are likewise contact chemoreceptors.

The scolopendromorph hypopharynx is unique among centipedes in forming an elongate, ventrally convex swelling instead of a tongue, i.e. the hypopharynx lacks a marked backside (Fig. 1a–c,j). Nevertheless it comprises the same components as in lithobiomorphs: a proximal Schlundplatte (Fig. 1h: spl) forms a distinct flap in front of the mouth and distally continues into an elongate pair of membranous lips that are laterally...
Fig. 5. Histological sections of the head of *Scolopendra oraniensis*. (a) Paramedian sagittal section, showing the topography of epi- and hypopharynx; scale bar = 100 μm. (B–D) Series of horizontal sections at levels indicated in A by stippled arrows, showing (b) median sensilla cluster on epipharynx; scale bar = 20 μm; (c) lateral sensilla cluster on epipharynx; scale bar = 100 μm; and (d) bullet-shaped sensilla between transverse bulge on epipharynx; scale bar = 100 μm. (e) Higher magnification of lateral sensilla cluster as indicated in C; scale bar = 20 μm. (f) Hypopharyngeal sensilla on *Schlundplatte* in front of mouth; scale bar = 20 μm; arrows point to dendrites penetrating the cuticle. (g) Higher magnification of epipharynx at border between labral and clypeal parts as shown in D showing sensory cells and associated cuticular channels of bullet-shaped sensilla; scale bar = 50 μm. Abbreviations: br, brain; bu, transverse bulge; cly, clypeus; ep, epipharyngeal epidermis; hb, hypopharyngeal bar of tentorial complex; hy, hypopharynx; lbg, lateral buccal gland; lf, lateral fold of hypopharynx; lsc, lateral sensilla cluster of epipharynx; mbg, median buccal gland; mcl, mandibular comb lamellae; md, mandible; mdt, mandibular teeth; mo, mouth; msc, median sensilla cluster of epipharynx; msp, median spine field; mxI, first maxilla; pc, preoral cavity; rbs, row of bullet-shaped sensilla; se, sensory cell; spl, hypopharyngeal *Schlundplatte*; tp, labral tooth plate; vlb, ventro-lateral bar.
covered by longitudinal rows of simple or branching bristles (Fig. 4a). Schlundplatte and lip-bearing parts are variably separated by a tuft of plumose bristles (Fig. 1c,j; tu; see Appendix 2, character 62). The tuft bristles originate from the mesial margin of lateral flaps that flank the hypopharynx and bear the darkly pigmented hypopharyngeal bars of the tentorial complex (Fig. 1c,h,j; hb). Another pair of faintly pigmented sclerotized bars (Fig. 1b,h; vlb) extends in between the lateral flaps and the longitudinal bristle rows from shortly beneath the Schlundplatte ventrolaterally towards the posterior apex of the hypopharynx. Button-shaped sensilla (Fig. 1c,j; bsc; Fig. 4c) are consistently distributed over the whole length of the membranous lips. A second cluster of nipple-shaped sensilla may be positioned on the Schlundplatte (Fig. 1h: nsc, 1I, 4b, 5f); presence and arrangement of these sensilla show significant variation (see Appendix 2, character 61).

Cladistic analysis

TNT analysis with the procedures described above yielded 16 shortest cladograms of 155 steps [consistency
index (CI) 0.57; retention index (RI) 0.82; rescaled consistency index (RCI) 0.47], the strict consensus of which is depicted in Fig. 6. The results described below characterize the major nodes of the shortest cladograms, all of which were examined under unambiguous, fast and slow optimizations with WINCLADA. Unless indicated otherwise, apomorphies described in the following section are unambiguous on all 16 shortest cladograms. Figure 7 depicts unambiguous changes on the single shortest cladogram favoured by implied
character weights (Goloboff, 1993), as implemented in TNT (default concavity function, $K = 3$; branches that are not strictly supported were collapsed after character optimization).

The monophyly of Scolopendromorpha receives support from a new character of the peristomial structures, a single row of bullet-shaped sensilla at the proximal margin of the spine field between the labral and clypeal parts of the epipharynx (character 53). Scolopendromorph monophyly is otherwise defended by traditional characters: the mandibular laminae intersecting at a cruciform suture (character 7), the dorsal brush on the second maxillary tarsus (character 8), composite tergite of the maxillipede and first pedigerous segments (character 9), and a lack of female gonopods (character 10). As noted above, several additional characters of the genital system and spermatophores are apomorphic for Scolopendromorpha. This list of autapomorphies can probably be expanded as several further characters that currently have limited sampling are more fully surveyed, such as the presence of spiracular muscles, i.e. muscles that attach to the dorsal and ventral sides of each spiracular pouch (Hilken, 1998), and a gizzard with plicate walls being differentiated at the end of the foregut (Balbiani, 1890; Lewis, 1981a).

The fundamental split within Scolopendromorpha resolves the Cryptopidae s.l. (i.e. sensu Attems, 1930) as a paraphyletic group within which a clade composed of Kethopinae, Newportiinae, Plutoniuminae, and Scolopocryptopinae is sister to all other taxa. Cryptopinae unite with Scolopendridae based on a reduction of the left oviduct (character 63) and, under accelerated transformation, a lenticular field of sensilla on the clypeal part of the epipharynx that cryptopines share with Asanada, the basal scolopendrid (character 54, state 4). We caution that the former character has very limited sampling in the Plutoniuminae + Scolopocryptopinae clade, known only from Theatops, but in that instance symmetrical gonodonts are interpreted as pleisiomorphic. The node unifying Cryptopinae and Scolopendridae has a very low jackknife frequency, collapses with the addition of one step to the shortest cladograms, and must be regarded as weakly supported.

Kethopinae, Newportiinae, Plutoniuminae, and Scolopocryptopinae form a clade supported by new synapomorphies from the peristomial structures. An unambiguous apomorphy of this group is the presence of lateral clusters of sensilla in front of the mouth on the clypeal part of the epipharynx closely approximating each other near the midline (character 58). Paired groupings of sensilla on the hypopharyngeal Schlundplatte (character 61) are additionally autapomorphic for this clade under delayed transformation. These two apomorphies are unique and unreversed. Although this node receives weak jackknife support it withstands the addition of an extra step to the shortest cladograms; across all 16 shortest cladograms the group has three unambiguous apomorphies but these are supplemented with an additional four or six apomorphic characters under delayed and accelerated transformation, respectively. Among these, the absence of bristle tufts on the lateral flaps of the hypopharynx (character 62, state 0), shared by all examined members of the group, is apomorphic for Kethopinae, Newportiinae, Plutoniuminae, and Scolopocryptopinae under accelerated transformation. Of the two unambiguous autapomorphies for this group from systems other than the peristomial structures, titial spurs (character 38) are convergent with Otostigmini within the Scolopendridae, and a coxopleural process on the ultimate leg (character 39) is convergent with Scolopendridae exclusive of Asanada.

Two alternative resolutions describe the interrelationships of Kethopinae and Newportiinae relative to Scolopocryptopinae and Plutoniuminae, both supported by characters of the epipharynx. In the eight shortest cladograms that resolve Newportia rather than Kethops as closest relative of Scolopocryptopinae + Plutoniuminae, that relationship is supported by sclerotization on the labral part of the epipharynx being confined to the region immediately proximal to the median tooth, and discontinuous with the border with the clypeal part of the epipharynx (character 48, state 2). The alternative resolution with Kethops closer to Scolopocryptopinae + Plutoniuminae is supported by the presence of spinose scales across its proximal labral part (character 51).

The sister group relationship between Plutonium and Theatops, Plutoniuminae sensu Shelley (1997), is defended by characters cited by Shelley (1997), i.e. depigmented eye spots (character 17), an elongated ultimate tergite (character 30) that has a complete longitudinal median suture (character 31), and pincer-like ultimate legs (character 41), as well as tooth plates (character 22, state 1) that are convergent with similar serrate endites in Scolopendridae. Although the peristomial structures do not contribute additional corroborative information for this node, neither do they force any homoplasy, and codings for the peristomial characters are identical for Theatops and Plutonium. The three characters with which Theatops posticus unites with Plutonium zwierleini to the exclusion of Theatops erythrocephalus all exhibit homoplasy (poison calyx extending into maxillipede coxosternite; absence of a coxopleural process and spinous processes/spines on the ultimate leg).

Scolopocryptopidae (sensu Shelley, 2002) is resolved as paraphyletic because of the inclusion of Plutoniuminae...
within it. The node that unites Scolopocryptopinae with Plutoniumiinae to the exclusion of either Kethopsinae (Kethops) or Newportiinae (Newportia) has a low jackknife frequency but is supported by four unambiguous apomorphic characters for both alternative resolutions of Newportia and Kethops: glabrous basal antennal articles (character 18), a trochanteroprefemoral process on the maxillipede (character 23), a long poison calyx (character 25, state 3), and sparse setae on the locomotory legs (character 35) are all homoplastic with Scolopendridae. Twenty-three trunk leg pairs have a single origin in Kethopinae, Newportiinae, and Scolopocryptopinae but do not unambiguously serve as a sclerocryptopid autapomorphy, and reversal (to 21 pairs) is forced in Plutoniumiinae. Scolopocryptopinae has strong (91%) jackknife support, uniquely supported by collared antennal sensilla (character 19), together with a suppression of paratergites (character 27), margins on multiple tergites (character 28: homoplastic with Scolopendridae and Lithobiomorpha), and fan bristles expanded onto the mandibular lamina dentifera (character 44: convergent within Scolopendridae).

Monophyly of Cryptopinae, here sampled by Cryptops + Paracryptops, is supported by several traditional characters, such as a hook-like, flanged second maxillary claw (character 21), lateral crescentic sulci on the tergites (character 29; optimized as convergent with Newportia), a line of skeletal thickening crossing the sternites (character 32), and saw teeth on leg 21 (character 43; convergent in Kethopinae). The strong accessory denticles on the mandibular teeth (character 45) of Cryptopinae are optimized as homoplastic with those of Lithobiomorpha. New apomorphies for Cryptopinae from the peristomatic structures are lid-like covers along the distal edge of sensilla on the medial clypeal part of the epipharynx (character 57), lateral longitudinal bands of scales that are mediolaterally confluent on the clypeal part of the epipharynx (character 60), and an absence of sensilla on the Schlundplatte of the hypopharynx (character 61); all of these characters are unique and unreversed. Endosternites (character 34) are apomorphic for Cryptopinae (and convergent in Newportia and Kethops) under delayed transformation only, versus apomorphic for Scolopendromorpha under accelerated transformation.

Monophyly of Scolopendridae (jackknife frequency 78%, Bremer support 4) is unambiguously defined by eyes, arranged as a rhomboid cluster of four ocelli (character 16), bipartite tarsi (character 36), and four characters that are convergent within Scolopocryptopinae [‘‘glabrous’’ basal antennal articles (character 18), a trochanteroprefemoral process on the maxillipede (character 23), a long poison calyx (character 25, state 3), suppression of setae on the locomotory legs (character 35)], together with three new characters from the peristomatic structures. The labral bristle bands are expanded to cover completely the distal sclerotization of the submarginal armature (character 50), an elongate or figure-of-eight-shaped group of two smooth scutes surrounds each sensillum on the clypeal part of epipharynx (character 56), and tufts of bristles on the lateral flaps of the hypopharynx form a continuous field with identical bristles medially (character 62, state 2).

Asanada is resolved as basal within Scolopendridae, rendering the traditional Scolopendrinidae (= Asanadini + Scolopendrini) a paraphyletic grouping. The clade uniting the remaining scolopendrids is defined by loss of pretergites (character 27), extended tergite marginal spines (character 28), a coxopleural process on the ultimate leg (character 39), and the labral bristles being differentiated into a band of short, simple bristles laterally and longer simple bristles medially rather than a uniform band of long, simple bristles (character 49). The arrangement of sensilla on the clypeal part of the epipharynx (character 54) is modified at the same node but the apomorphic state (1 or 2) is topology-dependent. A Z-shaped offset in the bristle band fringing the mandibular gnathal edge (character 44) defines the same group under accelerated transformation. Characters 27, 28 and 44 exhibit homoplasy with Scolopocryptopinae and the jackknife value for the node that isolates Asanada from other Scolopendridae is low (<50%), although it receives a Bremer support of 2.

Monophyly of Otostigmini is supported by tibial spurs (character 38) and a strongly arched border between the labral and clypeal parts of the epipharynx (character 52); in some resolutions, oblique testicular vesicles are also apomorphic for Otostigmini (character 65). In half of the shortest cladograms Edentistoma is resolved as sister group to Otostigmini, whereas in the other half it is sister to Otostigmini + Scolopendrini. The grouping of Edentistoma and Otostimini, i.e. Otostigmata sensu Attems (1930), finds supports from the sensillar fields on the clypeal part of the epipharynx being divided into lateral clusters (character 54, state 1) and the humped floor of the spiracular atrium (character 15). The alternative resolution in which Edentistoma is excluded from Otostigmini + Scolopendrini is unambiguously supported in some shortest cladograms by spines on the ventral side of the ultimate leg prefemur (character 42), but in other topologies it is supported only by optimization-dependent characters, e.g. the tripartite claw on the second maxilla (character 21, state 2) under accelerated transformation.

Scolopendrini is unambiguously defended as a clade based on a dorsomedial prefemoral process on leg 21 (character 40) and the bristle tufts on the lateral flaps being connected by scales or spines (character 62). In particular minimal length topologies, additional unam-
biguous apomorphies include the spiracles having a three-valved atrial cover (character 14), complete para-
median sutures along the trunk (character 33) (both of these characters shared with Asanada), and prefemoral
spines on the ultimate legs (character 42). Groupings within Scolopendri receive low jackknife values. In
addition to the two clades in the strict consensus (Fig. 6), Hemiscolopendra is resolved as sister to the
remaining Scolopendri in all shortest cladograms but without unambiguous support. The characters depicted
in Fig. 7 in support of a Cormocephalus + Campylo-
stigmus group (basal plates on the head, character 20; median embayment in the margin of the maxillipede
coxosternite, character 24) and a clade uniting Arthrop-
habdius, Scolopendra, and Scolopendropsis (median
suture on the ultimate tergite, character 31; tarsal spurs,
character 37) are stable across all minimal length
resolutions.

Discussion

Historically, controversies in scolopendromorph sys-
tematics since Attems’ (1930) monograph have focused
on three character systems: number of trunk segments,
loss of eyes, and the segmental distribution of spiracles.
The cladograms permit a reappraisal of evolutionary
patterns in these and other morphological character
systems.

Trunk segmentation

The distinction between Scolopendromorpha with 21
versus 23 pedigerous trunk segments has been recog-
nized as of significance as high as the deepest division
of scolopendromorph classification. Schileyko (1992)
avovated a split between Scolopocryptopidae (23 leg
pairs) and Scolopendra (21 leg pairs) as fundamental,
with no homoplasy in this character. Other recent
workers have alternatively advocated the utility of this
variation at a lower taxonomic level, e.g. for distingui-
ishing Scolopocryptopidae from Cryptopidae and
Scolopendridae (Shelley, 2002). Exceptionally and in
only one part of the Scolopendromorpha does number
of leg pairs (21 or 23) vary within a small monophyletic
group, indeed allegedly within a single species of
Scolopendropsis fide Schileyko (2006). The view that
Scolopendropsis is related to scolopocryptopids with 23
leg pairs (Schileyko, 1992) has been abandoned (Schil-
leyko, 2006), and in the present analysis Scolopendropsis
is resolved within the Scolopendri, as in Attems (1930)
monograph. The 23-segmented Scolopocryptopinae,
Newportiinae, and Kethopinae together are resolved
as paraphyletic rather than monophyletic, and the
number of trunk segments at the base of the Scolop-
endromorpha is equivocal, with two equally parsimo-
nious optimizations. If 23 segments are plesiomorphic,
the 21-segmented condition is independently acquired in
Plutoniuminae and Cryptopinae + Scolopendridae. If 21
segments are instead plesiomorphic, the 23-
segmented state in Kethopinae, Newportiinae, and
Scolopocryptopinae has a single origin at the base of
the Scolopocryptopidae but is forced to reverse (to 21)
in Plutoniuminae. In either case, homoplasy is forced on
the cladogram even discounting the clearly independent
evolution of the 23-segmented state (from a 21-
segmented ancestor) in Scolopendropsis.

Eye loss

In contrast to the basal node of Scolopendromorpha
being based on leg counts, the traditional classification
of Scolopendromorpha (Kraepelin, 1903; Attems, 1930)
alternatively recognized a basic division between blind
taxa and those with four ocelli. If eye loss is not coded as
irreversible, the loss of ocelli is optimized on the shortest
cladograms as having occurred in the common ancestor
of Epimorpha (= Scolopendromorpha + Geophило-
morpha), forcing a re-evolution of ocelli in Scolopen-
dridae. This two-step (loss-regain) optimization is more
parsimonious than forcing three independent losses of
ocelli in Geophilomorpha, the clade composed of
Kethopinae + Newportiinae + Plutoniuminae + Sco-
lopocryptopinae, and Cryptopinae. Re-gain of ocelli in
Scolopendridae carries the consequence that ocellar fine
structure is conserved, because the ocelli of Lithobiidae
(Müller and Rosenberg, 2006) display detailed similarities
with those of scolopendrids (Müller and Meyer-
Roehow, 2006) that strongly argue for homology at a
fine structural level, i.e. autapomorphies of all plein-
occisphoran chilopods. The most parsimonious opti-
mization would be consistent with the common ancestor
of Epimorpha being hypogean rather than inferring
parallel evolution of hypogean habits in three lineages.
Alternatively, the implied transformation of eye re-gain
from blind ancestors could be rejected in favour of
parallel loss of ocelli in geophilomorphs and in two
scolopendromorph lineages, at a cost of one step.

The same character state distribution (and optimi-
zation) for ocellar loss is observed for tarsal division
(character 36), with the three blind lineages all sharing
an undivided tarsus. Fusion of the tarsus–metatarsus
articulation is routinely ascribed “to adaptation to a
hypogean mode of life” (Schileyko and Pavlinov, 1997,
p. 36).

Spiracle distribution

Plutonium zwierleini is exceptional in the context of
Scolopendromorpha as a whole in having a spiracle
distribution otherwise observed only in Geophilomor-
pha, with spiracles on all but the last pedigerous trunk
segment. Schileyko and Pavlinov polarized characters with an assumption that the spiracle distribution of *Plutonium* was plesiomorphic, a view promulgated earlier by Fahlander (1938), but the position of *Plutonium* in the present analysis rejects this view. The proliferation of spiracles in *Plutonium* and Geophilomorpha is convergent, a conclusion also drawn by Prunescu (1969) from characters of the male genital system. Schileyko and Pavlinov (1997) further inferred a basal position of *Plutonium* in the Scolopendromorpha in part by coding “anisosegmentation” (their character 1) as absent (“as in annelid-like ancestors” *fide* them) in *Plutonium* and the hypothetical ancestor but present in all other scolopendromorphs. We excluded this character from consideration because *Plutonium zwierleini* has as clear an alternation of relatively longer and shorter tergites anteriorly on the trunk as does *Theatops*. It is in no sense lacking anisosegmentation (contra claims to the contrary by Manton, 1965, p. 289). Finally, a basal position of *Plutonium* within the Scolopendromorpha was argued based on the lack of an atrium in the spiracle, an absence coded by Schileyko and Pavlinov (1997) in *Plutonium, Ethmostigmus*, and a hypothetical ancestor, versus the presence of an atrium in all other scolopendromorphs. Discussion of character 14 in Appendix 2 instead argues that the spiracles of *Plutonium* (Fig. 8) and *Ethmostigmus* both possess an atrium into which the tracheae open, and no uniquely plesiomorphic character of spiracle structure is observed in *Plutonium*.

The present results call into question the reliance on presence or absence of a spiracle on the seventh trunk segment as a fundamental taxonomic character. For example, *Dinocryptops* Crabill, 1953, was separated from *Scolopocryptops* based on the presence (*Dinocryptops*) or absence (*Scolopocryptops*) of this spiracle (character 13, states 1 and 0, respectively). The shortest cladograms (Figs 6 and 7) resolve *Scolopocryptops* as paraphyletic with respect to *Dinocryptops*, a topology supported by the peculiarly serpentine poison calyx (character 26) shared by *Dinocryptops miersii* and some but not all species of *Scolopocryptops*. In some respects it is puzzling that so much taxonomic weight has been placed on the segment 7 spiracle given that Crabill (1955) showed that it is exceptionally developed (i.e. present in one aberrant individual) in a species, *Scolopocryptops sexspinosus*, that typically lacks it. A spiracle on segment 7 has multiple origins on the cladogram exclusive of those instances in which all trunk segments bear spiracles.

**Poison calyx**

Although the gross morphology and in some cases ultrastructure of the poison glands have long been documented in Scolopendromorpha (Duboscq, 1898;
and in Arthrorhabdus case of some Pincer-like ultimate legs extend far into the coxosternum (state 4) as many as in Scolopocryptopinae, some Plutoniuminae, and extends deeply into the trochanteroprefemur (state 3), cladograms pincer-like legs are synapomorphic for and it is found to have four or five independent origins, morphology (character 41) is tested by the cladogram, of the trochanteroprefemur (state 1), optimized as a general state for Epimorpha, i.e. inherited from com- pendrini, and in some topologies Edentistoma is resolved stemward of a clade composed of Otostigmini and Scolopendrini.

The most significant result of the present analysis for scolopendromorph systematics is the discovery of a monophyletic group composed of the Plutoniuminae and Scolopocryptopidae sensu Shelley (2002). As reported in the Results section above, this clade is supported by two unique, unreversed apomorphies of the peristomatic structures, at least three unambiguous autapomorphies in all shortest cladograms and as many as six additional optimization-dependent apomorphies. Although this grouping had not been proposed based on previous morphological investigations, it was retrieved by Regier et al. (2005, figs 1b and 2) in an analysis based on three nuclear coding genes. In their analyses, Theatops and Scolopo-cryptops united to the exclusion of Cryptops. Although the pattern of paraphyly of Cryptopidae s.l. (sensu Attems, 1930) depicted in Fig. 6 is weakly supported, the union of Kethopinae, Newportiinae, Plutoniuminae, and Scolopocryptopinae is the strongest previously unrecognized signal to emerge from the present analysis.

Because study of the peristomatic structures demands dissection and electron microscopy, we have not been able to include a few monotypic genera that are known from extremely limited material, in several cases from the holotype of their type species alone. Examples of such single specimen taxa include Mimops orientalis (family Mimopidae Lewis, 2006), and Sterropristes sarasinorum Attems, 1934 and Malacolabis metallica Verhoeff, 1937 (subfamily Sterropristinae). New collections of any of these would be useful additions to the dataset, as are some distinctive but rare taxa, like the tropical American subfamily Ectonocryptopinae (Shelley and Mercurio, 2005). We defer extensive revision of scolopendromorph classification until such taxa are added to the character sample and molecular data are more broadly sampled; existing molecular analyses (Edgecombe and Giribet, 2004; Regier et al., 2005) lack data for Kethopinae, Newportiinae, Plutonium, and several pivotal scolopendrids, such as Asanada and Edentistoma. In light of the current results, however, the recently favoured familial groupings of Cryptopinae and

A strongly thickened, pincer-like leg 21 (or 23 in the case of some Scolopendropsis) is developed in numerous scolopendromorphs. The cladistic reliability of this morphology (character 41) is tested by the cladogram, and it is found to have four or five independent origins, depending on cladogram topology. In all shortest cladograms pincer-like legs are synapomorphic for Theatops and Plutonium, but they have an independent origin (or two origins) in Asanada and Edentistoma as well as either one or two origins in Arthrorhabdus and Scolopendropsis. Accordingly, the development of pincers from slender ultimate legs is identified as highly homoplastic.

**Peristomatic structures: systematic implications**

The present study found that peristomatic structures provide novel support for the monophyly of several major groupings in the Scolopendromorpha. Such traditional taxa as Cryptopinae, Scolopendridae, Scolopendrini, and Otostigmini are reinforced by additional apomorphies of their peristomatic structures. In contrast, the present analysis disputes the monophyly of a few widely recognized groupings, here being resolved as paraphyletic or polyphyletic rather than monophyletic: these include a grouping of Plutoniuminae and Cryptopinae as a family Cryptopidae (Shelley, 2002) or Newportiinae and Cryptopinae as families in a superfamily Cryptopoidea (= Cryptopina Verhoeff, 1906), the union of Asanada (tribe Asanadini) with Scolopendrini to form the subfamily Scolopendrinae (Attems, 1930), and the exclusive grouping of Kethopinae, Newportiinae, and Scolopocryptopinae as a family Scolopocryptopidae (Shelley, 2002). The union of Edentistoma (tribe Arrhabdotini) with Otostigmini to form the subfamily Otostigmatae (Attems, 1930) is variably monophyletic or paraphyletic in the shortest cladograms. Asanada, and in some topologies Edentistoma, is resolved stemward of a clade composed of Otostigmini and Scolopendrini.

Bücherl, 1946; Ménez et al., 1990), the extent, position, and form of the poison duct and calyx have only recently been subjected to a detailed comparative treatment (Chao and Chang, 2006). We have modified a character for the highly variable length and position of the poison calyx in chilopods in general and scolopendromorphs in particular (character 25), and also coded its most elaborate morphological modification (character 26). The results reported here treat character 25 as unordered, although assuming an ordered multi-state transformation series involving elongation of the poison calyx from the outgroup state (i.e. ordering states 0-1-2-3-4) does not contribute homoplasy because the same 16 shortest cladograms of the same length are obtained by TNT irrespective of whether or not the character is ordered. Length of the poison calyx exhibits slightly more homoplasy (CI 0.50) than the dataset as a whole (CI 0.57). The inferred basal state for Scolopendromorpha is a calyx extending into the distal part of the trochanteroprefemur (state 1), optimized as a general state for Epimorpha, i.e. inherited from common ancestry with Mecistocephaus. A calyx that extends deeply into the trochanteroprefemur (state 3), as in Scolopocryptopidae, some Plutoniuminae, and most Scolopendridae, is independently lengthened to extend far into the coxosternum (state 4) as many as three times, within Theatops and Plutonium, in Asanada, and in Arthrorhabdus (Fig. 9).

**Pincer-like ultimate legs**

A strongly thickened, pincer-like leg 21 (or 23 in the case of some Scolopendropsis) is developed in numerous scolopendromorphs. The cladistic reliability of this morphology (character 41) is tested by the cladogram, and it is found to have four or five independent origins, depending on cladogram topology. In all shortest cladograms pincer-like legs are synapomorphic for Theatops and Plutonium, but they have an independent origin (or two origins) in Asanada and Edentistoma as well as either one or two origins in Arthrorhabdus and Scolopendropsis. Accordingly, the development of pincers from slender ultimate legs is identified as highly homoplastic.

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The most significant result of the present analysis for scolopendromorph systematics is the discovery of a monophyletic group composed of the Plutoniuminae and Scolopocryptopidae sensu Shelley (2002). As reported in the Results section above, this clade is supported by two unique, unreversed apomorphies of the peristomatic structures, at least three unambiguous autapomorphies in all shortest cladograms and as many as six additional optimization-dependent apomorphies. Although this grouping had not been proposed based on previous morphological investigations, it was retrieved by Regier et al. (2005, figs 1b and 2) in an analysis based on three nuclear coding genes. In their analyses, Theatops and Scolopo-cryptops united to the exclusion of Cryptops. Although the pattern of paraphyly of Cryptopidae s.l. (sensu Attems, 1930) depicted in Fig. 6 is weakly supported, the union of Kethopinae, Newportiinae, Plutoniuminae, and Scolopocryptopinae is the strongest previously unrecognized signal to emerge from the present analysis.

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Fig. 9. Extent of poison calyx (character 25) in scolopendromorphs optimized as an unordered multistate character (cladogram topology as in Fig. 7). Dashed lines indicate ambiguous nodal state. Species with maxillipeds and detail of poison calyx shown at right are indicated by enlarged names on cladogram, in same sequence. White arrow marks termination of poison calyx.
Plutoniuminae (as Cryptopidae) and Kethopinae, Newportiinae and Scolopocryptopinae (as Scolopocryptopidae) are modified in light of the hypothesis that Plutoniuminae is nested within Scolopocryptopidae (Fig. 6). The scope of Cryptopinae, Plutoniuminae, Kethopinae, Newportiinae, and Scolopocryptopinae can be maintained as those groups were delimited by Shelley (2002) (Fig. 6, Table 1). Pending testing with additional data, Plutoniuminae is presently reclassified in Scolopocryptopidae rather than Cryptopidae to maintain monophyly of familial groups according to the cladograms while minimizing changes to the current classification. The diagnostic basis for Scolopocryptopidae employed by Shelley (2002), 23 pairs of trunk legs, is not unambiguously autapomorphic for the group, and the combined data favour an internal clade, Plutoniuminae, having 21 pairs of trunk legs.

**Peristomatic structures: evolutionary aspects**

Some complex variability in epipharyngeal morphology exhibits a high measure of fit on the cladogram. Notable in this regard are the arrangements of a median sensilla cluster or clusters on the clypeal part of the epipharynx (character 54). Optimized on the topology in Fig. 7, this character specifies a transformation series between the four states observed within the Scolopendromorpha, without the necessity of invoking homoplasy. The implied transformation identifies a proximal cluster of median sensilla near the mouth (state 0) in scutigeromorph and lithobiomorph outgroups, a medial band of sensilla near the spine field (state 3) at the base of the Epimorpha and retained in basal scolopendromorphs, a rhomboid cluster of sensilla in the same position (state 4) in Cryptopinae and retained in basal Scolopendridae, two groups of sensilla positioned laterally (state 1) in Edentistoma and Otostigmini, and a large medial field of sensilla situated well behind the spine field (state 2) in Scolopendriini. Examining character optimizations on the cladograms, a correlated pattern of homoplasy in the preoral chamber is detected between the scolopendrids *Edentistoma* (endemic to Borneo and Palawan) and *Campylostigmus* (six species endemic to New Caledonia).

![Fig. 10. Epipharynx of Scolopendromorpha. SEM images. (a,b) *Edentistoma octosulcatus*: (a) epipharynx; scale bar = 200 μm; (b) labral bristles; scale bar = 15 μm. (c,d) *Scolopocryptops ferrugineus*: (c) epipharynx; scale bar = 20 μm; (d) labral bristles; scale bar = 10 μm. (e) *Campylostigmus orientalis*, labral bristles; scale bar = 50 μm. (f) *Cormocephalus hartmeyeri*, labral bristles, showing differentiation of two bands; scale bar = 30 μm. Abbreviations: db, distal bar of submarginal armature; msp, median spine field; tp, tooth plate.](image-url)
Edentistoma and Campylostigmus are resolved as members of the Otostigminae or sister to Otostigmini + Scolopendrini and within Scolopendrini, respectively. Although these two taxa are separated on the cladograms, they exhibit a striking convergence in three characters from the epipharynx and mandibles. In Edentistoma and Campylostigmus alone, the medial labral part of the epipharynx is reduced to a narrow strip (character 47), associated with a small median labral tooth (Fig. 10a,e, respectively, for the two genera) and a broad expanse of the labral bristle field, which encroaches on the medial sclerotized strip more so than in any other Scolopendromorpha. Additionally, unique to Edentistoma (Fig. 11c,d) and Campylostigmus (Fig. 11e,f) is a field of fan bristles that covers the entire lamina dentifera of the mandible (character 44, state 2). We have coded these characters of the epipharynx and mandible as independent indicators of phylogeny but recognize that their homoplastic covariation allows for the possibility that they are linked to an overall increase in the extent of bristle fields in the preoral chamber in these two lineages. Additionally, the mandibular teeth of Edentistoma (Fig. 12a) and Campylostigmus (Fig. 11e) are smaller than those of other Scolopendromorpha (character 46). On the shortest cladograms these three characters are acquired independently. Further functional and ecological studies are needed to shed light on possible similarities in feeding style between these otherwise distinctive centipedes. Lewis (1981b) speculated that an absence of tooth plates on the maxillipede and the broad, straight coxosternal margin in Edentistoma could signal an unusual diet, such as scraping cryptogams off bark; Campylostigmus, in contrast, has the typical scolopendrid tooth plates, serrate endites that function as a “can opener” or spade in tearing the cuticle of prey (Manton, 1965). Campylostigmus does not share the peculiar locomotory characters of Edentistoma, perhaps the most morphologically and behaviourally remarkable scolopendromorph with respect to its slow gait, apparently arboreal habits, and superficial resemblance to a polydesmoid millipede (Lewis, 1981b). Campylostigmus also lacks the characters associated with tergal strengthening seen in Edentistoma, such as reinforcement by

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**Fig. 11.** Gnathal edge of mandibles of Scolopendromorpha, with details of fan bristles on lamina dentifera (b,d,f). SEM images. (a,b) Scolopocryptops ferrugineus, scale bars = 50 μm, 10 μm. (c,d) Edentistoma octosulcatus, scale bars = 100 μm, 30 μm. (e,f) Campylostigmus orientalis, scale bars = 50 μm, 10 μm.
longitudinal ridges that run along the lengths of the trunk tergites, which superficially (Cook, 1897) resemble the keels on the tergum in *Alipes* and in some species of *Otostigmus*. Observations of feeding in *Edentistoma* and *Campylostigmus* should illuminate their unexpected similarity in details of the preoral chamber.

Acknowledgements

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References


Appendix 1

Data matrix representing the 65 morphological characters coded for the relationships of scolopendromorphs and outgroups as described in Appendix 2. Question marks (?) indicate missing data; dashes (-) indicate inapplicable character states.

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Appendix 2

Morphological character descriptions (data matrix in Appendix 1). Descriptive terminology follows Lewis et al. (2005) except where otherwise indicated.

Outgroup characters/ingroup monophyly

1. Shape of head capsule: (0) domed; (1) flattened [Dohle, 1985; Edgecombe et al., 1999, character 6].
2. Trochanter on second maxilla: (0) separated from pretarsus; (1) fused to pretarsus with incomplete articulation [Borucki, 1996; Edgecombe et al., 1999, character 36].
3. Coxosternite of maxilliped slerotized in midline: (0) coxae separated medially; (1) coxal plates meeting medially, hinge flexible; (2) midline sclerotized, inflexible. Ordered following Edgecombe et al. (1999, character 44).
4. Maxilliped tarsungulum: (0) separate tarsus and pretarsus; (1) tarsus and pretarsus fused [Borucki, 1996; Edgecombe et al., 1999, character 4].
5. Position of spiracle: (0) dorsal; (1) pleural.
6. Coxal organs: (0) absent; (1) present [Edgecombe et al., 1999, character 108].
7. Four laminae of mandible intersecting at cruciform suture: (0) absent; (1) present [Edgecombe and Giribet, 2004, character 130].
8. Dorsal brush on tarsus of second maxilla: (0) absent; (1) present [Edgecombe and Giribet, 2004, character 161].
9. Tergite of maxilliped segment and first pedigerous segment: (0) separate tergites; (1) single tergite.
10. Gonopods in female: (0) present; (1) absent.
11. Hinge between articles of maxilliped telopodite: (0) absent (entire femur and tibia); (1) hinge between trochanteroprefemur and tibia; (2) hinge between trochanteroprefemur and tarsungulum [Edgecombe and Giribet, 2004, character 48].

Ingroup characters for Scolopendromorpha

12. Number of pedigerous post-maxilliped 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 maxilliped and ultimate pedigerous segment.
14. Atrium of spiracle covered by three-valved flap: (0) absent; (1) present. Schileyko and Pavlinov (1997, character 4) coded for the absence (hypothetical ancestor, Plutonium, Ethnostigmus) or presence (other scolopendromorphs) of an atrium in the spiracle. This distinction between Ethnostigmus and Plutonium and other scolopendromorphs was maintained by Schileyko (2002, p. 493). The concept of an atrium fide Schileyko does not appear to rely on the differentiation of a subatrial cavity (i.e. a cavity into which the tracheae open, largely isolated from the atrium proper by a diaphragm) because Scolopocryptops lacks a subatrial cavity (Verhoeff, 1941) but was scored by Schileyko and Pavlinov (1997) as having an atrium. The spiracles of Ethnostigmus differ from those of Rhysida only in having the atrial floor (identity of the atrium indicated by its trichomes) raised closer to the level of the stigmatopleurite. In all other respects, spiracle structure in Ethnostigmus shows detailed similarity to that of Alipes and Rhysida (Verhoeff, 1941; Lewis et al., 1996) (see character 15), and we regard it as inaccurate to regard it as lacking an atrium. Plutonium has the tracheae opening on the floor of a trichome-bearing pocket (Fig. 8) that corresponds to the atrium of other chilopods. Accordingly we dispute the notion that either Plutonium or Ethnostigmus lacks an atrium or that they uniquely share any aspect of spiracle structure with each other to the exclusion of other scolopendromorphs, and remove presence or absence of an atrium as an informative character. We retain a character state for the well-documented (e.g. Lewis et al., 1996) triplicate flaps that cover the subatrial cavity in Scolopendridae (Schileyko and Pavlinov, 1997, character 4, state 2).
15. Spiracle with floor of atrium raised into humps: (0) humps absent, tracheae unconstucted at openings to atrium; (1) humps present, tracheae narrowed at their openings between the humps. A humped atrial floor, with constriction of the tracheal openings between the humps, is shared by Alipes (Verhoeff, 1941; figs 5 and 6), Ethnostigmus, and Rhysida (Lewis et al., 1996), whereas Otostigmos spinosus was described as having a sac-like spiracle (Verhoeff, 1941; figs 3 and 4) with wider tracheal openings like those of Scolopendridae (Verhoeff, 1941; figs 10 and 11). Humps are developed on the atrial floor in the Otostigmos species coded here, O. astenus. The cribiform spiracles of Plutonium (Fig. 8) and Edentistoma are coded the same.
16. Eyes: (0) present; (1) absent.
17. Depigmented ocular patches: (0) absent; (1) present [Shelley, 1997; Edgecombe and Giribet, 2004, character 144].
18. Setation of basal antennal articles: (0) basal few articles bear numerous setae dorsally, with setation grading in density as short sensilla become more numerous on more distal articles; (1) basal articles with few setae dorsally, with abrupt transition to more distal articles that have dense, short sensilla. This character codes for information in Lewis’ (2006, table 1) character for glabrous basal antennomeres, although with a more precise description to accommodate variation in distribution of antennal setae (Lewis, 2000). Although in many Scolopendridae an abrupt distinction can be made between a glabrous 2.5-4 basal articles and densely setose articles distal to that, in other taxa, such as Scolopocryptops (Lewis, 2000; fig. 6; Shelley, 2002; figs 115–135), the basal articles are not strictly glabrous but rather have scattered setae. The coding here distinguishes taxa that have a more gradational setation (such as Cryptops and Paracryptops; see Lewis, 2000; fig. 4, for the former) from those such as Scolopocryptops that have an abrupt change. Antennal sensilla: (0) mostly normal trichoid sensilla; (1) dense, mostly collared sensilla [Lewis, 2000; Edgecombe and Giribet, 2004, character 141].
Trichoid antennal sensilla of most scolopendromorphs (Lewis, 2000; figs 10 and 11) contrast with distinctive sensilla in Scolopocryptops and Dinocryptops, which have a tall basal collar from which a seta extends (Lewis, 2000; fig. 12; Edgecombe and Giribet, 2004; fig. 8h).
20. Basal plates at posterolateral corners of head plate: (0) absent; (1) present. Basal plates (Lewis, 1986) are delimited by postmedially orientated sutures at the corner of the head plate in Cornocephalus and Campylostigmus, are also present in some species of Scolopendra (= Trachycormocephalus; Lewis, 1986), and are variably developed in Scolopendridae.
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 [Edgecombe and Giribet, 2004, character 38].

States of the second maxillary claw in Scolopendromorpha are depicted in Fig. 13. States 1 and 6 describe variation in outgroups (Lithobiomorpha and Scutigeromorpha, respectively).
22. Tooth plates of maxillipes: (0) plates absent; (1) plates developed as anteriorly projecting, serratate endites; (2) strongly chitinized anterior margin of coxosternite without plates; (3) plates hyaline rather than strongly sclerotized, bearing no tooth margin [Schileyko and Pavlinov, 1997; character 6]; Schileyko and Pavlinov, 2000; fig. 6).
23. Trochanteroprefemoral processes on maxilliped: (0) absent; (1) present [Schileyko and Pavlinov, 1997, character 17, “medial tooth on maxilliped prefemur”].
24. Median embayment in posterior margin of maxillipede coxosternite: (0) absent; (1) present. The posterior margin of the maxillipede coxosternite is evenly convex posteriorly or in part approximately transverse in most scolopendromorphs. In a few taxa, such as Scolopendropsis/Dinocryptops, Newportia, and Campylostigmus, each half of the coxosternite is recurved forwards near the midline to contribute a bilobate, medially embayed posterior margin (Fig. 9).

25. Position of poison calyx: (0) poison duct and calyx not extending beyond tibia; (1) extending into distal part of trochanteroprefemur; (2) extending half length of trochanteroprefemur; (3) extending to proximal part of trochanteroprefemur or to articulation with coxosternum; (4) extending deeply into coxosternum [modified from Chao and Chang, 2006].

The variable elongation of the poison calyx in scolopendromorphs relative to other chilopods is scored as a multistate character. States 2–4 above are scored to distinguish an especially long poison calyx coded as character 4 by Chao and Chang (2006, fig. 18). Chao and Chang observed the calyx to extend into the coxosternum only in certain Geophilomorpha (Mecistocephalidae: Prolamnonyx = Arrup) but a comparable extension into the coxosternum (state 4 above) occurs in several scolopendromorphs as well (Arrhrothorax formosus, Asanada socotrina, Plutonium zwierleini, Theatops posticus) (Fig. 9). The outgroup condition of a short poison calyx (state 0) is reinforced by our observations on Craterostigmus tasmanianus (order Craterostigmomorpha), in which the calyx does not continue beyond the tarsus. Although both species of Cryptops examined here code as state 1, some congeners have been depicted with a longer calyx, comparable with state 2 (e.g. Cryptops lobatus; Verhoeff, 1931; fig. 9).

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

The serpentine poison calyx documented by Chao and Chang (2006, fig. 10) in two species of Scolopendropsis is confirmed for S. spinicaudus and Dinocryptops miersii but not S. ferrugineus, which has an arched calyx as in Scolopendridae (in scolopendrids an elaborate twisting of the calyx, when present, is confined to its terminal part; see Campylostigmus orientalis in Fig. 9). Elsewhere in Scolopendromorpha, a serpentine calyx is observed in Theatops erythrocephalus. Chao and Chang (2006) used a round versus cylindrical shape of the poison calyx to distinguish Cryptops (round calyx) from other scolopendromorphs and outgroups. Some species of Cryptops, such as C. australis and C. spinipes, have a cylindrical calyx, and the round calyx accordingly appears to unite a restricted clade within Cryptops.

27. Pre- and metatergites: (0) pretergite incompletely defined; (1) strong pretergite set off from metatergite by continuous transverse furrow [modified from Edgecombe et al., 1999, character 57].

28. Tergite margination: (0) margins present on more than last tergite; (1) restricted to last tergite only [Schileyko and Pavlinov, 1997, character 16].

29. Lateral crescentic sulci on tergites: (0) absent on all tergites; (1) present on most tergites. Crescentic sulci that are impressed on the lateral part of most tergites in Cryptops and Paracryptops, associated with an internal ridge, are not developed in other terminals coded herein apart from Newportia longitarsis.

30. Shape of ultimate tergite: (0) not substantially longer than penultimate tergite; (1) nearly twice as long as penultimate tergite [Shelley, 1997].

31. Median suture on ultimate tergite: (0) absent, (1) present. A median suture on the ultimate tergite is complete in Scolopendropolis, Plutonium, and Theatops but is variably complete or restricted to the anterior part of the tergite in Scolopendrum spp.

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

Crytots and Paracryptops share a skeletal thickening across the sternum from sternite 2 that runs posteromedially across each half of the metasternite, represented externally as a dark line (Eason, 1964).

33. Strong, complete paramedian sutures on sternum along length of trunk: (0) absent; (1) present.

Coding of state 1 is restricted to those taxa in which a complete pair of paramedian sutures is sharply impressed along all of sternites 2-20, and thus excludes species (such as Ototrigus australianus) in which the sutures
34. Endosternites: (0) absent or indistinct; (1) well developed on anterior part of trunk.

Endosternites in Cryptopinae are posterior prolongations of a sternite that underlie the anterior part of the following sternite (e.g. Brolemann, 1930; figs 334 and 335). Elsewhere in Scolopendromorpha, comparable elongation of the sternum is observed in Kethops and Newportia (e.g. Verhoeff, 1906; fig. 32). Endosternites were accordingly identified by Verhoeff (1906) as a diagnostic character of his taxon Cryptopina (= Cryptopinae + Newportiinae in the modern sense).

35. Setae on locomotory legs: (0) strong, numerous; (1) slender, sparse [Lewis, 2006; table 1].

36. Structure of tarsi of locomotory legs: (0) divided into two articles; (1) fused, at least internally [Schileyko and Pavlinov, 1997, character 13].

37. Tibial spurs of locomotory legs: (0) absent; (1) present [Schileyko and Pavlinov, 1997, character 14].

Tibial spurs of locomotory legs do not precisely covary in Scolopendromorpha and are accordingly coded as independent characters.

38. Coxopleural process of ultimate leg: (0) absent; (1) present [Schileyko and Pavlinov, 1997, character 8].

The extension of the posteromedial corner of the ultimate leg coxopleuron as a distally spined process is most elaborate within Scolopendridae, but is also well developed in Kethopinae, Newportiinae, and Scolopocryptopinae. An apically acuminate extension that bears a blackened spur distally in Theatops erythrocephalus (Shelley, 1997, figs 40 and 41) is coded as homologous.

40. Dorso medial prefemoral process on ultimate leg: (0) absent; (1) present.

The distal end of the prefemur of leg 21 in scolopendrids variably bears a process at its dorso medial edge (dorso medial prefemoral tubercle of Shelley, 2002), the process bearing a cluster of spines that generally varies in number within a species (see, for example, Shelley, 2002, figs 29–41). The process is generally absent in Kethopinae and Newportiinae.

41. Strongly thickened, pincer-shaped ultimate legs: (0) absent (1) present.

Schileyko and Pavlinov (1997) coded for the structure of the ultimate leg as an unordered multistate character that recognized several modifications of an ultimate leg that is not radically dissimilar to the locomotory legs on preceding segments, the general state for Scolopendromorpha. Some of their apomorphic states are autapomorphies (leaf-shaped distal part in Alipes) or are restricted to single terminals herein and thus uninformative (e.g. multisegmental tarsus 2 in Newportia). One of their apomorphic states (their character 9, state 1) is retained and employed herein.
42. Armature of ventral side of prefemur of ultimate leg: (0) spines and spinous processes absent, as on locomotory legs; (1) spine(s) or spinous process(es) present.

Schileyko and Pavlinov (1997) coded for terminal leg armature as a multistate character that grouped “prefemoral spines”, considered in the present character, and the saw teeth on the tibia and tarsus I of Cryptopinae. This allows spurious transformations between non-homologous variation, and the armature of the distal part of the leg is accordingly treated as a separate character (character 43 below).

Shelley and Mercurio (2005, their character 2) made a distinction between the large “spinous processes” of scolopocryptopids and the generally smaller spines of scolopendrids, identifying the former as direct cuticular outgrowths and the latter as being dislodgable to isolate a rounded hump. Examined by SEM, these structures are direct cuticular outgrowths in both groups and we regard them as homologous. The coding for state 1 encompasses a substantial range of variability in spine arrangements, from taxa with a single ventral spine (e.g. *Theatops erythrocephalus*; Shelley, 1997, figs 40 and 41) at one extreme to *Scolopocryptops* with up to five rows of spines aligned in rows on the ventral, medial and dorsomedial sides of the prefemur at the other extreme.

43. Saw teeth on ventral side of ultimate leg tibia and tarsus I: (0) absent; (1) present [Schileyko and Pavlinov, 1997, character 10, state 2].

An expanded field of fan bristles, characterized by a Z-shaped offset in the bristle band that fringes the mandibular biting edge (Fig. 12d), had been identified as a character shared by Scolopendridae (Edgecombe and Giribet, 2004), and is seen in the scolopendrids studied herein apart from *Asanada socotrana* (Fig. 12c). A scolopendrid-like expansion of the bristle field is also observed in *Scolopocryptops* (Fig. 11a,b) and *Dinocryptops*. An elaboration of the expanded field of fan bristles is shared by *Edentistoma* (Fig. 11c,d) and *Camylostigmus* (Fig. 11e,f), both of which have a bristle field covering the entire lamina dentifera (state 2 above). An ordered multistate coding (0-1-2) groups conditions in which fan bristles cover a variable extent of the lamina dentifera.

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 [Edgecombe and Giribet, 2004, character 152].

An expanded field of fan bristles, characterized by a Z-shaped offset in the bristle band that fringes the mandibular biting edge (Fig. 12d), had been identified as a character shared by Scolopendridae (Edgecombe and Giribet, 2004), and is seen in the scolopendrids studied herein apart from *Asanada socotrana* (Fig. 12c). A scolopendrid-like expansion of the bristle field is also observed in *Scolopocryptops* (Fig. 11a,b) and *Dinocryptops*. An elaboration of the expanded field of fan bristles is shared by *Edentistoma* (Fig. 11c,d) and *Camylostigmus* (Fig. 11e,f), both of which have a bristle field covering the entire lamina dentifera (state 2 above). An ordered multistate coding (0-1-2) groups conditions in which fan bristles cover a variable extent of the lamina dentifera.

45. Accessory denticles on mandibular teeth: (0) absent or at most weakly developed on part of dorsalmost tooth; (1) strong, triangular denticles on all teeth [Edgecombe and Giribet, 2004, character 153].

State 1, involving a strongly developed field of accessory denticles on all mandibular teeth, is similarly developed in Lithobiomorpha and Cryptopinae. Accessory denticles can be discerned to a variable degree in *Theatops* and *Scolopocryptops*, but they are more subdued on the dorsal tooth than in *Cryptops* (Edgecombe and Giribet, 2004; fig. 3b) or *Paracryptops* (Fig. 12c) and are indistinct on the more ventral teeth (Fig. 11a). Examined Scolopendridae lack accessory denticles apart from *Alipes*, which has an incomplete covering of small accessory denticles confined to the dorsalmost tooth (Fig. 12f).
46. Size of mandibular teeth: (0) teeth large, tooth row much more than half length of gnathal edge; (1) teeth small, tooth row less than half length of gnathal edge. States 0 and 1 are defined so as to distinguish the small mandibular teeth of *Edentistoma* (Fig. 12a) and *Campylostigmus* (Fig. 11e) in comparison with those of other scolopendromorphs (Figs 11a and 12b–d), in which larger teeth contribute to the tooth row occupying a much longer extent of the gnathal edge. The coding for *Scutigera* is complicated by the short tooth row resulting from a small tooth number and a relatively long molar part of the mandible, but the teeth themselves are relatively large. Although this character covaries with elaborate fan bristles in the same taxa (character 44) we see no reason to assume non-independence.

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. *Edentistoma* (Fig. 10a) and *Campylostigmus* (Fig. 10e), which share a relatively diminutive median labral tooth compared with other scolopendromorphs (Figs 3a, 10c and 14a), lithobiomorphs, and scutigeromorphs, also have the area between the labral bristle bands reduced to a narrow strip (Fig. 1e).

48. Medial sclerotisation of labral part of epipharynx: (0) absent (paired lateral bars); (1) sclerotization continuous from median tooth to border with clypeal part; (2) sclerotization confined to region immediately proximal to median tooth, discontinuous with border with clypeal part. Scolopocryptopinae, *Newportia*, and Plutoniuminae differ from other scolopendromorphs in having a drop-shaped sclerotization of the medial labral part of the epipharynx that terminates in advance of the border with the clypeal part of the epipharynx (Fig. 1g). Although the shape of the medial sclerotized region varies in the other scolopendromorphs (e.g. narrow and elongate in *Campylostigmus* and *Edentistoma*, short in Otostigmini: Fig. 1e and f, respectively), sclerotization is continuous with the border to the clypeal part, generally assuming an anchor-shape where sclerotization continues transversely across the border (Fig. 1d). Continuous sclerotization is also developed on the tooth plate throughout Lithobiomorpha (Koch and Edgecombe, 2008).

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. Most Scolopendridae have a distinctive differentiation of the labral bristles, with an outer band composed of simple bristles that are markedly shorter than the simple bristles in the inner band (Fig. 10f). This is not coded as homologous with the differentiation of labral bristles into two bands in Scutigeromorpha (Koch and Edgecombe, 2006; fig. 5b) and Lithobiomorpha (Koch and Edgecombe, 2008; fig. 6d), which have pectinate (rather than simple) bristles in their outer band (state 0 above). *Asanada* (Fig. 14a) and the blind scolopendromorphs (Fig. 14b) lack two bristle bands, having either uniformly simple bristles of similar length across the field or

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Fig. 16. Mediolateral clusters of sensilla on clypeal part of epipharynx in Otostigmini. (a,b) *Ethmostigmus rubripes*: (a) clypeal part of epipharynx; scale bar = 50 µm; (b) sensilla cluster; scale bar = 10 µm. (c,d) *Otostigmus astenus*; scale bars = 15 µm, 5 µm. (e) *Allipes crotalus*; scale bar = 15 µm. (f) *Rhysdia nuda*; scale bar = 15 µm. Abbreviations as in Figure 15.
having a series of short, multifurcating scales (Fig. 10c,d) that fringes the simple bristles to a variable length. These scales are a continuation of a field on the clypeal part of the epipharynx. *Edentistoma* is unique in having an outer band of scales that, unlike the scattered groupings in, for example, scolopocryptopines, form elongate, continuous rows (Fig. 10b). However, more medial to these scale bands, simple bristles are differentiated into two rows, the innermost composed of longer bristles, as in other scolopendrids (state 1).

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

A wide expanse of the labral bristle field to cover the entire distal bar in Scolopendridae (Figs 1d, 3a and 10a,c) is usually associated with a two-band arrangement of the bristles (character 49, state 1) but codings for the two characters in *Asanada* demonstrate that they do not precisely co-vary.

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

*Plutoniuminae* (Fig. 15d), Scolopocryptopinae (Figs 10c and 15c), *Kethops*, and some Cryptopinae (*Paracryptops*) have a well-developed field of node- or spine-like scales across the proximalmost labral part of the epipharynx. In *Cryptops* (Fig. 15c), the corresponding region is variably rugose but discrete scales cannot be detected.

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

*Otostigmini* share a more strongly arched border between the labral and clypeal parts of the epipharynx (Figs 1f and 16a,c) than other scolopendromorphs, in which this border varies continuously from nearly transverse (Figs 1g and 15f) to distally convex (Figs 1d and 15a,c,d).

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.

All scolopendromorphs have similarly shaped sensilla evenly spaced along the field of branching spines (rbs in Figs 1d, 3b, 5g, 14c, 15c and 16a,b,d). They are not homologous with glandular structures in lithobiomorphs that have a different composition and morphology (bottle- versus bullet-shaped), and a different position (distal rather than proximal to the field of branching spines; Koch and Edgecombe, 2008).

54. Sensillar field(s) on clypeal part of epipharynx: (0) medial cluster of sensilla proximally, near mouth opening; (1) ovoid crescentic fields of sensilla laterally (Figs 1f, 14c,f and 16); (2) large field of sensilla across medial clypeal part of epipharynx, separated from spine field by a substantial expanse that bears scattered pores (Figs 1d and 3c,d); (3) band of sensilla medially, immediately proximal to spine field (Figs 10c and 15d–f); (4) lenticular field of sensilla immediately proximal to spine field (Fig. 15a,b).

Despite their variable positions, homology between different conditions of sensilla clusters in Scolopendridae (either discrete lateral fields: state 1, or a large median field: state 2) is indicated by a similarity in morphology of the sensilla and their surrounding region (see character 56 for details). State 0 accommodates Scutigeromorpha (sensilla cluster s5 of Koch and Edgecombe, 2006; fig. 1c) and Lithobiomorpha (“msc” of Koch and Edgecombe, 2008; fig. 2c).

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.

Coding is restricted to taxa with a large median field of sensilla positioned relatively proximally on the clypeal part of the epipharynx (character 54, state 2), i.e. Scolopendrini. State 1 homologizes a sensilla cluster that is differentiated within the main field of sensilla, as in *Scolopendra canidens* (Fig. 17a) and *Scolopendrops bahiensis*, and morphologically similar sensilla (Fig. 17d) that are likewise differentiated from the main cluster in *Scolopendra cingulata* but are instead positioned wholly proximal to the main cluster (Fig. 17b).

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

In all examined Scolopendridae except *Campylostigma*, a pair of scutes in which the clypeal sensilla are housed have a transversely narrowed outline that is a variably figure-of-eight-shaped depression (Figs 3d,f, 16c,d and 17a,b). The region surrounding the sensilla in Cryptopinae (Fig. 15b), *Plutoniuminae* (Fig. 15d), Scolopocryptopinae (Fig. 15c), *Kethopinae*, and Newportiinae (Fig. 15f) is not similarly modified.

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Fig. 17. Proximal median clypeal part of epipharynx. (a) *Scolopendra canidens*, triangular cluster of button-shaped sensilla; scale bar = 10 μm. (b,d) *Scolopendra cingulata*, proximal band of button-shaped sensilla, detail in d; scale bars = 20 μm, 5 μm. (c) *Paracryptops weberi*, polygonal scales across median region; scale bar = 5 μm.
57. Lid-like cover along distal edge of sensilla on medial clypeal part of epipharynx: (0) absent; (1) present. *Cryptops* and *Paracryptops* uniquely have a partial covering of their clypeal sensilla, with the distal edge overhung by the surrounding cuticle (Fig. 15b).

58. Paired lateral cluster of sensilla on clypeal part of epipharynx: (0) both clusters positioned laterally, widely separated from each other; (1) positioned relatively medially, with each cluster closely approximating each other near midline.

State 1 identifies a cluster of paired sensilla situated in front of the mouth opening in Plutoniuminae and other Scolopocryptopidae (lsc: Fig. 14d) as homologous with a lateral cluster of sensilla that is generally present in Scolopendromorpha (Figs 1d, 3e and 5e), rather than with similarly positioned (i.e. close to the mouth) sensilla in Lithobiomorpha. This homology accounts for the distinct bilateral symmetry of the scolopendromorph sensilla clusters, which are in all cases discontinuous across the midline, in contrast to the medial, unpaired nature of the lithobiomorph sensilla (median sensilla cluster, “msc” of Koch and Edgecombe, 2008; Fig. 2c). It also accounts for the presence of the lateral sensilla cluster of other scolopendromorphs in the Newportiinae, Scolopocryptopinae, and Plutoniuminae, rather than having to posit their loss. In outgroups, a lateral sensilla cluster is present only in Scutigeromorpha (“s6” of Koch and Edgecombe, 2006; figs 1c and 7e).

59. Elongate, distally branching spines with apices directed distomedially, strongly differentiated from lateral longitudinal band of scales on clypeal part of epipharynx: (0) absent; (1) present. Long, branching spines with a distomedial orientation are developed medial to a lateral band of scales in *Edentistoma* (Fig. 14f) and some Otostigmus (Fig. 14e and 16a), whereas other Otostigmus (Alipes, Rhysida) have only a band of scales with their apices directed proximally. The scale band is a general character for scolopendromorphs, the spines having a more restricted distribution.

60. Extent of lateral longitudinal band of scales on clypeal part of epipharynx: (0) not confluent across midline; (1) confluent across midline, developed proximomedially as polygonal scales. *Cryptops* and *Paracryptops* have the lateral longitudinal bands of scales of other scolopendromorphs grading into polygonal scales medially (Fig. 17c), and the scale field completely covers the proximomedial area of the clypeal part of the epipharynx (Fig. 15a). *Newportia longitarsus* (Fig. 15f) and *Kethops utahensis* have relatively expanded scale bands as well, but both have a clear median strip that is devoid of scales. In other scolopendromorphs the scales are confined to lateral bands (Fig. 10a).

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

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Fig. 18. Proximal part of lateral flaps and *Schlundplatte* on median part of hypopharynx of Scolopendromorpha. (a) *Cryptops spinipes*, showing discrete tufts of bristles on lateral flaps; scale bar = 10 µm. (b) *Plutonium zwierleini*, showing absence of bristles on lateral flaps; scale bar = 30 µm. (c) *Otostigmus astenus*, showing bristles on lateral flaps confluent across midline; scale bar = 20 µm. (d,f) *Scolopendra cingulata*, showing bristles on lateral flaps connected by short spines; scale bars = 40 µm, 15 µm. (e) *Scolopocryptops ferrugineus*; scale bar = 15 µm. Abbreviations: lf, lateral flap; nsc, cluster of nipple-shaped sensilla; spl, *Schlundplatte*; tu, tuft of bristles on lateral flap.
Lateral groupings of sensilla on the *Schlundplatte* in Newportiinae, Kethopinae, Scolopocryptopinae (nsc: Figs 1h and 18e), and Plutoni-

uminae (Figs 4a,b and 18b for *Theatops* and *Plutonium*, respectively) contrast with a single medially situated cluster of sensilla in Scolopendridae (Figs li and 5f) and an absence of *Schlundplatten-
sensilla* in Cryptopinae (Fig. 18a). A single medial cluster (state 0) is shared with the scutigeromorph (“s1” of Koch and Edgecombe, 2006; fig. 1a) and lithobiomorph (“nsc” of Koch and Edgecombe, 2008; figs 2d and 11a–c) outgroups.

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.

The lateral flaps of scolopendromorphs and lithobiomorphs bear a tuft of bristles proximally except in Plutoniuminae and other Scolopocryp-
topidae (state 0: Figs 4a and 18b), which are devoid of bristles on the corresponding part of the flaps. Three states are recognized to describe variation between the bristles on the lateral flaps and the adjacent median part of the hypopharynx. The median region may be smooth, thus emphasizing the discreteness of the tufts (state 1: Fig. 18a), or it may bear bristles identical to those on the lateral flaps so as to form a continuous bristle field (state 2: Fig. 18c), or the tufts on the lateral flaps may be separated by scales or short spines medially (state 3: Fig. 18d,f).

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

Although surveyed in few species, this character is coded to distinguish *Theatops erythrocephalus* (state 0) from other sco-
lopendromorphs (state 1) (Prunescu, 1997). Data are at hand for *Scolopendra cingulata* and the outgroup species of *Scutigera* (Prunescu, 1967) and *Lithobius* (Rilling, 1968), but congeneric proxies are used for Asanada (*A. brevicornis* for *A. socotrana*; Prunescu, 1997), *Corno-
cephalus* (*C. anceps* for *C. aurantiipes*; Brunhuber, 1969; Brunhuber and Hall, 1970), *Ethmostigmus* (*E. trigonopodas* for *E. rubripes*; Prunescu, 1965a) and *Cryptops* (*C. anomalans* and *C. parisi* for *C. australis*; Prunescu, 1965b).

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

Coding for the presence or absence of a ventral invagination in the spermatophore uses data for several congeners described by Demange and Richard (1969) as proxies: this applies to *Cryptops* (also Demange, 1945; Zalesskaja and Schileyko, 1991; fig. 22), *Ethmostigmus* (also Rajulu, 1969), *Hemiscelopendra*, *Newportia*, and *Otostigmus*. *Rhysida nuda*, *Scolopendra cingulata* and *Scolopocryptops ferrugineus* are coded following Demange and Richard (1969), and *S. canidens* from Zalesskaja and Schileyko (1991).

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

Longitudinal and oblique testicular vesicles are observed in Scolopendrinae/Cryptopidae s.l. and Otostigminae, respectively (Demange and Richard, 1969). Congeneric proxies for *Asanada*, *Cornocephalus*, *Cryptops*, *Ethmostigmus*, *Hemiscelopendra*, *Newportia*, and *Otostigmus* are, as for characters 63 and 64, mostly from Demange and Richard (1969) and Prunescu (1997). Data are additionally available for *Plutonium zwierleini* (Prunescu, 1997). Coding is inapplicable for *Scutigera* and *Lithobius*, which have an elongate, non-vesicular testis.