316

Zoological Journal of the Linnean Society (1995), *115*: 185–209. With 25 figures

The sternal pore areas of geophilomorph centipedes (Chilopoda: Geophilomorpha)

ALESSANDRA TURCATO, GIUSEPPE FUSCO, AND
ALESSANDRO MINELLI, F.L.S.

Dipartimento di Biologia dell'Università, Via Trieste, 75, I 35121 Padova, Italy

Received October 1994, accepted for publication January 1995

Most geophilomorph centipedes have segmental clusters of exocrine glands whose opening pores are arranged in more or less well-defined sternal pore areas. We describe here the cuticular structures forming and/or accompanying the gland openings on the sternites and the shape of the pore areas along the body axis in representatives of most geophilomorph families. The cuticular ring around the pore may exhibit either of two forms. In Himantariidae (*Himantarium*) and in Dignathodontidae (*Henia*) the ring looks like a continuous ribbon with a visible suture, whereas in the representatives of the remaining families no suture is seen. As to the distribution of the pores on ventral surface of the body, we record the presence of pores on the last leg-bearing segment of *Clinopodes flavidus*, whereas that segment was described as poreless in all geophilomorphs. We also provide a taxonomic survey of shape and distribution of pore areas in the individual families, where the pore areas may take very different shapes that we regard as transformational homologues. As for the segmental distribution of sternal pore areas, there is a considerable amount of complexity along the trunk of geophilomorph centipedes, in contrast to the apparently uniform trunk structure.

ADDITIONAL KEY WORDS:—homology – serial homology – positional homology.

CONTENTS

INTRODUCTION

Most geophilomorph centipedes have voluminous clusters of exocrine glands whose opening pores are arranged in ventral areas known as sternal pore areas (SPAs).

These glands have been studied from a histological point of view by Brade-Birks & Brade-Birks (1920) and by Koch (1927); their fine structure

0024–4082/95/010185+25 $12.00/0

has been investigated more recently by Turcato & Minelli (1990) on *Pleurogeophilus mediterraneus* (Meinert, 1870) and by Hopkin & Anger (1992) on *Henia vesuviana* (Newport, 1844). We are very poorly informed about the chemistry of the secretion of the glands, which seems to be quite different within the order: Jones *et al.* (1976) reported the presence of cyanide derivatives in the secretion of a '*Geophilus vittatus*' (true identity uncertain), whereas Hopkin *et al.* (1990) identified proteinaceous components in the glue-like secretion of *Henia vesuviana.*

In the present paper we deal with the morphology of the cuticular structures forming and/or accompanying the gland openings on the sternites, and the shape and distribution of SPAs along the body axis.

Since the nineteenth century, taxonomists have recognized the diagnostic importance of the differences in size, form and distribution of SPAs among geophilomorph centipedes. Some references to SPAs are found in Koch (1863) and Bergsøe & Meinert (1866), but the first true comparisons and illustrations of many species were given by Meinert (1870). The prominence of these characters in geophilomorph taxonomy can be fully appreciated by a perusal of Attems' monograph (1929) and of the more recent literature. However, we do not know in detail how variable these characters are within a species and to what degree they change with age and maturity. More important, the different kinds and different segmental arrangements of SPAs have never been rationally compared with due regards to questions of serial and special homology. In addition, no effort has been made to define the polarity of the evolutionary changes between the different character states exhibited by the different taxa. Therefore, it has not been possible to identify the likely instances of homoplasy. As we will see, homoplasy seems to have occurred many times, especially when rudimentation or disappearance of the pore areas are involved.

In this paper we provide an overall review of the structure and taxonomic distribution of geophilomorph SPAs.

MATERIALS AND METHODS

By scanning electron microscopy (SEM), using a Cambridge Stereoscan 250, we examined the individual pores and the surrounding cuticular area of the following species representative of most geophilomorph families currently recognized: *Himantarium gabrielis* (Linnaeus, 1767) (Himantariidae); *Henia bicarinata* (Meinert, 1870) (Dignathodontidae); *Schendyla carniolensis* Verhoeff, 1902 (Schendylidae); *Ballophilus* sp. (Ballophilidae); *Orya barbarica* (Gervais, 1835) (Oryidae); *Geophilus richardi* (Brölemann, 1904), *Geophilus insculptus* Attems, 1895, *Clinopodes flavidus* Koch, 1847 and *Pleurogeophilus mediterraneus* (Meinert, 1870) (Geophilidae); *Strigamia crassipes* (Koch, 1835) (Linotaeniidae); *Dicellophilus carniolensis* (Koch, 1847) (Mecistocephalidae).

Size, shape and distribution along the body axis of SPAs have been observed on lactophenol cleared specimens of *c.* 100 species. For species we were unable to study personally, we obtained information from Attems (1929) and more recent literature (see Table 1). Taxonomic work of the senior author currently in progress has been incorporated into our database.

During our original investigations we quickly realized the unreliability of

TABLE 1. Homogeneous and heterogeneous SPASPs in the individual families of Geophilomorpha. Letters refer to the SPAs patterns shown in Fig. 25. Ø no pores on the sternite; # sparse pores on the sternite.

Family	SPASPs	Refs.
Himantariidae	hom: Ø, #, B, C, D het: ABC, BC, BØ, CØ, DØ	*1–26*
Dignathodontidae	hom: Ø, E, F, G	*1, 27*
Oryidae	hom: Ø, #, H, I, L, M het: HN, ILK, ILN, JL, JØ	*1, 28–41*
Eriphantidae	het: OP	*42*
Gonibregmatidae	hom: Ø, Q, U, V, W het: QRQ, WTS, WU	*1, 33, 43–45*
Schendylidae	hom: Ø, d, f het: aha, bcb, dc, df, dh, ed, eh, ehe, fhf, gfd, aØ, bØ, cØ, dØ, dcØ, dfØ, dhØ, eØ, ehØ, fØ	*1–2, 7–8, 18, 23, 27–28, 33, 37, 39, 41, 46–87*
Ballophilidae	hom: #, i, j, k, l, m, n,	*1, 3, 8, 30, 32, 37, 39, 41, 48, 59–60, 88–98*
Geophilidae	hom: Ø, #, *a, c, d, e, f, g, h, j, m* het: Ø*bcb*, Ø*e, cdg, cf, cg, cgc, df, dg, dgd, dge, dfg, dgh, dmjf, eg, ege, egm, fc, fd, fe, fg, fge, fgf, fhf, foj, ghg, gj, glf, hf, hg, hj, ihjh, jgf, jhj, klf, mhg, nm, c*Ø, *d*Ø, *df*Ø, *dg*Ø, *e*Ø, *f*Ø, *fc*Ø, *fg*Ø, *g*Ø, *h*Ø, *i*Ø	*1–4, 6–9, 11, 22–23, 26–28, 30, 32–33, 37, 39, 46, 48–49, 51–52, 58–61, 66, 72, 82, 86–90, 96–146*
Linotaeniidae	hom: Ø, *p, q, s* het: *pq, qp, qr*	*1, 6–7, 33, 61, 63, 91, 147–156*

Numbers refer to the following references: *1* Attems, 1929; *2* Attems, 1934a; *3* Attems, 1947; *4* Attems, 1951; *5* Chamberlin, 1930a; *6* Chamberlin, 1938; *7* Chamberlin, 1941a; *8* Chamberlin, 1943a; *9* Chamberlin, 1944b; *10* Chamberlin, 1946c; *11* Chamberlin, 1953b; *12* Chamberlin, 1964; *13* Crabill, 1953; *14* Crabill, 1959c; *15* Crabill, 1960b; *16* Crabill, 1969b; *17* Eason, 1962; *18* Lignau, 1929a; *19* Lignau, 1929b; *20* Matic & Darabantu, 1969; *21* Matic & Darabantu, 1974; *22* Verhoeff, 1930; *23* Verhoeff, 1934a; *24* Verhoeff, 1938c; *25* Verhoeff, 1938d; *26* Verhoeff, 1943; *27* Folkmanova & Dobroruka, 1960; *28* Attems, 1952b; *29* Chamberlin, 1939; *30* Chamberlin, 1941b; *31* Chamberlin, 1941c; *32* Chamberlin, 1950b; *33* Chamberlin, 1955–56; *34* Crabill, 1959a; *35* Crabill, 1968b; *36* Crabill, 1968c; *37* Demange, 1963; *38* Lawrence, 1953; *39* Lawrence, 1960; *40* Machado, 1951; *41* Turk, 1955; *42* Crabill, 1970; *43* Attems, 1930b; *44* Chamberlin, 1963; *45* Chamberlin, 1965; *46* Attems, 1934b; *47* Attems, 1939; *48* Attems, 1953; *49* Chamberlin, 1940d; *50* Chamberlin, 1942a; *51* Chamberlin, 1942b; *52* Chamberlin, 1946b; *53* Chamberlin, 1946d; *54* Chamberlin, 1947a; *55* Chamberlin, 1947b; *56* Chamberlin, 1948; *57* Chamberlin, 1950a; *58* Chamberlin, 1952b; *59* Chamberlin, 1953a; *60* Chamberlin, 1957; *61* Chamberlin, 1960a; *62* Chamberlin, 1962b; *63* Chamberlin & Mulaik, 1940; *64* Crabill, 1958; *65* Crabill, 1959b; *66* Crabill, 1960a; *67* Crabill, 1960c; *68* Crabill, 1961a; *69* Crabill, 1968a; *70* Demange, 1969; *71* Dobroruka, 1959; *72* Folkmanova, 1956; *73* Hoffman & Pereira, 1991; *74* Kaczmarek, 1962; *75* Kaczmarek, 1969; *76* Mauriès, 1968; *77* Pereira, 1981b; *78* Pereira, 1984a; *79* Pereira, 1984b; *80* Pereira & Coscarón, 1975–76; *81* Pereira & Demange, 1991; *82* Pereira & Hoffman, 1993; *83* Shear & Peck, 1992; *84* Shinohara, 1970; *85* Titova, 1972; *86* Verhoeff, 1937a; *87* Verhoeff, 1940; *88* Archey, 1936; *89* Chamberlin, 1940a; *90* Chamberlin, 1943b; *91* Chamberlin, 1944a; *92* Chamberlin, 1945; *93* Chamberlin, 1958; *94* Crabill, 1960b; *95* Demange & Pereira, 1985; *96* Matic, Negrea & Fundora Martinez, 1977; *97* Verhoeff, 1939a; *98* Verhoeff, 1951; *99* Attems, 1930a; *100* Attems, 1937; *101* Attems, 1938; *102* Attems, 1952a; *103* Capuse, 1968; *104* Chamberlin, 1928a; *105* Chamberlin, 1928b; *106* Chamberlin, 1930b; *107* Chamberlin, 1940b; *108* Chamberlin, 1940c; *109* Chamberlin, 1941d; *110* Chamberlin, 1946a; *111* Chamberlin, 1951; *112* Chamberlin, 1952a; *113* Chamberlin, 1955; *114* Chamberlin, 1956; *115* Chamberlin, 1960b; *116* Chamberlin, 1962a; *117* Crabill, 1949; *118* Crabill, 1963; *119* Crabill, 1964; *120* Crabill, 1969a; *121* Dobroruka, 1969; *122* Dobroruka, 1973; *123* Fahlander, 1935; *124* Folkmanova, 1928; *125* Folkmanova, 1959; *126* Jones, 1989; *127* Kaczmarek, 1970; *128* Lawrence, 1955; *129* Lawrence, 1959; *130* Lewis, Jones & Keay, 1988; *131* Loksa, 1971; *132* Machado, 1953; *133* Minelli, 1982a; *134* Minelli, 1983; *135* Pereira, 1981a; *136* Pereira, 1984c; *137* Silvestri, 1935a; *138* Silvestri, 1935b; *139* Verhoeff, 1928; *140* Verhoeff, 1937b; *141* Verhoeff, 1938a; *142* Verhoeff, 1939b; *143* Verhoeff, 1941a; *144* Verhoeff, 1941b; *145* Verhoeff, 1942a; *146* Verhoeff, 1945; *147* Chamberlin, 1954; *148* Chamberlin, 1966; *149* Crabill, 1954; *150* Crabill, 1962a; *151* Crabill, 1962b; *152* Shinohara, 1981; *153* Silvestri, 1929; *154* Verhoeff, 1934b; *155* Verhoeff, 1935; *156* Verhoeff, 1938b.

many old descriptions. For example, we were able to see a few scattered pores on the last leg-bearing segment of *Clinopodes flavidus*, whereas all current descriptions in the literature consider that segment to be poreless in all geophilomorphs (cf. below, p. 193). An original redescription of all known species is far beyond the scope of this article. However, we are confident that the sample we have studied provides sufficient evidence to reveal some patterns of taxonomic importance.

RESULTS AND DISCUSSION

Morphology of gland pores

With the exception of *Geophilus richardi* and *Dicellophilus carniolensis*, all species we have investigated by SEM have gland openings (Figs 1–19) in the form of cuticular pores circumscribed by a ring. The diameter of individual pores ranges from 2 to 4 μm, according to species and does not change with age and shows no substantial variation, either within a single area, or between sternites.

Two kinds of cuticular rings may be recognized. In *Himantarium* and in *Henia* ring type 1 looks like a continuous ribbon with a visible suture. (Fig. 6, arrow), whereas in the remaining species (ring type 2) no suture is seen (Fig. 19). These different structures are probably the result from different morphogenetic processes. We wonder whether these differences are also mirrored in function (cf. Hopkin *et al.*, 1990).

This structural difference allows, Himantariidae and Dignathodontidae, both with ring type 1, to be distinguished from the remaining families, all with ring type 2. We have no data concerning ring type in the males of *Brahmaputrus poriger* Verhoeff, 1942, the only representative within the generally poreless Mecistocephalidae with sternal pores.

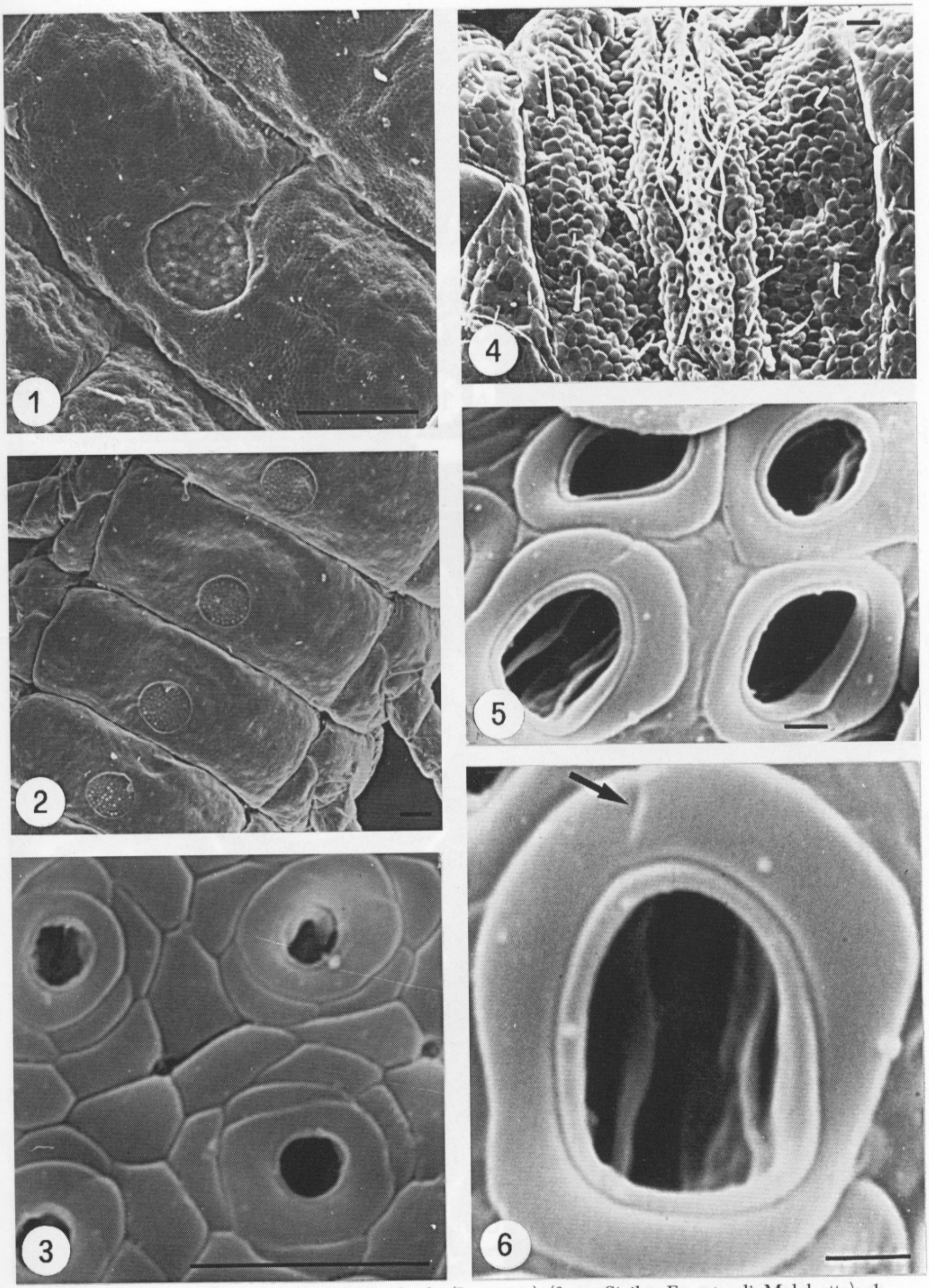
Concerning the polygonal fields of the cuticle ('cells'), those bearing pores are surrounded by several simple cells. Both the spatial arrangement of these cells and the distance between pores vary according to species. However, closely related species such as *Pleurogeophilus mediterraneus*, *Geophilus insculptus* and *Clinopodes flavidus* (Figs. 17, 18), all belonging to the family Geophilidae, exhibit a very similar arrangement of cells: between two neighbouring pores there are nearly always three or more conventional cells and the mean distance between two neighbouring pores is about 10 μm.

In *Schendyla* (Fig. 13), both the shape of the cuticular cells and the mean distance between pores are similar to those in geophilids; however, owing to the larger average size of the conventional cuticular cells in *Schendyla*, there is a smaller number of these cells between neighbouring pores.

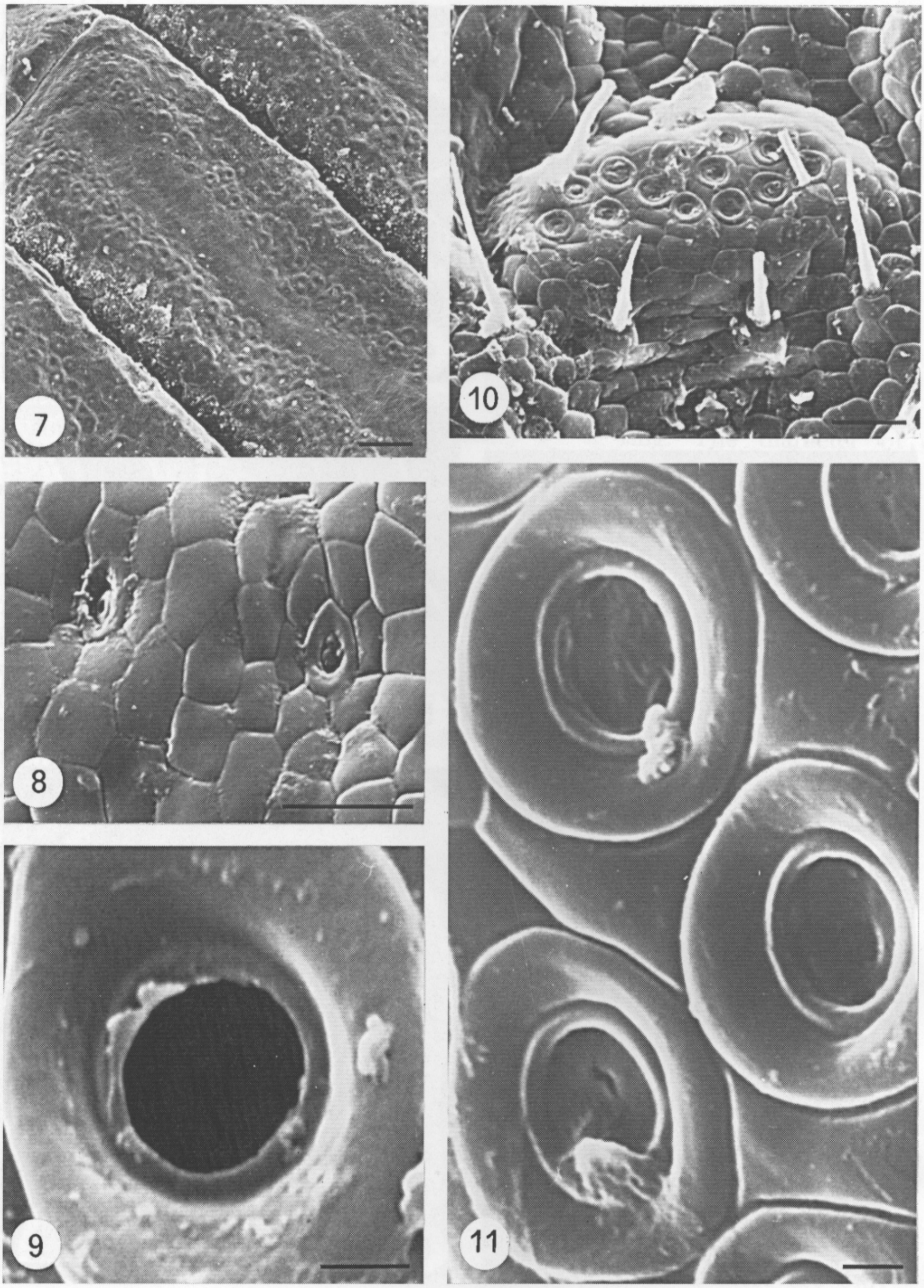
In *Strigamia crassipes* (Fig. 16), the arrangement is quite similar, with three or more conventional cells between neighbouring pores; but these are only about 6 μm apart.

At variance with the previous genera, in *Henia* (Figs 5, 6) the pore-lining cells are often contiguous, without conventional cells in between; accordingly, the pore-to-pore distance is reduced to 4 μm.

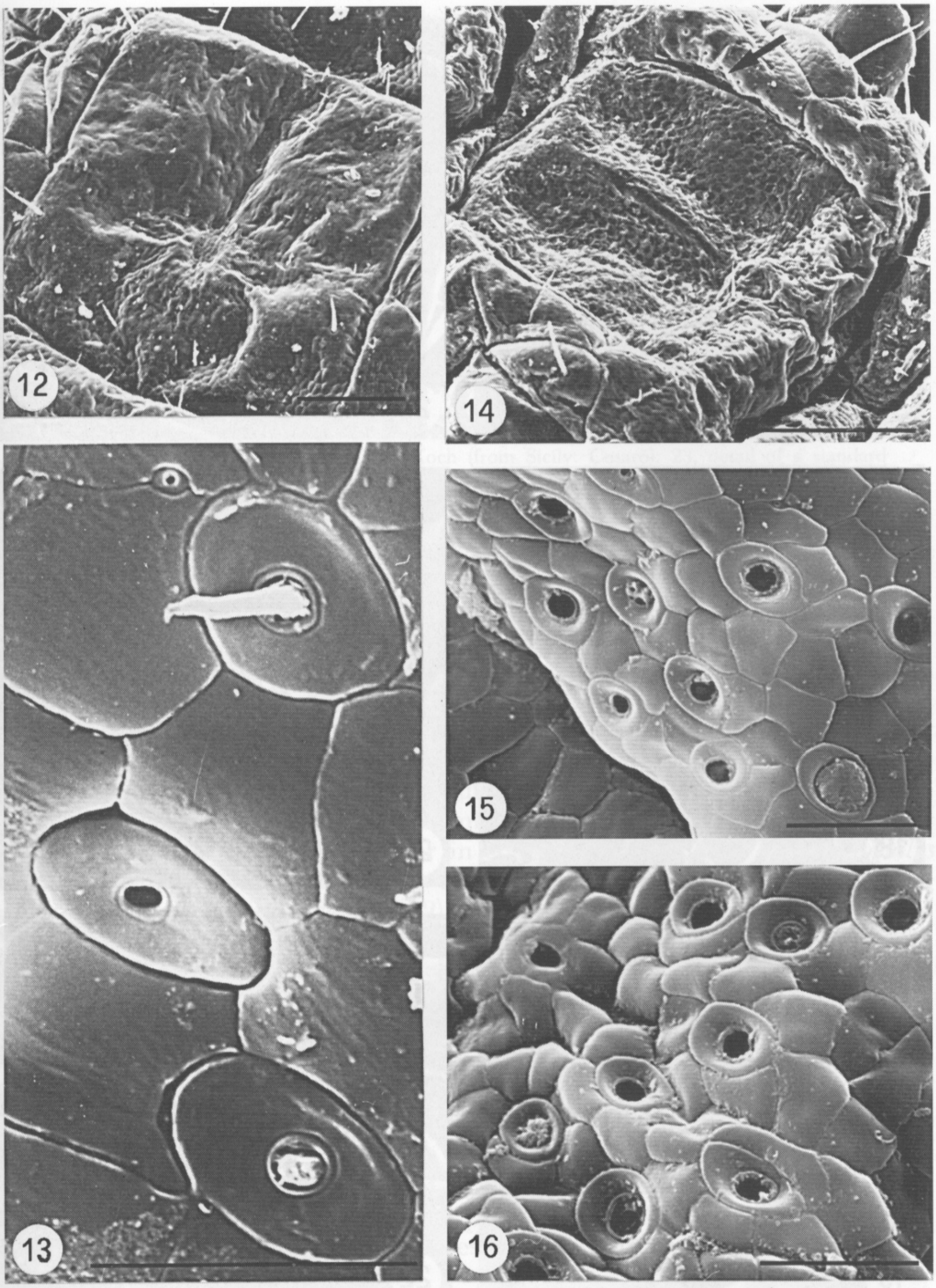
Different again, and very characteristic, is the arrangement of the pores in *Himantarium gabrielis* (Fig. 3), where each pore is surrounded by a rosette of



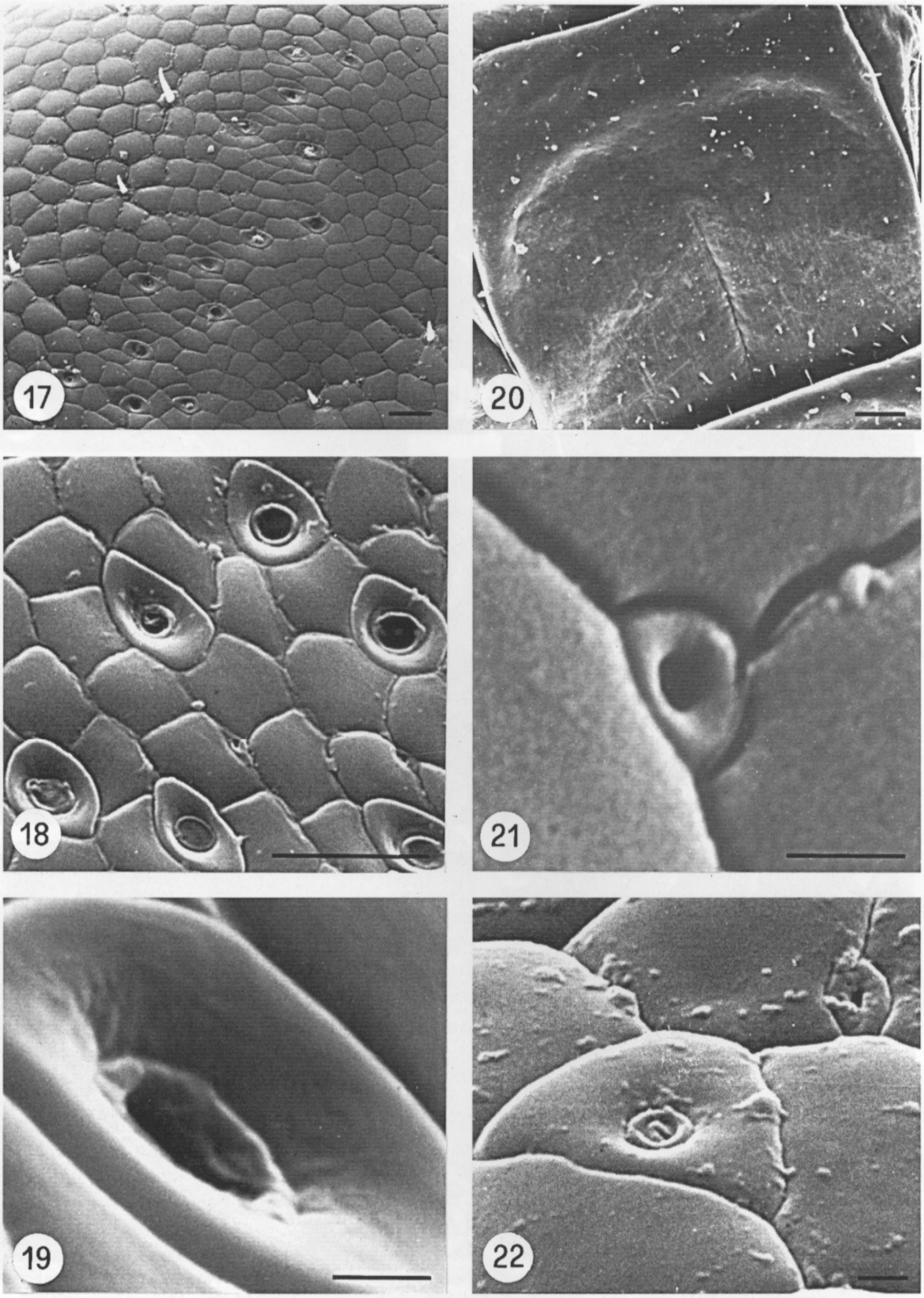
Figures 1–6. Figs 1–3. *Himantarium gabrielis* (Linnaeus) (from Sicily: Foresta di Malabotta): 1, ventral pore area of the second leg-bearing segment: the pore field is depressed and linked to the anterior edge of the segment by a narrow groove; the first leg-bearing segment (right top corner of the picture) only bears a longitudinal groove, without a pore field; 2, pore areas of some posterior segments, all without anterior groove; 3, enlarged detail of a part of a ventral pore area. Figs 4–6, *Henia bicarinata* (Meinert) (from Italy: Gubbio): 4, ventral pore area of the fourth leg-bearing segment; 5 and 6, enlarged details of the same. The arrow points to the suture in the ring surrounding the pore. Scale bar = 100 μm (1 and 2); = 10 μm (3 and 4); = 1 μm (5 and 6).



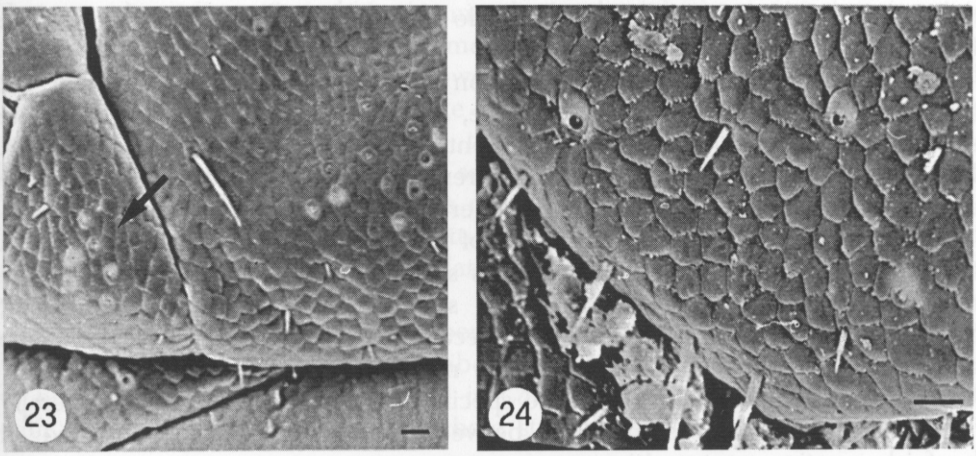
Figures 7–11. Figs 7–9. *Orya barbarica* (Gervais) (from Algeria: 32 km E from Azarga): 7, ventral pore area of a segment at mid-body level; 8 and 9, enlarged details of the same. Figs 10, 11. *Ballophilus* sp. (from the Virgin Islands); 10, ventral pore area of VI segment; 11, enlarged detail of the same. Scale bar = 100 μm (7); = 10 μm (8 and 10); = 1 μm (9 and 11).



Figures 12–16. Figs 12, 13. *Schendyla carniolensis* Verhoeff (from Italy: Varazze): 12, ventral pore area of the XIV segment; 13 enlarged detail of the same. Figs 14–16. *Strigamia crassipes* (C. L. Koch) (from Croatia: Biokovo): 14, ventral view of the IV leg-bearing segment: the pores are distributed along the posterior edge of the sternite (enlarged detail in Fig. 16) as well as on the hypocoxae (arrow: enlarged detail in Fig. 15). Scale bar = 100 μm (12 and 14); = 10 μm (13, 15 and 16).



Figures 17–22. Figs 17–19. *Clinopodes flavidus* C. L. Koch (from Sicily: Cesarò): 17, ventral pore area of the IV leg-bearing segment; 18, detail of the ventral pore area of the fourth-last segment; 19, a pore. Figs 20, 21. *Dicellophilus carniolensis* (from Italy: Dolomites, Val Cadino): 20, ventral view of a leg-bearing segment, devoid of pore areas; 21 enlarged view of a micropore. Fig. 22. *Geophilus richardi* Brölemann (from Italy: Badalucco), an isolated pore and a micropore of the IV leg-bearing segment. Scale bar = 10 μm (17 and 18); = 1 μm (19, 21 and 22); = 100 μm (20).



Figures 23, 24. *Clinopodes flavidus* C. L. Koch (from Sicily: Cesarò): 23, detail of a standard trunk segment with scattered pores on the hypocoxa (arrow); 24, the sternite of the last leg-bearing segment, also with pores. Scale bar = 10 μm.

5–6 cells. At least 5 to 6 poreless cells lay between neighbouring pores, which are about 10 μm apart.

In *Ballophilus* (Fig. 11), the sparsely arranged pores are nearly as crowded as in *Henia*, despite the different nature of the rings. Pore-to-pore distance is about 5–6 μm.

In all geophilomorph species we have studied by SEM, some smaller pores, less than 0.5 μm in diameter, also occur on the sternites. These micropores are not bounded by a cuticular ring, but instead open in the middle of a very small cell. These micropores occur within the pore area as well as outside it and also occur in species lacking SPAs. In *Dicellophilus carniolensis* (Figs 20, 21) only these micropores are present on the sternites, whereas in *Geophilus richardi* (Fig. 22), where typical ventral pores of 2–4 μm are absent, the sternites bear a small number of pores of 0.5–1 μm, similar to the usual ventral pores, in that they are bounded by their own cuticular ring. Small pores of similar size and shape also occur on the hypocoxa of *Strigamia* (Fig. 15).

The micropores have nothing to do with ventral glands, whereas the small pores of *G. richardi* are possibly the remnants of typical ventral pores, their reduction being perhaps a correlate of overall miniaturization (Hanken & Wake, 1993).

The presence of the hypocoxa of pores of the same kind as those of the SPAs is very seldom described, but probably widespread. We provide an illustration (Fig. 23) of hypocoxal pores in *Clinopodes*, which were previously unknown in this genus.

Morphology of pore areas

Out of 949 geophilomorph species included in our survey, 485 possess SPAs and 302 lack them. For the remaining 162 species, very poor descriptions in the literature prevent safe assignment. In so far as the generic placement of these species is correct, we may guess that they belong mainly to groups with SPAs. However, we do not refer to them further in the following discussion.

As a rule, SPAs are more evident on the anterior sternites, the first 1-2 (-3) excepted, and, to a lesser degree, on the penultimate sternites. The sternite of the last leg-bearing segment is always described as poreless. However, we found a few scattered pores in *Clinopodes flavidus* (Fig. 24); we also expect a similar occurrence in other species.

We can distinguish two main kinds of SPA segmental pattern (SPASP). In the first, SPAs occur as a homogeneous series along the whole length of the trunk, without any major variation in shape. In the second arrangement, SPAs form an heterogeneous series, because of major differences in shape along the body length; several sternites may also lack SPAs.

The SPASP displayed by a single specimen is often complex but generally 'smooth,' the differences in shape between contiguous SPAs being bridged by fairly continuous transitions.

The SPASPs we recognize are summarized in Table 1. For key references see the Appendix. The shapes of different SPAs recorded for each family and the pattern of transition between SPAs in the heterogeneous series are summarized in Figure 25.

The segmental pattern of sternal pore areas: a taxonomic survey

Himantariidae

SPAs are generally arranged in homogeneous series. In most species SPAs occur from the second sternite to the penultimate one. The individual areas are slightly depressed with respect to the sternal surface, have well-defined outlines and circular, oval or kidney-like shape.

In a few species, the series is more or less heterogeneous: in *Mesocanthus latisternus* Attems, 1934, for example, the areas are ovally elongated on the first segments, circular in the following ones and transversally oval in the rear part of the body. *Himantarium gabrielis* shows individual variability in SPASPs: generally, SPAs are circular in the midbody segments but towards the ends of the trunk they are often oval, with either transversal or longitudinal main axes (Minelli, Pasqual & Etonti, 1984).

In a few species, the series is abruptly truncated at about two thirds body length. The site of the transition (given as the ratio of the average pediferous segment number with the last SPA to the average total number of pediferous segments) is 66/165 in *Nesoporogaster excavata* Verhoeff, 1924; 45/103 in *N. souletina* (Brölemann, 1907), 41/93 (males) or 49/99 (females) in *N. s. brevior* Eason, 1962; 72/163 in *N. hispanica* Matic & Darabantu, 1979 and 50/115 in *N. mediterranea* Matic & Darabantu, 1979; 36/73 in *Stenophilus rothi* Chamberlin, 1953, 50/85 in *Stigmatogaster subterranea* (Leach, 1817) and 60/125 in *S. dimidiata* (Meinert, 1870). This means that this site is roughly the same for several of these species. In fact, dealing with serial homology leads one to discuss whether there is any meaning in *specifically* homologizing the *n*th segment of the body (or trunk), or the *n*th copy of a metameric feature, say, the *n*th pair of legs or the SPA of the *n*th trunk segment in one animal with the *n*th segment, or feature, of another animal. Our answer is that these features are positionally homologous in a strict sense if and only if their position is specified, in both animals, in absolute terms, i.e. by counting units (segments, or a proxy for segments) starting with the same (reasonably, the anterior) end of the body. However, position is very often determined in relative rather than in absolute terms. This implies that the features occurring at the *n*th segment of two animals are, in a broader sense, homologous, if the total number of segments in the two animals is the same. If, on the contrary, the two animals differ in their total number of segments, then it seems to be appropriate to regard as positional homologues two features occurring at the same relative position even though they are on different segments (Minelli, 1992).

Meinertophilus californicus Chamberlin, 1930 and *Stenophilus coloradanus* Chamberlin, 1946 have been described as poreless, but this condition needs to be confirmed. Still more unusual is *Causerium tuxtlanum* Chamberlin, 1964 with pores distributed across the whole sternal surface.

Dignathodontidae

In *Henia*, SPAs are distributed in homogeneous series, generally from the first or second to the penultimate sternite. Areas are always well defined and generally depressed and circular, sometimes elongated in longitudinal or transversal sense. This agrees with a possible kinship between this family and the Himantariidae.

No SPA occurs in the other two genera of the family: *Dignathodon* and *Agnathodon*.

Oryidae

All the different SPAs occurring in this family are easily understood as different degrees of expressions of a square pattern. The square can be reduced to two transversal rows or even to a single transversal band just in front of the hind border of the sternite. Generally, but not always, SPASPs are of the homogeneous type. In *Metaxythus austrinus* Crabill, 1968, SPAs disappear at about half way along the trunk. Two genera, *Keporya* and *Rhysonotum*, lack SPAs.

In *Trematorya sternalis* Brölemann, 1909 numerous pores are sparsely distributed over the whole surface of the sternite; this arrangement is unusual within Oryidae and seems to justify the usual placement of this genus in a distinct family-level taxon, Trematoryinae.

Eriphantidae

In the single species belonging to this family, *Eriphantes telluris* Crabill, 1970, the SPASP is a heterogeneous series from the very first segment to the penultimate one.

Gonibregmatidae

Most SPAs can be regarded as different modifications of a square pattern. The basic pattern, however, seems to be richer than in Oryidae, because of the development of a longitudinal median stripe. SPASPs are generally of the homogeneous type. *Eucratonyx meinerti* (Pocock, 1889), *Eu. hamatus* Pocock, 1898 and *Himantosoma porosum* Pocock, 1891 have heterogeneous SPASPs.

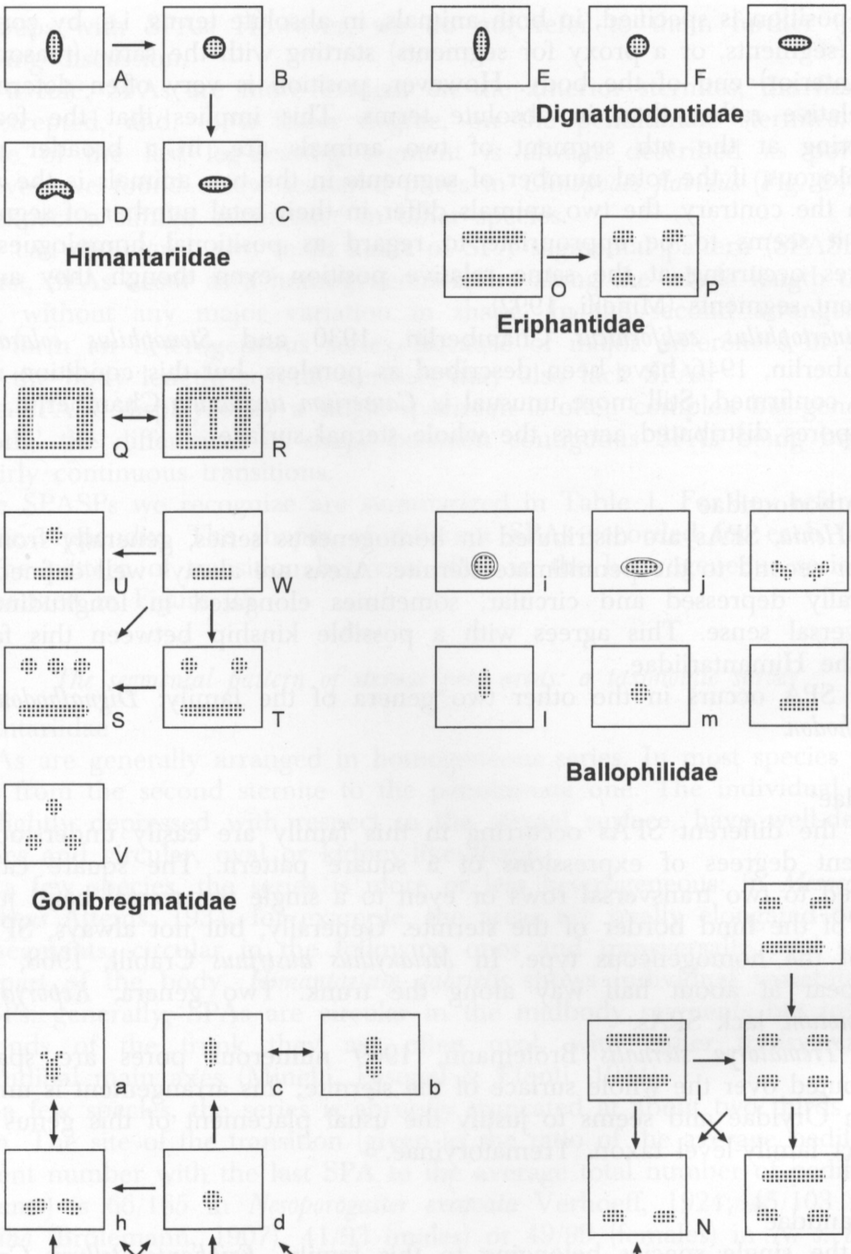
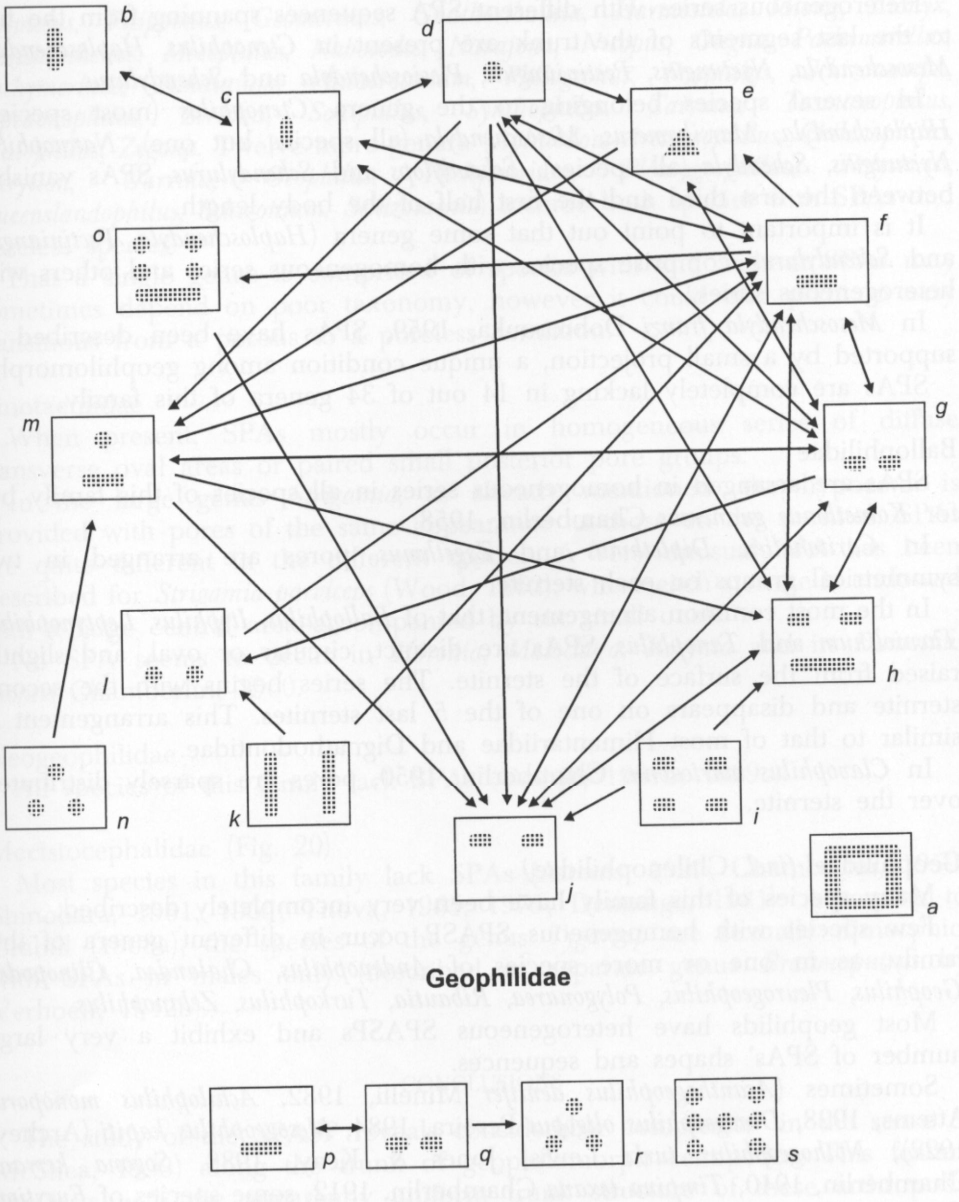
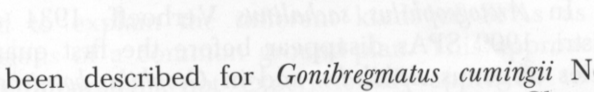


Figure 25. A schematic summary of the kinds of sternal pore areas (SPAs) occurring in the individual families of geophilomorph centipedes. Couples of SPAs occurring together in the same animal are connected by a line. Arrows indicate the antero-posterior polarity, i.e. which one of the SPAs precedes the other along the trunk. Codes for SPAs are the same as in Table 1.



Geophilidae



Linotaeniidae

Figure 25.—*continued.*

No SPA has been described for *Gonibregmatus cumingii* Newport, 1842, *Eremorus becki* Chamberlin, 1963 and *Ketampa brattstromi* Chamberlin, 1956.

Schendylidae

Only a few species belonging to the genera *Ctenophilus*, *Lithoschendyla*, *Nyctunguis*, *Schendylellus* and *Schendylurus* have homogeneous SPASP beginning with the first or second sternite.

Heterogeneous series with different SPA sequences spanning from the first to the last segments of the trunk are present in *Ctenophilus*, *Haploschendyla*, *Mesoschendyla*, *Nyctunguis*, *Pectiniunguis*, *Plesioschendyla* and *Schendylurus.*

In several species belonging to the genera *Ctenophilus* (most species), *Haploschendyla*, *Marsikomerus*, *Mesoschendyla* (all species but one), *Nannophilus*, *Nyctunguis*, *Schendyla* (all species), *Schendylops* and *Schendylurus*, SPAs vanishes between the first third and the first half of the body length.

It is important to point out that some genera (*Haploschendyla*, *Pectiniunguis* and *Schendylurus*) comprise species with homogeneous series and others with heterogeneous series.

In *Mesoschendyla franzi* Dobrorouka, 1959, SPAs have been described as supported by a small projection, a unique condition among geophilomorphs.

SPAs are completely lacking in 14 out of 34 genera of this family.

Ballophilidae

SPAs are arranged in homogeneous series in all species of this family but for *Koinethmus guanereus* Chamberlin, 1958.

In *Caritohallex*, *Diplethmus* and *Zygethmus*, pores are arranged in two symmetrical groups on each sternite.

In the most common arrangement, that of *Ballophilus*, *Ityphilus*, *Leptynophilus*, *Taeniolinum* and *Tanophilus*, SPAs are distinct, circular or oval, and slightly raised from the surface of the sternite. The series begins with the second sternite and disappears on one of the 5 last sternites. This arrangement is similar to that of most Himantariidae and Dignathodontidae.

In *Clavophilus maricaonus* Chamberlin, 1950, pores are sparsely distributed over the sternite.

Geophilidae *(incl.* Chilenophilidae*)*

Many species of this family have been very incompletely described.

Few species with homogeneous SPASP occur in different genera of this family, as in one or more species of *Andenophilus*, *Chalandea*, *Clinopodes*, *Geophilus*, *Pleurogeophilus*, *Polygonarea*, *Ribautia*, *Turkophilus*, *Zelanophilus.*

Most geophilids have heterogeneous SPASPs and exhibit a very large number of SPAs' shapes and sequences.

Sometimes (*Acanthogeophilus dentifer* Minelli, 1982, *Achilophilus monoporus* Attems, 1928, *Dinogeophilus oligopus* Pereira, 1984, *Mesogeophilus kapiti* (Archey, 1922), *Nothogeophilus turki* Lewis, Jones & Keay, 1988, *Sogona kerrana* Chamberlin, 1940, *Timpina texana* Chamberlin, 1912, some species of *Eurytion*, *Geophilus*, *Ribautia*, *Schizoribautia*), SPAs are present in the first segments of the trunk and then vanish, generally between the first third and the first half of the body. In *Arctogeophilus sachalinus* Verhoeff, 1934 and *Dinogeophilus pauropus* Silvestri, 1909 SPAs disappear before the first quarter of the trunk.

In two species of genus *Aphilodon* and in *Geophilus bosniensis* Verhoeff, 1895 SPAs occur in the last trunk segments only.

Sparse pores evenly distributed across the whole sternal surface have been described in *Achilophilus pachypus* Verhoeff, 1937, *Arctogeophilus macrocephalus* Folkmanova & Dobroruka, 1960 and *Queenslandophilus goetschi* Verhoeff, 1934.

One third of geophilid genera lack SPAs. These are *Alloschizotaenia*, *Barrophilus*, *Bebekium*, *Brachygeophilus*, *Brachygonarea*, *Cephalodolichus*, *Condylona*, *Dysmesus*, *Filipponus*, *Geomerinus*, *Gnathoribautia*, *Harmostela*, *Idiona*, *Lionyx*, *Mecistauchenus*, *Mecophilus*, *Nabocodes*, *Navajona*, *Nicopus*, *Oligna*, *Pachymerellus*, *Pachymerinus*, *Pandinium*, *Philacroterium*, *Philogeonus*, *Poaphilus*, *Schizonampa*, *Sepedonophilus*, *Serrona*, *Soniphilus*, *Synthophilus*, *Taiyuna*, *Tasmanophilus*, *Watophilus*, *Zygona*. Twelve more genera (*Aphilodon*, *Arctogeophilus*, *Chilenophilus*, *Eurytion*, *Garrina*, *Geophilus*, *Pachymerium*, *Pleurogeophilus*, *Polycricus*, *Queenslandophilus*, *Schizonium*, *Schizotaenia*) include both species with SPAs and poreless species.

That a single genus is comprised of species with and without SPAs may sometimes depend on poor taxonomy, however it could also point to easy transitions from a porous to a poreless condition.

Linotaeniidae

When present, SPAs mostly occur in homogeneous series of diffuse transverse oval areas or paired small posterior pore groups.

In the large genus *Strigamia*, as already mentioned, the hypocoxa is provided with pores of the same appearance as those on the sternites. SPAs are quite different in the different species. A very unusual SPA has been described for *Strigamia parviceps* (Wood, 1862), where each sternite is endowed with a large central area accompanied by six small ones.

No SPA seems to occur in *Horonia*, *Malochora*, *Korynia* and in *Damothus montis* Chamberlin, 1960.

Neogeophilidae

All species of this family lack SPAs (Crabill, 1961b; 1969c).

Mecistocephalidae (Fig. 20)

Most species in this family lack SPAs (Attems, 1929; Chamberlin, 1959; Shinohara, 1961, 1965; Titova, 1965, 1975; Demange, 1981). According to Crabill (1968a), the species of the genus *Tygarrup* are sexually dimorphic, with SPAs in males only (described as separate genus *Brahmaputrus* by Verhoeff, 1942b).

CONCLUSIONS

The study of the SPASP reveals considerable complexity (in the sense of McShea, 1993) along the trunk of geophilomorph centipedes. This feature contrasts with the apparently uniform trunk structure of these arthropods, and is perhaps a bit unexpected in a group with strictly epimorphic development.

We have tried to explain the different kinds of SPAs as more or less divergent expressions of a common ground-plan. This approach is similar to the traditional (comparative, not experimental) approach to the study of butterfly wing patterns (reviewed in Nijhout, 1991). The argument develops as follows.

First, within one individual, the SPASP is, according to the species, either homogeneous or heterogeneous. Therefore, it seems to be safe to regard as 'related'–i.e. as different expressions of a common ground-type–the different kinds of SPAs which occur within one animal with heterogeneous SPASP.

Second, one type of SPA may be associated with different types of SPA in different species. Therefore, in some way, we can also regard as 'related' two SPAs which may both associate with a third SPA, although they never occur together in the same animal.

Actually, in the graphs of co-occurrence of SPAs in the different families (Fig. 25) there are many links. In Eriphantidae and Schendylidae, all SPAs recorded appear to be 'related.' In four more families, only one SPA remains out of the connected network. Only in Gonibregmatidae does the connectivity graph show three separate clusters of SPAs. This, however, may be due to the very low number of species described in the family or to the possible polyphyly of this unrevised group.

Within the individual families, the patterns summarized in Figure 25 support the hypothesis that the most different SPAs are but variations on a common theme, that is to say that these structures are transformational homologues. Obviously, we cannot apply this approach to the families in which only homogeneous series occur (Dignathodontidae and Ballophilidae).

Sternal pores are, possibly, an autapomorphy of Geophilomorpha. Therefore, the widespread (and scattered) poreless condition should be regarded as a derived homoplastic state. A little puzzling, however, is the situation in the Mecistocephalidae. There is a possibility that Mecistocephalidae are the sister-group to all remaining Geophilomorpha. Verhoeff (1902–25) contrasted them as superfamily Placodesmata to a superfamily Adesmata with all remaining geophilomorphs. In that case, the poreless condition would be ancestral to the whole of Geophilomorpha, thus retained by Mecistocephalidae as a plesiomorphy.

The occurrence of scattered pores in some representatives of Himantariidae, Ballophilidae and Geophilidae, is certainly homoplastic.

At the present stage of knowledge we have not attempted comparisons between genera not belonging to the same family. This means that we do not feel confident in the degree of generalization our comparative approach may warrant. The same happened, in the past, when considering the wing patterns of Lepidoptera. At present, we simply lack more detailed knowledge of geophilomorph SPAs as well as a reliable phylogenetic arrangement of genera and suprageneric taxa.

Priorities for further research on geophilomorph sternal pores include:

(1) An adequate re-description of a large fraction of the named species. Recent revisionary work on several genera (e.g. Minelli 1982b; Hoffman & Pereira, 1991; Pereira & Demange, 1991) has abundantly demonstrated that many old descriptions, even among those of famous (and prolific) authors like Silvestri and Verhoeff, were often wrong, owing to inadequate clearing of the specimens, poor optics, careless observation, bad typesetting, lack of proof reading, or a mixture of these different causes;

(2) A study of the developmental series. Routine examination of large series, likely including all post-embryonic stages of a few common species, does not reveal any major ontogenetic change in shape and distribution of pore areas, but a systematic investigation has not yet been performed;

(3) An adequate study of intraspecific variability, especially in the himantariid species with abruptedly truncated SPASP;

(4) A more sensible specification of the position of the individual pore area on the sternal surface. To simply qualify a transversal bar, or a couple of spots, as 'anterior' or 'posterior' is but a first approximation, to be refined by taking into account either metric parameters or, perhaps better, the association of 'normal,' glandular and accompanying 'cells.'

ACKNOWLEDGEMENTS

We are grateful to Claudio Friso for assistance with the drawings and to Claudio Furlan for help with the scanning electron microscope. Research supported by grants of the Italian National Research Council (CNR) and the Italian Ministry of University and Scientific and Technological Research (MURST) to AM.

REFERENCES

Archey G. 1936. Revision of the Chilopoda of New Zealand. *Record of the Auckland Institute and Museum* **2:** 43–70.

Attems C. 1929. Myriapoda. 1. Geophilomorpha. *Das Tierreich*, Berlin, Water de Gruyter **52:** 1–388.

Attems C. 1930a. Myriopoden von Java, Sumatra und Bali. *Archiv für Hydrobiologie* **8:** 115–182.

Attems C. 1930b. Myriopoden der Kleinen Sunda-Inseln, Gesammelt von der Expedition Dr. Rensch. *Mitteilungen aus dem Zoologischen Museum in Berlin* **16:** 117–184.

Attems C. 1934a. Einige neue Geophiliden und Lithobiiden des Hamburger Museums. *Zoologischer Anzeiger* **107:** 310–317.

Attems C. 1934b. The Myriopoda of Natal and Zululand. *Annals of the Natal Museum* **7:** 459–522.

Attems C. 1937. Chilopoden und Symphylen des Belgischen Congo. *Revue de Zoologie et de Botanique Africaines* **29:** 317–332.

Attems C. 1938. Myriopoden von Hawaii. *Proceedings of the Zoological Society of London, Series B* **108:** 365–387.

Attems C. 1939. Étude sur les Myriopodes recueillis par M. Henri Gadeau de Kerville pendant son voyage zoologique en Asie Mineure (Avril–Mai 1912). In: Gadeau de Kerville H, ed. *Voyage Zoologique en Asie Mineure.* Paris: **1:** 17–28.

Attems C. 1947. Neue Geophilomorpha des Wiener Museums. *Annalen des naturhistorischen Museums Wien* **55:** 50–149.

Attems C. 1951. Ergebnisse des Österreichischen Iran-Expedition 1949/50. Myriopoden vom Iran gesammelt von der Expedition Heinz Loeffler und Genossen 1949/50. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Abteilung I* **160:** 387–426.

Attems C. 1952a. Eine *Chalandea* im Obirgebiet. (Aus der Ordnung der Tausendfuessler und der Familie der Erdkreicher). *Carinthia II* **142:** 50–52.

Attems C. 1952b. Myriopoden der Forschungsreise Dr. H. Franz in Spanien 1951 nebst Übersicht über die gesamte Iberische Myriopodenfauna. *Eos* **28:** 323–366.

Attems C. 1953. Myriopoden von Indochina. Expedition von Dr. C. Dawydoff (1938–1939). *Mémoires du Muséum d'Histoire naturelle, Paris, nouvelle série* **5A:** 133–230.

Bergsøe V, Meinert F. 1866. Danmarks Geophiler. *Naturhistorisk Tidsskrift* (3)**4:** 81–108.

Brade-Birks HK, Brade-Birks SG. 1920. Notes on Myriapoda. XX. Luminous Chilopoda, with special reference to *Geophilus carpophagus* Leach. *Annals and Magazine of natural History (9)* **5:** 1–34.

Capuse I. 1968. Contribution à l'étude des espèces appartenant aux genres *Insigniporus* Att. et *Pachymerium* C. L. Koch (Geophilomorpha, Geophilidae). *Travaux du Muséum d'Histoire naturelle "Grigori Antipa"* **8:** 699–719.

Chamberlin RV. 1928a. Some chilopods and diplopods from Missouri. *Entomological News* **39:** 153–155.

Chamberlin RV. 1928b. Notes on chilopods and diplopods from South-eastern Utah. *Entomological News* **39:** 307–311.

Chamberlin RV. 1930a. A new geophiloid chilopod from Potter Creek Cave, California. *University of California Publications in Zoology* **33:** 297–300.

Chamberlin RV. 1930b. On some centipeds and millipeds from Utah and Arizona. *Pan-Pacific Entomologist* **6:** 111–121.

Chamberlin RV. 1938. Three new geophiloid chilopods. *Entomological News* **49:** 254–255.

Chamberlin RV. 1939. On a collection of chilopods from the East Indies. *Bulletin of the University of Utah, Biological Series* **5:** 1–13.

Chamberlin RV. 1940a. On some chilopods from Barro Colorado Island. *Psyche* **47:** 66–74.

Chamberlin RV. 1940b. A new *Geophilus* from San Nicholas Island, California. *Pan-Pacific Entomologist* **16:** 4.

Chamberlin RV. 1940c. Diagnoses of ten new chilopods with a new genus of Sogonidae and a key to the species of *Lophobius. Pan-Pacific Entomologist* **16:** 49–56.

Chamberlin RV. 1940d. Two new Geophiloid chilopods from Mexico and Texas. *Proceedings of the biological Society of Washington* **53:** 65–66.

Chamberlin RV. 1941a. New genera and species of North American geophiloid centipedes. *Annals of the entomological Society of America* **34:** 773–790.

Chamberlin RV. 1941b. On a collection of myriopods from Venezuela. *Proceedings of the biological Society of Washington* **54:** 137–142.

Chamberlin RV. 1941c. On a collection of millipedes and centipedes from Northeastern Peru. *Bulletin of the American Museum of Natural History* **78:** 473–535.

Chamberlin RV. 1941d. New chilopods from Mexico. *Pan-Pacific Entomologist* **17:** 154–188.

Chamberlin RV. 1942a. Notes on a collection of centipeds chiefly from Louisiana, Arkansas and Missouri (Chilopoda). *Entomological News* **53:** 184–188.

Chamberlin RV. 1942b. On ten new centipedes from Mexico and Venezuela. *Proceedings of the biological Society of Washington* **55:** 17–24.

Chamberlin RV. 1943a. On Mexican centipeds. *Bulletin of the University of Utah, Biological Series* **7:** 1–55.

Chamberlin RV. 1943b Some records and descriptions of American chilopods. *Proceedings of the biological Society of Washington* **56:** 97–108.

Chamberlin RV. 1944a. Some chilopods from the Indo-Australian Archipelago. *Notulae Naturae of the Academy of natural Science of Philadelphia* **147:** 1–14.

Chamberlin RV. 1944b. Chilopods in the collections of Field Museum of Natural History. *Field Museum of Natural History, Zoological Series* **28:** 175–216.

Chamberlin RV. 1945. Two new centipeds from Trinidad. *Entomological News* **56:** 171–174.

Chamberlin RV. 1946a. A new chilopod genus of the family Sogonidae. *Canadian Entomologist* **78:** 69–71.

Chamberlin RV. 1946b. On the chilopods of Alaska. *Annals of the Entomological Society of America* **39:** 177–189.

Chamberlin RV. 1946c. A new American genus in the chilopod family Himantariidae. *Proceedings of the biological Society of Washington* **59:** 35–38.

Chamberlin RV. 1946d. A new Schendyloid chilopod from California. *Pan-Pacific Entomologist* **22:** 69–70.

Chamberlin RV. 1947a. On four new American chilopods. *Pan-Pacific Entomologist* **23:** 37–39.

Chamberlin RV. 1947b. A few chilopods taken in Panama by N. L. H. Krauss. *Entomological News* **58:** 146–149.

Chamberlin RV. 1948. A new geophiloid centiped taken at the Mexican border. *Entomological News* **58** (1947): 260.

Chamberlin RV. 1950a. Neotropical chilopods and diplopods in the collections of Tropical Research, New York Zoological Society. *Zoologica, New York* **35:** 133–144.

Chamberlin RV. 1950b. Some chilopods from Puerto Rico. *Proceedings of the biological Society of Washington* **63:** 155–160.

Chamberlin RV. 1951. Records of American millipeds and centipeds collected by Dr. D. Elden Beck in 1950. *Great Basin Naturalist* **11:** 27–35.

Chamberlin RV. 1952a. A new geophiloid centiped from the littoral of Southeast Alaska. *Proceedings of the biological Society of Washington* **65:** 83.

Chamberlin RV. 1952b. The centipeds (Chilopoda) of South Bimini, Bahama Islands, British West Indies. *American Museum Novitates* **1576:** 1–8.

Chamberlin RV. 1953a. Geophiloid chilopods of the Hawaiian and other Oceanic islands of the Pacific. *Great Basin Naturalist* **13:** 75–85.

Chamberlin RV. 1953b Two new Oregon chilopods of the order Geophilida. *Psyche* **60:** 37–39.

Chamberlin RV. 1954. Notes on the chilopod genera *Linotaenia* and *Tomotaenia* with description of a new *Korynia. Entomological News* **65:** 117–122.

Chamberlin RV. 1955. Four new American chilopods. *Proceedings of the biological Society of Washington* **68:** 179–181.

Chamberlin RV. 1955–56. Reports of the Lund University Chile Expedition 1948–49. The Chilopods of the Lund University and California Academy of Science Expeditions. *Acta Universitatis Lundensis* **51**(5): 1–61.

Chamberlin RV. 1956. A new chilopod from Chile. *Entomological News* **67:** 11–12.

Chamberlin RV. 1957. Geophiloid chilopods taken in the Northern Andes in 1954–1955. *Proceedings of the biological Society of Washington* **70:** 21–30.

Chamberlin RV. 1958. Five new south American chilopods. *Proceedings of the biological Society of Washington* **71:** 57–60.
Chamberlin RV. 1959. Entomologische Ergebnisse der Deutschen Indien-Expedition 1955–1958. On some chilopods from India. *Entomologische Mitteilungen aus dem zoologischen Staatsinstitut und zoologischem Museum Hamburg* **19:** 1–4.
Chamberlin RV. 1960a. Five new western geophilid chilopods. *Proceedings of the biological Society of Washington* **73:** 239–244.
Chamberlin RV. 1960b. A new marine centiped from California littoral. *Proceedings of the biological Society of Washington* **73:** 99–101.
Chamberlin RV. 1962a. Chilopods secured by the Royal Society Expedition to Southern Chile in 1958–1959. *University of Utah, Biological Series* **12**(4): 1–23.
Chamberlin RV. 1962b. New records and species of chilopods from Nevada and Oregon. *Entomological News* **73:** 134–138.
Chamberlin RV. 1963. A new genus in the chilopod family Tampiyidae. *Proceedings of the biological Society of Washington* **76:** 33–36.
Chamberlin RV. 1964. A new American genus in the chilopod family Himantariidae. *Entomological News* **75:** 66–68.
Chamberlin RV. 1965. A new genus and species in the chilopod family Tampiyidae. *Great Basin Naturalist* **25:** 39–42.
Chamberlin RV. 1966. A new genus of the chilopod family Dignathodontidae with proposal of two subfamilies (Chilopoda: Geophilomorpha). *Proceedings of the biological Society of Washington* **79:** 215–220.
Chamberlin RV, Mulaik S. 1940. On a collection of centipeds from Texas, New Mexico and Arizona (Chilopoda). *Entomological News* **51:** 107–110.
Crabill RE. 1949. A new centipede from the Eastern United States (Chilopoda: Geophilidae). *Entomological News* **60:** 210–213.
Crabill RE. 1953. A new Himantariid from the Eastern United States (Chilopoda: Geophilomorpha: Himantariidae). *Bulletin of the Brooklyn entomological Society* **48:** 85–88.
Crabill RE. 1954. Concerning *Tomotaenia* and *Paraplanes*, with the description of a new dignathodontid centipede from Missouri (Chilopods: Geophilomorpha: Dignathodontidae). *Canadian Entomologist* **86:** 416–419.
Crabill RE. 1958. A new schendylid from the Eastern United States, with notes on distribution and morphology (Chilopoda: Geophilomorpha: Schendylidae). *Entomological News* **69:** 153–160.
Crabill RE. 1959a. A new centipede from Okinawa (Chilopoda: Oryidae). *Pacific Insects* **1:** 173–176.
Crabill RE. 1959b. A new Floridan *Pectiniunguis*, with re-appraisal of its type species and comments on the status of *Adenoschendyla* and *Litoschendyla* (Chilopoda: Geophilomorpha: Schendylidae). *Journal of the Washington Academy of Sciences* **49:** 324–330.
Crabill RE. 1959c. A synonymical list of American Himantariidae, with a generic key and description of a new genus (Chilopoda: Geophilomorpha: Himantariidae). *Entomological News* **70:** 117–126, 153–159.
Crabill RE. 1960a. Centipedes of the Smithsonian Bredin Expedition to the West Indies. *Proceedings of the United States Museum* **111:** 1–15.
Crabill RE. 1960b. Concerning the aberrant genus *Nothobius*, with a redescription of its type species (Chilopoda: Geophilomorpha: Himantariidae). *Entomological News* **71:** 87–99.
Crabill RE. 1960c. On the identities of *Ctenophilus* and *Pleuroschendyla* (Chilopoda: Geophilomorpha: Schendylidae). *Revue de Zoologie et Botanique africaines* **62:** 145–160.
Crabill RE. 1961a. A catalogue of the Schendylinae of North America including Mexico, with a generic key and proposal of a new *Simoporus* (Chilopoda: Geophilomorpha: Schendylinae). *Entomological News* **72:** 29–36.
Crabill RE. 1961b. Concerning the Neogeophilidae, with a proposal of a new genus (Chilopoda: Geophilomorpha: Neogeophilidae) *Entomological News* **72:** 155–159, 177–190.
Crabill RE. 1962a. A new interpretation of some troublesome dignathodontid species and genera (Chilopoda: Geophilomorpha). *Entomological News* **73:** 179–186.
Crabill RE. 1962b. A new *Damothus* and a key to the North American dignathodontid genera (Chilopoda: Geophilomorpha: Dignathodontidae). *Psyche* **69:** 81–86.
Crabill RE. 1963. A preliminary review of *Zelanophilus* with description of a new Australian species (Chilopoda: Geophilomorpha: Geophilidae). *Psyche* **70:** 164–169.
Crabill RE. 1964. A preliminary review of *Maoriella*, with description of a new species from the Chatham Islands (Chilopoda: Geophilomorpha: Chilenophilidae). *Entomological News* **75:** 85–97.
Crabill RE. 1968a. Two new species of *Mesoschendyla* from the old world tropics, with a key to their congeners (Chilopoda; Geophilomorpha: Schendylidae). *Revue de Zoologie et Botanique africaines* **77:** 283–288.
Crabill RE. 1968b. Concerning the evolution of the Oryidae, with description of a primitive new genus (Chilopoda: Geophilomorpha: Oryidae). *Entomologische Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischem Museum Hamburg* **3:** 243–248.

Crabill RE. 1968c. A new Oryid genus and species from Africa, with generic key and notes on evolution within the family Oryidae (Chilopoda: Geophilomorpha). *Entomological News* **79:** 248–253.

Crabill RE. 1969a. Review of *Arenophilus* and key to all species. *Entomological News* **80:** 7–11.

Crabill RE. 1969b. Tracheotaxy as a generic criterion in Himantariidae, with proposal of two new Bothriogastrine genera (Chilopoda: Geophilomorpha). *Smithsonian Contributions to Zoology* **12:** 1–9.

Crabill RE. 1969c. Revisionary conspectus of Neogeophilidae with thoughts on a phylogeny. *Entomological News* **80:** 38–43.

Crabill RE. 1970. A new family of centipedes from Baja California with introductory thoughts on ordinal revision (Chilopoda: Geophilomorpha: Eriphantidae). *Proceedings of the entomological Society of Washington* **72:** 112–118.

Demange JM. 1963. La réserve naturelle intégrale du Mont Nimba. Chilopoda. *Mémoires de l'Institut français d'Afrique Noire* **66:** 41–118.

Demange JM. 1969. Myriapodes Chilopodes du Gabon. *Biologia Gabonica* **4**(1968)**:** 281–294.

Demange JM. 1981. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles (Mission P. L. Benoit-J. J. Van Mol, 1972). Myriapoda-Chilopoda. *Revue de Zoologie africaine* **95:** 623–652.

Demange JM, Pereira LA. 1985. Géophilomorphes (Myriapoda, Chilopoda) de la Guadeloupe et ses Dépendances. *Bulletin du Muséum national d'Histoire naturelle, Paris,* 4e série, 7, section A: 181–199.

Dobroruka LJ. 1959. *Mesoschendyla franzi* nov. spec., eine neue Chilopoden-Art aus dem Tschadgebiet. *Annalen des naturhistorischen Museums Wien* **63:** 414–415.

Dobroruka LJ. 1969. Some Chilopoda from Zambia. *Revue de Zoologie et Botanique africaines* **79:** 352–358.

Dobroruka LJ. 1973. Chilopoda from Kenya. *Revue de Zoologie et Botanique africaines* **87:** 829–834.

Eason EH. 1962. The chilopod genus *Nesoporogaster* Verhoeff. *Proceedings of the Zoological Society of London* **138:** 123–132.

Fahlander K. 1935. Ein japanischer *Nesogeophilus* nebst Bemerkungen über zwei amerikanische Geophiliden. *Arkiv för Zoologi, Stockholm* **28b**(7)**:** 1–4.

Folkmanova B. 1928. Chilopoda Republiky Ceskoslovenské Dil I. Chilopoda Cech. *Fauna et Flora Cechoslovenica v Praze* **3:** 1–131.

Folkmanova B. 1956. On new forms of Geophilomorpha from the Southern provinces of U.S.S.R. to the knowledge of the Myriapoda of U.S.S.R. *Zoologicheskii Zhurnal* **35,** 1633–1646.

Folkmanova B. 1959. Ueber neue Formen der Chilopoda aus U.d.S.S.R. *Zoologicheskii Zhurnal* **38:** 183–192.

Folkmanova B, Dobroruka LJ. 1960. Beitrag zur Kenntnis der Chilopoda der U.d.S.S.R. *Zoologicheskii Zhurnal* **39:** 1811–1818.

Hanken J, Wake DB. 1993. Miniaturization of body size: organismal consequences and evolutionary significance. *Annual Review of Ecology and Systematics* **24:** 501–519.

Hopkin SP, Anger HS. 1992. On the structure and function of the glue-secreting glands of *Henia vesuviana* (Newport, 1854). *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplementum* **10:** 71–79.

Hopkin SP, Gaywood MJ, Vincent JFV, Mayes-Harris EV. 1990. Defensive secretion of proteinaceous glues by *Henia* (*Chaetechelyne*) *vesuviana* (Chilopoda Geophilomorpha). In: Minelli A, ed. *Proceedings of the 7th International Congress of Myriapodology.* Leiden, E. J. Brill: 175–181.

Hoffman RL, Pereira LA. 1991. Systematics and biogeography of *Marsikomerus* Attems, 1938, a misunderstood genus of centipedes (Geophilomorpha: Schendylidae). *Insecta Mundi* **5:** 45–60.

Jones RE. 1989. On a new species of centipede (Chilopoda, Geophilomorpha) from the Isles of Scilly. *Journal of Natural History* **23:** 627–633.

Jones TH, Conner WE, Meinwald J, Eisner HE, Eisner T. 1976. Benzoyl cyanide and mandelonitrile in the cyanogenetic secretion of a centipede. *Journal of Chemical Ecology* **2:** 421–429.

Kaczmarek J. 1962. *Schendyla furcidens* nov. sp. eine neue *Schendyla*-Art aus Polen. *Bulletin de la Société des Amis des Sciences et des Lettres de Poznán (D)* **3:** 99–104.

Kaczmarek J. 1969. Beiträge zur Kenntnis bulgarischer Chilopoden. Teil I. *Bulletin de la Société des Amis des Sciences et des Lettres de Poznán (D)* **9:** 263–277.

Kaczmarek J. 1970. Beiträge zur Kenntnis bulgarischer Chilopoden. Teil III. *Bulletin de la Société des Amis des Sciences et des Lettres de Poznán (D)* **11:** 81–89.

Koch A. 1927. Studien an leuchtenden Tieren. I. Das Leuchten der Myriapoden. *Zeitschrift für Morphologie und Ökologie der Tiere* **8:** 241–270.

Koch CL. 1863. *Die Myriapoden getreu nach der Natur abgebildet und beschrieben.* Halle, Schmidt.

Lawrence RF. 1953. Zoological results of a fifth expedition to East Africa. V. Chilopoda (Myriopoda). *Bulletin of the Museum of Comparative Zoology, Harvard College, Cambridge* **110:** 409–423.

Lawrence RF. 1955. A revision of centipedes (Chilopoda) of Natal and Zululand. *Annals of the Natal Museum* **13:** 121–174.

Lawrence RF. 1959. A collection of Arachnida and Myriapoda from the Transvaal Museum. *Annals of the Transvaal Museum* **23:** 363–386.

Lawrence RF. 1960. Myriapodes-Chilopodes. *Faune de Madagascar* **12:** 1–123.

Lewis JGE, Jones RE, Keay AN. 1988. On a new genus and species of centipede (Chilopoda, Geophilomorpha, Chilenophilidae) from the British Isles. *Journal of Natural History* **22:** 1657–1663.

Lignau N. 1929a Zur Kenntnis der zentralasiatischen Myriopoden. *Zoologischer Anzeiger* **85:** 159–175.

Lignau N. 1929b. Neue Myriopoden aus Zentralasien. *Zoologischer Anzeiger* **85:** 204–218.

Loksa I. 1971. Die von K. Lindberg in Afghanistan gesammelten Chilopoden. *Senckenbergiana biologica* **52:** 103–112.

Machado A. 1951. Novos dados sobre os Chilopodes de Angola (Colheitas de A. de Barros Machado, 1949). *Publicações Culturais da Companhia de Diamantes de Angola* **11:** 49–74.

Machado A. 1953. Alguns miriapodes de Espanha (Colheitas de J. Mateu). *Archivos del Instituto de Aclimatación* **1:** 77–92.

McShea DW. 1993. Evolutionary change in the morphological complexity of the mammalian vertebral column. *Evolution* **47:** 730–740.

Matic Z, Darabantu C. 1969. Contributo alla conoscenza del genere *Nesoporogaster* Verhoeff, 1924 (Geophilomorpha). *Memorie del Museo Civico di Storia Naturale di Verona* **16:** 447–454.

Matic Z, Darabantu C. 1974. Contributions à la connaissance du genre *Thracophilus* Verhoeff (Geophilomorpha, Himantariidae). *Bulletin de l'Institut de Zoologie et du Musée, Academie Bulgare des Sciences* **40:** 93–98.

Matic Z, Negrea S, Fundora Martinez C. 1977. Recherches sur les Chilopodes hypogés de Cuba. *Résultats de l'expédition biospéologique cubano-roumaine à Cuba.* Bucuresti, Editions de l'Académie de la Republique Socialiste Roumaine **2:** 277–301.

Mauriès JP. 1968. Myriapodes de l'île aux Singes (Makokou, Gabon) récoltés par J. A. Barra. *Bulletin du Muséum national d'Histoire naturelle, Paris, 2e série,* **40:** 768–771.

Meinert F. 1870. Myriapoda Musaei Hauniensis. Bitrag til Myriapodernes morphologi og systematik. I. Geophile. *Naturhistorisk Tidsskrift* (3)**7:** 1–128.

Minelli A. 1978. Secretions of centipedes. In: Bettini S, ed. *Arthropod venoms.* (*Handbook of experimental Pharmacology, 48*) Heidelberg, Springer: 73–84.

Minelli A. 1982a. Un nuovo chilopodo italiano, *Acanthogeophilus dentifer* n. g. n. sp. (Geophilomorpha Geophilidae). *Bollettino del Museo civico di Storia naturale di Verona* **8** (1981): 235–240.

Minelli A. 1982b. Contributo alla revisione dei chilopodi geofilomorfi finora riferiti ai generi *Henia* e *Chaetechelyne* (Chilopoda Geophilomorpha). *Memorie della Società entomologica Italiana* **60** (1981): 253–268.

Minelli A. 1983. On Sardinian centipedes (Chilopoda). *Bollettino di Zoologia* **49** (1982): 1–16.

Minelli A. 1992. Towards a new comparative morphology of myriapods. *Berichte des naturwissenschaftlich-medizinischen Vereins Inssbruck, Supplementum* **10:** 37–46.

Minelli A, Pasqual C, Etonti G. 1984. I chilopodi geofilomorfi del genere *Himantarium* C. L. Koch con particolare riferiamento alle popolazioni italiane. *Lavori della Società Veneziana di Scienze Naturali* 9(1): 73–84.

Nijhout HF. 1991. *The Development and Evolution of Butterfly Wing Patterns.* Washington and London: Smithsonian Institution Press.

Pereira LA. 1981a. Estudios sobre Geofilomorfos neotropicales. III. Sobre la presencia del género *Geoperingueyia* Attems, 1926 en la región neotropical (Chilopoda: Geophilomorpha: Geophilidae). *Revista de la Sociedad entomológica Argentina* **40:** 11–25.

Pereira LA. 1981b. Estudios sobre Geofilomorfos neotropicales. IV. Sobre cuatro especies nuevas del genero *Schendylurus* Silvestri, 1907. *Revista de la Sociedad entomológica Argentina* **40:** 115–138.

Pereira LA. 1984a. Estudio sobre Geofilomorfos neotropicales. VIII. Sobre una nueva especie perteneciente al genero *Schendylurus* Silvestri 1907 (Chilopoda: Geophilomorpha: Schendylidae). *Neotropica* 30(83); 63–74.

Pereira LA. 1984b. Estudios sobre Geofilomorfos neotropicales. IX. Acerca de la verdadera identidad de "*Brachyschendyla pectinata* Attems, 1934" (Chilopoda: Geophilomorpha: Schendylidae). *Revista de la Sociedad entomológica Argentina* **43:** 239–246.

Pereira LA. 1984c. Estudios sobre Geofilomorfos neotropicales X. Contribución al conocimiento del género *Dinogeophilus* Silvestri, 1909 (Chilopoda: Geophilomorpha: Geophilidae). *Bollettino del Laboratorio di Entomologia agraria Filippo Silvestri* **41:** 119–138.

Pereira LA, Coscarón S. 1975/76. Estudios sobre Geofilomorfos neotropicales. I. Sobre dos especies nuevas del genero *Pectiniunguis* Bollman (Schendylidae–Chilopoda). *Revista de la Sociedad entomológica Argentina* **35:** 59–75.

Pereira LA, Demange JM. 1991. Sur les espèces du genre *Ctenophilus* Cook, 1896 (Chilopoda, Geophilomorpha, Schendylidae). *Bulletin du Muséum national d'Histoire naturelle, Paris,* 4e série, **13,** section A: 81–96.

Pereira LA, Hoffman RL. 1993. The American species of *Escaryus,* a genus of holarctic centipedes (Geophilomorpha: Schendylidae). *Jeffersoniana* **3:** 1–72.

Shear WA, Peck SB. 1992. Centipedes (Chilopoda) and Symphyla of the Galápagos Islands. Equador. *Canadian Journal of Zoology* **70:** 2260–2274.

Shinohara K. 1961. Taxonomical and morphological studies of Myriapoda. VII. Two new species of Mecistocephalidae (Chilopods). *Zoological Magazine, Tokyo* **70:** 212–216.

Shinohara K. 1965. A new species of Chilopoda from Himalaya. *Journal of the College of Arts and Sciences of the Chiba University, Natural Sciences Series* **4:** 303–306.

Shinohara K. 1970. Taxonomical and morphological studies of Myriapoda. 9. A new genus of geophilid centipeds from Japan. *Zoological Magazine, Tokyo* **79:** 53–55.

Shinohara K. 1981. Two new species of the genus *Strigamia* (Chilopoda: Geophilidae) from Japan. *Acta Arachnologica* **30:** 41–48.

Silvestri F. 1928. Description of a new genus and species of Geophilidae (Myriapoda, Chilopoda) from Madras (India). *Record of the Indian Museum, Calcutta* **36:** 263–267.

Silvestri F. 1929. Risulati zoologici della Missione inviata dalla R. Società Geografica Italiana per l'esplorazione dell'oasi di Giarabub. Myriapodi e Chilopodi. *Annali del Museo di Storia naturale, Genova* **53:** 308–312.

Silvestri F. 1935a. Myriopoda from the Society Islands. *Bulletin of the Bishop Museum, Honolulu* **113:** 131–134.

Silvestri F. 1935b. Chilopoda. In: Visser-Hooft C, ed. *Wissenschaftliche Ergebnisse der Niederländischen Expedition in den Karakorum und die angrenzenden Gebiete 1922, 1925, und 1929–30.* Leipzig, F. A. Brockhaus: 194–204.

Titova LP. 1965. A new chilopod *Tygarrup numinabadicus* Titova sp. n. (Mecistocephalidae, Chilopoda) from South Tadzhikistan. *Zoologicheskii Zhurnal* **44:** 871–876.

Titova LP. 1972. Novuie vidui roda *Escaryus* Cook et Collins (Schendylidae, Chilopoda). *Ekol. Pocvinn. Besposvonocn.* Moskva, Nauka: 94–119.

Titova LP. 1975. Geophilids of the family Mecistocephalidae (Chilopoda) in the fauna of the U.S.S.R. *Zoologicheskii Zhurnal* **44:** 39–48.

Turcato A, Minelli A. 1990. Fine structure of the ventral glands of *Pleurogeophilus mediterraneus* (Meinert) (Chilopoda, Geophilomorpha). In: Minelli A, ed. *Proceedings of the 7th International Congress of Myriapodology.* Leiden, E.J. Brill: 165–173.

Turk FA. 1955. The Chilopods of Peru with description of new species and some zoogeographical notes on the Peruvian Chilopod fauna. *Proceedings of the Zoological Society of London* **125:** 469–504.

Verhoeff KW. 1908–25. Chilopoda. In: Bronn HG, ed. *Die Klassen und Ordnungen des Tier-Reichs,* 5:2. Leipzig, Akademische Verlagsgesellschaft.

Verhoeff KW. 1928. Geophilomorphen-Beiträge und eine *Lithobius*-Form. *Mitteilungen aus dem Zoologischen Museum in Berlin* **14:** 229–286.

Verhoeff KW. 1930. Über Myriapoden aus Turkestan. *Zoologischer Anzeiger* **91:** 243–266.

Verhoeff KW. 1934a. Beiträge zur Systematik und Geographie der Chilopoden. *Zoologische Jahrbücher, Abeilung für Systematik* **66:** 1–112.

Verhoeff KW. 1934b. Schwedisch-Chinesische wissenschaftliche Expedition nach den nordwestlichen Provinzen Chinas, unter der Leitung von Dr. Sven Hedin und Prof. Su Ping-chang. Myriapoda. *Arkiv för Zoologi, Stockholm* **26a** (10): 1–41.

Verhoeff KW. 1935. Über *Scolioplanes* (Chilopoda). *Zoologischer Anzeiger* **111:** 10–23.

Verhoeff KW. 1937a. South African Geophilomorpha (Myriopoda). *Annals of the South African Museum* **32:** 95–116.

Verhoeff KW. 1937b. Chilopoden aus Malacca, nach den Objecten des Raffles Mus. Singapore. *Bulletin of the Raffles Museum Singapore* **13:** 198–270.

Verhoeff KW. 1938a. Zur Kenntnis südafrikanischer Geophilomorphen. *Zoologischer Anzieger* **121:** 181–194.

Verhoeff KW. 1938b. Über einige amerikanische Myriapoden. *Zoologischer Anzeiger* **122:** 273–284.

Verhoeff KW. 1938c. Über einige Chilopoden des Zoologischen Museums in München. *Zoologischer Anzeiger* **123:** 123–130.

Verhoeff KW. 1938d. Myriapoden aus Marokko. *Zoologischer Anzeiger* **123:** 295–302.

Verhoeff KW. 1939a. Chilopoden der Insel Mauritius. *Zoologische Jahrbücher, Abteilung für Systematik* **72:** 71–98.

Verhoeff KW. 1939b. Polydesmoideen, Colobognathen und Geophilomorphen aus Südafrika, besonders den Drakensbergen, Natal. *Annals of the Natal Museum* **9:** 203–224.

Verhoeff KW. 1940. Aliquid novi ex Africa. III–Chilopoda–Epimorpha. *Zoologischer Anzeiger* **132:** 49–62.

Verhoeff KW. 1941a. Asyanin zoogeografiyasi ve hayvan sistematige hakkinda. Asiatische Beiträge. II–Türkische Chilopoden. *Revue de la Faculté des Sciences de l'Université d'Istambul* **6B:** 85–110.

Verhoeff KW. 1941b. Myriapoden der Insel Fernando Po. X. Beitrag zu den wissenschaftlichen Ergebnissen der Forschungsreise H. Eidmann nach Spanisch-Guinea 1939–40 (Schluss). *Zoologischer Anzeiger* **136:** 89–98.

Verhoeff KW. 1942a. Myriapoden der Insel Fernando Po und über den Ankerapparat und die Spermaleitung der Spirostreptoideen (XVI. Beitrag zu den wissenschaftlichen Ergebnissen der Forschungsreise nach Spanisch-Guinea 1939–40). *Zeitschrift für Morphologie und Ökologie der Tiere* **39:** 76–97.

Verhoeff KW. 1942b. Chilopoden aus innerasiatischen Hochgebirgen. *Zoologischer Anzeiger* **137:** 35–52.

Verhoeff KW. 1943. Über Chilopoden der Türkei. III. Aufsatz. *Zoologischer Anzeiger* **143:** 116–140.

Verhoeff KW. 1945. Asya hayvanlari ve zoogeografiyasi hakkinda–Asiatische Beiträge VIII. *Revue de la Faculté des Sciences de l'Université d'Istanbul* **9B:** 307–347.

Verhoeff KW. 1951. Chilopoden und Diplopoden. *Beiträge zur Fauna Perus* **2:** 1–68.

APPENDIX

Papers containing useful descriptions of sternal pore areas in the genera quoted in the text.

Himantariidae	
Causerium	Chamberlin, 1964
Himantarium	Attems, 1929
Meinertophilus	Attems, 1929; Chamberlin, 1930a; Verhoeff, 1938d
Mesocanthus	Attems, 1929, 1934a, 1947
Nesoporogaster	Attems, 1929; Eason, 1962; Matic & Darabantu, 1969
Stenophilus	Chamberlin, 1946c, 1953b
Stigmatogaster	Attems, 1929; Verhoeff, 1938c
Dignathodontidae	
Agnathodon	Folkmanova & Dobroruka, 1960
Dignathodon	Attems, 1929
Henia	Attems, 1929; Minelli, 1982b
Oryidae	
Keporya	Chamberlin, 1941b
Metaxythus	Crabill, 1968b
Rhysonotum	Attems, 1952b
Trematorya	Attems, 1929
Eriphantidae	
Eriphantes	Crabill, 1970
Gonibregmatidae	
Eremorus	Chamberlin, 1963
Eucratonyx	Attems, 1929
Gonibregmatus	Attems, 1929, 1930b
Himantosoma	Attems, 1929
Ketampa	Chamberlin, 1955–56
Schendylidae	
Ctenophilus	Pereira & Demange, 1991
Haploschendyla	Attems, 1929; Lawrence, 1960
Litoschendyla	Attems, 1929
Marsicomerus	Hoffman & Pereira, 1991
Mesoschendyla	Attems, 1929; Crabill, 1968a; Verhoeff, 1937a, 1940; Dobroruka, 1959
Nannophilus	Attems, 1929
Nyctunguis	Attems, 1929, 1939; Crabill, 1958; Chamberlin, 1941a, 1946d, 1962b; Turk, 1955
Pectiniunguis	Attems, 1929; Crabill, 1959b; Camberlin, 1941a; Pereira & Coscarón, 1975–76
Plesioschendyla	Attems, 1929
Schendyla	Attems, 1929; Kaczmarek, 1962, 1969, Verhoeff, 1934a
Schendylellus	Attems, 1929
Schendylops	Attems, 1929
Schendylurus	Attems, 1929, 1934a; Chamberlin, 1957; Crabill, 1960a; Demange, 1963; Pereira, 1981b, 1984a; Turk, 1955
Ballophilidae	
Ballophilus	Archey, 1936; Attems, 1929, 1953; Chamberlin, 1944a, 1950b, 1953a; Demange, 1963; Lawrence, 1960; Verhoeff, 1939a, 1951
Caritohallex	Crabill, 1960
Clavophilus	Chamberlin, 1950b
Diplethmus	Attems, 1929, 1947; Chamberlin, 1940a; Turk, 1955
Ityphilus	Attems, 1929; Chamberlin, 1943a, 1943b, 1957; Crabill, 1960a
Koinethmus	Chamberlin 1958
Leptynophilus	Chamberlin, 1940a
Taeniolinum	Attems, 1929; Chamberlin, 1940a
Tanophilus	Attems, 1929
Zygethmus	Chamberlin, 1957

Geophilidae (inc. Chilenophilidae)	
Acanthogeophilus	Minelli, 1982a
Achilophilus	Attems, 1929, Verhoeff, 1937a
Alloschizotaenia	Attems, 1929, 1937
Andenophilus	Verhoeff, 1951
Aphilodon	Attems, 1929; Lawrence, 1955; Verhoeff, 1937a, 1938a
Arctogeophilus	Attems, 1929, 1947; Chamberlin, 1941a; Folkmanova & Dobroruka, 1960; Verhoeff, 1934a
Barrophilus	Chamberlin, 1940a
Bebekium	Verhoeff, 1945
Brachygeophilus	Attems, 1929, 1934a, 1952b; Chamberlin, 1938, 1941a, 1943a, 1952a, 1953b; Crabill, 1949; Folkmanova, 1956
Brachygonarea	Attems, 1929, 1934a
Cephalodolichus	Verhoeff, 1938a
Chalandea	Attems, 1929, 1952a
Chilenophilus	Attems, 1929; Chamberlin, 1962a
Chilerium	Chamberlin, 1955–56
Clinopodes	Attems, 1929; Loksa, 1971
Condylona	Chamberlin, 1941a
Dinogeophilus	Attems, 1929; Pereira, 1984c
Dysmesus	Chamberlin, 1944b
Eurytion	Attems, 1929; Dobroruka, 1969; Verhoeff, 1937a, 1940
Filipponus	Chamberlin, 1962a
Garrina	Attems, 1929; Chamberlin, 1943a, 1943b, 1944b
Geomerinus	Attems, 1929
Geophilus	Archey, 1936; Attems, 1929, 1951, 1952b; Chamberlin, 1928a, 1928b, 1930b, 1940b, 1941a, 1943b, 1951; Folkmanova, 1928; Kaczmarek, 1970; Minelli, 1983; Silvestri, 1935b; Verhoeff, 1928, 1939a, 1943b
Gnathoribautia	Attems, 1929
Harmostela	Chamberlin, 1941a
Idiona	Chamberlin, 1946a
Lionix	Chamberlin, 1960b; Pereira & Hoffman, 1993
Mecistauchenus	Attems, 1929
Mecophilus	Attems, 1929
Mesogeophilus	Attems, 1929, 1947
Nabocodes	Chamberlin, 1940a
Navajona	Chamberlin, 1930b
Nicopus	Attems, 1947
Nothogeophilus	Lewis, Jones & Keay, 1988
Oligna	Chamberlin, 1943a
Pachymerellus	Attems, 1929
Pachymerinus	Attems, 1929
Pachymerium	Attems, 1929, 1934b, 1947; Capuse, 1968; Chamberlin, 1960a; Lawrence, 1960; Matic, Negrea & Fundora Martinez, 1977; Verhoeff, 1943
Pandinium	Chamberlin, 1955–56, 1956, 1962a
Philacroterium	Attems, 1929
Philogeonus	Attems, 1929
Pleurogeophilus	Attems, 1929, 1947; Folkmanova, 1956; Verhoeff, 1934a
Poaphilus	Attems, 1929
Polycricus	Chamberlin, 1940a, 1941d, 1943a, 1944b
Polygonarea	Attems, 1929; Chamberlin, 1955–56; Lawrence, 1959; Verhoeff, 1937a, 1938a, 1941b, 1942a
Queenslandophilus	Attems, 1929; Verhoeff, 1934a
Ribautia	Attems, 1929; Chamberlin, 1941b, 1957; Demange, 1963; Lawrence, 1960; Verhoeff, 1939b
Schizonampa	Attems, 1929
Schizonium	Chamberlin, 1955–56, 1962a
Schizoribautia	Chamberlin, 1957; Verhoeff, 1951
Schizotaenia	Attems, 1929; Dobroruka, 1969, 1973; Folkmanova & Dobroruka, 1960
Sepedonophilus	Attems, 1929; Chamberlin, 1940c
Serrona	Chamberlin, 1941a
Sogona	Attems, 1929, 1947; Chamberlin, 1940d, 1943a
Soniphilus	Attems, 1929

Synthophilus	Chamberlin, 1946b
Taiyuna	Attems, 1929; Chamberlin, 1941a
Tasmanophilus	Attems, 1929
Timpina	Attems, 1929
Turkophilus	Verhoeff, 1941a
Watophilus	Attems, 1929; Chamberlin, 1928b
Zelanophilus	Archey, 1936; Crabill, 1963
Zygona	Chamberlin, 1960a; Pereira & Hoffman, 1993
Linotaeniidae	
Damothus	Chamberlin, 1960a; Crabill, 1962b
Horonia	Chamberlin, 1966
Korynia	Chamberlin, 1941a, 1954
Malochora	Chamberlin, 1941a
Strigamia	Attems, 1929; Shinohara, 1981; Verhoeff, 1935, 1938b