

**A scolopocryptopid centipede (Chilopoda: Scolopendromorpha)
from Mexican amber: synchrotron microtomography and
phylogenetic placement using a combined morphological and
molecular dataset**

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Abstract

The first scolopocryptopid centipede described from the fossil record is a specimen of the subfamily Scolopocryptopinae in Miocene amber from Chiapas, southern Mexico. It is described as *Scolopocryptops simojovelensis* n. sp., displaying a distinct combination of morphological characters compared to extant congeners. Anatomical details of the fossil specimen were acquired and quantified by non-invasive 3D synchrotron microtomography using x-ray phase contrast. The phylogenetic position of the new species is inferred based on a combination of morphological data with sequences for six genes (18S and 28S nuclear rRNA, nuclear protein-coding Histone H3, and mitochondrial 12SrRNA, 16S rRNA and COI) for extant Scolopendromorpha. The dataset includes eight extant species of *Scolopocryptops* and *Dinocryptops* from the Neotropics, North America and east Asia, rooted with novel sequence data for other blind scolopendromorphs. The molecular and combined datasets, analysed in a parsimony/direct optimization framework, identify a stable pattern of two main clades within Scolopocryptopinae. North American and Asian species of *Scolopocryptops* are united as a clade supported by both morphological and molecular characters. Its sister group is a Neotropical clade that nests *Dinocryptops* within a paraphyletic assemblage of *Scolopocryptops* species. The strength of support for the relationships of extant taxa from the molecular data allow the Chiapas fossil to be assigned with precision, despite ambiguity in the morphological data; the fossil is resolved as sister species to the Laurasian clade.

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ADDITIONAL KEYWORDS: Chiapas amber, Miocene, Scolopocryptopidae, *Scolopocryptops*

INTRODUCTION

Scolopocryptopinae are widely distributed through tropical parts of the world, with occurrences that extend into the temperate region in the northern hemisphere. Their distribution is largely circum-Pacific, including western North America from Baja California to southern Alaska, most of the eastern United States (see Shelley, 2002: fig.75 for North American distribution) throughout Mexico, Central America and the Caribbean, South America as far south as Argentina and southern Brazil, east Asia (mainland China, Taiwan, Korea, Japan), Vietnam, the Philippines, the Indonesian Archipelago, New Guinea, and Fiji. They also occur widely through tropical west Africa (Demange, 1963; 1968).

In the Neotropical region, the group is represented by five currently recognised species of *Scolopocryptops* Newport, 1845, and one species of *Dinocryptops* Crabill, 1953, following revisions by (Chagas, 2003; 2004). After a long period of taxonomic confusion and nearly universal application of the name *Otocryptops* Haase, 1887, for what taxonomists now call *Scolopocryptops* (Chagas, 2003 for a historical review), the modern concept of the genera took shape when Crabill (1953) erected *Dinocryptops*. Distinction between the two genera relies on a taxonomic character that had figured in the group's systematics since a revision by Pocock (1895-1910), the absence (*Scolopocryptops*) or presence (*Dinocryptops*) of a spiracle on trunk segment 7.

The fossil record of Scolopendromorpha, though extending as far back as the Late Carboniferous, consists of just a few species, most of which are known from a small number of specimens (Edgecombe, 2011) The only published fossil representative of Scolopocryptopinae is a specimen from Dominican amber (Miocene) illustrated by Poinar & Poinar (1999, fig. 87). The specimen has 23 leg-bearing segments and a single strong ventral spinose process on the prefemur of the last leg pair, both of these being diagnostic characters for Scolopocryptopinae. Herein we provide the first formal description of an extinct species of Scolopocryptopinae, provided by a single complete individual (Fig. 1A) in Miocene amber from Chiapas State in southern Mexico.

Most amber fossils from Chiapas are sourced from mines in marine calcareous sandstones and shales near the village of Simojovel de Allende (Solórzano Kraemer, 2007; 2010), and the fossil treated here comes from these sites. The amber occurs in the La Quinta or Simojovel Formation (dated to the early Miocene based on its foraminiferans, corals and pollen) and the Mazantic Shale, variably dated to the Oligocene-Miocene boundary based on isotopic signatures in mollusc shells (Vega, Nyborg, Coutiño et al., 2009), early Miocene based on its molluscs (Perrilliat, Vega & Coutiño, 2010), or early middle Miocene based on a correlation with Dominican and Puerto Rican ambers (Solórzano Kraemer, 2010). A single record of amber in a third stratigraphic unit, the Balumtun Sandstone, may be reworked from the Mazantic Shale (Solórzano Kraemer, 2007). The correlation with Dominican amber (age data listed by Penney, 2010) is indicated by close similarities in their respective insect faunas (Solórzano Kraemer, 2007), and dates the Chiapas occurrences to between 15 and 20 My.

The fossil scolopocryptopine is preserved in a piece of amber that includes numerous insect inclusions. The large size of the centipede and the undulating configuration of its trunk make standard preparation techniques for small amber inclusions untenable. Several taxonomically important characters used in the systematics of Scolopocryptopinae could not be examined in light microscopy because they were obscured by another structure. Accordingly, we employed synchrotron microtomography in order to extract more anatomical details. Because of the large specimen diameter and the need to resolve small features, a local tomography approach was employed where only the volume of interest remained in the beam, e.g. (Stock, 2008). The data were reconstructed a) as measured, i.e. with a mixture of inline X-ray phase contrast and absorption, and b) after phase-retrieval, i.e. after processing using an algorithm based on the transport-of-intensity equations.

The microtomographic and light microscopic data for the Miocene fossil permit it to be coded in a morphological dataset alongside its extant congeners, and a complimentary molecular dataset was built for extant Scolopocryptopidae. Analysis of the combined data – morphological and molecular – provides a basis for inferring the systematic position of the fossil.

MATERIAL AND METHODS

Synchrotron microtomography and data visualization

Synchrotron microtomography of the amber specimen was performed at station 2-BM of the Advanced Photon Source, Argonne National Laboratory (De Carlo, Xiao & Tieman, 2006). Radiographs of the specimen were recorded every 0.12° and with 20.7 keV monochromatic radiation. After each set of projections were recorded, the specimen was translated vertically (along the centipede's body axis) in order to cover a new portion of the fossil. The separation between the detector and the tomography rotation axis was 30 mm, and either a 2.5X or 5X objective lens was used in the detector system (producing isotropic reconstructed volume elements, voxels, $2.9\ \mu\text{m}$ or $1.45\ \mu\text{m}$ in size, respectively). Because this level of resolution was required to study the features of interest in the fossil and the detector consisted of 2K elements in the plane of reconstruction, only a fraction of the amber remained in the beam at all angles. The region-of-interest stayed in view for all angles and was centred on the centipede's body. This approach is termed local tomography and provides accurate geometry but shifted values of linear attenuation coefficient (Xiao, De Carlo & Stock, 2007). Reconstructions were on a 2K x 2K grid with software modified from Gridrec (Dowd et al., 1999) applied directly to the measured data or were with a filtered back projection algorithm after phase-retrieval based on the transport-of-intensity equations (Paganin et al., 2002) and implemented in ANKPhase (Weitkamp et al., 2011).

Data processing and visualization were carried out using Avizo Fire 7.0 (Visualization Sciences Group). The 32-bit raw data were downsampled to 16-bits and the data were filtered with $7 \times 7 \times 7$ kernel median filter in order to remove ring artefacts and noise. Segmentation was performed manually.

Taxonomic sampling

Our phylogenetic data consist of 16 extant species belonging to the family Scolopocryptopidae and the Chiapas amber fossil, together with 9 species belonging to the families Cryptopidae, Plutoniumidae and Scolopendridae (see Table 1 for list,

Appendix 1 for voucher details). Previous analyses including multi-locus sequence data agreed on the monophyly of Scolopocryptopidae and identified the blind families Cryptopidae and Plutoniumidae as their closest relatives (Murienne, Edgecombe & Giribet, 2010; Vahtera, Edgecombe & Giribet, 2012). Accordingly members of these families are used as outgroups for rooting Scolopocryptopidae, the sample including two species of the plutoniumid *Theatops* Newport, 1844, four species of the cryptopid *Cryptops* Leach, 1815, and one of the closely-allied *Paracryptops* Pocock, 1891. Because the interrelationships of the three blind families have been unstable (Koch, Edgecombe & Shelley, 2010; 2009; Vahtera et al., 2012) we include a few more distantly-allied outgroups. These sample one representative of each of the two diverse subgroups of Scolopendridae, the otostigmine *Otostigmus astenus* (Kohlrausch, 1881) and the scolopendrine *Cormocephalus aurantiipes* (Newport, 1844). These taxa were selected for the completeness of the molecular character set.

Scolopocryptopinae for which the genes used in our study (see “*Character sampling*”) are available from previous work are *Scolopocryptops sexspinosus* (Say, 1821) and *S. nigridius* McNeill, 1887 (Edgecombe & Giribet, 2004; Murienne et al., 2010) and *Dinocryptops miersii* (Vahtera et al., 2012). Here we add novel data for these and the two additional markers (see below) for *S. mexicanus* Humbert & Saussure, 1869 (sensu Chagas, 2008), *S. macrodon* (Kraepelin, 1903) (sensu Chagas, 2008), *S. melanostoma* Newport, 1845, *S. rubiginosus* Koch, 1878, *S. spinicauda* Wood, 1862, and *S. nipponicus* Shinohara, 1990. The latter species was placed in synonymy with *S. spinicauda* by Shelley (2002), but the molecular evidence presented in our study strongly indicates that a Japanese species (*S. nipponicus*) is distinct from the western United States species *S. spinicaudus*, and we refer to the Japanese taxon by its valid, available name. The analysis includes recently generated sequence data for other subfamilies of Scolopocryptopidae as well (members of Ectonocryptopinae and Newportiinae analysed by Vahtera et al., 2012), to which we here add novel data for three additional species of *Newportia*.

When possible, we included more than one specimen per species in order to cover the geographical range better. The two geographically widespread species of *Scolopocryptops* that occur throughout the Neotropical region are sampled from different parts of their geographic ranges: *S. mexicanus* samples are from the Dominican Republic, Colombia, and Ecuador; samples of *S. melanostoma* were sourced from Costa Rica and Fiji.

Character sampling

Morphological data consist of 52 characters (Table 2; Appendix 2), mostly extracted from our previously published dataset (Vahtera et al., 2012). To that are added several new characters (chs. 5, 7, 11, 20, 34, and 37 in Table 2) that are cladistically informative for species-level interrelationships of Scolopocryptopinae.

For the most part, molecular laboratory work followed the same protocols as in Vahtera et al. (2012), which used the two nuclear ribosomal markers (18S and 28S rRNA) and the two mitochondrial markers (16S rRNA and cytochrome oxidase-*c* subunit I) employed herein. The only differences involve the two new additional markers: nuclear protein-encoding Histone H3 (hereafter H3) and mitochondrial ribosomal 12S rRNA were applied in this study. H3 was amplified using the primer pair H3aF - H3aR (Colgan et al., 1998) and 12SrRNA using 12Sai -12Sbi (Kocher, Thomas, Meyer et al., 1989). The optimal annealing temperatures were 51°C for H3 and 45° for 12SrRNA. Chromatograms were visualized and assembled using Sequencher 4.9 or 4.10.1 (Gene Codes Corp., Ann Arbor, MI, USA).

Phylogenetic analyses

The sequences of each fragment were compared simultaneously in *Se-Al* v2.0a11 sequence alignment editor (Rambaut, 1996). The two amplified parts of 28S rRNA were aligned using MUSCLE alignment software (Edgar, 2004). Since the 28S fragments contained several long (<150 bp) insertions, GBlocks (Castresana, 2000) was used to remove the parts that were not present for all terminals. The six genes together sum to ca 4600 b.p. per terminal.

The phylogenetic analyses were conducted parallel using the computer package POY ver. 4.1.2 (Varón, Vinh & Wheeler, 2010) on Odyssey cluster at Harvard University, FAS Research Computing group (<http://www.odyssey.fas.harvard.edu>). The Direct Optimization approach (Wheeler, 1996) was used with parsimony as the optimality criterion. The COI, H3 and 28S data were treated as prealigned, the other fragments analysed unaligned. All fragments were analysed both individually and in combination. For both individual and combined molecular data sets, we conducted

sensitivity analysis (Wheeler, 1995) in order to explore the sensitivity of the data to parameter variation. We explored a parameter space of two variables (indel/transversion ratio and transversion/transition ratio) for a total of six parameter sets: 111, 121, 211, 221, 3211 and 3221. The first number in each parameter set reflects the ratio between indel/transversion and the two subsequent values represent the transversion/transition ratio. In two of them (3211, 3221), a cost for gap opening and extension is also specifically defined (i.e. in 3221 a gap opening costs 3, a gap extension 1, and all nucleotide transformations cost 2). All parameters were analysed per each fragment or combination using a timed search (3 h for each analysis). In order to test how long it takes the combined molecular tree length to stabilize, we conducted four different rounds of sensitivity analysis with and without auto sequence partitioning command. After each round we reported the tree length in order to see when the length stabilizes. The parameter set that minimized the incongruence length difference (ILD) among the data set was chosen as optimal. For both the combined molecular data as well as the combined molecular and morphological data, the parameter set of the lowest ILD value was 3221 (gap opening = 3, gap extension = 1, transversion = 2, transition = 2). We used this optimal parameter set in the final, deeper search (15 h each for both combined molecular data alone and together with equally weighted morphological data).

The morphological data were analyzed separately with TNT (Goloboff, Farris & Nixon, 2008) using heuristic search strategies. For analysis of morphology on its own, implied character weights (Goloboff, 1993) were used, testing sensitivity of clades to different concavity constants ($k=2, 3, 4, 5, 6$). Searches involved 1000 random stepwise addition sequences of the taxa, saving up to 100 trees per replicate, and swapping on those trees with tree bisection-reconnection (TBR). Multistate characters were all treated as non-additive (unordered). One multistate character that exhibited polymorphism (either of states 0 or 1 in different specimens) was analysed using the “NONA” option in TNT, i.e., analysed as either of the two states. Clade support under implied weights was evaluated with symmetric sampling (measured by the GC ratio of Goloboff et al., 2003), with 1000 replicates each having a 33% change probability.

For the molecular and combined datasets, jackknife resampling (Farris et al., 1996) was used to estimate the nodal support. 1000 jackknife replicates were each set with a 36 % probability of each fragment being deleted.

Systematics

Order Scolopendromorpha Pocock, 1895

Family Scolopocryptopidae Pocock, 1896

Subfamily Scolopocryptopinae Pocock, 1896

Scolopocryptops Newport, 1845

Type species. *Scolopocryptops melanostoma* Newport, 1845, by subsequent designation of Lucas (1849).

Included species. Twenty-two valid species are recognised in Chilobase (<http://chilobase.bio.unipd.it>) (Minelli et al. 2006 onwards; accessed 24 May 2012). One has been placed in synonymy since the most recent update; *S. verdecens* Chamberlin, 1920, is a junior subjective synonym of *S. melaonstoma* Newport *vide* Chagas (2010).

Scolopocryptops simojovelensis n. sp. (Figs. 1-3)

Diagnosis. *Scolopocryptops* lacking margination on cephalic plate; paramedian sutures terminating on tergite 21; anterior margin of forcipular coxosternite lacking lateral tooth or bulge, median part of margin projecting anterior to lateral part; coxopleural process long, terminating in a strong spine; two tibial spurs on legs 1-19, ventral spur only on leg 20; moderately developed pair of pretarsal accessory spurs.

Holotype. AMNH Ch-SH7, American Museum of Natural History amber arthropod collection, from Simojovel de Allende, Chiapas, Mexico.

Etymology. For Simojovel de Allende, the most prolific source of Chiapas amber.

Description. Length of body (anterior margin of cephalic plate to posterior margin of tergite 23) 29 mm. Cephalic plate lacking margination either laterally or posteriorly, its posterior margin overlying tergite 1 (Figs. 1C, 3A). 17 articles in right antenna (left antenna preserves only basal few articles, the remainder eroded from the inclusion);

moderately long setae numerous over length of articles to at least article 8; articles 2 and 3 bearing a similar, moderate number of setae dorsally (neither is sparsely setose); short, dense setae on article 4 and more distal parts of antenna.

Anterior margin of forcipular coxosternite partly covered (Fig. 3C), only visible on lateral half of right side; exposed part of margin approximately straight, its more medial part anterior to its lateral part, lacking lateral tooth or lateral bulge.

Complete pair of paramedian sutures on TT16-21 (Fig. 2A, B), anterior to this to at least T8 (and apparently as far as T5) a pair of lines of surficial crust run parallel to the course of the paramedian sutures on TT16-21 and evidently represent deposits along the sutures; paramedian sutures absent on TT1-3 and 22. Posterior part of tergites bearing several subtransverse anastomosing grooves, more prominent posterior on trunk to ca segment 21.

Paired tibial spurs on legs 1-19, smaller anterodorsal spur and larger ventral spur; ventral spur only on leg 20 (Fig. 1B), lacking on legs 21-23. Single tarsal spur on legs 1-21 (Fig. 1B, C), lacking on legs 22 and 23. Pretarsi of legs 1-22 with moderately developed pair of accessory spurs (Fig. 1D); ultimate leg with small accessory spurs. Sternite of segment 23 with evenly concave posterior margin. Coxopleural pore field extending close to base of coxopleural process ventrad, posterior margin of pore field sinuous but without a re-entrant field devoid of pores dorsad (Fig. 3D). Dorsomedial spinose process of ultimate leg prefemur more than half the length of strong ventral spinose process (Fig. 2C, D). Setal density on distal articles of ultimate leg (Fig. 2D) apparently similarly sparse to that on proximal part (no evidence for clustered “bottle brush” setae on any article).

RESULTS AND DISCUSSION

Morphological data

The identification of the fossil as Scolopocryptopinae is based on its lack of ocelli, 23 pedigerous trunk segments, strong anastomosing grooves parallel to the posterior margin of the tergites (Fig. 2A, B), single tarsal article on legs 1-21 and bipartite tarsi on legs 22 and 23, slender ultimate leg on which the prefemur bears a single dorsomedial spinose process and a single large ventral spinose process (Fig. 2C), a

coxopleural process that terminates as a single strong spine (Fig. 2C), and presence of paired tibial spurs on most trunk legs that are reduced to a single (ventral) spur on one or two more posterior legs (Fig. 1B).

As noted in the introduction, the sole basis for distinguishing between *Scolopocryptops* and *Dinocryptops* is the absence or presence of a spiracle on the seventh trunk segment. Spiracles have not been detected in the fossil because of poor preservation of the pleuron; even the spiracle on segment 3, which can be large in *Scolopocryptopinae*, is not seen in light microscopy, and the synchrotron imagery did not clarify the presence or absence of the spiracle on segment 7. This seemingly prohibits making an assignment to one of either *Scolopocryptops* or *Dinocryptops* according to the traditional criteria. In fact, the monophyly of *Scolopocryptops* is contradicted; given that the two genera are distinguished by alternative states of the same character, one is expected to be paraphyletic with respect to the other, and morphology-based analyses suggest that recognition of *Dinocryptops* leaves *Scolopocryptops* as a paraphyletic grouping (Edgecombe & Koch, 2008; Koch et al., 2010; 2009). The phylogenetic analyses described below strongly support the paraphyly of *Scolopocryptops* with respect to *Dinocryptops*. We have assigned the fossil species to *Scolopocryptops* because that name would have priority were *Dinocryptops* placed in synonymy, and none of our phylogenetic analyses (morphological or combined morphological and molecular) unite the fossil more closely to the type species of *Dinocryptops* (*D. miersii*) than to the type species of *Scolopocryptops*, *S. melanostoma*.

The fossil can be reliably distinguished from each of the five extant Neotropical species of *Scolopocryptops*. Perhaps the most pertinent comparisons are with the two most geographically widespread species, *S. mexicanus* Humbert & Saussure, 1869, and *S. melanostoma* Newport, 1845, because their distributions suggest the highest probability of an age consistent with a Miocene fossil history. Both of these species occur in southern Mexico and range throughout Central America and the Caribbean, throughout which they are the only extant members of *Scolopocryptopinae* (Chagas, 2008). Compared to *S. melanostoma* the fossil has more strongly developed pretarsal accessory spurs (Fig. 1D), possesses both dorsal and ventral tibial spurs on leg 19 (versus a ventral spur only on leg 19 in *S. melanostoma*), and has a ventral tibial spur on leg 20 (Fig. 1B). The slope of the short extent of the forcipular coxosternal margin that is visible in the fossil suggests that the medial part of the margin is anterior to the

lateral part (versus the opposite in *S. melanostoma*). Following Chagas (2008), we apply the name *S. mexicanus* to Neotropical material that has generally been identified as *S. ferrugineus* (Linné, 1767). Compared to *S. mexicanus*, the Chiapas specimen lacks a lateral tooth on the forcipular coxosternal margin, and has a substantially longer coxopleural process (both a longer spinose distal part as well as a more sloping posterior margin when seen in lateral view (Fig. 2C), cf. (Attems, 1930: fig. 347 for *S. ferrugineus*). It appears to differ from both of these species in that antennal articles 2 and 3 bear numerous setae dorsally.

Character coding for *S. simojovelensis* was aided by the synchrotron imaging. Light microscopy demonstrated the presence of the coxopleural pore field but did not permit the shape of the field to be visualised. An embayment (a pore-free area) in the pore field on its posterodorsal side (Attems, 1930: fig. 350) is shared by some Neotropical Scolopocryptopinae (*S. macrodons*, *S. melanostoma*, *Dinocryptops miersii*), and its presence was coded as character 37. The synchrotron data allowed the complete pore field to be documented in the fossil (Fig. 3D), and show the absence of a posterodorsal embayment (character state 0). In total, the fossil can be coded for 33 of 52 characters in the dataset (Table 2), many of the missing codings applying to characters of the peristomatic organs (Edgecombe and Koch, 2008) and the foregut (Koch et al., 2009).

The morphological cladistic analysis supports the assignment of *S. simojovelensis* to Scolopocryptopinae, that group being retrieved in all 9 best-fit cladograms (Fig. 4). These nine cladograms and their consensus in Fig. 4 are stable across the range of explored concavity constants. All identify Newportiinae as sister group of Scolopocryptopinae, i.e., monophyly of Scolopocryptopidae. *Dinocryptops miersii*, the type species of that genus, is nested within a paraphyletic *Scolopocryptops*, and its closest relatives within *Scolopocryptops* are other Neotropical species, *S. macrodon* and *S. melanostoma*. The Asian and North American members of *Scolopocryptops* unite as a clade, united by margination of the cephalic plate (character 7), a character that is lacking in *S. simojovelensis* (Fig. 3A). Within that group, species with incomplete paramedian sutures on the tergites (character 20) are monophyletic to the exclusion of the sampled species that has complete sutures (*S. rubiginosus*). The precise placement of *S. simojovelensis* within Scolopocryptopinae is subject to some ambiguity, the species being resolved in three alternative positions: either it or *S. mexicanus* is sister species to the other

Scolopocryptopinae, or *S. simojovelensis* is sister species to the clade composed of *S. macrodon*, *S. melanostoma* and *D. miersii*.

Molecular data

The parameter set that minimised incongruence for the molecular data is 3221 (Table 3). The single most parsimonious cladogram for the combination of the six genes (length 14465 steps) is shown in Fig. 5. This topology is congruent with the morphological cladogram (Fig. 4) with respect to the monophyly of Scolopocryptopidae and its sister group relationship to Plutoniumidae. The former has a jackknife frequency (hereafter JF, reported as percentages) of only 61 and is contradicted in two of the explored parameter sets (211, 221). These two contradicting parameter sets ally Plutoniumidae more closely to Scolopocryptopinae than either is to Newportiinae. The clade composed of Plutoniumidae and Scolopocryptopidae is better supported (JF 83 and monophyletic under all explored parameters). Within Scolopocryptopidae, Newportiinae (JF 94) and Scolopocryptopinae (JF 94) are well supported clades, both being monophyletic under all parameters. Relationships within Scolopocryptopinae are very stable to varied transition-transversion and indel costs: monophyly of two main subclades described below as well as every grouping within them apart from the placement of two species (*Scolopocryptops nigradius* and *S. spinicauda*) with respect to each other is retrieved across the six explored parameter sets.

The molecular data are congruent with morphology in nesting *Dinocryptops miersii* within a paraphyletic *Scolopocryptops*, and with the same Neotropical species resolved as its closest relatives (*Scolopocryptops melanostoma* and *S. macrodon*) with JF 95. The molecular data permit a more decisive resolution of the interrelationships of these species, with *S. macrodon* being strongly supported as the sister species of *D. miersii* (JF 100). The molecules assign *S. mexicanus* to the cladogram with more precision than was achieved with morphology alone: that species groups with the Neotropical clade (JF 94). As a result, Scolopocryptopinae is divided into two groups that have an apparent vicariant pattern. One clade includes the Neotropical species (some of which, such as *S. melanostoma*, are more widely distributed into the Old World tropics) and we infer that the west African species are parts of this group based on their morphological similarity to *S. mexicanus*; this would be effectively a West

Gondwanan clade. The other clade is the same Asian/North American grouping as retrieved based on morphology (JF 100 for the molecular data).

Within the Asian/North American clade, the molecular cladogram resolves the Japanese *S. nipponicus* as sister species of *S. rubiginosus* (JF 99). This provides a strong counterargument to the proposal that *S. nipponicus* is a subjective synonym of the Western North American species *S. spinicauda* (Shelley, 2002); the two taxa are separated on the tree and accordingly cannot be regarded as a widespread species with a Transpacific distribution.

The molecular cladogram is more explicit than the morphological with respect to relationships within Newportiinae. As was the case for morphology, the nesting of Ectonocryptopinae (sampled by *Ectonocryptoides quadrimeropus*) within Newportiinae is found for the molecular data under the most congruent parameters but two suboptimal parameter sets resolved Ectonocryptopinae as sister to a monophyletic Newportiinae. When Newportiinae is paraphyletic, the same species of *Newportia* (*N. monticola* and *N. longitarsis*) are allied with *Ectonocryptoides* for both molecules and morphology. The molecular data resolve a clade within *Newportia* that was ambiguous based on morphology alone, one composed of *N. divergens*, *N. ernsti* and *N. stolli* (JF 99 and stable across the six parameter sets). This group corresponds to *Scolopendrides* Saussure, 1858, formerly employed as a subgenus of *Newportia* but discarded by Schileyko & Minelli (1998), who left *Newportia* undivided. A possible apomorphy for this group is the traditional defining character of *Scolopendrides*, irregular boundaries between the tarsomeres of tarsus 2 of the ultimate leg (character 30, state 1). Within this clade, the sequence data expose an unanticipated resolution: *N. stolli* is non-monophyletic under all studied parameter sets, its two sampled specimens failing to unite with each other. Similarly, *N. divergens* is most likely non-monophyletic, its specimens grouping together only under one sub-optimal parameter set (221). This contrasts strikingly with the situation for species of Scolopocryptopinae that were sampled from different parts of their geographic ranges (*Scolopocryptops mexicanus*, *S. melanostoma*, *Dinocryptops miersii*), in which the two samples united with each other with JF 100. The non-monophyly of two species of *Newportia* throw open the question of species delineation in that genus; work in progress involving much more intensive sampling of these putative species and other Mesoamerican *Newportia* species will focus on this issue.

Combined analysis

Incongruence between morphology and the six genes is minimised under parameter set 3221, the same parameters that were optimal for the molecular data alone. The single shortest cladogram (length 14570 steps) for the combined data under these parameters (Fig. 6) has an identical topology to the molecules-only cladogram (Fig. 5) with respect to the interrelationships of extant taxa across the entire tree. As was likewise the case for the molecules alone, relationships within Scolopocryptopinae are very stable across the explored parameter space.

In the total evidence cladogram, *Scolopocryptops simojovelensis* is resolved in a different position to the best fit morphological cladograms with implied weights, the combined data resolving it as sister group of the Laurasian clade. That placement is stable across the six explored parameter sets (JF 95 for the optimal parameters). This resolution is affected by a different placement of some extant species (such as *S. mexicanus*) for the morphological and molecular data, and also reflects a difference in character weighting. The combined analysis applied equal weights to the morphological data partition, and the resolution of *S. simojovelensis* at the base of the Laurasian clade is found in a subset of the shortest morphological cladograms under equal weights. In those morphological trees that resembling the total evidence tree in resolving *S. sexspinosus* at the base of the Laurasian clade, the alliance of *S. simojovelensis* with that group is supported by character 5, state 2 (the basal antennal article alone being sparsely setose).

Discussion

Inferring relationships within Scolopocryptopinae has been greatly aided by the availability of a multi-locus molecular dataset. Although some of the deeper relationships within the group were retrieved by morphology on its own (e.g., monophyly of the Laurasian clade, monophyly of a group of Neotropical species), the relationships of some species that were ambiguous with morphology alone, such as *Scolopocryptops mexicanus*, were decisively resolved with the molecular data. The same applies to the placement of the new fossil species, even though it (obviously) lacks the entire molecular character set. The greater degree of precision of the molecular data for resolving the interrelationships of the extant species allowed for

the choice of a single optimal position of the fossil on the cladogram, instead of the multiple placements that were permitted by morphology on its own. This pattern reflects a phenomenon that had been detected with real and simulated datasets, i.e., molecular data improving the accuracy with which the relationships of fossils can be inferred (Wiens, Kuczynski, Townsend et al., 2010).

The biogeographic significance of the fossil *Scolopocryptops* is also affected by the difference between morphological and total evidence analyses. Morphology resolved the fossil species either at or near the base of Scolopocryptopinae or detected an alliance with a Neotropical clade (= *S. macrodon* + *S. melanostoma* + *D. miersii*). In contrast, the cladogram based on the combined datasets resolved the Mexican amber species as more closely allied to a Laurasian group than it is to species from the Neotropics or any part of Gondwana. In the Miocene, Chiapas was situated near the southern edge of the North American Plate and was separated from the South American Plate by the Central American Seaway. Affinities of the fossil to species from North America rather than those from the South American Neotropics may reflect a geographic isolation that had been in effect since the Mesozoic. The Neotropical affinities of extant species of *Scolopocryptops* in Mexico (*S. mexicanus* and *S. melanostoma*) likely reflect range expansion in the Great American Interchange.

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Figure 1. *Scolopocryptops simojovelensis* n. sp. Holotype AMNH Ch-SH7. A, dorsolateral view of complete specimen, scale 5 mm. B, dorsolateral view of cephalic plate and right antenna, scale 1 mm. C, distal part of leg 20, showing tibial spur (*ti*) and tarsal spur (*ta*), scale 0.5 mm. D, distal part of tarsus and pretarsus of leg 20, showing accessory spurs (*ac*), scale 0.1 mm.

Figure 2. *Scolopocryptops simojovelensis* n. sp. Holotype AMNH Ch-SH7. Scales 1 mm except C, 0.5 mm. A, nearly dorsal view of tergites 17-22; arrows on TT17 and 18 indicate complete paramedian sutures. B, dorsolateral view of tergites 17-20. C, dorsal view of segment 23, showing tergite (*T23*), coxopleural process (*cp*), dorsomedial spinose process (*ds*) and ventral spinose process (*vs*) of prefemur. D, dorsolateral view of leg pairs 21-23.

Figure 3. *Scolopocryptops simojovelensis* n. sp. Visualizations of synchrotron tomography data of holotype. A, B, dorsolateral and oblique anterodorsal views of head. C, ventral view of forcipules. D, lateral view of coxopleuron of leg 23.

Figure 4. Strict consensus of 9 best-fit cladograms based on morphological data in Table 2 under implied weights ($k=2, 3, 4, 5$ and 6). GC values $>50\%$ shown above branches for concavity constant $k=3$. Position of *Scolopocryptops simojovelensis* highlighted.

Figure 5. Single shortest cladogram for six genes in combination (14465 steps) under parameter set 3221. Numbers above branches are jackknife frequencies $>50\%$. Navajo rugs below branches depict monophyly (black) or non-monophyly (white) of clades under the six parameter sets shown at left; grey box indicates monophyly in some but not all shortest cladograms.

Figure 6. Single shortest cladogram for six genes and morphology in combination (14470 steps) under parameter set 3221. Numbers above branches are jackknife frequencies >50%. Navajo rugs (as explained in Fig. 5.) for the six parameter sets shown below branches.

<i>Newportia stollii</i>	DNA103975	MCZ	Colombia	new	new	new	new	new	new
<i>Newportia stollii</i>	DNA103988	MCZ	Guatemala	new	new	new	new	new	new
<i>Dinocryptops miersii</i>	DNA104699	AMNH LP3868	French Guiana	HQ402510	HQ402528	new	HQ402545	new	new
<i>Dinocryptops miersii</i>	DNA101160	MCZ	Brazil	new	-	new	new	new	new
<i>Scolopocryptops macrodon</i>	DNA105858	MCZ	Guyana	new	-	new	new	new	new
<i>Scolopocryptops melanostoma</i>	DNA104714	AMNH LP6249	Costa Rica	new	-	new	new	new	new
<i>Scolopocryptops melanostoma</i>	DNA104006	MCZ	Fiji	new	-	new	new	new	new
<i>Scolopocryptops mexicanus</i>	DNA103980	MCZ	Colombia	new	new	new	new	new	new
<i>Scolopocryptops mexicanus</i>	DNA105626	MCZ	Ecuador	new	new	new	new	-	new
<i>Scolopocryptops nigridius</i>	DNA105919	MCZ	USA	new	new	new	new	new	-
<i>Scolopocryptops nipponicus</i>	DNA105913	MCZ	Japan	new	new	new	new	new	new
<i>Scolopocryptops sexspinosus</i>	DNA100808	MCZ	USA	AY288694	AY288710	AY288726	AY288745	-	new
<i>Scolopocryptops rubiginosus</i>	DNA105912	MCZ	Taiwan	new	-	new	new	new	new
<i>Scolopocryptops spinicauda</i>	DNA104717	AMNH LP6385	USA	new	new	new	new	new	new
<i>Otostigmus (Otostigmus) astenus</i>	DNA102463	MCZ	Fiji	HQ402515	HQ402532	HM453221	HM453312		-
<i>Otostigmus (Otostigmus) astenus</i>	DNA103943	MCZ	Vanuatu					new	
<i>Cormocephalus aurantiipes</i>	DNA103951	MCZ	Australia	HQ402509	HQ402527	HQ402492	HQ402543	new	-

Table 2. Characters used in phylogenetic analysis (fossil in bold), corresponding to list in Appendix 2.

	1	11	21	31	41	51
<i>Cormocephalus aurantiipes</i>	0010000100	-1010-0000	000100100-	00000103-0	00003000--	--
<i>Otostigmus astenus</i>	0010300000	-1010-0000	000000100-	11000103-0	00002000--	--
<i>Theatops erythrocephalus</i>	0001000030	-110100110	011100110-	11101101-0	001101010-	00
<i>Theatops posticus</i>	0001000030	-100100110	011100110-	10101000-0	001101010-	00
<i>Cryptops hortensis</i>	0000100121	00010-0010	110011010-	00000000-0	100010110-	00
<i>Cryptops lamprethus</i>	0000100021	00010-0010	110011010-	00000000-0	110?10????	??
<i>Cryptops niuensis</i>	0000100121	00?10-0010	110011010-	00000000-0	110?10????	??
<i>Cryptops sarasini</i>	0000100221	0000101010	110011000-	00000000-0	11????????	??
<i>Paracryptops weberi</i>	0000100?22	00010-0010	110011010-	00000000-0	100110110-	00
<i>Ectonocryptoides quadrimeropus</i>	1100100011	0000101010	110001010-	0000010201	0010010110	11
<i>Newportia divergens</i>	1100100111	0100110010	1100010111	1110010201	0010010111	11
<i>Newportia ernsti ernsti</i>	1100100111	0100100010	1100010111	1110010201	001?01????	??
<i>Newportia longitarsis stechowi</i>	1100100?11	0000100010	1100010110	0100010201	0010010110	11
<i>Newportia monticola</i>	1100100111	0000101010	1100010110	0100010201	0011010110	11
<i>Newportia stolli</i>	1100100111	0000100010	1100010111	1110010201	0010010111	11
<i>Scolopocryptops macrodon</i>	1000010011	01?0100000	000000110-	1110011210	00????????	??
<i>Scolopocryptops melanostoma</i>	1000010011	01?0100000	000000110-	1111011210	001?01????	??
<i>Scolopocryptops mexicanus</i>	1000010011	1100100000	000000110-	1110010210	001101011?	11
<i>Scolopocryptops nigridius</i>	1000311011	01?0100001	000000110-	1110010210	001?01????	??
<i>Scolopocryptops nipponicus</i>	1000311011	01?0100001	000000110-	1110010210	00????????	??
<i>Scolopocryptops rubiginosus</i>	1000311011	0110100000	000000110-	1110010210	001?01????	??
<i>Scolopocryptops sexspinosus</i>	1000211011	01?0100001	000000110-	1110010210	00????????	??
<i>Scolopocryptops spinicauda</i>	1000311011	0110100001	000000110-	1110010210	0011010110	11
<i>Scolopocryptops simojovelensis</i>	1?002?00?1	0??0?00000	00000?110-	1110010210	00????????	??
<i>Dinocryptops miersii</i>	1100010011	0110100000	000000110-	1110011210	0011010110	11

Table 3. Most parsimonious tree lengths for different data partitions analysed and incongruence length difference (ILD) between the data sets. The parameter set shown in bold minimizes the incongruence and is chosen as optimal.

	COI	16S	12S	28Sa	28Sb	H3	18S	MOL comb	ILD
111	2065	2094	1533	43	250	385	868	7582	0.045370615
121	2977	3461	2525	56	334	533	1456	11973	0.052701913
211	2065	2619	1878	43	250	385	1310	9248	0.075475779
221	2977	4434	3153	56	334	385	2329	15183	0.099782652
3211	2972	3311	2481	56	334	532	1141	11194	0.032785421
3221	4130	4067	3025	86	500	770	1423	14465	0.032077428

	Morphology	MOL + morphology combined	ILD MOL + morphology combined
111	95	7688	0.046175858
121	95	12079	0.053150095
211	95	9364	0.076783426
221	95	15299	0.100398719
3211	95	11301	0.033536855
3221	95	14570	0.032532601

Appendix 1. Voucher details for the specimens sequenced. Institutional abbreviations: AMNH, American Museum of Natural History, New York, New York, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

Cormocephalus aurantiipes (Newport, 1844)—32°45'45"S 116°04'36"E; Australia: Western Australia: Lane Poole Reserve, S. of Dwellingup; 21.I.2006; G.D. Edgecombe, G. Giribet; MCZ DNA103951

Cryptops (Cryptops) hortensis (Donovan, 1810)—U.K.: Putney Heath, London; 18.XI.2007; G.D. Edgecombe; MCZ DNA102579

Cryptops (Cryptops) lamprethus Chamberlin, 1920—37°55'42"S 174°55'20"E; New Zealand: North Island: creek on road near Te Mata, WO; 17.I.2003; S. Boyer, C. D'Haese, G. Giribet; MCZ DNA103950

Cryptops (Cryptops) niuensis Chamberlin, 1920—16°51'58.8"S 179°54'18.8"E; Fiji: Taveuni Island: coastal forest along waterfall trail, Lavena village; 10.VIII.2008; J. Murienne, P. Sharma; MCZ DNA104828

Cryptops (Trigonocryptops) sarasini Ribaut, 1923—22°3'S 166°28'E; New Caledonia: Mt. Dzumac road, QM Berlesate 1059; 31.X.2001; G. B. Monteith; MCZ DNA103948

Dinocryptops miersii Newport, 1845—4°33'35"N 52°12'25.3"W; French Guiana: Approuague-Kaw, Kaw Mountains, area around Amazone Nature Lodge, several trails through primary tropical rainforest; 21-25.XII.2004; J. Huff; AMNH code LP3868, MCZ DNA104699. Brazil: Paraná State: Usina Santa Clara; 21.XII.2003; C.E. Conte; MCZ DNA101160

Ectonocryptoides quadrimeropus Shelley & Mercurio, 2005—México: Jalisco: Puerto Vallarta; 5.VII.2009; F. Cupul Magaña; MCZ DNA104639

Newportia divergens Chamberlin, 1922—16°10'N 93°36'W; LLAMA MCZ81365, MGB669: México: Chiapas: 18.5 km ENE Tonalá; 16.VII.2007; M. G. Branstetter; MCZ DNA103991. 15.0840726N, 89.94547974W; LLAMA Wa-B-01-1-all: Guatemala: El Progreso: Cerro Pinalón: cloud forest, oak trees, pine trees, tree ferns, bamboo sometimes present; 30.VI.2009; MCZ DNA104725 (MCZ catalog no. 89511)

Newportia ernsti ernsti Pocock, 1891—Dominican Republic; VI 2010; purchased from pet trade; MCZ DNA105917

Newportia longitarsis (Newport, 1845)—4°30'22.6"N 52°3'29.9"W; French Guiana: Approuague-Kaw, Kaw Mountains, end of Kaw road to boat ramp, trail on left through primary tropical rainforest; 24.XII.2004; J. Huff; AMNH LP 3871; MCZ DNA104706

Newportia monticola Pocock, 1890—5°42'34"N 73°27'36"W; Colombia: Departamento de Boyacá: mixed forest dominated by *Quercus humboldti*, Loc. 335: Santuario de Fauna y Flora Iguaque; 31.X.2004; L. Benavides; D. Campos, G. Giribet; MCZ DNA103974

Newportia stollii (Pocock, 1896)—5°42'34"N 73°27'36"W; Colombia: Departamento de Boyacá: Santuario de Fauna y Flora Iguaque; 30.X.2004; L. Benavides, D. Campos, G. Giribet; MCZ DNA103975. 15°5'N 89°56.65'W; LLAMA MGB1028, Guatemala: El Progreso: Sierra de las Minas, Cerro Pinalón; 21.IX.2008; M.G. Branstetter; MCZ DNA103988

Otostigmus astenus (Kohlrausch, 1878)—17°45'18.2S 167°20'19.2" E; Vanuatu: Efate Island: private conservation area, road to Erakor; 16.VIII.2008; P. Sharma, J. Muriene; MCZ DNA103943

Paracryptops weberi Pocock, 1891—5°02'32"S 119°44'07"E; Indonesia: Sulawesi: Bantimurang-Bulusoraung National Park; 28.VI.2006; G. Giribet, R. Clouse, C. Rahmadi; MCZ DNA102459

Theatops erythrocephalus (C.L. Koch, 1847)—Spain: Barcelona Province; XI.1995;

A. Serra; MCZ DNA103996

Theatops posticus Say, 1821—USA: North Carolina: Durham, Duke Forest; R.M. Shelley, S.B. Bauer; 30.iii.1998; MCZ DNA100806. 30°33'53"N 84°57'5"W; USA: Florida: Torreya State Park, Weeping Ridge trail; 19.III.2010; P. Sharma, R. Clouse MCZ DNA105630

Scolopocryptops inversus Chamberlin, 1921—58°56.774'W, 1°23.307'N; Guyana: Upper Takutu-Upper Essequibo, Acarai Mts., near Romeo's Camp, 282 m; 7.X.2006; T. R. Schultz; MCZ DNA105858

Scolopocryptops melanostoma Newport, 1845—9°46'69"N 83°45'6"W; Costa Rica: Cartago Province, Pejibaye, Cartago, Reserva Biológica “El Copal”; 15.V.2006; V. Vignoli, C. Viquez, H. Ajuria; AMNH code LP6249, MCZ DNA104714. 18°4'15"S 178°26'39.9"E; Loc. 531: Fiji: Viti Levi Island: Savura park along ridge trail; 31.VII.2008; J. Muriene, P. Sharma; MCZ DNA104006

Scolopocryptops mexicanus Humbert & Saussure, 1869—S 0.95274 W 77.7468; Ecuador: Napo Province: Sacha Wagra Lodge, 10 km Road Archidona-Rio Hollin; 29.XI.2009; L. Benavides; MCZ DNA105626. 1°20'10"N 77°15'47"W; Loc 356: Colombia: Departamento de Nariño: Chachagüi, Reserva de Común; 12.XI.2004; L. Benavides; L. Cabrera; G. Castillo; C. Florez, G. Giribet; M. Romo, V. Solarte; MCZ DNA103980

Scolopocryptops nigridius McNeill, 1887—35°43'52.4"N 81°53'59.2"W; USA: North Carolina; McDowell County, Lake James S.P.; 16.VI.2005; R. Clouse; MCZ DNA105919

Scolopocryptops nipponicus Shinohara, 1990— 35°2.07'N 136°54.01'E; Japan: Honshu: Nagoya, Tokai, Shinnitetsumae station, city park; 25.IV.2010; Z. Korsós; MCZ DNA105913

Scolopocryptops rubiginosus L. Koch, 1878—24°45'44"N 121°35'57"E; 201. Taiwan: Llan County, Fushan Botanical Garden, primary forest; 22.V.2010; Z. Korsós, Y. Nakamura; MCZ DNA105912

Scolopocryptops sexspinosus (Say, 1821)—USA: North Carolina: Durham, Duke Forest; R.M. Shelley, S.B. Bauer; 30.III.1998; MCZ DNA100808

Scolopocryptops spinicauda Wood, 1862—38°14'18.6"N 122°30'23.4"W; USA: California: Sonoma Co., Hwy 116 between Petaluma and Sonoma, under rocks and dry river bed; 20.VIII.2006; J. Huff, W. Savary; AMNH code LP6385, MCZ DNA104717

Appendix 2. Morphological characters coded in Table 2.

1. Number of pedigerous post-forcipular segments: (0) 21; (1) 23.
2. Spiracle on segment 7: (0) absent; (1) present.
3. Eyes: (0) absent; (1) cluster of four ocelli.
4. Depigmented ocular patches: (0) absent; (1) present.
5. Number of sparsely hirsute basal antennal articles: (0) at least three sparsely hirsute articles; (1) basal articles with numerous setae dorsally, with gradational trend to distal articles with shorter, denser seta; (2) basal article alone sparsely hirsute dorsally; (3) basal two articles sparsely hirsute dorsally, third at least distally as densely hirsute as subsequent articles.
6. Structure of antennal sensilla: (0) mostly normal trichoid sensilla; (1) mostly sensilla that project from a basal tubercle or collar.
7. Head plate margined laterally and posteriorly: (0) margins absent; (1) margins present.
8. Longitudinal sutures on head plate: (0) absent; (1) paired, confined to extremities of head plate; (2) paired, complete along entire length of head plate.
9. Structure of claw of second maxillary telopodite: (0) robust median claw with a slender spine on each side; (1) pectinate claw; (2) hook-like claw with ventral flange; (3) two curved processes, one above the other.
10. Tooth plates of forcipules: (0) plates with strongly chitinized tooth margins; (1) strongly chitinized anterior margin of coxosternite without plates; (2) hyaline, lobate plates lacking teeth.
11. Forcipular margin with inner and outer tooth pair: (0) margin lacking well-defined teeth; (1) tooth pair present.
12. Trochanteroprefemoral process on forcipule: (0) absent; (1) present.
13. Form of poison calyx: (0) straight or arcuate; (1) serpentine.
14. Relationship between head plate and T1: (0) head plate overlapping anterior margin of T1; (1) T1 overlapping head plate.
15. Anterior transverse suture on T1: (0) absent; (1) present.
16. Continuity of anterior transverse suture on T1: (0) continuous medially and

- laterally; (1) interrupted between paramedian sutures.
17. W-shaped sutures on T1: (0) absent (paramedian sutures, when present, either continuous to anterior transverse suture or terminating behind that suture); (1) present (paramedian sutures originate at posterior apices of the W).
 18. Inverted Y-shaped sutures on T1 (anterior median suture and divergent posterior sutures): (0) absent; (1) present.
 19. Pre- and metatergites: (0) pretergite and metatergite merged; (1) strong pretergite set off from metatergite by continuous, transverse suture.
 20. Completeness of paramedian sutures on tergum: (0) complete on at least some tergites; (1) none extending more than posterior one-third of tergite length.
 21. Crescentic sulci on tergites: (0) absent on all tergites; (1) present on most tergites.
 22. Tergite margination: (0) margins present on more than last tergite; (1) restricted to last tergite only.
 23. Shape of ultimate tergite: (0) not substantially longer than penultimate tergite; (1) nearly twice as long as penultimate tergite.
 24. Median suture on ultimate tergite: (0) absent; (1) present.
 25. Line of skeletal thickening across sternites originating at coxa: (0) absent; (1) present.
 26. Endosternite: (0) absent; (1) present.
 27. Setae on locomotory legs: (0) strong, numerous; (1) slender, sparse.
 28. Structure of tarsi of locomotory legs: (0) divided into two articles; (1) fused, at least internally.
 29. Tarsomeres in tarsus 2 of ultimate leg: (0) undivided tarsus 2; (1) tarsus 2 with numerous tarsomeres.
 30. Definition of tarsomeres in tarsus 2 of ultimate leg: (0) regular tarsomere boundaries; (1) irregular tarsomere boundaries.
 31. Tarsal spurs of locomotory legs: (0) absent; (1) present.
 32. Dorsolateral tibial spur: (0) absent on all locomotory legs; (1) present on one or more locomotory legs.
 33. Ventral tibial spur: (0) absent on all locomotory legs; (1) present on most locomotory legs.
 34. Pretarsal accessory spurs on locomotory legs: (0) well-defined; (1) rudimentary.

35. Strongly thickened, forcipulate ultimate leg: (0) absent; (1) present.
36. Coxopleural process of ultimate leg: (0) absent; (1) present (represented at least by spur).
37. Embayment in posterodorsal margin of coxopleural pore field: (0) absent; (1) present.
38. Armature of ventral side of ultimate leg prefemur: (0) spines and spinous processes absent, as on locomotory legs; (1) single small spine on each prefemur and femur; (2) large spinous process(es); (3) spines in ordered rows.
39. Arrangement of spinous processes on ultimate leg prefemur: (0) a few processes in an irregular row; (1) single large ventral process and smaller dorsomedial process.
40. Ventral spinose processes on ultimate leg femur: (0) absent; (1) present.
41. Saw teeth on ventral side of ultimate leg tibia and tarsus I: (0) absent; (1) present.
42. Saw teeth on ultimate leg femur: (0) absent; (1) one or two distally.
43. Medial sclerotisation of labral part of epipharynx: (0) sclerotisation continuous from median tooth to border with clypeal part; (1) sclerotisation confined to region immediately proximal to median tooth, discontinuous with border with clypeal part.
44. Node- or spine-like scales across proximal labral part of epipharynx: (0) absent; (1) present.
45. Sensillar field(s) on clypeal part of epipharynx: (0) band of sensilla coeloconica medially, immediately proximal to spine field; (1) lenticular field of sensilla coeloconica immediately proximal to spine field; (2) crescentic field of sensilla coeloconica laterally; (3) large field of sensilla coeloconica across median clypeal part, separated from spine field by a substantial expanse that bears scattered pores.
46. Paired lateral cluster of sensilla on clypeal part of epipharynx: (0) both groups positioned laterally, widely separated from each other; (1) positioned medially, with each group closely approximating each other near midline.
47. Extent of lateral longitudinal bands of scales on clypeal part of epipharynx: (0) not confluent across midline; (1) confluent across midline, developed proximomedially as polygonal scales.
48. Gizzard structure: (0) plicae covered with scales that each bear a single spine;

- (1) posterior part of foregut organised as a sieve with stiff, anteriorly-directed projections.
- 49.** Anterior gizzard projections with pigmented bases bearing spinose scales or spines, distal part translucent, tapering, bearing dense hairs: (0) absent; (1) present.
- 50.** Terminal part of large pineapple-shaped projections of gizzard: (0) projections evenly tapering, tip filamentous; (1) projection bifid, with a short conical tip emerging from the notch.
- 51** Shape of main zone of sieve projections: (0) evenly curved; (1) kinked near midlength, with distal part more strongly directed forwards.
- 52** Longitudinally patterned bands of trichomes on basal half of sieve projections: (0) absent (trichomes, if present, not patterned); (1) present.