The phylogenetic position of *Dinogeophilus* and a new evolutionary framework for the smallest epimorphic centipedes (Chilopoda: Epimorpha)

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Abstract

The centipedes of the clade Epimorpha change slightly during post-embryonic growth but there is huge variation between species in the maximum body size. New specimens of the rarely collected Neotropical genus *Dinogeophilus* provide further evidence that this genus comprises the smallest species of the Epimorpha, with a recorded maximum length of 5.5 mm. Up to now *Dinogeophilus* has been invariantly classified in Geophilidae but different sources of evidence (examination by SEM, cladistic evaluation of morphology, similarity and phylogenetic analysis of molecular data) agree on a very different phylogenetic hypothesis: *Dinogeophilus* is actually a derived lineage of Schendylidae, only distantly related to Geophilidae, and possibly belong to a mainly Neotropical subgroup of schendylids. A comparison of *Dinogeophilus* with the most closely related taxa suggests that body miniaturization was accompanied by possibly paedomorphic traits, including lower number of some multiple elements (antennal sensilla, processes on the mouth-parts, coxal organs) and shorter setae. Possibly associated with miniaturization are also a few novel features of *Dinogeophilus*, among which the unique subterminal denticles of the forcipules, suggesting a possible change in the feeding behaviour.

Contents

Introduction

Within the extant centipedes (Chilopoda), two thirds of the species (nearly two thousand) are in the clade Epimorpha, all of which form all their trunk segments and appendages before or very shortly after hatching (Minelli and Sombke, 2011; Brena, 2014). Nevertheless, different species of Epimorpha grow up to very different body sizes and their maximum length spans two orders of magnitude, from millimetres to decimetres. Such huge differences are found within each of the two major clades within the Epimorpha, *i.e.* the Scolopendromorpha (~700 species) and the Geophilomorpha (>1200 species). Among scolopendromorphs, at least two species of *Scolopendra* Linnaeus, 1758 have been reported to overreach 30 cm in length, *i.e. S. gigantea* Linnaeus, 1758 and *S. galapagoensis* Bollman, 1889 (Shear and Peck, 1992; Shelley and Kiser, 2000; Kronmüller, 2013). Among geophilomorphs, individuals surpassing 20 cm have been reported in a few species of *Himantarium* Koch, 1847, *Orya* Meinert, 1870 and *Titanophilus* Chamberlin, 1915, all in the superfamily Himantarioidea (Attems, 1929; Bonato *et al.*, 2011; C. Kronmüller, pers. comm.). At the opposite extreme, body miniaturization evolved repeatedly in the history of the Epimorpha (Lewis, 2002; Foddai *et al.*, 2003; Pereira, 2013a) but the smallest species are hard to single out, mainly because many candidate species are known from single or very few specimens only, preventing a confident estimate of the maximum length that they may reach at full growth (Appendix 1). The available data point to the species of *Dinogeophilus* Silvestri, 1909 as the smallest species in the Epimorpha, but this has been rarely highlighted in the literature.

Up to now no more than half a dozen specimens of *Dinogeophilus* have been reported, all from a narrow region in South America, partly in Argentina and partly in Uruguay. The first specimen was collected in the early 20th century (Silvestri, 1909a, 1909b) and described as *D. pauropus* Silvestri, 1909, as the first representative of a distinct genus. Another five specimens were collected much later and described (Pereira, 1984) as belonging to a second species *D. oligopodus* Pereira, 1984. All these specimens are less than 5.5 mm long.

Since its discovery and over more than a century, *Dinogeophilus* has been almost invariantly considered a member of the family Geophilidae. This taxonomic position has been explicitly maintained also in recent taxonomic synopses (Foddai *et al.* 2000; Bonato *et al.*, 2011), in evolutionary analyses of anatomical features (Minelli and Bortoletto, 1988; Turcato *et al.*, 1995) and in biogeographical overviews (*e.g.*, Pereira *et al.*, 1997; Bonato and Zapparoli, 2011). However, new specimens collected by one of us (L.A. Pereira) and a recent molecular phylogenetic analysis of the Geophilomorpha (Bonato *et al.*, 2014) have provided evidence that *Dinogeophilus* does not belong to the family Geophilidae but to the family Schendylidae, which is morphologically very different and only distantly related to the former (Edgecombe and Giribet, 2007; Bonato *et al.*, 2014). Geophilidae and Schendylidae have been recently classified in different superfamilies (Geophiloidea and Himantarioidea, respectively; Bonato *et al.*, 2014) and their separation has been estimated to date back from the Mesozoic (Murienne *et al.*, 2010).

Such preliminary evidence prompted us to reassess the phylogenetic position of *Dinogeophilus* by means of both morphological and molecular evidence. In particular, we tested the two competing hypotheses (Geophilidae vs. Schendylidae) by (i) examining newly available specimens, also applying scanning electronic microscopy for the first time to this taxon, (ii) performing similarity analyses and phylogenetic analyses on the molecular data recently obtained, and (iii) revisiting critically all previously published data and opinions on *Dinogeophilus*. This allowed us to (iv) reinterpret the morphology of these peculiarly miniaturized centipedes in a more solidly established evolutionary context, especially exploring morphological correlates of miniaturization, including putative paedomorphic traits and novelties.

Material and methods

We examined a specimen of *D. oligopodus* from Puerto Iguazù, Argentina [female, 15.xi.1980, L.A. Pereira lg; indicated in the original description as the allotype of the species; Pereira, 1984] and seven new specimens from La Plata, Argentina [two males and five females, 19.xii.1985, 14.iv-3.v.1986, 22-23.viii.2009, L.A. Pereira lg]. Specimens are preserved in the collections of the Museum of La Plata, Argentina, and in the Minelli-Bonato collection at the Department of Biology, University of Padova, Italy.

The specimens were examined with light microscopy (LM), with a Leica DMLB microscope equipped with a Leica DFC420 camera. A male and a female were also examined with scanning electron microscopy (SEM), using a Cambridge Stereoscan 260. For both LM and SEM, the head was detached from the trunk. For LM, the specimens were mounted in temporary slides, following standard protocols for geophilomorphs (Pereira, 2000). For SEM, the samples were gradually hydrated, post-fixed in 4% formaldehyde in water, rinsed with 0.5% Triton-X 100 in water, briefly sonicated, rinsed in water, cleaned with 3% H_2O_2, dehydrated in graded ethanol series, dried with hexamethyldisilazane (Sigma), and coated with gold.

The entire body of two specimens (collected in 2009 and fixed in absolute ethanol) were used for DNA extraction, with the aim to amplify and sequence the genes most commonly used in phylogenetic analyses in Chilopoda (CO1 and 16S rRNA from the mitochondrial genome; 18S and 28S rRNA from the nuclear genome; *e.g.*, Murienne *et al.*, 2010). We followed a protocol previously optimized in our laboratory for a broad sample of geophilomorphs (described in detail in Bonato *et al.*, 2014). Because of difficulties due to limited mass and poor quality of preservation of the samples, we were successful in obtaining well readable sequences only for the three subunits of rRNA and only for one of the specimens.

In order to test the two competing hypotheses on the phylogenetic position of *Dinogeophilus* (within Geophilidae vs. within Schendylidae; see Introduction), the sequences of *Dinogeophilus* (16S, 18S, 28S rRNA) were compared with all homologous sequences available in GenBank for species of Geophilidae and Schendylidae. Following the cladistic revision proposed by Bonato *et al.* (2014), the two families are here intended in a broader sense than the traditional one, including subgroups that have been traditionally distinguished as distinct families: Geophilidae includes

Table 1. Morphological characters that are considered informative on the phyletic position of *Dinogeophilus* within either Geophilidae or Schendylidae. Characters are listed in anatomical order, anterior to posterior.

character	Geophilidae	Schendylidae	*Dinogeophilus*	illustrations	phylogenetic interpretation of character state in *Dinogeophilus*
cephalic plate: scutes: average area	usually <80 µm^2	usually >80 µm^2	100 µm^2	Fig. 1A	synapomorphy of Schendylidae, but with instances of convergence and reversal
labrum: posterior margin: denticles	absent	present	present, few	Fig. 2A Pereira, 1984: Fig. 26	synapomorphy of Himantarioidea
mandible: lamellae: number	1	2	1	Fig. 2A Pereira, 1984: Fig. 27	synapomorphy of Geophiloidea
second maxillae: pretarsus: shape of distal part	usually uniformly tapering	flattened	flattened	Fig. 2B Pereira, 1984: Fig. 42	synapomorphy of Himantarioidea
second maxillae: pretarsus: filaments	absent	present	present, few	Fig. 2B Pereira, 1984: Figs 42-43	? symplesiomorphy shared with Schendylidae
trunk: anterior metasternites: pore-fields: number and position	1 or more, often posterior	1, usually sub-central	1, sub-central	Fig. 2C Pereira, 1984: Figs 32-34	? symplesiomorphy shared with Schendylidae
leg: pretarsus: posterior accessory spines: number	1	>1	2	Fig. 2F Pereira, 1984: Fig. 50	synapomorphy of Schendylidae, but with instances of convergence
ultimate leg-bearing segment: telopodite: shape	often inflated in male	often inflated in both sexes, especially mesalwards	inflated in both sexes, especially mesalwards	Fig. 2G Pereira, 1984: Figs 36, 44	synapomorphy of part of Schendylidae
postpedal segments: female gonopods: separation	no	yes	yes	Fig. 2H	symplesiomorphy shared with Schendylidae
postpedal segments: female gonopods: structure and shape	uni-articulate, shortened	bi- or uni-articulate,	uni-articulate, rounded-tipped	Figs 1C, 2H	synapomorphy of part of Schendylidae

'Aphilodontidae', 'Dignathodontidae' and 'Linotaeniidae'; Schendylidae includes 'Ballophilidae'. We considered all species of Geophilidae and Schendylidae for which sequence fragments were available and alignable for at least two of the three genes. Many of these sequences had been obtained directly in our laboratory using the same protocol (Bonato *et al.*, 2014). Homologous sequences were aligned for the single genes by means of ClustalW implemented in MEGA 6.06 (Tamura *et al.*, 2013).

We performed a similarity analysis of the molecular sequences by estimating alternative measures of pairwise distance (proportion of positions with different nucleotides, p-distance; distance according to the Kimura 2-parametres model, K2P) and clustering by the neighbour joining algorithm (NJ). Standard errors of the estimates were calculated by means of 1000 bootstrap replicates. This approach mirrors the common DNA-barcoding methodology for species identification, extended to above-species taxa (Wilson *et al.*,
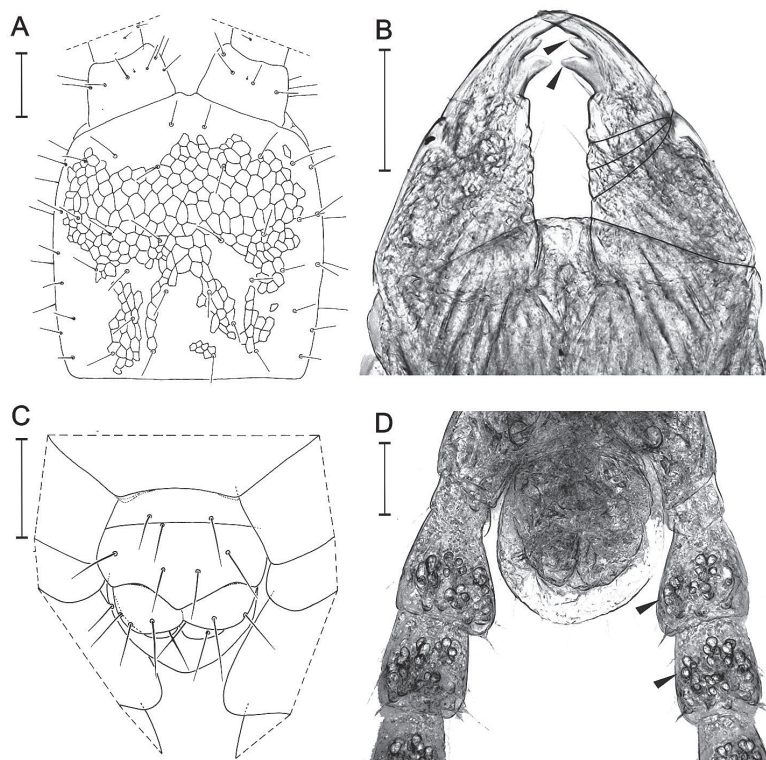
Fig. 1. Dinogeophilus oligopodus, LM. A. Cephalic plate, dorsal view; scutes are partially omitted. B. Forcipules, ventral view; articulations are marked on the left forcipule; arrow-heads indicate the subterminal denticles. C. Postpedal segments, ventral view; setae are partially omitted. D. Basal part of the legs of the ultimate pair, ventral view; arrow-heads indicate internal vesicular structures. Scale bars: 50 μm. Photographs taken from a 4.5 mm long female from Puerto Iguazú, 15.vi.1985. Line-drawings from a 5.5 mm long female from La Plata, 14.iv-3.v.1986.

2011). We also performed the analysis by applying the minimum evolution (ME) criterion.

We performed a phylogenetic analysis of the molecular sequences, employing alternative criteria of optimization, including maximum likelihood (ML) and maximum parsimony (MP). The trees were rooted assuming the monophyly of the Schendylidae, which is supported by all previous molecular analyses (Edgecombe and Giribet, 2004; Murienne *et al.*, 2010; Bonato *et al.*, 2014). For the ML, the best-fit models of nucleotide substitution were selected according to the corrected Akaike information criterion (AICc) and the Bayesian information criterion (BIC). The statistical support of the nodes was tested by means of 1000 bootstrap replications. The MP tree was searched by 1000 replicates of random additions, using the Tree-Bisection-Reconnection algorithm.

For the terminology of the anatomical parts we follow Bonato *et al.* (2010). The analyses of the molecular sequences were performed with MEGA 6.06 (Tamura *et al.*, 2013). The three genes were analysed both separately and concatenated. Differences of genetic distances between groups were tested for statistical significance with the Mann-Whitney U test (MW).

Results

Morphological evidence

After LM and SEM examination of representative specimens, and after revisiting all previously published descriptions and illustrations, we found different morphological characters that are possibly informative on the phylogenetic position of *Dinogeophilus*. These are summarised in Table 1 and described in the following lines. A complete revised diagnosis of *Dinogeophilus* is provided in Appendix 2.

Cephalic plate. When comparing the polygonal reticulation of the head of different species of Geophilomorpha (Moretto *et al.*, 2015), the average area of the scutes in *Dinogeophilus* (about 100 μm^2; Fig. 1A) is well within the range of variation estimated for the Schendylidae to the exclusion of the ballophilines (about 80-120 μm^2, calculated on five species), whereas it is remarkably higher than the range of variation estimated for the Geophilidae (40-80 μm^2, calculated on 9 species) with the only exception of a subgroup distinguishable as Ribautiinae (80-100 μm^2, measured in five species).
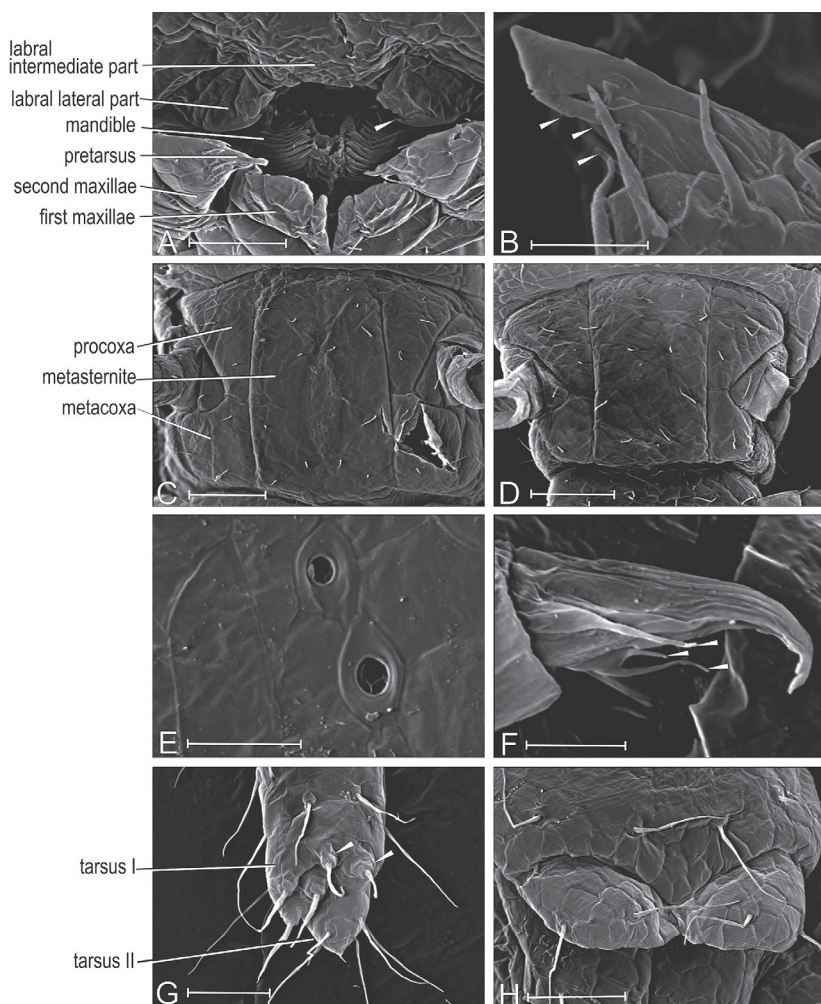
Fig. 2. Dinogeophilus oligopodus, SEM. A. Mouth, with surrounding labrum, mandibles and maxillae; arrow-heads indicate labral denticles. B. Left pretarsus of the second maxillae; arrow-heads indicate filaments. C. Leg-bearing segment 3. D. Leg-bearing segment 28. E. Glandular pores on metasternite of leg-bearing segment 7. F. Pretarsus of the left leg of the pair 10; arrow-heads indicate the accessory spines. G. Distal part of the right leg of the ultimate pair; arrow-heads indicate two of the large setae associated with internal vesicular structures (Fig. 1D). H. Gonopods. All pictures are in ventral view. Scale bars: 5 μm (B, E, F); 20 μm (A, G, H); 50 μm (C, D). Micrographs from a 5.5 mm long male (C, E) and a 5.0 mm long female (A-B, D, F-H), both from La Plata, 19. xii.1985.

Labrum. Along the posterior margin of the labrum, one or two projections are present on each lateral part (Fig. 2A). In ventral view, these projections are subtriangular, stout and pointing mesally. These features distinguish the so-called 'denticles' (present exclusively on the labrum of the Himantarioidea, which includes Schendylidae) from other kinds of projections. The condition found in *Dinogeophilus* (denticles very few, inconspicuous, and limited to the lateral part of the labral margin) is similar to the condition documented in some Schendylidae, especially in ballophiline species classified either in *Ballophilus* Cook, 1896 or in *Ityphilus* Cook, 1899 (*e.g.*, Ribaut, 1914; Pereira *et al.*, 1994). Instead, it is different from the most common and putatively basal condition found in Geophilidae (intermediate 'tubercles' and lateral 'bristles') and other derived conditions found in this family

(Bonato *et al.*, 2014). It is quite different with respect to cases of remarkable reduction of labral projections, *e.g.* in the aphilodontines (*e.g.*, Silvestri, 1909b; Attems, 1929).

Mandible. The distal margin of the mandible of *Dinogeophilus* bears a single row of projections (Silvestri, 1909b; Pereira, 1984; Fig. 2A). Shape, size and sclerotization of the projections vary only slightly and gradually along the row, without any abrupt transition suggesting a composite origin of the apparently single lamella. Moreover, we could not recognise any rudiment of other lamellae. The presence of a single pectinate lamella on the mandible is a well-established synapomorphy of the Geophiloidea, while two lamellae have been invariantly recognized in all Schendylidae and more than two in all other Geophilomorpha (Bonato *et al.*, 2014). However, the mandibles are quite

variable within the Schendylidae: the two lamellae may be aligned and contiguous, with one often more sclerotized and modified in shape, or instead imbricated and similar to each other; in some species (*e.g.*, *Plesioschendyla confossa* Ribaut, 1923), the two lamellae are aligned but weakly distinguishable from each other (Ribaut, 1923).

Second maxillary pretarsus. The pretarsus of the second maxillae of *Dinogeophilus* has a rounded tip, which is distinctly flattened (Fig. 2B). Three projections emerge from the basal part of the pretarsus, one on the ventral side, the other two on the dorsal side. These projections are elongate and point distally. A shallow-domed sensillum is present at about midlength on the ventral side of the pretarsus. A more or less evident flattening of the pretarsus towards the tip is a synapomorphy of the Himantarioidea, although weakly manifested in some derived clades (Chalande and Ribaut, 1909). The presence of elongate projections ('filaments') like those in *Dinogeophilus* is common to different geophilomorph families, among which the Schendylidae, and could be a basal condition in the Adesmata, which comprises Geophiloidea and Himantarioidea (Bonato *et al.*, 2014). On the contrary, no filaments are present in some other families, including Himantariidae and Geophilidae, possibly because of convergent evolution (Bonato *et al.*, 2014).

Ventral pore-fields. Clusters of glandular pores are present on the ventral side of the trunk of *Dinogeophilus* (Fig. 2C), but only on the approximately anterior fourth of the trunk (Fig. 2D) and to the exclusion of the first leg-bearing segment. The microstructural features of these pores (Fig. 2E) and their arrangement suggest that they are homologous to the so-called pore-fields known in most Adesmata. In particular, in *Dinogeophilus* a single pore-field is present on each metasternite, in a subcentral position, and can be described as approximately subelliptical and remarkably elongate longitudinally (Fig. 2C). For their sub-central position on the metasternites, the pore-fields of *Dinogeophilus* resemble most closely those found in some Schendylidae (*e.g.*, in some species of *Ityphilus*, where pore-fields are however rarely elongate longitudinally; Pereira, 2013b). Conversely, they are very different from the putative basal condition within the Geophilidae (pore-fields wider than long, centred on the posterior part of the metasternite, and often accompanied by additional anterior pore-fields; Bonato *et al.*, 2014), as well as from all the many derived conditions found in some Geophilidae (Turcato *et al.*, 1995).

Legs. The locomotory legs of *Dinogeophilus* are provided with a total of three accessory spines: besides a single anterior spine, two posterior spines are usually detectable, even though one is often shorter and narrower than the other (Fig. 2F). While in most centipedes the pretarsi of the legs are provided with only two accessory spines, one anterior and one posterior, in all Mecistocephalidae and all Schendylidae they bear a third spine, close to the posterior one, or even more additional spines (Bonato *et al.*, 2014). Such conditions could be interpreted as independently evolved in the two families.

Ultimate leg-bearing segment. In *Dinogeophilus* the legs of the ultimate pair are distinctly different from those of all other pairs: all articles are conspicuously inflated and especially the prefemur is distinctly bulging on its mesal side at its distal end; additionally, the leg ends with a single short spine instead of a claw-like pretarsus (Fig. 2G). The same condition is common to male and female adults, without obvious sexual dimorphism. The legs of the ultimate pair are variously modified in most Epimorpha, but the particular combination of modified features found in *Dinogeophilus* (legs mesally inflated and ending with a spine, in both sexes) is found only in some schendylids, especially in species belonging to some of the largest genera, like *Schendyla* Bergsøe and Meinert, 1866, *Pectiniunguis* Bollman, 1889 and *Schendylops* Cook, 1899 (see, *e.g.*, Brolemann, 1930; Pereira and Minelli, 1996). Conversely, somehow similar conditions are very rare among the diverse Geophilidae, like *e.g.* in *Dignathodon* Meinert, 1870 (however without mesal bulges, and with some trace of claws; Brolemann, 1930).

Gonopods. In *Dinogeophilus* females, the gonopods are two paired appendages, touching each other at their bases but distinctly separated. The contour of each gonopod is stoutly rounded and no intermediate articulation is detectable (Fig. 2H). In shape, structure and relative position, these gonopods resemble those commonly found in the females of most Schendylidae (Brölemann and Ribaut, 1912). Indeed, paired, uni-articulate, rounded-tipped gonopods could be a synapomorphy of a subgroup of Schendylidae. Conversely, in all female Geophilidae the pair of gonopods is invariantly represented by a single, significantly shorter lamina, at most shallowly bilobate. In most other geophilomorphs, instead, female gonopods are separate, but usually bi-articulated at full development and pointed at the tip (Bonato *et al.*, 2014).

Summing up, in *Dinogeophilus* we detected many characters (referring to different body parts) that may correspond to synapomorphies for the Schendylidae, or for a subgroup of Schendylidae, or for the parental superfamily Himantarioidea. Conversely, in *Dinogeophilus* we found a single character (referring to the shape of the mandible) that could be interpreted as a synapomorphy for the superfamily Geophiloidea. Additionally, *Dinogeophilus* shares with Schendylidae other characters that are represented in Geophilidae by a different state, which is recognised as a synapomorphy of the latter.

Molecular evidence

After aligning the sequences of the 16S, 18S and 28S rRNA genes of *Dinogeophilus* with those of 21 species of Geophilidae and 7 species of Schendylidae (Appendix 3), we obtained a concatenated sequence of 5913 positions. The average genetic distance between species of Geophilidae was found similar to the average distance between species of Schendylidae (Table 2; MW: p = 0.70 for both p-distances and K2P distances), and the average distance between species in different families was found significantly higher than between species in the same family (MW: p = 0.00 for both Geophilidae and Schendylidae, and for both distances). The sequence of *Dinogeophilus* was found more similar on average to those of Schendylidae than to those of Geophilidae, even though without statistical significance (MW: p = 0.16 for p-distances, p = 0.18 for K2P distances). In both NJ and ME analyses (Fig. 3A), *Dinogeophilus* clustered together with all Schendylidae, and to the exclusion of all Geophilidae, with high statistical support. This came out from alternative analyses performed on p-distances and K2P distances, the only differences regarding the relative positions of some species within Geophilidae and within Schendylidae.

For the ML phylogenetic analysis of the concatenated sequences, the GTR+G+I substitution model (selected as the best-fit model under AIC) and the K2P+G+I model (selected under BIC) produced two fully consistent trees (Fig. 3B). *Dinogeophilus* was found well nested within the Schendylidae, and the entire group of Schendylidae including *Dinogeophilus* was strongly supported. The species of Schendylidae included in the analysis were found representatives of four moderately to strongly supported clades: (i) *Plesioschendyla confossa* (New Caledonia) (ii) species of *Pectiniunguis* and *Schendylops* (mainly Neotropical schendylines), (iii) species of *Hydroschendyla* and *Schendyla* (mainly Palearctic schendylines), and (iv) species of *Ballophilus* and *Ityphilus* (ballophilines). *Dinogeophilus* was found to belong to clade ii, together with schendylines from the Neotropical region.

From the MP of the concatenated sequences, we obtained four equally most parsimonious trees, from 1352 informative positions, with consistency index 0.40 and retention index 0.51. The MP trees were 821 step long and their strict consensus (Fig. 3C) was consistent with the ML tree (Fig. 3B) in recovering a monophyletic Schendylidae including *Dinogeophilus*, but with a more ambiguous position of the latter either closer to the Neotropical schendylines or the ballophilines.

Discussion

The phyletic position of Dinogeophilus

The anatomical and molecular data presented here concur in providing compelling evidence that *Dinogeophilus* originated within the Schendylidae rather than within the Geophilidae as previously thought. The phyletic position of *Dinogeophilus* has been hitherto remarkably misunderstood, because the two families are only very distantly related according to the consensus phylogeny of the Geophilomorpha derived from modern analyses of molecular and morphological data (Edgecombe and Giribet, 2007; Murienne *et al.*, 2010; Bonato *et al.*, 2014): after the basal emergence of the Mecistocephalidae, the separation between Geo-

Table 2. Pairwise genetic distances between species, including *Dinogeophilus oligopodus*, 21 species of Geophilidae and 7 species of Schendylidae (Appendix 3). Averages are given, together with the range of variation in squared brackets.

	within Geophilidae	within Schendylidae	Geophilidae vs. Schendylidae	*Dinogeophilus* vs. Geophilidae	*Dinogeophilus* vs. Schendylidae
p-distance (%)	12.8 [3.6-20.7]	12.6 [5.0-18.6]	16.6 [4.7-22.0]	17.4 [10.2-19.8]	14.9 [10.7-18.6]
K2P distance (%)	14.2 [3.7-24.3]	14.0 [5.2-21.4]	18.6 [4.9-26.3]	20.0 [11.0-23.1]	16.7 [11.6-21.5]

philoidea (including Geophilidae) and Himantarioidea (including Schendylidae) was most probably the deepest split within the remaining geophilomorphs (Adesmata) (Bonato *et al.*, 2014), and this separation has been estimated to date back between 350 and 250 million years ago (Murienne *et al.*, 2010).

The long-lasting misconception appears even more remarkable if we consider that Silvestri (1909a) hypothesized that *Dinogeophilus* could be close to *Apogeophilus* Silvestri, 1905, which is undisputedly a geophilid, although still very poorly understood. Silvestri's hypothesis was eventually dismissed, because it was based on an erroneous interpretation of the articular structure of the legs of the ultimate pair in *Dinogeophilus* (Pereira, 1984). While most authors maintained *Dinogeophilus* in the Geophilidae, a very different arrangement was elaborated by Verhoeff (1925), who included *Dinogeophilus* in a very heterogeneous subfamily Chaetechelyninae inside a family Scolioplanidae, together with other genera currently recognised in different lineages of Geophilidae. Verhoeff's proposal was based on erroneous interpretations of the structure of the labrum that are now largely superseded (Koch and Edgecombe, 2012).

Many of the morphological characters supporting the evolutionary emergence of *Dinogeophilus* within the Schendylidae had been already described and illustrated correctly, at least for *D. oligopodus* (Pereira, 1984): denticle-like projections on the labral margin, branching pretarsi on the second maxillae, longitudinally elongate pore-fields, additional minute accessory spines on the leg pretarsi, peculiarly modified legs of the ultimate pair, uni-articulate and separate gonopods in the female. However, some of these characters have been hitherto underestimated for their value in inferring phylogeny and driving classification, or even fully ignored (especially the structure of the female gonopods; Bonato *et al.*, 2014). Conversely, a major role in perpetuating the misplacement of *Dinogeophilus* within the Geophilidae has been played most probably by the primary diagnostic value so far attributed to the shape of the mandibles, especially to the number and diversity of the lamellae (*e.g.*, Attems, 1929). Our observations confirm previous reports (Silvestri, 1909a; Pereira, 1984) that the mandibles of *Dinogeophilus* resemble more the unilamellate mandibles of the Geophilidae than the bilamellate mandibles of the Schendylidae. Therefore, we should hypothesize that the unilamellate mandible found in *Dinogeophilus* derives from the bilamellate mandible of Schendylidae, independently from the similarly unilamellate mandible of

A   0.02
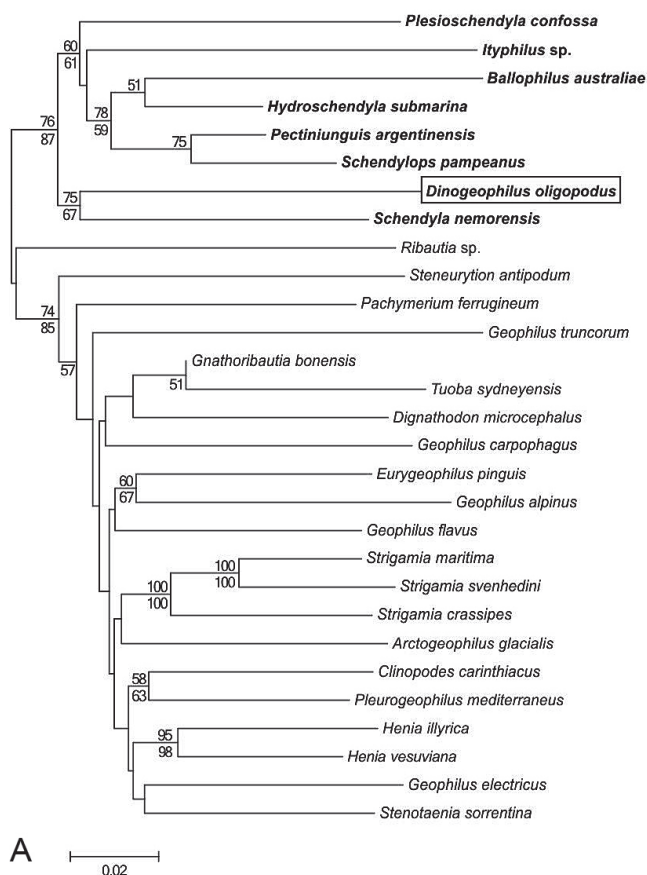
all Geophiloidea, which instead derives from a multilamellate mandible (Bonato *et al.*, 2014).

Miniaturization, paedomorphosis and evolutionary novelties in Dinogeophilus

While for most species of Epimorpha accurate measurements of body size are scarce and poorly comparable, for *Dinogeophilus* a more satisfactory estimate of maximum body length is allowed by multiple and unusually precise measures. All thirteen specimens collected so far are adults or at least subadults (according to the shape and relative size of the gonopods) and all have been measured with a precision of at least 0.5 mm. All these specimens have been found to be between 4.5 mm long (most specimens of *D. oligopodus*)
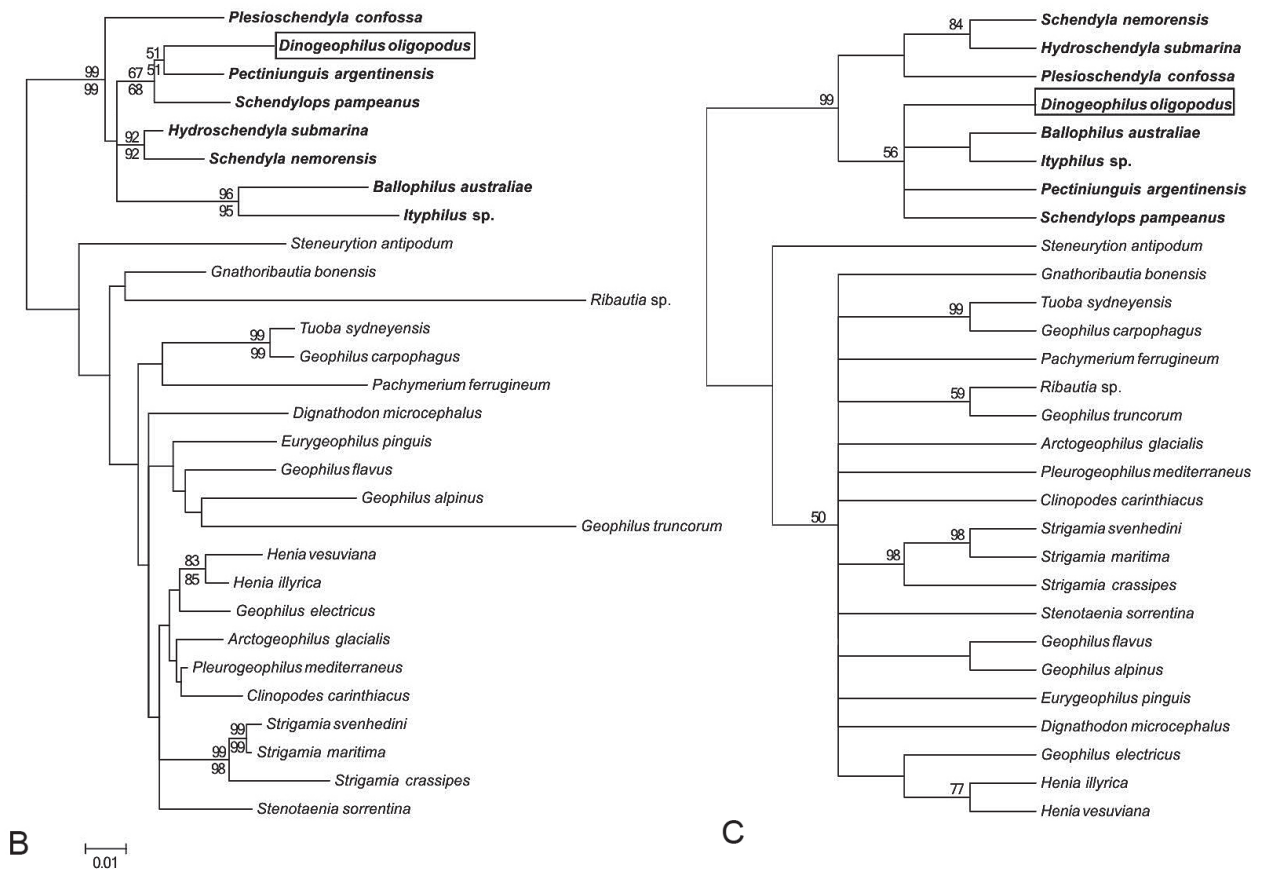
Fig. 3. Similarity analysis and phylogenetic analyses of the concatenated sequences of 16S, 18S and 28S rRNA genes of *Dinogeophilus oligopodus* and representative species of Geophilidae and Schendylidae. Bootstrap percentages are not shown when <50%. A. NJ and ME tree (bootstrap percentages: above node, using p-distances; below nodes, using K2P distances). B. ML tree (bootstrap percentages: above node, using the GTR+G+I model; below nodes, using the K2P+G+I model). C. MP consensus tree. Species of Schendylidae are in bold.

and 5.5 mm long (only the single specimen of *D. pauropus*; Silvestri, 1909a). Therefore, as far as known, with an estimated maximum length of 5.5 ± 0.5 mm, *Dinogeophilus* comprises the smallest species in the Epimorpha. A maximum body length of at least 7 mm has been found in all other species for which at least half a dozen specimens have been measured, and no less than 6.5 mm are reported for the species known from a single adult only (Appendix 1). When considering the whole of Chilopoda, the minute body size of *Dinogeophilus* is paralleled by a few lineages of lithobiomorphs, which are reported to be as short as about 5 mm at full growth, or even smaller, especially among the Anopsobiinae and the Lithobiinae (Bonato *et al.*, 2011).

Considering the larger body size of all other extant

Schendylidae (most of which grow up to more than one or few centimetres; reviewed in Bonato *et al.*, 2011), it is probable that the evolutionary differentiation of *Dinogeophilus* was accompanied by body miniaturization, *i.e.* by a distinct reduction of the overall size (Hanken and Wake, 1993). Actually, a thorough evaluation of this hypothesis would require comparing *Dinogeophilus* with the most closely related species, considering also the internal anatomy and focussing on the earlier postembryonic stages, which are expected to be the critical stages constraining body miniaturization (Polilov, 2015). However, the precise phyletic position of *Dinogeophilus* among the schendylids is still uncertain (Fig. 3) and anatomical and developmental investigations are currently unpractical for small and rarely collected epimorphic centipedes (see, *e.g.*, Brena, 2014).

Structural and morphological correlates of body miniaturization have been detected in many animal groups, providing evidence that size reduction may sometimes be so dramatic as to reach a critical size at which physical constraints or physiological processes may favour or require major changes (Hanken and Wake, 1993; Polilov, 2015). Thorough investigations have been carried on especially in lineages of vertebrates, hymenopterans and coleopterans, not so in myriapods.

When comparing *Dinogeophilus* with all other Schendylidae or the schendylid clades that are possibly most closely related to *Dinogeophilus* (the other mainly Neotropical genera *Pectiniunguis schendylops*, as suggested by our phylogenetic analysis; Fig. 3B-C), different morphological elements that are usually found in multiple numbers in adult schendylids are greatly reduced in number in *Dinogeophilus*. This is the case for the antennal sensilla, the filaments on the second maxillary pretarsi, the denticles on the labrum, and the coxal organs (Pereira, 1984; Table 1). In all geophilomorphs, all these integumental elements increase in number with growth, moult after moult, but in *Dinogeophilus* the number found at full growth is lower than usually found in adults of other species. In the same way, some structural elements that usually grow in size along with the entire body are significantly smaller in adult *Dinogeophilus* than in the adults of other schendylids. This is especially the case of the setae covering most part of the body (up to about 30 μm long, with the exception of longer setae on the ultimate pair of legs). As a matter of fact, because adults of *Dinogeophilus* resembles juveniles of other schendylids (including the possibly most closest relatives) in the number and/or the size of these elements, these reductions may represent paedomorphic traits, like those recognised in other miniaturised animals (Hanken and Wake, 1993; Rundell & Leander, 2010). However, in *Dinogeophilus* they are not so obviously related to body miniaturization, because they occur also in other schendylids with broadly variable body size, including relatively large species. For instance, some species surpassing centimetres in length have nevertheless very few or no filaments on the second maxillary pretarsi also when adult (*e.g.*, in the genus *Schendyla*; Brolemann, 1930), or their labral margin is almost entirely smooth (*e.g.*, in *Ityphilus*; Pereira, 2013b), or even they maintain a single coxal organ per side at full growth (*e.g.*, in *Australoschendyla* Jones, 1996, *Marsikomerus* Attems, 1938, *Mesoschendyla* Attems, 1909; reviewed in Crabill, 1968; Hoffman and Pereira, 1991; Jones, 1996).

Besides these putative paedomorphic traits, no remarkable changes are evident in *Dinogeophilus* in many other structures of obvious functional value, *e.g.* the fine shape of the maxillary complex, the articulation and the poison apparatus of the forcipules, the system of tracheae and spiracles, the array of the ventral glands or the locomotory legs. Also with respect to the sensory apparatus *Dinogeophilus* develops the complete array of different types of sensilla that is common to all other geophilomorphs, even though for each type the number of sensilla produced during growth is lower than in other larger species. In particular, all different types of antennal sensilla found in the Schendylidae have been detected in *Dinogeophilus* as well, with the exception of the peculiar sclerotized sensilla accompanying brachyconic sensilla on the articles V, IX and XIII in most (but not all) Schendylidae (Bonato *et al.*, 2014: Table S2; often referred to as 'type c sensilla', *e.g.* Pereira, 2013b).

A few features of *Dinogeophilus* appear actually unique, or at least very unusual, in comparison to all other Schendylidae and the Epimorpha as a whole. Peculiar tubercles are present on the most posterior leg-bearing segments of the single known specimen of *D. pauropus* (Silvestri, 1909a: Figs 8-9; Pereira, 1984: Fig. 9) and have been assumed to be a diagnostic feature for that species, at least in the adult males (see Appendix 2). Moreover, at least in *D. oligopodus* (both sexes), the legs of the ultimate pair are provided with internal vesicular structures associated with large ventral setae (Figs 1D, 2G; Pereira, 1984: Figs 41, 47, 48, 57). However, it remains to investigate whether similar tubercles or vesicles occur also in other geophilomorphs. A novel feature of *Dinogeophilus* is represented by the conspicuous denticles close to the tips of the forcipules: a couple of pointed projections aligned along the intermediate part of each forcipular tarsungulum, on the concave side (Fig. 1B; Pereira, 1984: Figs 6, 7, 58). The outline of these additional denticles is remarkably uniform between specimens, and without any obvious difference between the two species *D. pauropus* and *D. oligopodus*. In the evolutionary history of the Epimorpha, bumps, tubercles or denticles originated and disappeared repeatedly, but almost exclusively on the proximal part of the tarsungula, usually basal to the rudimentary suture between the two ancestral articles comprising the entire tarsungulum (Dugon and Arthur, 2012; Maruzzo and Bonato, 2014). Conversely, additional projections evolved very rarely along the intermediate part of the tarsungula: projections in this

position are found only in single species or small lineages comprising very few species, only distantly related to each other, and are very different in shape and size. Worth noting is that most of these cases are known within the Schendylidae, *e.g.* in the single species of *Falcaryus* Shinohara, 1970 and in some species of *Ityphilus* from South America (Shinohara, 1970; Pereira, 2012, 2013b), but only weakly resembling those of *Dinogeophilus*. The peculiar denticles of *Dinogeophilus* may therefore represent an evolutionary novelty of this lineage. However, like the putatively paedomorphic traits, this novelty is not obviously associated with miniaturization, because projections in the same positions evolved also in larger species (at least 13 mm long in *Falcaryus*, and up to 9 cm in species of *Ityphilus* with denticles; Turk, 1955). The mouth parts, the poisonous apparatus and other feeding-related structures in *Dinogeophilus* are very similar to those found in all other centipedes, and any dramatic deviation can be ruled out from the predatory ecology assumed to be common to all centipedes (Edgecombe and Giribet, 2007). Nevertheless, the unique shape of the forcipules of *Dinogeophilus* (strongly tapering into strong trifurcate tips; Fig. 1B) is suggestive of some functional changes in the mechanics of the preying apparatus and, possibly, in the feeding habits. In general, however, the trophic ecology and predatory behaviour are almost completely unexplored in the entire Geophilomorpha.

Acknowledgements

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Appendix 1

Species of Epimorpha for which the maximum body length measured in adults is 11 mm or less. In squared brackets: maximum length, number of measured specimens to the exclusion of those reported as juveniles, main references.

Cryptopidae: *Cryptops angolensis* Machado, 1951 [7 mm; 6 exx.; Machado, 1951], *C. calinus* Chamberlin, 1957 [11 mm; 2 exx.; Chamberlin, 1957], *C. cubanus* Matic, Negrea & Fundora Martinez, 1977 (11 mm; 1 ex.; Matic *et al.*, 1977), *C. daszaki* Lewis, 2002 [7.5 mm; 6 exx.; Lewis, 2002], *C. erkowiti* Lewis, 1967 [8.5 mm; 1 ex.; Lewis, 1967], *C. ethophor* Chamberlin, 1920 [9 mm; ≥2 exx.; Chamberlin, 1920a], *C. heathi* Chamberlin, 1914 [10 mm; 1 ex.; Chamberlin, 1914], *C. livius* Chamberlin, 1951 [10 mm; >2 exx.; Chamberlin, 1951], *C. manni* Chamberlin, 1915 [9.5 mm; 1 ex.; Chamberlin, 1915], *C. melanotypus* Chamberlin, 1941 [8.5-9 mm; 1 ex.; Chamberlin, 1941], *C. micrus* Chamberlin, 1922 [10 mm; 1 ex.; Chamberlin, 1922], *C. nanus* Attems, 1938 [9 mm; 2 exx.; Lewis, 2011a][1], *C. navigans* Chamberlin, 1913 [11 mm; 2 exx.; Chamberlin, 1913], *C. navis* Chamberlin, 1930 [10 mm; 1 ex.; Chamberlin, 1930], *C. omissus* Ribaut, 1915 [9 mm; 1 ex.; Ribaut, 1915], *C. sankuruensis* Schubart, 1938 [9 mm; 1 ex.; Schubart, 1938], *C. stabilis* Chamberlin, 1944 [11 mm; 2 exx.; Chamberlin, 1944; Lewis, 2011b], *C. venezuelae* Chamberlin, 1939 [10 mm; 1 ex.; Chamberlin, 1939][2]

Scolopocryptopidae: *Newportia kraepelini* (Crabill, 1977) [11 mm; 1 ex.; Crabill, 1977; Shelley & Mercurio, 2008][3], *Newportia pelaezi* Chamberlin, 1942 [10 mm; 1 ex.; Chagas Junior & Shelley, 2003][4]

Mecistocephalidae: *Nannarrup hoffmani* Foddai, Bonato, Pereira & Minelli, 2003 [10.3 mm; 1 ex.; Foddai *et al.,* 2003]

Geophilidae: *Aphilodon modestus* Silvestri, 1909 [9 mm; 1 ex.; Silvestri, 1909a], *Apogeophilus claviger* Silvestri, 1905 [10 mm; 1 ex.; Silvestri, 1905], *Geophilus minimus* Verhoeff, 1928 [9.5 mm; 2 exx.; Verhoeff, 1928; Foddai & Minelli, 1999], *G. piae* Minelli, 1983 [11 mm; 15 exx.; Minelli, 1983; Zapparoli, 2011][5], *G. pinivagus* Verhoeff, 1928 [10 mm; 1 ex.; Verhoeff, 1928], *G. pusillus* Meinert, 1870 [11 mm; 5 exx.; Meinert, 1870; Bonato & Minelli, 2014], *G. richardi* Brölemann, 1904 [10 mm; >20 exx.; Minelli, 1983; Zapparoli, 2011], *Hyphydrophilus projectus* Pereira, Minelli & Barbieri, 1994 [10 mm; >20 exx.; Pereira *et al.*, 2000], *Mecophilus neotropicus* Silvestri, 1909 [8 mm; 1 ex.; Silvestri, 1909a], *'Orinophilus' platensis* Silvestri, 1898 [9 mm; ≥3 exx.; Silvestri, 1898][6], *Poaphilus kewinus* Chamberlin, 1912 [6.5 mm; 1 ex.; Chamberlin, 1912], *Ribautia combinata* Pereira, Uliana and Minelli, 2006 [9 mm; 1 ex.; Pereira *et al.,* 2006][7], *Schizotaenia prognatha* Cook, 1896 [11 mm; 13 exx.; Crabill, 1964], *Sogona vera* (Chamberlin, 1943) [10 mm; 1 ex.; Chamberlin, 1943]

Schendylidae: *Ballophilus pallidus* Attems, 1938 [11 mm; ≥3 exx.; Attems, 1938], *Caritohallex minyrrhopus* Crabill, 1960 [10 mm; 2 exx.; Crabill, 1960], *Dinogeophilus* spp. [5.5 mm; 13 exx.; Silvestri, 1909a; Pereira, 1984; this paper], *Leucolinum trinidadense* Chamberlin, 1945 [9 mm; >2 exx.; Chamberlin, 1945], *Marsikomerus arcanus* (Crabill, 1961) [10 mm; 1 ex.; Hoffman & Pereira, 1991], *Mesoschendyla franzi* Dobroruka, 1959 [10 mm; 1 ex.; Dobroruka, 1959], *M. javanica* (Attems, 1907) [10 mm; 1 ex.; Attems, 1907][8], *Morunguis morelus* Chamberlin, 1943 [10 mm; 1 ex.; Chamberlin, 1943], *Schendyla armata* Brölemann, 1901 [11 mm; >20 exx.; Brolemann, 1930; Zapparoli, 2011], *S. gracillima* Verhoeff, 1934 [10 mm; ≥2 exx.; Verhoeff, 1943], *S. verneri* (Folkmanová & Dobroruka, 1960) [10 mm; ≥2 exx.; Folkmanová & Dobroruka, 1960], *Schendylellus hodites* Chamberlin, 1920 [7.5 mm; 1 ex.; Chamberlin, 1920b], *Schendylops minutus* (Pereira & Minelli, 1993) [11 mm; 1 ex.; Pereira & Minelli, 1993], *S. oligopus* Pereira, Minelli & Barbieri, 1995 [10 mm; >20 exx.; Pereira, 2013a], *S. ramirezi* Pereira, 2013 [7 mm; 11 exx.; Pereira, 2013a], *Sogolabis scapheus* Chamberlin, 1920 [8 mm; 1 ex.; Chamberlin, 1920b], *Taeniolinum panamicum* Chamberlin, 1940 [11 mm; 1 ex.; Chamberlin, 1940]

Notes. [1] both specimens are suspected to be juveniles (Lewis, 2011a); [2] the congeneric *C. gracillimus* Machado, 1951 is known for a single specimen, 6.0 mm long, which however is almost certainly a juvenile (Lewis, 2013); [3] the very similar *Newportia sandrops* (Schileyko, 2009) is known for a single specimen, 11-12 mm long (Schileyko, 2009); [4] the single known specimen has been considered a juvenile (Chagas Junior & Shelley, 2003); [5] measured specimens up to 12 mm long belong to either this species or the very similar *G. minimus*, and a single specimen of *G. piae* has been measured 15 mm long but it features as an outlier (Zapparoli, 2011); [6] the taxonomic position is uncertain, possibly a species of *Ribautia* (Pereira, 2014); [7] the single known specimen has been reported as a

female (Pereira *et al.*, 2006), but the anatomy of the genital region suggests a juvenile without gonopods; [8] the measure has been taken including the antennae (Attems, 1907).

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Appendix 2

Taxonomic account

Superfamily Himantarioidea Bollman, 1893
Family Schendylidae Cook, 1896
Genus *Dinogeophilus* Silvestri, 1909

Type-species. *Dinogeophilus pauropus* Silvestri, 1909 (by original designation)
Other species included. *Dinogeophilus oligopodus* Pereira, 1984

Diagnosis. Schendylids without denticles on the intermediate part of the labral margin, only a few denticles on the lateral parts; a single lamella on the mandible; second maxillary pretarsus slightly spatulate and with a few slender spines; forcipular coxosternite with incomplete chitin-lines; forcipules with denticles along the intermediate part of the tarsungulum; pore-fields elliptical, longitudinally elongate only on the anterior part of the trunk; a single coxal pore on each coxopleuron, corresponding to a homogeneous coxal organ; telopodite of the ultimate leg pair of six articles, swollen in both sexes, without claw but with a tiny apical spine; female gonopods uniarticulate, touching only at their bases; no anal pores.

Notes on the differences between species. The distinction of two species of *Dinogeophilus* was originally based on a series of differences found between the two male holotypes (Pereira, 1984). However, an adequate evaluation of the diagnostic value of most characters is hindered by the fact that a single specimen is known for *D. pauropus* and this is in bad conditions, lacking the head, and included in a microscopic slide (Pereira, 1984). Actually, some of the putative differences originally scored appear today of questionable diagnostic value, because they may be affected by intraspecific variation, as demonstrated in other geophilomorphs. This is the case of the position of the tips of the forcipules relative to the anterior margin of the head, the density of setae on the trunk (especially on the posterior part of the body), the number of sternal pores and the longitudinal extent of the pore-fields along the series of the trunk segments, the density of setae on the ventral side of the ultimate leg-bearing segment (especially on the posterior part of the metasternite and the mesal part of the coxopleura) at least in adult males, and the elongation of the metatergite of the ultimate leg-bearing segment. Although the intraspecific variability of *D. pauropus* remains un-known, candidate differential characters between the two species are the following: presence (*D. pauropus*) vs. absence (*D. oligopodus*) of tubercles on the surface of the most posterior leg-bearing segments, at least in adult males; 31 pairs of legs (*D. pauropus*) vs. 29 pairs of legs (*D. oligopodus*).

Geographical distribution. Specimens of *Dinogeophilus* have been collected so far in three localities, all in the lower and middle part of the basin of the Paraná and Uruguay rivers, between the Brazilian Highlands and the northern part of Pampas: near Salto, along the Uruguay river (Silvestri, 1909a; *D. pauropus*); near Puerto Iguazu, close to the Paraná river (Pereira, 1984; *D. oligopodus*); La Plata, close to the mouth of the rivers (new record; *D. oligopodus*).

Appendix 3

Species of Geophilidae and Schendylidae for which DNA sequences were analysed, with collection codes of the specimens (localities and dates of collection given in Bonato *et al.*, 2014: Table S1), GenBank accession codes of the sequences and total length of the concatenated sequences.

family	species	specimen code	28S	18S	16S	base pairs
-	*Dinogeophilus oligopodus* Pereira, 1984	PD1003	KF569284	KF569263	KF569240	3890
Geophilidae	*Arctogeophilus glacialis* (Attems, 1909)	UAM100040031a	KF569268	KF569247	KF569224	4462
	Clinopodes carinthiacus (Latzel, 1880)	PD568	KF569269	KF569248	KF569225	4435
	Dignathodon microcephalus (Lucas, 1846)	PD583	–	KF569245	KF569221	2585
	Eurygeophilus pinguis (Brölemann, 1898)	PD535	KF569271	KF569249	KF569226	3614
	Geophilus alpinus Meinert, 1870	PD626	KF569271	KF569250	KF569227	4363
	Geophilus carpophagus Leach, 1815	PD611	KF569272	KF569251	KF569228	4447
	Geophilus electricus (Linnaeus, 1758)	-	HM453296	AY288700	AY288732	3719
	Geophilus flavus (De Geer, 1778)	PD699	KF569273	KF569252	KF569229	4167
	Geophilus truncorum Bergsøe & Meinert, 1866	PD956	KF569274	KF569253	KF569230	4610
	Gnathoribautia bonensis (Meinert, 1870)	PD700	KF569275	KF569254	–	1799
	Henia illyrica (Meinert, 1870)	PD656	KF569267	KF569246	KF569222	4375
	Henia vesuviana (Newport, 1845)	PD761	HM453304	AF173255	KF569223	2832
	Pachymerium ferrugineum (Koch, 1835)	-	HM453301	AY288702	AF370863	2976
	Pleurogeophilus mediterraneus (Meinert, 1870)	PD694	KF569277	KF569255	KF569232	4303
	Ribautia sp.	-	HM453300	AF173263	AY288736	3754
	Steneurytion antipodum (Pocock, 1891)	-	HM453299	AF173261	AY288734	4248
	Stenotaenia sorrentina (Attems, 1903)	PD601	KF569278	KF569256	KF569234	4227
	Strigamia crassipes (Koch, 1835)	PD692	KF569282	KF569261	KF569238	4358
	Strigamia maritima Leach, 1817	-	HM453303	AF173265	AY288733	3762
	Strigamia svenhedini (Verhoeff, 1933)	ZMUC1006	KF569283	KF569262	KF569239	3944
	Tuoba sydneyensis (Pocock, 1891)	-	HM453297	AF173260	HM453231	3840
Schendylidae	*Ballophilus australiae* Chamberlin, 1920	-	HM453292	AF173258	–	3827
	Hydroschendyla submarina (Grube, 1872)	PD957	–	KF569264	KF569241	2392
	Ityphilus sp.	PD1278	KF569266	KF569244	KF569220	4152
	Pectiniunguis argentinensis Pereira & Coscarón, 1975	-	HM453294	AF173256	HM453230	2694
	Plesioschendyla confossa Ribaut, 1923	-	HM453295	AY288699	AY288731	3389
	Schendyla nemorensis (Koch, 1837)	PD631	KF569287	KF569265	KF569243	3869
	Schendylops pampeanus (Pereira and Coscarón, 1976)	-	HM453293	AF173257	–	3752