

# ***Stenotaenia* Koch, 1847: a hitherto unrecognized lineage of western Palaearctic centipedes with unusual diversity in body size and segment number (Chilopoda: Geophilidae)**

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Based on morphological evidence, we newly define the genus *Stenotaenia* Koch, 1847 (= *Scnipaeus* Bergsøe & Meinert, 1866; = *Simophilus* Silvestri, 1896; = *Onychopodogaster* Verhoeff, 1902; = *Insigniporus* Attems, 1903; = *Notadenophilus* Verhoeff, 1928; = *Bithyniphilus* Verhoeff, 1941; = *Schizopleres* Folkmanova, 1956; = *Euronesogeophilus* Matic, 1972; all **syn. nov.**) as including the following 15 species: *Stenotaenia linearis* (Koch, 1835) (= *Geophilus simplex* Gervais, 1835; = *Geophilus brevicornis* Koch, 1837; = *Scnipaeus foveolatus* Bergsøe & Meinert, 1866; = *Himantarium caldarium* Meinert, 1886 **syn. nov.**; = *Geophilus* (*Geophilus*) *linearis* var. *polyporus* Verhoeff, 1896 **syn. nov.**; = *Geophilus ormanyensis* Attems, 1903 **syn. nov.**, after lectotype designation; = *Insigniporus acuneli* Căpușe, 1968 **syn. nov.**) from central and northern Europe; *Stenotaenia frenum* (Meinert, 1870) from northern Africa; *Stenotaenia romana* (Silvestri, 1895) (= *Geophilus silvestrii* Verhoeff, 1928 **syn. nov.**) and *Stenotaenia sorrentina* (Attems, 1903) (= *Geophilus forficularius* Fanzago, 1881 **syn. nov.**; = *Geophilus linearis abbreviatus* Verhoeff, 1925 **syn. nov.**) from the Italian peninsula and Sardinia; *Stenotaenia antecribellata* (Verhoeff, 1898) (= *Simophilus albanensis* Attems, 1929 **syn. nov.**), *Stenotaenia cribelliger* (Verhoeff, 1898), *Stenotaenia palpiger* (Attems, 1903), *Stenotaenia rhodopensis* (Kaczmarek, 1970), and *Stenotaenia sturanyi* (Attems, 1903) from the Balkan peninsula; *Stenotaenia naxia* (Verhoeff, 1901) (= *Geophilus graecus* Verhoeff, 1902) from the Aegean islands; *Stenotaenia asiaeaminoris* (Verhoeff, 1898) and *Stenotaenia bosporana* (Verhoeff, 1941) from Anatolia; *Stenotaenia giljarovi* (Folkmanova, 1956) from western Caucasus; *Stenotaenia fimbriata* (Verhoeff, 1934) and *Stenotaenia palaestina* (Verhoeff, 1925) from Palestine; with the only exception of *S. linearis*, all of these binomens are **comb. nov.** In *Stenotaenia*, a strongly conserved overall morphology is matched by an unusual interspecific variation in both the body size of fully grown specimens (from 1.7 cm in *S. romana* to 7.7 cm in *S. sturanyi*) and the number of leg-bearing segments (from 43 in male *S. romana* to 115 in female *S. sturanyi*). The number of segments correlates with maximum body size. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **153**, 253–286.

**ADDITIONAL KEYWORDS:** evolution – geographical distribution – morphology – segmental structure – species diversity – taxonomic revision.

## INTRODUCTION

Within the dramatic evolutionary radiation of arthropods, geophilomorph centipedes (Geophilomorpha) are represented by more than a thousand described species. This group is very distinct and is quite

conservative in most anatomical traits, but is very diverse in general body features such as size at full growth (total length ranging from c. 5 mm in *Dinogeophilus* to more than 200 mm in some Himantariidae and Oryidae), overall shape (from delicately slender, as in some Schendylidae and Geophilidae, to stout, as in some Himantariidae), and segmental composition (the number of leg-bearing segments ranging from 27 in some *Schendylops oligopus* (Pereira,

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Minelli & Barbieri, 1995) to 191 in some *Gonibregmatus plurimipes* Chamberlin, 1920; Minelli & Bortoletto, 1988; Minelli *et al.*, 2000). For these features, geophilomorphs are appealing targets for researchers of evolutionary developmental biology that are aiming to explore evolutionary patterns and to unveil morphogenetic processes involved in the shaping of arthropod body structure (Minelli & Bortoletto, 1988; Minelli *et al.*, 2000; Minelli & Fusco, 2004; Arthur & Chipman, 2005). However, any effort in this sense needs to be based on a satisfactory understanding of the actual diversity of the group, as well as on a reliable scenario for their evolution. Conversely, current taxonomic knowledge for most geophilomorph taxa is still largely inadequate, and therefore it could provide a misleading framework for comparative analyses addressing any kind of biological questions.

This is true even for the geophilomorph fauna of the western Palaearctic, despite the fact that it has been more thoroughly investigated than that of any other region of the world. Primary taxonomic work in the past was usually very limited in geographical scope, and comprehensive revisions have been rare. As a result, the taxonomy and nomenclature currently in use are very heterogeneous, and are largely inconsistent, even at the supraspecific level.

More than one half of the geophilomorph species of the western Palaearctic, and almost half of all those described throughout the world, are assigned to the family Geophilidae, the largest and most widely distributed geophilomorph family. Indeed, different authors proposed different circumscriptions for the family Geophilidae, sometimes separating minor groups as distinct families, but a recently compiled catalogue of world centipedes (Minelli, 2006) adopted a relatively inclusive circumscription, and listed c. 560 species and c. 110 genera in the Geophilidae. These species are found almost worldwide (in the Americas, from the Arctic to the southernmost regions, the whole temperate part of Eurasia, from Macaronesia and the Mediterranean region to the Japanese islands, most of Africa, Madagascar, and the Australian region including New Zealand and some islands in the Pacific Ocean). The highest species richness is in North America, particularly in the Californian and Mexican regions, and in southern Europe; relatively high numbers of species are also hosted by South America, the southernmost part of Africa, Australia, and New Zealand; conversely, only few species are known from southern and south-eastern Asia. Morphological diversity among geophilids is remarkable, but all proposals to split them into different families, or to arrange them in subfamilies (see especially Verhoeff, 1902–25; Brölemann, 1909a; Attems, 1926, 1929a, 1947; Crabill, 1970), resulted in unsatisfactory arrangements that were

not followed by recent authors. Furthermore, in all phylogenetic analyses performed to date, upon either morphological or molecular data, geophilids were found to be a paraphyletic assemblage, particularly with respect to clades that have long been recognized as clearly diagnosed families, namely the Linotaenidae and Dignathodontidae (Edgecombe, Giribet & Wheeler, 1999; Foddai & Minelli, 2000; Edgecombe & Giribet, 2002, 2004). Also, the genus-level taxonomy is very heterogeneous and unsatisfactory: some large genera, as currently circumscribed, are obviously composite (polyphyletic), and many monotypic genera are still accepted as valid, but their identity and affinities need further evaluation.

In the context of an on-going reassessment of the taxonomic system of the geophilids, we found compelling evidence for the existence of a well diagnosable genus-level group, which has hitherto gone largely unrecognized. After a critical evaluation of the relevant literature, and a comparative morphological analysis of representative specimens, we propose here an original circumscription of this genus, together with a preliminary revision of the included species, as well as a full, updated synthesis of their geographical distribution. We also analyse and discuss the unusual interspecific diversity in body size and trunk segmentation, which suggests this arthropod lineage as an attractive model system within which to investigate evolutionary patterns and developmental processes in segmental structure and body size.

## MATERIAL AND METHODS

Through an exhaustive survey of the taxonomic literature on Geophilidae, we compiled a full catalogue of citations, taxonomic opinions, and geographical records for all nominal species recognizable in the genus as defined here. We provide here a selected list of citations, including all those relevant for taxonomy and morphological description of the individual taxa, whereas the full database is available upon request.

We also performed comparative morphological analysis on 143 specimens from throughout the geographical range of the genus, which are representative of different nominal taxa, of various sizes and both sexes (see Appendix). In order to minimize variation in the subjective interpretation of morphological traits, all specimens were examined comparatively by one of us (LB) under light microscopy, following standard procedures (Pereira, 2000; Foddai, Minelli & Pereira, 2002). Micrographs of representative specimens were taken after clearing in lactophenol.

Direct examination of type material was not needed for most nominal species, as we were able to recognize their identity and taxonomic position confidently from published information, or through the examination of

representative specimens assigned confidently to those taxa, or based on unpublished information provided by colleagues who examined the type specimens. Of the few nominal species of uncertain identity or dubious assignment, we could examine the syntypes of *Himantarium caldarium* Meinert, 1886, whereas we could not locate the type material of *Geophilus forficularius* Fanzago, 1881, *Geophilus linearis* var. *polyporus* Verhoeff, 1896, and *Geophilus ungviculatus* Daday, 1889.

In order to analyse the geographical occurrence of taxa we evaluated all published data, as well as unpublished records based on about 230 specimens from our own or museum collections (database available on request). As different authors followed different nomenclature and diagnostic criteria, each published identification was only considered as reliable when evidence was available on the criteria adopted, or when the identification was consistent with other sources. Identification and mapping of localities was based on the Geographic Names Data Base of NGIA (<http://www.nga.mil/geonames/GNS>). Data were mapped upon a grid of 30' latitude  $\times$  30' longitude; a more precise resolution was not practicable because of the limited precision of most of the published records.

As a measure of body size, we selected the maximum head width (measured by means of a micrometer mounted on one ocular lens of the microscope) instead of body length or other longitudinal measures, as these latter measurements are affected by the degree of relaxation of the trunk and are expected to be correlated, at least in part, with segment number.

## RESULTS

### GENUS *STENOTAENIA* KOCH, 1847

*Stenotaenia* Koch, 1847: 85, 187. Bergsøe & Meinert, 1866: 99. Pocock, 1890: 66. Attems, 1929a: 330.

*Scnipaeus* Bergsøe & Meinert, 1866: 95. Cook, 1896: 75. Pocock, 1901: 330. **Syn. nov.**

*Simophilus* Silvestri, 1896: 154. Attems, 1903: 170, 272; 1926: 362; 1929a: 195; 1929b: 334; 1947: 109. Brölemann, 1909a: 332. *Geophilus* (*Simophilus*): Verhoeff, 1941a: 89. **Syn. nov.**

*Onychopodogaster* Verhoeff, 1902: 560; 1925: 73. Attems, 1926: 362. *Geophilus* (*Onychopodogaster*): Brölemann, 1909b: 211. Verhoeff, 1924a: 413; 1928: 267; 1934a: 9; 1934b: 114; 1937a: 97; 1938: 346; 1941a: 89; 1943b: 79; 1945: 311. **Syn. nov.**

*Insigniporus* Attems, 1903: 269; 1909: 36; 1926: 362; 1929a: 208; 1947: 108. Brölemann, 1909a: 332. Folkmanova, 1928: 124; 1929: 36; 1956: 1641 (misspelled as *Insigniporus*). Căpușe, 1968: 699. Matic, 1972: 121. **Syn. nov.**

*Notadenophilus* (subgenus of *Geophilus*) Verhoeff, 1928: 268. **Syn. nov.**

*Bithyniphilus* Verhoeff, 1941b: 40; 1945: 4, 6. Chamberlin, 1952: 198. **Syn. nov.**

*Schizopleres* Folkmanova, 1956: 1640. **Syn. nov.**

*Euronesogeophilus* (subgenus of *Nesogeophilus*) Matic, 1972: 99. **Syn. nov.**

*Type species: Geophilus linearis* Koch, 1835; by subsequent designation (Pocock, 1890: 66).

*Brief description (based on an adult):* Head capsule: cephalic plate only slightly longer than wide; frontal line not evident. Antennae: about two or three times as long as the head; apical sensilla spear-like, only slightly swollen at mid-length, c. 10–12- $\mu$ m long; club-like sensilla, c. 10–12- $\mu$ m long, on both sides of antennal article XIV. Clypeus: uniformly areolate, without 'clypeal areas', i.e. distinct areas with finer areolation; setae arranged approximately in two or three transverse rows, on the anterior part of the clypeus; a pair of distinct, not areolate, transversally elongated areas along the posterior margin. Labrum: margin slightly projecting backwards into a medial, obtuse angle with concave sides; a row of slender, pointed, finely ciliated filaments along the margin, projecting backwards; a few stout tubercles sometimes present at the mid-point of the margin. Mandible: ventral side swollen, covered with dense, hair-like projections. First maxillae: one or two pairs of lappets covered with scales. Second maxillae: telopodite bearing a slender, pointed claw. Forcipular segment: tergum c. 2.0–2.5 times as wide as long; exposed part of coxosternum wider than long, anterior margin without evident teeth, pleurocoxal margins completely ventral, evidently convergent backwards; chitin lines evident, either reaching the condyles of the coxosternum or not; forcipules shorter than the maximum width of the coxosternum, basal article wider than long, evidently narrowing distad; intermediate articles extremely short to apparently coalescent; tarsungulum gradually narrowing, its internal margin entire; mesal sides of forcipules without any evidence of tubercles; calyx of poison gland elongated, reaching the basal article. Leg-bearing segments: sternal pores arranged into a single, rounded to oval, medio-posterior area on each of the anteriormost and posteriormost segments, but arranged into two distinct, transversally paired areas on each of the intermediate segments; anterior margin of sterna without evident 'carphophagus' sockets. Last leg-bearing segment: tergum subtrapezoid, wider than long; sternum subrectangular to trapezoid, wider than long, either not evidently or only slightly narrowing backwards; channels of coxal glands mostly converging into two pouches on the internal margin of each coxopleuron, which open on

the anterior end and on the ventral median point, respectively; telopodite only slightly longer than the telopodite of the penultimate leg-bearing segment; relatively dense, short setae on the ventral side of the telopodite; claw well developed. Terminal segments: female gonopods in the shape of an entire, short, slightly bilobate lamina.

*Differential diagnosis (differences from most similar and possibly most closely related genera; see also Table 1 and Fig. 1):* *Stenotaenia* Koch, 1847 differs from *Geophilus* Leach, 1814 mainly in having a relatively shorter basal article of the forcipule, forcipular tarsungulum without basal tubercle, trunk sterna without 'carpophagus' sockets, sternal pores in the anterior part of the trunk arranged in a longitudinally elongate oval area, instead of a transversally elongate band, and coxal glands opening in common pouches, instead of through independent pores. *Stenotaenia* Koch, 1847 differs from *Clinopodes* Koch, 1847 mainly in having sternal pores in the anterior part of the trunk arranged in a longitudinally elongate oval area, instead of a transversally elongate band, and legs of the last pair bearing well-developed claws. *Stenotaenia* Koch, 1847 differs from *Tuoba* Chamberlin, 1920 mainly in having a relatively shorter basal article of the forcipule, forcipular tarsungulum without basal tubercle, trunk sterna without 'carpophagus' sockets, sternal pores in the anterior part of the trunk arranged in a longitudinally elongate oval area, instead of a transversally elongate band, and coxal glands opening in two pouches, instead of a single pouch.

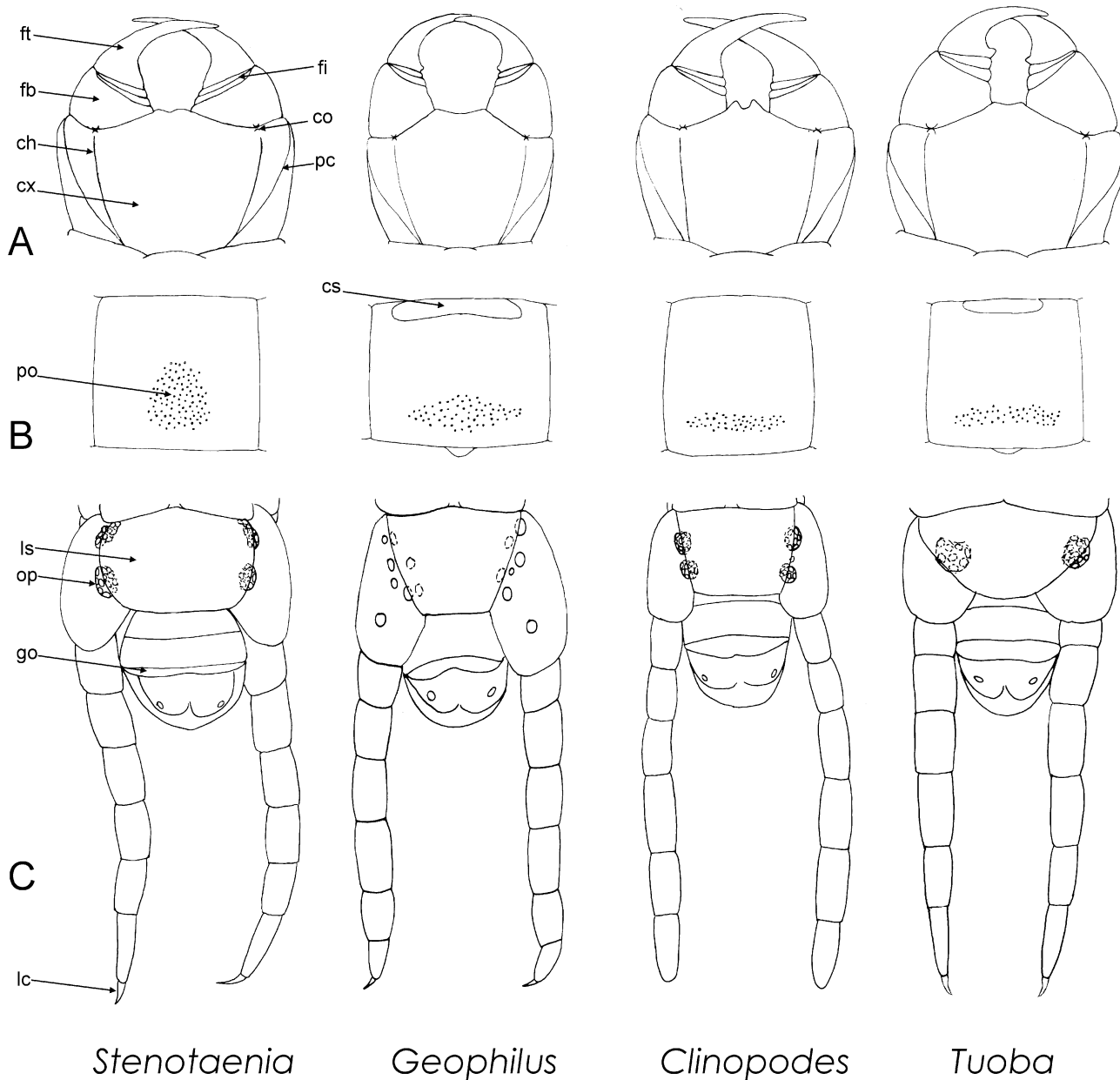
*Taxonomic history:* *Stenotaenia* Koch, 1847 is the oldest among all of the available genus-group names of which the type species are included here in this genus. Koch (1847) introduced *Stenotaenia* to include the two species *Geophilus linearis* Koch, 1835 and *Geophilus acuminatus* Leach, 1815, but failed to select a type species. Most subsequent authors recognized that these two species are so different as to deserve being assigned to different genera, as *G. linearis* and *Scolioplanes acuminata*, respectively (Latzel, 1880, 1885; Haase, 1881; Sselivanov, 1884; Daday, 1889a; Attems, 1895, 1903; Verhoeff, 1902–25). Therefore, *Stenotaenia* was most often considered as an invalid taxon, and was usually listed as a synonym of both *Geophilus* Leach, 1814 and *Scolioplanes* Bergsøe & Meinert, 1866, mostly ignoring that *G. linearis* had been validly designated as the type species of *Stenotaenia* by Pocock (1890), and even irrespective of the principle of priority (Latzel, 1880; Haase, 1881; Sselivanov, 1884; Daday, 1889a; Verhoeff, 1902–25; Attems, 1903; Berlese, 1903; Brade-Birks, 1934; Matic, 1972). In his fundamental monograph on world geophilomorphs, Attems (1929a)

**Table 1.** Main differential characters between *Stenotaenia* and other close genera to which species of *Stenotaenia* have been assigned, to date

	<i>Stenotaenia</i> Koch, 1847	<i>Geophilus</i> Leach, 1814	<i>Clinopodes</i> Koch, 1847	<i>Tuoba</i> Chamberlin, 1920
Type species	<i>Geophilus linearis</i> Koch, 1835	<i>Scolopendra electrica</i> Linnaeus, 1758	<i>Clinopodes flavidus</i> Koch, 1847	<i>Tuoba curticeps</i> Chamberlin, 1920 (junior synonym of <i>Geophilus sydneyensis</i> Pocock, 1891)
Forcipule: basal article	Less long than wide	About as long as wide	Less long than wide	About as long as wide
Forcipule: basal tubercle on tarsungulum	Absent	Present	Absent	Present
Anterior part of trunk: 'carpophagus' sockets	Absent	Present	Absent	Present
Anterior part of trunk: sternal pore areas	Oval, longitudinally elongate	Transversally elongate	Transversally elongate	Transversally elongate
Last leg-bearing segment: anterior margin of sternum	Only slightly wider than the posterior margin	Much wider than the posterior margin	Much wider than the posterior margin	Much wider than the posterior margin
Last leg-bearing segment: openings of coxal glands	Two pouches	Independent pores	Two pouches	One pouch
Last leg-bearing segment: claw of telopodite	Present	Present	Absent	Present

Characters are based on type species only. Differences in respect to *Stenotaenia* are in italics.





**Figure 1.** Main differential characters between *Stenotaenia* and related genera to which species of *Stenotaenia* have been assigned, to date. Drawings represent the type species of each genus (see Table 1): A, forcipular segment, ventral; B, sternum at about one third of the length of the trunk, ventral; C, last leg-bearing segment and terminal segments in the female, ventral. Abbreviations: ch, chitin line; co, condyle of forcipular coxosternum; cs, 'carphophagus' socket; cx, forcipular coxosternum; fb, forcipular basal article; fi, forcipular intermediate articles; ft, forcipular tarsungulum; go, gonopods; lc, claw of last leg; ls, sternum of last leg-bearing segment; op, openings of coxal glands; pc, forcipular pleurocoxal margin; po, sternal pore area.

registered *Stenotaenia* as a taxon of uncertain status. Indeed, the name *Stenotaenia* was not used as valid after Fanzago (1881a).

#### Remarks on synonyms

*Scnipaeus* Bergsøe & Meinert, 1866. The genus *Scnipaeus* was introduced by Bergsøe & Meinert

(1866) to include the two new species *Scnipaeus sodalis* Bergsøe & Meinert, 1866 and *Scnipaeus foveolatus* Bergsøe & Meinert, 1866, but no type species was fixed at that time. *Scnipaeus foveolatus* was subsequently designated as the type species by Cook (1896). For a long time these two nominal species were recognized as junior synonyms of *Geophilus*

*carpophagus* Leach, 1815 and *G. linearis*, respectively. As a consequence, *Scnipaeus* was regarded most often as a synonym of *Geophilus* (Meinert, 1870; Latzel, 1880; Sselivanov, 1881, 1884; Attems, 1903, 1929a; Crabill, 1954), or as a synonym of *Clinopodes* (Brölemann, 1930). Indeed, it was not cited as valid since Pocock (1901). *Scnipaeus* is recognized here as a junior synonym of *Stenotaenia*, as its type species is recognized as being identical to the type species of *Stenotaenia* [see *Stenotaenia linearis* (Koch, 1835)].

*Simophilus* Silvestri, 1896. The genus *Simophilus* was introduced by Silvestri (1896) for the single species *Geophilus frenum* Meinert, 1870, which thus is the type species by monotypy. Attems (1929b) described another species under this genus, namely *Simophilus albanensis* Attems, 1929, and also moved *Geophilus palaestinus* Verhoeff, 1925 under it (Attems, 1929a); the latter combination was not accepted in the subsequent literature. As the identity of both *G. frenum* and *S. albanensis* remained unclear, *Simophilus* continued to be cited as a genus of uncertain identity in all major works (Verhoeff, 1902–25, 1945; Brölemann, 1909a; Attems, 1929a, 1947). Occasionally, it was treated as a subgenus of *Geophilus* (Verhoeff, 1941a). *Simophilus* is recognized here as a junior synonym of *Stenotaenia*, as its type species is very similar to the type species of *Stenotaenia* [see *Stenotaenia frenum* (Meinert, 1870)], and deserves to be considered congeneric with it. Silvestri's (1896) original diagnosis is fully compatible with the diagnosis of *Stenotaenia* provided here, even in major diagnostic traits such as the shape of the sternal pore areas and the last pair of legs.

*Onychopodogaster* Verhoeff, 1902. *Onychopodogaster* was first introduced by Verhoeff (1902) only citing *Onychopodogaster graecum* [sic] as an alternative, 'in litteris' name for his new species *Geophilus graecus*. *Onychopodogaster* was explicitly used as a valid taxon in different publications (Verhoeff, 1902–25, 1924a, 1925, 1928, 1934a, 1934b, 1937a, 1938, 1941a, 1943b, 1945; Brölemann, 1909b; Attems, 1926; Folkmanova, 1952). Therefore, as already discussed by Jeekel (2005), *Onychopodogaster* is an available name dating from 1902 (ICZN: art. 11.6; International Commission on Zoological Nomenclature, 1999), its author is Verhoeff (ICZN: art. 50.7), and its type species is *Geophilus graecus* Verhoeff, 1902 by monotypy (ICZN: art. 67.12). *Onychopodogaster* was not used as a valid taxon name after Folkmanova (1952); it was considered to be a synonym of *Clinopodes* Koch, 1847, based on the unwarranted opinion of a close affinity of its type species with *Clinopodes flavidus* Koch, 1847 (Brölemann, 1909a; Brölemann, 1930; Matic, 1972), or as a synonym of *Geophilus* Leach, 1814 (Foddai *et al.*, 1995), or was even com-

pletely ignored (Attems, 1929a). *Onychopodogaster* is recognized here as a junior synonym of *Stenotaenia*, as its type species has been considered very close to the type species of *Stenotaenia* since it was introduced originally by Verhoeff (1902), and was later synonymized under *Geophilus naxius* Verhoeff, 1901 (Verhoeff, 1925), which is shown here to be congeneric with *Stenotaenia linearis* (Koch, 1835) [see *Stenotaenia naxia* (Verhoeff, 1901)].

*Insigniporus* Attems, 1903. The genus *Insigniporus* was introduced by Attems (1903) for his new species *Insigniporus sturanyi*, which is thus the type species by monotypy. The identity of this taxon has remained poorly understood, and different authors have proposed different affinities for it (Attems, 1909; Brölemann, 1909a), yet its validity remained unchallenged, and another species, *Insigniporus acuneli*, was later described under it by Căpușe (1968). *Insigniporus* is recognized here as a junior synonym of *Stenotaenia* because its type species is so close to the type species of *Stenotaenia* that it deserves to be included in the same genus. It is worth noting that *I. acuneli* is demonstrated here to be identical to *S. linearis* [see *Stenotaenia linearis* (Koch, 1835)]. Even the original diagnosis of *Insigniporus* is largely coincident with that of *Stenotaenia*, as revised here, in all characters that best differentiate the genus in respect to the other geophilids. The diagnosis of *Insigniporus* provided by Attems (1903, 1909, 1929a) departs from *Stenotaenia* only in two points, i.e. the putative presence of distinct labral sidepieces and the presence of a medial suture in the coxosternum of the second maxillae. However, direct examination of representative specimens of the type species *Stenotaenia sturanyi* (Attems, 1903) demonstrated that the published accounts were inaccurate on these points [see *Stenotaenia sturanyi* (Attems, 1903)].

*Notadenophilus* Verhoeff, 1928. *Notadenophilus* was introduced by Verhoeff (1928) as a subgenus of *Geophilus* for his new species *Geophilus (Notadenophilus) silvestrii*, which is thus the type species by monotypy. No other species has ever been included in it, and *Notadenophilus* was indeed ignored by most authors, even though its taxonomic validity was never rejected explicitly. *Notadenophilus* is considered here to be a junior synonym of *Stenotaenia* because its type species is recognized as a junior synonym of *Geophilus romanus* Silvestri, 1895, which clearly belongs to the genus *Stenotaenia* as diagnosed here [see *Stenotaenia romana* (Silvestri, 1895)].

*Bithyniphilus* Verhoeff, 1941. The genus *Bithyniphilus* was introduced by Verhoeff (1941b) for the single species *Bithyniphilus bosporanus*, which is the type species by monotypy. Its identity has remained poorly understood, and indeed Zapparoli (1999) doubted its validity. So far, however, its taxo-

nomic position has not been resolved. *Bithyniphilus* is recognized here as a junior synonym of *Stenotaenia* as its type species is very close to the type species of *Stenotaenia* [see *Stenotaenia bosporana* (Verhoeff, 1941)], as explicitly admitted by Verhoeff (1945) in providing a detailed description of *B. bosporanus*. Furthermore, the peculiar traits given by Verhoeff (1941b, 1945) as being diagnostic are indeed fully compatible with the morphological variation of *Stenotaenia*, as are the apparent coalescence of the intermediate articles of the forcipules, the elongation of the sternal pore areas, and the aggregated pattern of the coxal pores.

*Schizopleres* Folkmanova, 1956. The genus *Schizopleres* was introduced by Folkmanova (1956) for the new species *Schizopleres giljarovi*, which is thus the type species by original designation. No other species have since been included, and its status has remained undiscussed. *Schizopleres* is regarded here as a junior synonym of *Stenotaenia*, because its type species shares all the diagnostic characters of the genus with the type species of *Stenotaenia*, including all putative synapomorphies: above all, the shape of the labral margin, the conformation of the forcipules, the pattern of the sternal pores, and the pattern of the coxal pores. It is worth mentioning that Folkmanova (1956), in introducing *Schizopleres*, compared it with *Clinopodes* as well as with *Insigniporus*.

*Euronesogeophilus* Matic, 1972. *Euronesogeophilus* was introduced by Matic (1972) as a subgenus of *Nesogeophilus* Verhoeff, 1925 to include two species, namely *Geophilus ormanyensis* Attems, 1903, which he selected as the type species, and *Geophilus palpiger* Attems, 1903. *Euronesogeophilus* was ignored by all subsequent authors, and was listed under the synonyms of *Geophilus* by Foddai *et al.* (1995). *Euronesogeophilus* is considered here as a junior synonym of *Stenotaenia* because its type species is synonymized here under *G. linearis* [see *Stenotaenia linearis* (Koch, 1835)].

#### *STENOTAENIA ANTECRIBELLATA* (VERHOEFF, 1898)

*Geophilus cribelliger antecribellatus* Verhoeff, 1898: 347 (original description), figs 4–6. Attems, 1903: 222 (in key), 229 (redescription); 1929a: 176 (redescription); 1947: 112 (in key). *Geophilus antecribellatus*: Kos, 1992: 355. Stoev, 1997: 102.

*Simophilus albanensis* Attems, 1929b: 333 (original description), figs 1–4; 1929a: 196 (redescription and in key). Stoev, 2001: 103. **Syn. nov.**

*Type locality*: ‘Bosnaquelle bei Ilidce’ = Bosna springs, near Ilidza (Bosnia & Herzegovina).

*Type material*: Holotype, female, 25-mm long; held in the Museum für Naturkunde, Berlin, ZMB/Myr-13502 (Moritz & Fischer, 1979).

*Diagnosis*: A *Stenotaenia* species of medium body size (total length reaching at least 2.5 cm); c. 61–65 leg-bearing segments; first maxillae apparently without lappets; chitin lines of the forcipular coxosternum reaching the anterior condyles; anterior margin of the forcipular coxosternum angulated; forcipular intermediate articles distinctly separate; sternal pore areas in the anterior part of the trunk trapezoid-oval, slightly longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior pouch with pores and one posterior single pore (see also Tables 2 and 3).

*Taxonomic history*: After the original description by Verhoeff (1898), other specimens were referred to *G. cribelliger antecribellatus* by Attems (1903, 1929a, b). However, the identity and validity of this taxon remained undiscussed, and very recently it was treated as a distinct species, *G. antecribellatus* (Kos, 1992; Stoev, 1997).

*Assignment to Stenotaenia*: It is assigned confidently to *Stenotaenia* (**comb. nov.**) as the original description and illustrations, as well as the direct examination of the holotype by P. Stoev (pers. comm.), document a combination of characters that are diagnostic of this genus (Table 2). This is also suggested by the subsequent description of other material (Attems, 1903), as well as by the original treatment of this taxon as a subspecies of *Geophilus cribelliger* Verhoeff, 1898, which is also included here in *Stenotaenia* [see *Stenotaenia cribelliger* (Verhoeff, 1898)].

*Validity*: It is treated here as a distinct species only provisionally, as its original description and illustrations do not provide clear diagnostic traits in respect to other nominal species, in particular to the better known *Stenotaenia sorrentina* (Attems, 1903) (Table 3). Pending more thorough sampling and comparisons, we provisionally maintain *S. antecribellata* as distinct from *S. sorrentina*, as they apparently occur in nonoverlapping ranges: the Balkan Peninsula and the Italian Peninsula, respectively.

#### *Remarks on synonyms*

*Simophilus albanensis* Attems, 1929. *Simophilus albanensis* was described by Attems (1929b) on a single specimen from ‘Ljubeten’, putatively in Albania. As for the genus *Simophilus*, the true identity of *S. albanensis* has also remained obscure to date (e.g. Stoev, 2001), and no specimens, other than the holotype, were ever identified under this name.

**Table 2.** Occurrence of the diagnostic characters of the genus *Stenotaenia* in each of the species included here in the genus, according to the published descriptions (either text or illustrations) of the type material

	Source	Shape of labrum	Anterior margin of forcipular coxosternum	Chitin lines of forcipular coxosternum	Shape of forcipules	Internal margin of forcipules	Pattern of sternal pore areas	Shape of sternum of last leg-bearing segment	Pattern of coxal pores	Claw of legs of the last pair
<i>antecribellata</i>	Verhoeff, 1898	—	x	x	x	x	x	x	x	—
<i>asiaeminoris</i>	Verhoeff, 1898	—	x	x	x	x	x	x	x	x
<i>bosporana</i>	Verhoeff, 1941b, 1945	x	x	x	x	x	x	x	x	x
<i>cribelliger</i>	Verhoeff, 1898	—	x	x	x	x	x	x	x	x
<i>finbriata</i>	Verhoeff, 1934a	x	x	x	x	x	x	x	x	x
<i>frenum</i>	Meinert, 1870	—	—	x	—	x	x	x	—	—
<i>giljarovi</i>	Folkmanova, 1956	x	x	x	x	x	x	x	x	x
<i>linearis</i>	Koch, 1835, 1863	—	—	—	x	x	—	x	—	x
<i>naxia</i>	Verhoeff, 1901	—	—	x	x	x	x	—	x	x
<i>palaestina</i>	Verhoeff, 1925	—	—	x	—	—	x	—	x	x
<i>palpiger</i>	Attems, 1903	—	x	x	x	x	x	x	x	x
<i>rhodopensis</i>	Kaczmarek, 1970	—	x	x	x	x	x	x	x	x
<i>romana</i>	Silvestri, 1895; Minelli, 1983a	—	x	x	x	x	x	x	x	x
<i>sorrentina</i>	Attems, 1903; Lewis, 1994	x	x	x	x	x	x	x	x	x
<i>sturanyi</i>	Attems, 1903	x	x	x	x	x	x	x	x	x

However, according to the original description and illustration, the holotype of *S. albanensis* is clearly recognizable as a representative of the genus *Stenotaenia*, as it shares a combination of characters that are diagnostic for this genus, including features of the labrum, the forcipules, the forcipular coxosternum, the sternal pore areas, and the coxal pores. In particular, the number of leg-bearing segments (61 in the male holotype), the evident lappets of the first maxillae, the shape of the sternal pore areas, and the geographical origin, all suggest that *S. albanensis* is a junior synonym of *S. antecribellata*.

**Distribution:** Originally described from a locality in Bosnia (Fig. 2), *S. antecribellata* was later recorded from a few other localities in the Dinarides (Verhoeff, 1898; Attems, 1903, 1929a, b). Attems (1903, 1929a, b) listed a few other localities in the same region for *G. cribelliger antecribellatus*, which, however, had previously been listed by Verhoeff (1898) for *G. cribelliger*; Attems did not provide an explanation, and indeed maintained the two taxa as distinct. Therefore, as these subsequent identifications may be unwarranted, and because most recent authors virtually ignored *S. antecribellata*, the actual distribution of this species is at present unknown. In particular, some published records under the names *G. linearis* or *G. abbreviatus*, from different localities throughout the Dinarides, from Istria to Greek Macedonia, could actually represent *S. antecribellata*.

#### STENOTAENIA ASIAEMINORIS (VERHOEFF, 1898)

*Geophilus linearis asiae-minoris* Verhoeff, 1898: 349 (original description), 344 (in key), figs 16–19. Attems, 1903: 219 (in key; cited as *Geophilus linearis asiae minoris*). *Geophilus (Onychopodogaster) asiaeminoris*: Verhoeff, 1924a: 414. *Geophilus asiaeminoris*: Verhoeff, 1925: 73 (in key). *Clinopodes asiae minoris*: Attems, 1929a: 203 (in key), 206 (redescription). *Clinopodes linearis asiae minoris*: Attems, 1947: 120 (in key).

**Type locality:** ‘Cilicien, Kleinasien’ = Cilicia (Turkey).

**Type material:** Seven syntypes, of which two are males and five are females, 38–47-mm long; one syntype in the Museum für Naturkunde, Berlin, ZMB/Myr-3383 (Moritz & Fischer, 1979); the repository of the other syntypes is unknown.

**Diagnosis:** A *Stenotaenia* species of large body size (total length reaching over 4.5 cm); *c.* 75–79 leg-bearing segments; first maxillae without distinct lappets on the coxosternum and small lappets on the telopodites; chitin lines of the forcipular coxosternum

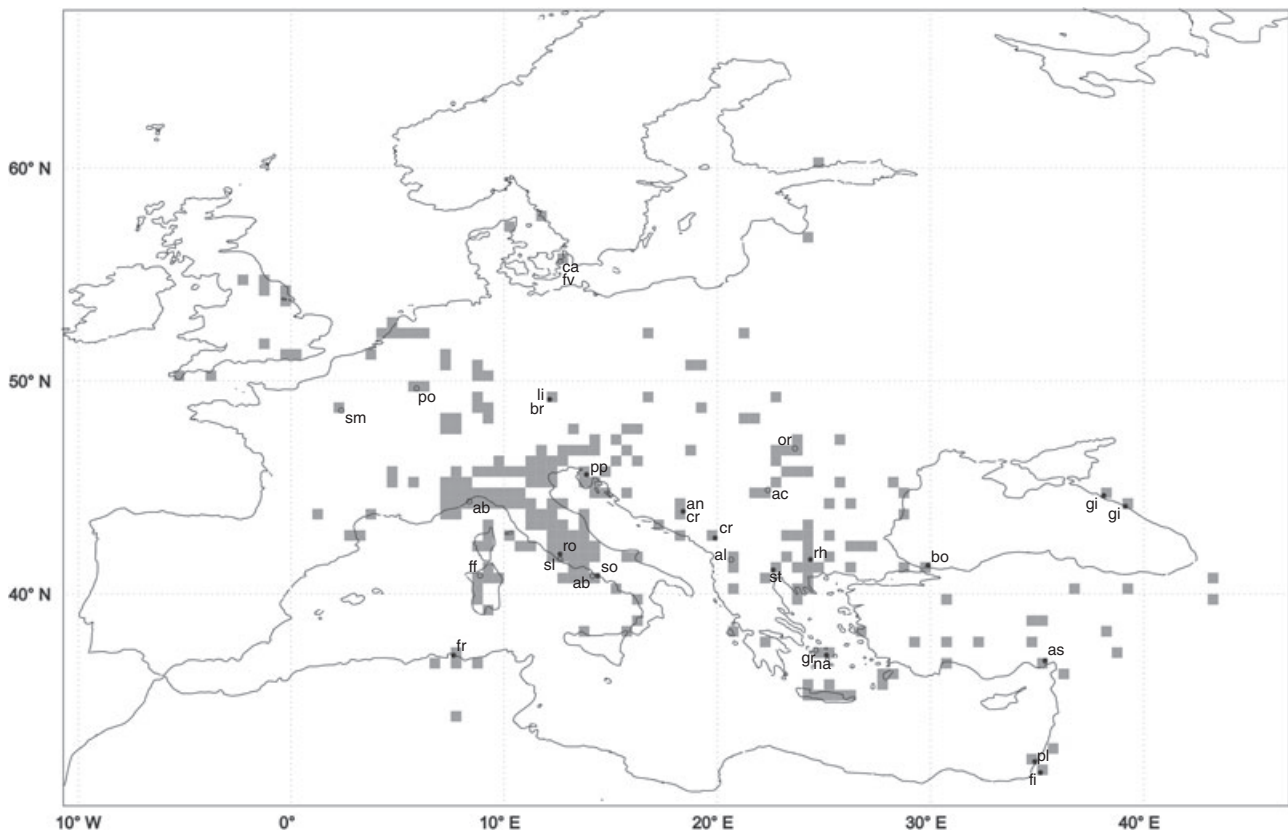


**Table 3.** Characters of possible diagnostic value for the species referred here to *Stenotaenia*

	Maximum body length	Number of leg pairs	Labrum: number of tubercles	Maxillae I: lappets on coxosternum	Maxillae I: lappets on telopodites	Forcicular coxosternum: chitin line reaching the anterior condyle	Forcicular: intermediate articles distinctly separate	Anterior part of trunk: shape of sternal pore area	Anterior part of trunk: position of sternal pore area	Coxopleuron: opening of posterior glands
<i>antecribellata</i>	25 mm (N = 6)	♂ 61–65 (N = 2) ♀ 61–65 (N = 4)	?	Absent	Absent	Yes	Angulated	Trapezoid-oval, slightly longer than wide	On the posterior half of sternum	One pore
<i>asiaeminoris</i>	47 mm (N = 7)	♂ 75 (N = 2) ♀ 77–79 (N = 5)	?	Absent	Reduced	Yes	Angulated	Trapezoid, wider than long	At mid-length of sternum	One pouch with pores
<i>bosporana</i>	45 mm (N = 1)	♀ 71 (N = 1)	?	Present	Present	Yes	Angulated	Oval, slightly longer than wide	On the posterior half of sternum	One pouch with pores
<i>cribelliger</i>	19 mm (N = 2)	♂ 51 (N = 1) ♀ 51 (N = 1)	?	Absent	Absent	Yes	?	Oval, much longer than wide	On the posterior half of sternum	One pore
<i>fimbriata</i>	19 mm (N = 2)	47–49 (N = 2)	0	Absent	Reduced	?	?	Rounded	On the posterior half of sternum	Two pores
<i>frenum</i> *	48 mm (N = 28)	♂ 77–91 (N = 15) ♀ 79–93 (N = 23) 75 (N = 1)	0–2	Present	Well developed	Yes	Almost straight	Oval, slightly longer than wide	On the posterior half of sternum	One pouch with pores
<i>giljarovi</i>	52 mm (N = 13)	81–89 (N = 13)	1–2	Present	Present	Yes	Almost straight	Rounded	At mid-length of sternum	One pouch with pores
<i>linearis</i> *	50 mm (N = some dozens)	♂ 63–75 (N = tens) ♀ 67–81 (N = tens)	0–1	Present	Well developed	Yes	Angulated	Oval, longer than wide	On the posterior half of sternum	One pouch with pores
<i>naxia</i>	68 mm (N = 3)	♂ 77 (N = 1) ♀ 83–85 (N = 2) 81–85 (N = at least 3)	?	?	Well developed	Yes	?	Oval, longer than wide	On the posterior half of sternum	One pouch with pores, coalescent with anterior pouch
<i>palaestina</i>	25 mm (N = 2)	♂ 65 (N = 1) 69 (N = 2)	4–5	Present	Absent	Yes	?	Oval, longer than wide	On the posterior half of sternum	One pouch with pores
<i>palpiger</i>	17 mm (N = 1)	♂ 49 (N = 1)	?	Present	Reduced	Yes	?	Oval, longer than wide	On the posterior half of sternum	One pore
<i>rhodopenis</i>	25 mm (N = 1)	55 (N = 1)	5	Absent	Reduced	Yes	Almost straight	Subtriangular, longer than wide	On the posterior half of sternum	One pore
<i>romana</i> *	17 mm (N = some dozens)	♂ 43–49 (N = tens) ♀ 45–49 (N = tens)	1–2	Absent	Absent	No	Angulated	Oval, longer than wide	On the posterior half of sternum	One pore or one pouch with a few pores
<i>sorrentina</i> *	35 mm (N = some dozens)	♂ 53–67 (N = tens) ♀ 57–67 (N = tens)	0–1	Present	Reduced	Yes	Angulated	Oval, longer than wide	On the posterior half of sternum	One pouch with pores
<i>sturanyi</i> *	77 mm (N = 6)	♂ 105 (N = 1) 111–115 (N = 5)	2	Present	Well developed	Yes	Angulated	Oval, with a median restriction both anteriorly and posteriorly	On the posterior half of sternum	One pouch with pores

Information is derived mainly from published accounts, to the exclusion of data based on possibly misidentified specimens.

\*Published data that have been checked and integrated through direct observation of new material.



**Figure 2.** Geographical distribution of *Stenotaenia* species. The previously published and new records have been plotted upon a grid of 30' latitude  $\times$  30' longitude. The type localities of all nominal taxa are indicated by circles (full circles for valid species, empty circles for synonyms), with the following abbreviations: ab, *abbreviatus*; ac, *acuneli*; al, *albanensis*; an, *antecribellatus*; as, *asiaeminoris*; bo, *bosporanus*; br, *brevicornis*; c, *caldarium*; cr, *cribelliger*; fi, *fimbriatus*; ff, *forficularius*; fv, *foveolatus*; fr, *frenum*; gi, *giljarovi*; gr, *graecus*; li, *linearis*; na, *naxius*; or, *ormanyensis*; pl, *palaestinus*; po, *polyporus*; pp, *palpiger*; rh, *rhodopensis*; ro, *romanus*; sl, *silvestrii*; sm, *simplex*; so, *sorrentinus*; st, *sturanyi*.

reaching the anterior condyles; anterior margin of the forcipular coxosternum angulated; forcipular intermediate articles not distinctly separate; sternal pore areas in the anterior part of the trunk trapezoid, wider than long, and placed at mid-length of each sternum; each coxopleuron with one anterior and one posterior pouch, with pores (see also Table 3).

**Taxonomic history:** After the original description by Verhoeff (1898), it was later recorded only by Matic (1980). This taxon was variously considered either a subspecies or a full species, under either *Geophilus* or *Clinopodes*, but its identity and validity remained unchallenged.

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original description and illustrations document the presence of a combination of characters that are diagnostic for this genus (Table 2). Additional support comes from its

original treatment as a subspecies of *G. linearis*, which is the type species of *Stenotaenia*.

**Validity:** It is recognized here as a distinct species only based on the published original description and illustrations, which indicate a peculiar shape of the sternal pore areas and other minor, possibly diagnostic, traits (Table 3). According to the original description, it should be unique within the geophilids in having a single recognizable intermediate article, instead of two, in each forcipule, a condition paralleled only in the unrelated Aphilodontidae (Verhoeff, 1937a). However, we observed that an apparent coalescence of the forcipular intermediate articles is also *chizopleres* found in *S. sturanyi*, and a similar condition was illustrated for *Schizopleres giljarovi* by Folkmanova (1956), was described by Verhoeff (1901, 1902) under *G. naxius* as well as under *G. graecus*, and was recognized as a general feature of *Onychopodogaster* by Verhoeff (1937a) himself. Further

investigation is required to evaluate the actual taxonomic status of *S. asiaeminoris* in respect to other nominal species, including *S. linearis*, *Stenotaenia palaestina* (Verhoeff, 1925), *S. naxia*, and *S. giljarovi*.

**Distribution:** Originally described from the southern part of Anatolia (Fig. 2), it was subsequently recorded from a locality in the western part of Anatolia, but evidence supporting a correct identification of the new material is lacking (Matic, 1980). As most recent authors working on faunistic surveys ignored this species, the actual distribution of *S. asiaeminoris* is at present unknown. In particular, published records of *S. linearis* from other localities in the Anatolia Peninsula could actually represent *S. asiaeminoris*.

#### *STENOTAENIA BOSPORANA* (VERHOEFF, 1941)

*Bithyniphilus bosporanus* Verhoeff, 1941a: 40 (original description); 1945: 312 (redescription), figs 9–12.

**Type locality:** 'Göksu süßen Wasser Asiens östlich des Bosphorus' (Verhoeff, 1945) = Goksu, east of Bosphorus (Turkey).

**Type material:** Holotype, female, 45-mm long; repository unknown (no specimen recognizable as holotype is present in the main repositories of Verhoeff's collection, i.e. the Museum für Naturkunde in Berlin, the Zoologische Staatssammlung München, and the Zoologisches Museum der Universität Hamburg; Weidner, 1960; Rack, 1974; Moritz & Fischer, 1979; J. Spelda, pers. comm.).

**Diagnosis:** A *Stenotaenia* species of large body size (total length reaching at least 4.5 cm); c. 71 leg-bearing segments; first maxillae with distinct lappets on both the coxosternum and the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; anterior margin of the forcipular coxosternum angulated; forcipular intermediate articles poorly distinct; sternal pore areas in the anterior part of the trunk oval, slightly longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior and one posterior pouch, with pores (see also Table 3).

**Taxonomic history:** This species was originally introduced by Verhoeff (1941a) and was only associated with a minimal diagnosis of its original genus *Bithyniphilus* in a key, whereas a detailed description and illustration was published later (Verhoeff, 1945). No other specimens have been referred to *B. bosporanus*, but its validity was never questioned, even though Zapparoli (1999) raised doubts about the validity of the genus *Bithyniphilus*.

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original descriptions and illustrations document a combination of characters that are diagnostic for this genus (Table 2). Other characters described for *B. bosporanus* are also compatible with *Stenotaenia*, including the elongation of the head and the antennae, the shape of the labrum, the structure of the second maxillae and their claws, the apparent coalescence of the intermediate articles of the forcipules, and the position of the forcipular poison glands. Apparently unusual characters are the angled internal margin of the forcipular tarsungulum, the absence of articulations in the telopodites of the first maxillae, the aggregation of coxal glands in four recognizable groups on each coxopleuron, but these may be either genuine, peculiar features of this species, that do not in any way challenge its assignment to *Stenotaenia*, or merely artifactual or misinterpreted traits of the only examined specimen. It is worth noting that Verhoeff (1945), in describing *B. bosporanus*, acknowledged its similarity to *G. linearis*, and provided a differential diagnosis of the two species.

**Validity:** It is treated here as a distinct species based only on the original description and illustrations (Table 3). In particular, according to Verhoeff (1945), it should be distinguished from *S. linearis* for the straighter chitin lines, an unusually shaped forcipular tarsungulum, more numerous pouches on the coxopleura, and a slightly wider sternum of the last leg-bearing segment. However, further investigation is needed to check whether these traits are actually invariant and diagnostic for this species.

**Distribution:** Only known from a locality east of Bosphorus (Fig. 2).

#### *STENOTAENIA CRIBELLIGER* (VERHOEFF, 1898)

*Geophilus cribelliger* Verhoeff, 1898: 346 (original description), 344 (in key), figs 1–3. Attems, 1903: 221 (in key); 1929a: 162 (in key), 175 (redescription); 1947: 112 (in key).

**Type localities:** 'Trebevic bei Sarajevo; Plasa bei Jablanica' = Trebević, near Sarajevo; Plasa, near Jablanica (Bosnia & Herzegovina).

**Type material:** Two syntypes, of which one is a male, 14-mm long, from Plasa, and one is a female, 18.5-mm long, from Trebević; both are held in the Museum für Naturkunde, Berlin, ZMB/Myr-13500 (male from Plasa) and ZMB/Myr-13501 (female from Trebević) (Moritz & Fischer, 1979).

**Diagnosis:** A *Stenotaenia* species of small body size (total length reaching 2 cm); c. 51 leg-bearing segments; first maxillae without distinct lappets on the coxosternum and on the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, much longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior pouch with pores and one posterior single pore (see also Table 3).

**Taxonomic history:** After the original description by Verhoeff (1898), other specimens have been referred to this species by Attems (1929b). This taxon was invariantly cited as a valid species under the genus *Geophilus* (e.g. Attems, 1929a, 1947; Kos, 1992; Stoev, 1997), but its identity and validity were never critically discussed.

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original description and illustrations, as well the direct examination of the syntypes by P. Stoev (pers. comm.), document a combination of characters that are diagnostic for this genus (Table 2). Verhoeff (1898), in describing *G. cribelliger*, recognized its closeness to *G. linearis*, which is the type species of *Stenotaenia*.

**Validity:** It is treated here as a distinct species only provisionally, as its original description and illustrations provide some evidence for diagnostic traits in respect to other species (Table 3), but its actual status in respect to the better known *S. sorrentina* and the poorly known *S. antecribellata*, *Schizopleres ormanyensis*, and, above all, *S. palpiger* (see below) should be evaluated through adequate sampling and comparisons.

**Distribution:** Originally described from two localities in Bosnia (Fig. 2), it was subsequently recorded from another two localities in the same region (Attems, 1929b), but these records are not accompanied by descriptive evidence, and therefore need to be reassessed. As most recent authors virtually ignored *S. cribelliger*, and its identity remained uncertain, the actual distribution of this species is at present unknown.

#### *STENOTAENIA FIMBRIATA* (VERHOEFF, 1934)

*Geophilus (Onychopodogaster) fimbriatus* Verhoeff, 1934a: 11 (original description), figs 18–19. *Clinopodes fimbriatus*: Attems, 1947: 120 (in key).

**Type locality:** 'bei Jerusalem [...] (Kirjat Anawim)' = Qiryat Anawim, near Jerusalem (Israel).

**Type material:** Two syntypes, of both sexes, 18–19-mm long; one syntype is held in the Museum für Naturkunde, Berlin, ZMB/Myr-13456 (Moritz & Fischer, 1979), and one syntype is held at the Zoologische Staatssammlung München, ZSM/Myr-A20030337 (J. Spelda, pers. comm.).

**Diagnosis:** A *Stenotaenia* species of small body size (total length reaching 2 cm); c. 47–49 leg-bearing segments; labrum without tubercles; first maxillae without distinct lappets on the coxosternum, and with small lappets on the telopodites; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk round, and placed on the posterior half of each sternum; each coxopleuron with one anterior pouch with pores, and one posterior couple of pores (see also Table 3).

**Taxonomic history:** After the original description by Verhoeff (1934a) no other specimens have been recorded. The species was moved to *Clinopodes* by Attems (1947), but its identity and status were never discussed further.

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original description documents a combination of characters that are diagnostic of this genus (Table 2). Verhoeff (1934a), in describing *G. fimbriatus*, assigned it to the subgenus *Onychopodogaster* and compared it with a juvenile stage of *G. linearis*, the type species of *Stenotaenia*.

**Validity:** It is recognized here as a distinct species only based on the published original description and illustrations. Potentially discriminating traits are the pattern of the sternal pore areas and the number of the trunk segments (Table 3).

**Distribution:** Only known from two close localities in Palestine (Fig. 2).

#### *STENOTAENIA FRENUM* (MEINERT, 1870)

*Geophilus frenum* Meinert, 1870: 74 (original description). *Simophilus frenum*: Silvestri, 1896: 154 (redescription). Attems, 1929a: 196 (redescription and in key).

**Type locality:** 'Bona' = Annaba (Algeria).

**Type material:** Twenty-four syntypes, of which eight are males and 16 are females, up to 48-mm long; all are held in the Zoological Museum, University of Copenhagen, without catalogue number (H. Enghoff, pers. comm.).



**Diagnosis:** A *Stenotaenia* species of large body size (total length almost reaching 5 cm); *c.* 75–93 leg-bearing segments; labrum without or with one or two tubercles; first maxillae with distinct lappets on both the coxosternum and the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; anterior margin of the forcipular coxosternum almost straight; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, slightly longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior and one posterior pouch with pores (see also Table 3).

**Taxonomic history:** After the original description by Meinert (1870), further specimens from a few other localities were identified by Silvestri (1896), who also redescribed the species and erected the new genus *Simophilus* for it. However, the true affinities of *S. frenum* were not recognized to date.

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**) based on the original description (Table 2), on Silvestri's (1896) redescription, as well as on our direct study of other specimens that are obviously representative of this species (Figs 3, 4). It is noted here that the original description of the coxal pores was imprecise, as Meinert (1870) dubiously recognized only two large pores on each coxopleuron; later, Silvestri (1896) demonstrated that Meinert had misinterpreted two pouches with

many glands each as two simple pores. Furthermore, indirect support to the placement of this species in *Stenotaenia* comes from the fact that Attems (1929b), in describing *Simophilus albanensis*, recognized that his new species, synonymized here under *S. antecribellata* (see above), was close to Meinert's *G. frenum*.

**Validity:** It is treated here confidently as a distinct species, as published accounts and direct examination of representative specimens revealed some distinguishing traits (Table 3), as well as a disjunct distribution in respect to all other species of *Stenotaenia*.

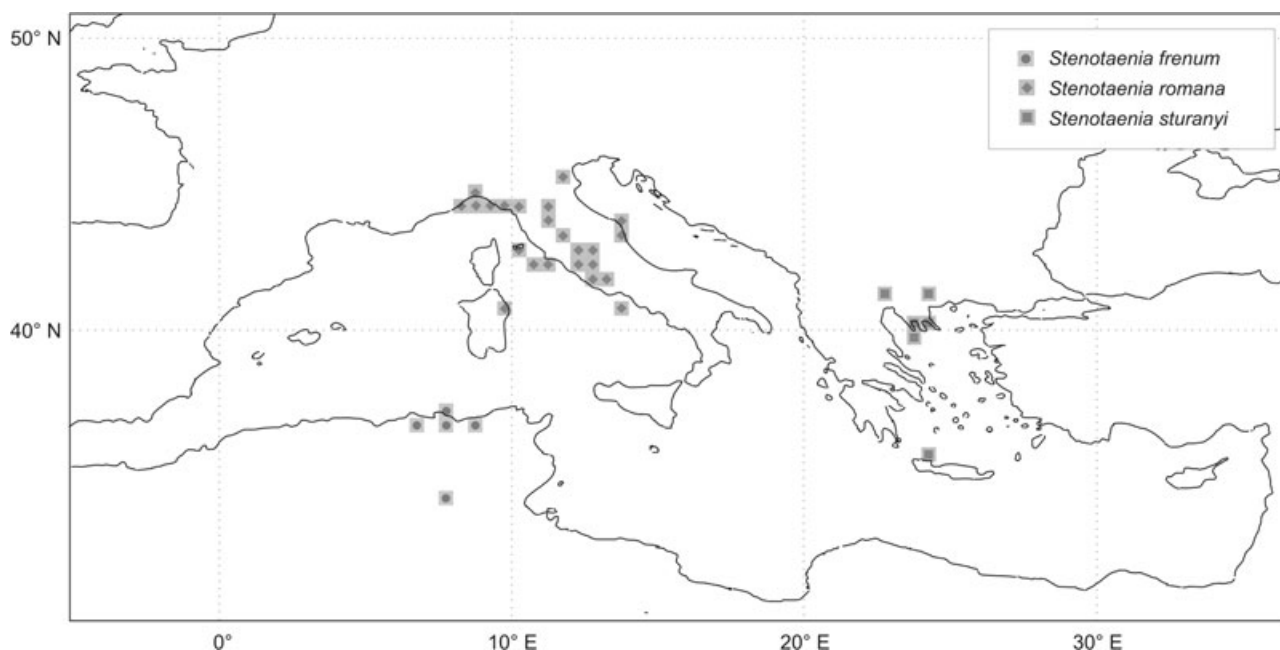
**Distribution:** As far as is known, it is limited to the Eastern part of the Atlas chain (Fig. 3). In particular, it is known from nine localities, five of which are published here as new (see Appendix).

#### *STENOTAENIA GILJAROVI* (FOLKMANOVA, 1956)

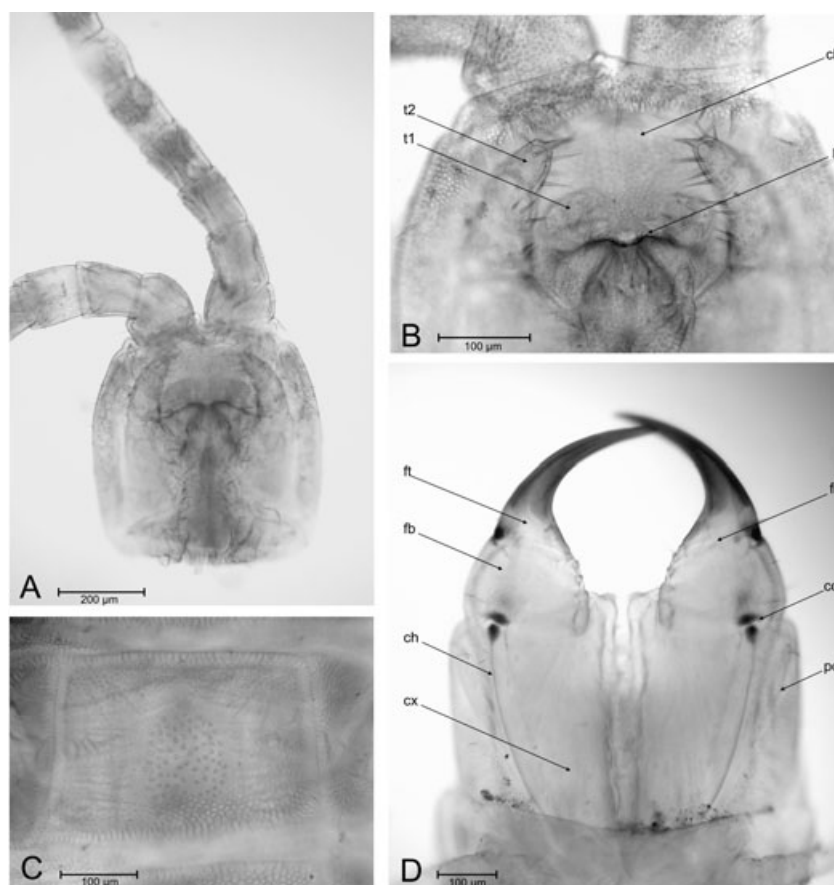
*Schizopleres giljarovi* Folkmanova, 1956: 1638 (original description), fig. 2.

**Type localities:** 'Krasnodarskij kraj (stanitsa Ehrivanskaya; Ubinskoe i Georgievskoe lesnichestva)' = Krasnodar region (Erivanskaya; Ubinskoe and Georgievskoe forestries) (Russia).

**Type material:** Thirteen syntypes, of which four are males and six are females, up to 52-mm long; repository unknown (A. Schileyko and K. Tajovský, pers. comm.).



**Figure 3.** Geographical distribution of *Stenotaenia frenum*, *Stenotaenia romana*, and *Stenotaenia sturanyi*. Both previously published and new records have been plotted upon a grid of 30' latitude × 30' longitude.



**Figure 4.** Microscopic images of a female specimen of *Stenotaenia frenum* (Meinert, 1870) from Baie de Tamanart (Algeria) (28-mm long, with 81 leg-bearing segments; 7-XI-1984, collection A. Minelli): (a) head, ventral; (b) clypeus and maxillary complex, ventral; (c) sternum of leg-bearing segment X; (d) forcipular segment, ventral. Abbreviations: ch, chitin line; cl, clypeus; co, condyle of forcipular coxosternum; cx, forcipular coxosternum; fb, forcipular basal article; fi, forcipular intermediate articles; ft, forcipular tarsungulum; la, labrum; pc, forcipular pleurocoxal margins; t1, telopodite of first maxillae; t2, telopodite of second maxillae.

**Diagnosis:** A *Stenotaenia* species of large body size (total length reaching 5 cm); c. 81–89 leg-bearing segments; labrum with one or two tubercles; first maxillae with distinct lappets on both the coxosternum and the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; anterior margin of the forcipular coxosternum almost straight; forcipular intermediate articles poorly distinct; sternal pore areas in the anterior part of the trunk round, and placed at the mid-length of each sternum; each coxopleuron with one anterior and one posterior pouch with pores (see also Table 3).

**Taxonomic history:** After the original description by Folkmanova (1956), no other specimen was identified, and the true affinities of this species remained unrecognized (Dobroruka, 1961).

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original description and illustrations document a combination of characters that are diagnostic for this genus (Table 2).

**Validity:** It is recognized here as a distinct species only provisionally. According to the original description and illustrations, *S. giljarovi* could be distinguished from most other species of *Stenotaenia* mainly for the number of trunk segments and the shape of the sternal pore areas (Table 3). However, further investigation should evaluate the putative diagnostic value of these characters, above all in respect to *S. linearis* and *S. asiaeminoris*.

**Distribution:** It is only known from the western part of Caucasus, north of the Black Sea (Fig. 2). A few

other published records of *S. linearis* from neighbouring regions in Anatolia (Zapparoli, 1999) should be reassessed.

#### *STENOTAENIA LINEARIS* (KOCH, 1835)

*Geophilus linearis* Koch, 1835: table 1 (original description). Latzel, 1880: 169 (in key), 189 (redescription). Folkmanova, 1952: 182 (in key), 188 (redescription), fig. 9. Lewis & Keay, 1994: 43 (redescription), figs 1–20. *Stenotaenia linearis*: Koch, 1847: 188; 1863: 120 (redescription), fig. 108. *Clinopodes linearis*: Attems, 1929a: 203 (in key), 205 (redescription); 1947: 120 (in key). Brolemann, 1930: 55 (in key), 143 (redescription), figs 201–207. Eason, 1964: 44 (in key), 107 (redescription), figs 147–152. Matic, 1972: 75 (in key), 93 (redescription), fig. 37. Kaczmarek, 1979: 62 (redescription and in key), figs 31 and 61.

*Geophilus simplex* Gervais, 1835: 9 (original description); 1937: 52 (in key). Newport, 1845: 435 (redescription); 1856: 88 (redescription). Berlese, 1903: (4) 10 (redescription). Synonymy by Gervais (1837: 52). *Geophilus brevicornis* Koch, 1837: table 3 (original description). Gervais, 1847: 319 (redescription). Synonymy by Koch (1847: 188).

*Scnipaeus foveolatus* Bergsøe & Meinert, 1866: 96 (original description). *Geophilus foveolatus*: Meinert, 1870: 66 (redescription). Synonymy by Latzel (1880: 189).

*Himantarium caldarium* Meinert, 1886: 148 (original description). Attems (1929a): 55. **Syn. nov.**

*Geophilus linearis* var. *polyporus* Verhoeff, 1896: 86 (original description). **Syn. nov.**

*Geophilus ormanyensis* Attems, 1903: 230 (original description). *Nesogeophilus ormanyensis*: Attems, 1929a: 184 (in key), 187 (redescription); 1947: 117 (in key). Matic (1972): 100 (redescription). **Syn. nov.**

*Insigniporus acuneli* Căpușe, 1968: 700 (original description), fig. 1. Matic, 1972: 122 (redescription; misspelled as *Insigniporus acunaeli*), fig. 48. **Syn. nov.**

*Type locality*: 'Regensburg' = Regensburg (Germany).

*Type material*: Holotype, possibly male; apparently there are no more specimens in existence, as no specimen recognizable as such was found by one of the authors (AM) in the main repository of Koch's centipedes, in the collections of the Natural History Museum, London, or in the collections of the Museum für Naturkunde, Berlin, where other materials from Koch's collection are preserved (Moritz & Fischer, 1979).

*Diagnosis*: A *Stenotaenia* species of large body size (total length reaching 5 cm); c. 63–81 leg-bearing segments; labrum either with or without a single tubercle; first maxillae with distinct lappets on both the coxosternum and the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; anterior margin of the forcipular coxosternum angulated; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior and one posterior pouch with pores (see also Table 3).

*Taxonomic history*: Most authors have referred this species either to *Geophilus* or to *Clinopodes*, whereas its treatment under *Stenotaenia* has been very limited (Koch, 1847, 1863; Fanzago, 1881a). Authors' opinions also differ in the circumscription of this species and the possible recognition of subspecies within it.

*Assignment to Stenotaenia*: It is the type species of the genus, by subsequent designation by Pocock (1890).

*Validity*: This is a well-known species, even though its taxonomic circumscription is currently uncertain, in particular with respect to similar species such as *S. naxia*, *S. giljarovi*, *S. palaestina*, and *S. asiaeminatoris* (Table 3).

#### *Remarks on synonyms*

*Geophilus simplex* Gervais, 1835. *Geophilus simplex* was described by Gervais (1835) from near Paris, but its original description was so incomplete that the use of this name was very limited. Gervais (1837, 1847) recognized that his *G. simplex* was identical to *G. linearis* Koch, 1835, and most other authors followed this view (e.g. Berlese, 1903; Bagnall, 1918). We accept this synonymy, as the original descriptions of the two species are fully overlapping and no evidence suggests we should reject this view. As for the priority between these two names, both were published in the same year, but the actual dates are unknown to us. Gervais (1837, 1847) deliberately adopted his name *G. simplex* as valid, based on his opinion that Koch's name had been published subsequently. He was followed by other authors (Newport, 1845, 1856; Berlese, 1903; Bagnall, 1918), even though Berlese obviously misinterpreted the species. Conversely, most other authors in the 20th century used *G. linearis* as the valid name, in tens of works dealing with faunistics, taxonomy, ecology, physiology, and anatomy, whereas *G. simplex* has never been used as valid after 1918. Therefore, for the purpose of stability, we propose to

consider *G. linearis* as the valid name for this species. If *G. linearis* is the senior synonym, it should be considered as the valid name following the principle of priority. Conversely, if it is the junior synonym, the conditions for the reversal of precedence (ICZN: art. 23.9) are not met, because *G. simplex* has been used as valid even after 1899 (e.g. see Koch, 1927; Attems, 1929a). Therefore, the matter has been referred to the International Commission of Zoological Nomenclature for a ruling under the plenary power (Bonato & Minelli, 2007).

*Geophilus brevicornis* Koch, 1837. *Geophilus brevicornis* was described by Koch (1837) from Germany, probably near Regensburg. It was later recognized as a junior synonym of *G. linearis* by the same author (Koch, 1847), and has never been used as valid since then. In particular, Koch (1847) recognized that he had described *G. linearis* and *G. brevicornis* from a male and a female, respectively, of the same species. Indeed, the original descriptions and illustrations of the two nominal species are largely congruent, but for minor details in body colour and number of leg pairs, 75 and 79, respectively. Wood (1862) described a distinct species from North America under the same name *G. brevicornis*, which was therefore a junior homonym of *Geophilus brevicornis* Koch, 1837. Wood's species is obviously unrelated to *Stenotaenia*, but its identity remains uncertain and no substitute name for it has been proposed so far.

*Scnipaeus foveolatus* Bergsøe & Meinert, 1866. *Scnipaeus foveolatus* was described by Bergsøe & Meinert (1866) from some specimens collected in the Botanic Garden of Copenhagen, and was redescribed by Meinert (1870) as *G. foveolatus* from other specimens from different localities. It was recognized as a junior synonym of *G. linearis* by Latzel (1880) and was not used as valid after that. On the basis of the original description and the secondary account by Meinert (1870), we confirm that *S. foveolatus* is identical to *G. linearis*, even in some traits that are diagnostic at the species level, including body size and number of trunk segments.

*Himantarium caldarium* Meinert, 1886. *Himantarium caldarium* was described by Meinert (1886) from four specimens of both sexes collected in the Botanical Garden of Copenhagen. As the original description was very inadequate no further specimens were ever referred to *H. caldarium*, and the identity and taxonomic position of this nominal species has remained unresolved (Attems, 1903, 1929a). Based on direct examination of the syntypes (preserved in the Zoological Museum, University of Copenhagen, without catalogue number), we found that *H. caldarium* is identical to *S. linearis*, as all the syntypes of the former fully agree with the latter species, particularly in the features of the clypeus, the

labrum, the maxillae and the forcipular segment, the shape of the sternal pore areas and its variation along the trunk, the number of trunk segments, and the features of the last leg-bearing segment. Therefore, we consider *H. caldarium* as a junior synonym of *S. linearis*. The original description of *H. caldarium* was inaccurate in the following points: the sternal pore areas of the anterior part of the trunk were described as rounded, but they are actually oval; coxal pores were described as opening independently, at least in the female, but actually all of them open in two common pouches in all syntypes; the claws of the legs of the last pair were described as sexually dimorphic in size, but they are actually similar in both sexes. It is worth noting that *S. linearis* is known to occur frequently in hothouses and other suitable anthropic habitats in northern Europe (e.g. Barber & Keay, 1988). In particular, the presence of this species in the Botanical Garden of Copenhagen in the second half of the 19th century is documented by the fact that some specimens collected there had been described previously by Bergsøe & Meinert (1866) as *Scnipaeus foveolatus* (see above). The presence of *S. linearis* in Copenhagen has been documented even more recently (Enghoff, 1973).

*Geophilus linearis* var. *polyporus* Verhoeff, 1896. *Geophilus linearis* var. *polyporus* was described by Verhoeff (1896) from an unknown number of specimens from the Rhineland in Germany. Based on the very poor diagnosis, it should differ from typical *G. linearis* only in having 30 or more coxal pores on each side, whereas the typical number for *G. linearis* was given as nine or ten. This nominal taxon was completely ignored in subsequent literature. We were not able to examine the type material, which is apparently neither preserved in Verhoeff's collections at the Museum für Naturkunde in Berlin (Moritz & Fischer, 1979) nor at the Zoologische Staatssammlung München (J. Spelda and M. Unsöld, pers. comm.). Extensive faunistic investigations in that region failed to secure other specimens referable to this taxon, instead they documented that the populations of *Stenotaenia* from that region may be obviously referred to the typical *S. linearis*. Furthermore, by considering that no other geophilid species closely resembling *S. linearis* actually lives in that region, we can accept Verhoeff's identification of the specimens as belonging to *S. linearis*, but we consider that their taxonomic distinction was unwarranted. Therefore, we consider *G. linearis* var. *polyporus* as a junior synonym of *G. linearis*. In any case, *Geophilus linearis* var. *polyporus* Verhoeff, 1896 is an invalid name, as it is a primary junior homonym of *Geophilus polyporus* Haase, 1887, a species from the D'Urville island off New Zealand, which is still of uncertain taxonomic position but is clearly unrelated to *Stenotaenia*.



*Geophilus ormanyensis* Attems, 1903. *Geophilus ormanyensis* was described by Attems (1903) from two specimens from a locality near Klausenburg, in Romania, but the identity of this nominal species remained unclear, and no other specimen has been referred to it. As the large difference in the number of leg pairs between the two syntypes (55 in a male, 73 in a female) is unusual within a single geophilomorph population, it is highly probable that they are not conspecific. Therefore, in order to fix the identity of *G. ormanyensis* unambiguously, we designate the female syntype as the lectotype of this species; the lectotype is preserved in the Naturhistorisches Museum in Wien, catalogue number NHMW4813 (V. Stagl, pers. comm.). Based on the original account, the lectotype may be confidently regarded as belonging to *S. linearis*, which is known to occur in the region, whereas it differs from other species of *Stenotaenia* known from the same region at least in the number of trunk segments. Therefore, we regard *G. ormanyensis* as a junior synonym of *G. linearis*. Instead, the male with 55 leg-bearing segments is probably closer to other nominal species, such as *S. antecribellata* or *S. cribelliger*.

*Insigniporus acuneli* Căpușe, 1968. *Insigniporus acuneli* was described by Căpușe (1968) from a single male from the Banat region in Romania. No other specimen has been referred to this nominal species, the status of which and validity have remained unassessed (Matic, 1972). Based on the detailed description and illustrations available (Căpușe, 1968; Matic, 1972), and considering the current knowledge of the centipede fauna of Romania, *I. acuneli* can be confidently recognized as a synonym of *S. linearis*. *Insigniporus acuneli* agrees with *S. linearis* in the general body shape and size, and in all diagnostic characters, including the shape of the cephalic shield and antennae, the sculpture and pattern of setae in the clypeus, the shape of the labrum, the hairiness and shape of the maxillae, the overall features of the forcipular segment, the number of trunk segments, the shape of the sternal pore areas and their variation along the trunk, the pattern of the coxal pores, the shape and other features of the legs of the last pair. The only apparent difference between the two nominal species is in the shape of the sternum of the last leg-bearing segment, which was illustrated as subtrapezoid in *I. acuneli*, whereas in *S. linearis* it usually appears subrectangular, only slightly narrowing backwards; however, this disagreement is perhaps explained by interindividual variation or by the incorrect interpretation of the microscopical evidence. It is worth noting that *S. linearis* is already known to occur in that region (Matic, 1972).

**Distribution:** Different authors have recorded *S. linearis* from throughout the entire range of *Stenotaenia*, as reconstructed here, often because they misidentified specimens belonging to other congeneric species. Based on the critical evaluation of the published accounts, as well as on the direct examination of representative specimens from different regions, we found that populations reliably referred to *S. linearis* occur mainly in Central Europe, westward to Great Britain and central France, northward to the Baltic region, including Denmark and southern Scandinavia, eastward to Latvia, the Carpathian chain, and the western coast of the Black Sea, and southward to the Alps, including the Maritime Alps, and Transylvania (Fig. 2). Published records from other regions need to be reassessed, with respect to other species of *Stenotaenia* occurring there, as for the southern part of France, most of the remaining Balkan Peninsula, the Aegean islands, and the entire region of Anatolia.

#### *STENOTAENIA NAXIA* (VERHOEFF, 1901)

*Geophilus* (*Geophilus*) *naxius* Verhoeff, 1901: 420 (original description). Attems, 1903: 219 (in key). *Clinopodes naxius*: Brölemann, 1909a: 332. *Geophilus* (*Onychopodogaster*) *naxius*: Brölemann, 1909b: 211 (in key). *Geophilus linearis naxius*: Verhoeff, 1925: 72 (redescription), 73 (in key). *Clinopodes linearis naxius*: Attems, 1929a: 203 (in key), 205 (redescription); 1947: 120 (in key). Kanellis, 1959: 38 (key). *Geophilus graecus* Verhoeff, 1902: 560 (original description), fig. 2; 1924a: 413. *Clinopodes graecus*: Brölemann, 1909a: 332. Synonymy by Verhoeff (1925: 73).

**Type locality:** 'Naxos' = Naxos, Naxos island (Greece).

**Type material:** Holotype, female, 44-mm long; held in the Museum für Naturkunde, Berlin, ZMB/Myr-13498 (Moritz & Fischer, 1979).

**Diagnosis:** A *Stenotaenia* species of large body size (total length almost reaching 7 cm); c. 77–85 leg-bearing segments; first maxillae with distinct lappets on the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; forcipular intermediate articles not distinctly separate; sternal pore areas in the anterior part of the trunk oval, longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior and one posterior pouch with pores, the two pouches apparently coalescent (see also Table 3).

**Taxonomic history:** After the original description by Verhoeff (1901), other specimens were referred to this species by different authors (Brölemann, 1904;



**Figure 5.** Microscopic images of a female specimen of *Stenotaenia romana* (Silvestri, 1895) from Isola del Cantone near Genova (Italy: Liguria) (12-mm long, with 47 leg-bearing segments; 5-XI-1978 Gardini lg, collection A. Minelli): (a) head, ventral; (b) clypeus and maxillary complex, ventral; (c) sternum of leg-bearing segment X; (d) forcipular segment, ventral.

Verhoeff, 1925; Chamberlin, 1952; Zapparoli, 1994, 1995, 2002; Simaiakis, Minelli & Mylonas, 2004). This taxon has been occasionally referred to either *Clinopodes* or *Onychopodogaster* (Brölemann, 1909a, b), has been treated as a subspecies of *S. linearis* (Verhoeff, 1925; Attems, 1929a, 1947; Chamberlin, 1952; Kanellis, 1959), or has even been considered as a full synonym of *S. linearis* (Matic, 1972; Kaczmarek, 1979).

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original description documents a combination of characters that are diagnostic for this genus (Table 2). Its affinity to some of the species recognized here as belonging in *Stenotaenia*, namely *S. linearis* and *S. cribelliger*, was recognized by Verhoeff (1901) himself, and was reflected by the fact that *G. naxius* has been occasionally referred to either *Clinopodes* or *Onychopodogaster*, has even been treated as a subspecies of *S. linearis*, or has even been considered a full synonym of *S. linearis*.

**Validity:** It is recognized here as a distinct species only based on published accounts, which assign diagnostic value to some characters including body size, the number of trunk segments, and the arrangement of the coxal pores (Table 3). However, further investigations should evaluate the taxonomic status of *S. naxia* in respect to other nominal species, above all *S. linearis*.

#### Remarks on synonyms

*Geophilus graecus* Verhoeff, 1902. *Geophilus graecus* was described by Verhoeff (1902) from one male and one female from Syros in the Aegean Sea, but no other specimen was later referred to it. *Geophilus graecus* was cited under either *Clinopodes* (Brölemann, 1909a) or *Geophilus* (Verhoeff, 1924a), until Verhoeff (1925) himself recognized that it was a junior synonym of *G. naxius*. The synonymy was accepted by all subsequent authors. Indeed, the original description of *G. graecus* is fully consistent with that of *G. naxius*, but for the putatively shorter sternal pore areas and the more numerous coxal glands, which,

however, may be related to the larger size of the syntypes of *G. graecus* with respect to the holotype of *G. naxius*. The two nominal taxa share some features that appear to be diagnostic with respect to other *Stenotaenia* species, namely body size, the number of trunk segments, and the peculiarly large and almost coalescent groups of coxal glands. It is worth noting that Verhoeff (1902), in describing *G. graecus*, disclosed his suspicion that it could be best treated as a subspecies of *G. naxius*.

**Distribution:** It occurs in the eastern part of the Mediterranean basin, where it has been reliably recorded from the islands of Syros, Naxos, Halki, Rhodes, and Crete, and from Palestine. A record from inland Anatolia (Chamberlin, 1952) should be reassessed, as supporting evidence is lacking, whereas a record from the southern coast of France (Brölemann, 1904) was recognized as erroneous by the same author (Brölemann, 1930).

*STENOTAENIA PALAESTINA* (VERHOEFF, 1925)

*Geophilus palaestinus* Verhoeff, 1925: 72 (original description), 73 (in key). *Simophilus palaestinus*: Attems, 1929a: 196 (in key), 197 (redescription).

**Type locality:** 'Chuldah bei Jaffa' = Chuldah, near Jaffo (Israel).

**Type material:** Holotype, sex unknown, 25-mm long; held in the Zoologische Staatssammlung München, ZSM/Myr-A20030436 (J. Spelda, pers. comm.).

**Diagnosis:** A *Stenotaenia* species of intermediate body size (total length reaching at least 2.5 cm); c. 65–69 leg-bearing segments; labrum with about four or five tubercles; first maxillae with distinct lappets on the coxosternum, apparently without lappets on the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior and one posterior pouch with pores (see also Table 3).

**Taxonomic history:** After the original description by Verhoeff (1925) it was never recorded further. Its identity and validity remained unchallenged, even though Attems (1929a) referred it to the genus *Simophilus*.

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original description documents a combination of characters that are

diagnostic for this genus (Table 2). Further support comes from the fact that Verhoeff (1925), in introducing *G. palaestinus*, explicitly considered it to be very close to *S. linearis*.

**Validity:** It is recognized here as a distinct species only provisionally, based on the published original description, which indicates a possible difference in respect to other species occurring in that region, at least in the number of trunk segments (Table 3). Indeed, its actual relations in respect to other species of *Stenotaenia* need to be thoroughly assessed.

**Distribution:** Only known from two close localities in Palestine, namely the type locality (Fig. 2) and Jerusalem (another specimen identified by K.W. Verhoeff, preserved in the Zoologische Staatssammlung München; J. Spelda, pers. comm.).

*STENOTAENIA PALPIGER* (ATTEMS, 1903)

*Geophilus palpiger* Attems, 1903: 231 (original description). *Nesogeophilus palpiger*: Attems, 1929a: 184 (in key), 187 (redescription); 1947: 117 (in key).

**Type locality:** 'Podgorje, Istrien' = Podgorje (Slovenia).

**Type material:** Holotype, male, 17-mm long; held in the Naturhistorisches Museum, Wien, NHMW4843 (V. Stagl, pers. comm.).

**Diagnosis:** A *Stenotaenia* species of small body size (total length reaching at least 1.5 cm); c. 49 leg-bearing segments; first maxillae with distinct lappets on the coxosternum and small lappets on the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior pouch with pores and one posterior single pore (see also Table 3).

**Taxonomic history:** After the original description by Attems (1903), no other specimens have been referred to this nominal species. Its validity has been questioned and its identity to *S. romana* has been suspected (Foddai *et al.*, 1995; Stoev, 1997).

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), as the original description documents a combination of characters that are diagnostic for this genus (Table 2).



**Validity:** It is treated here as a distinct species only provisionally, as further investigations are needed to evaluate its putative differences in respect to other species of *Stenotaenia*, especially *S. cribelliger* (Table 3). However, based on the original description, the suspected synonymization of *G. palpiger* under *S. romana* appears unwarranted, as body size and segment number of the holotype of *G. palpiger* are outside of the known range of variation for *S. romana*, and the two nominal species apparently also differ in the evidence and degree of elongation of the chitin lines; furthermore, the type locality of *G. palpiger* is outside of the known range of *S. romana*.

**Distribution:** Only known from a locality in Istria (Fig. 2).

*STENOTAENIA RHODOPENSIS* (KACZMAREK, 1970)

*Geophilus rhodopensis* Kaczmarek, 1970: 85 (original description), figs 2–3. Stoev, 2002: 90 (in key).

**Type locality:** ‘Devin (NW-Rhodopen)’ = Devin (Bulgaria).

**Type material:** Holotype, male (according to the original description, but see below), 25-mm long; the specimen was originally deposited in the collections of the Adam Mickiewicz University, Poznań.

**Diagnosis:** A *Stenotaenia* species of intermediate body size (total length reaching at least 2.5 cm); c. 55 leg-bearing segments; labrum with about five tubercles; first maxillae without distinct lappets on the coxosternum and with small lappets on the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; anterior margin of the forcipular coxosternum almost straight; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk subtriangular, longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior pouch with pores and one posterior single pore (see also Table 3).

**Taxonomic history:** After the original description by Kaczmarek (1970), it was recorded from other localities by Ribarov (1986, 1989, 1996) and by Stoev (2002). Its validity and its assignment to the genus *Geophilus* has never been questioned.

**Assignment to *Stenotaenia*:** It is assigned quite confidently to *Stenotaenia* (**comb. nov.**), as the detailed original description and illustrations document a combination of characters that are diagnostic for this

genus (Table 2). Actually, the coxal glands were described as independently opening on the surface, but the accompanying drawing may be interpreted as an anterior pouch of aggregated pores and a single, large posterior pore, i.e. a pattern that is typical of *Stenotaenia*. The legs of the last pair were described and illustrated as quite slender in the holotype, which was identified as a male, but the accompanying drawing of the genital region suggests conversely that the holotype could actually be a female. The putative presence of five tubercles on the labrum and the evidence of a socket along the anterior margin of the anteriormost sterna, resembling a ‘carpophagus’ socket, as in many *Geophilus* species, are quite unusual features compared with other *Stenotaenia* species. However, the combination of all the other traits strongly supports the inclusion of this species in *Stenotaenia*. It is worth noting that Kaczmarek (1970), in describing *G. rhodopensis*, stated explicitly that it was very similar to *S. linearis*, which is the type species of *Stenotaenia*. Direct examination of specimens putatively representative of *S. rhodopensis* (identified as such by P. Stoev; see also Stoev & Lapeva-Gjonova, 2005) confirmed that they share all major diagnostic characters of *Stenotaenia*, including the absence of carpophagus sockets and the arrangement of coxal pores.

**Validity:** It is treated here as a distinct species, based on the original description and illustrations (Table 3). However, some putative peculiar traits described in this species need to be evaluated in other specimens. It is worth noting that the putative specimens of *S. rhodopensis* examined directly by us (see Appendix) agree with the original description in the presence of some distinct tubercles on the labrum, namely two tubercles and two other close projections that resemble tubercles in colour. The actual relations of *S. rhodopensis* to other species deserve to be assessed, mainly in respect to *S. antecribellata* and *S. cribelliger*.

**Distribution:** It is known to occur in the Carpathian Mountains, the Rhodopes chain, and some neighbouring regions. It was recorded from differing localities from the Vitosha Mountains in the west, through the Sredna Gora, and the Rhodopes Mountains, to the Toundzha Plain and the Strandzha mountains in the east, but these subsequent records were not accompanied by evidence supporting the species identity in respect to other similar species.

*STENOTAENIA ROMANA* (SILVESTRI, 1895)

*Geophilus romanus* Silvestri, 1895: 194 (original description). Attems, 1903: 221 (in key); 1929a: 161



(in key), 179 (redescription); 1947: 112 (in key). Minelli, 1983a: 8 (redescription).

*Geophilus* (*Notadenophilus*) *silvestrii* Verhoeff, 1928: 269 (original description), figs 28–29. *Nesogeophilus silvestrii*: Attems, 1929a: 359 (redescription). **Syn. nov.**

*Type locality*: ‘Roma (Villa Pamphili)’ = Villa Doria Pamphili, in Rome (Italy).

*Type material*: Syntypes (number unknown), of both sexes, up to 16-mm long; held in the Museo civico di Storia naturale, Genova, without catalogue number.

*Diagnosis*: A *Stenotaenia* species of small body size (total length not reaching 2 cm); c. 43–49 leg-bearing segments; labrum with about one or two tubercles; first maxillae without distinct lappets on both the coxosternum and the telopodites; chitin lines of the forcipular coxosternum not reaching the anterior condyles; anterior margin of the forcipular coxosternum angulated; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior pouch with pores and one posterior single pore or a pouch with very few pores (see also Table 3).

*Taxonomic history*: After the original description by Silvestri (1895) the true identity of this species remained uncertain until Minelli’s (1983a) account, based upon the examination of the type material. *Geophilus romanus* was recorded from other Italian localities (Minelli, 1983a, 1992; Minelli & Zapparoli, 1985, 1992), but its assignment to the genus *Geophilus* was never questioned.

*Assignment to Stenotaenia*: It is assigned confidently to *Stenotaenia* (**comb. nov.**), based on the original description, as emended by Minelli (1983a) (Table 2), as well as on the examination of representative specimens from throughout the known range (Figs 3, 5). This species shares all major diagnostic characters of the genus, including the shape of the labrum, the features of the maxillary complex and the mandibles, the general shape of the forcipular segment, the pattern of sternal pore areas and of the coxal pores, and the features of the legs of the last pair. It is worth noting that Silvestri’s (1895) original description was inaccurate in recognizing only a single pore on the internal ventral side of each coxopleuron, whereas an anterior pouch is also invariably present, as demonstrated by Minelli (1983a) in the type material, and confirmed by our original observations in other specimens. The affinity between

*S. romana* and *S. linearis* was already acknowledged (Silvestri, 1895; Minelli, 1992), and indeed *S. romana* was even suspected by Verhoeff (1928) to represent just a juvenile stage of *S. linearis*.

*Validity*: It is recognized here as a very distinct species: distinguished from all other known species of *Stenotaenia* for the smaller body size, the lower number of trunk segments, the apparent incompleteness of the chitin lines, and the presence of an anterior pouch of coxal glands and a posterior single large pore on each coxopleuron, even in full grown specimens, which is possibly a paedomorphic trait (Table 3).

#### *Remarks on synonyms*

*Geophilus* (*Notadenophilus*) *silvestrii* Verhoeff, 1928. *Geophilus silvestrii* was described by Verhoeff (1928) from a single male from near Rome, and another specimen was later identified by the same author from Mt Argentario, along the Tyrrhenian coast (Verhoeff, 1934a). Its possible synonymy under *S. romana* has already been claimed (Minelli, 1983a; Foddai *et al.*, 1995). According to the detailed original description, *G. silvestrii* agrees fully with *S. romana*, especially in body size, the number of trunk segments, and other major traits in the forcipular segment, the sternal pore areas, the coxal pores, and the last pair of legs. Furthermore, the type localities of the two nominal species are only a few kilometres apart. The only putative diagnostic difference is in the elongation of the head, but the length-to-width ratio given by Verhoeff for *G. silvestrii* is hardly correct, as it is outside the known range of all *Geophilus* or *Stenotaenia* species. Therefore, we are confident in recognizing *G. silvestrii* as a junior synonym of *S. romana*.

*Distribution*: It occurs mainly along the Italian Peninsula, most frequently on the Tyrrhenian side from Liguria to Campania, including some minor islands, namely Elba, Giglio, and Ischia (new localities, see Appendix; M. Zapparoli, pers. comm.). It also occurs in Sardinia (Minelli, 1983a), in the western Alps (Minelli & Zapparoli, 1992), on the Euganean Hills (Minelli, 1992), and on Mt Conero along the Adriatic coast (new localities, see Appendix) (Fig. 3).

#### *STENOTAENIA SORRENTINA* (ATTEMS, 1903)

*Geophilus sorrentinus* Attems, 1903: 228 (original description); 1929a: 161 (in key), 175 (redescription); 1947: 111 (in key). Verhoeff, 1943b: 78 (redescription). Lewis, 1994: 39 (redescription; as synonym of *G. linearis*), figs 1–9.

*Geophilus forficularius* Fanzago, 1881b: 378 (original description); 1881a: 13 (redescription). **Syn. nov.** *Geophilus linearis abbreviatus* Verhoeff, 1925: 74 (original description); 1943a: 70 (redescription). *Clinopodes linearis abbreviatus*: Attems, 1929a: 203 (in key), 205 (redescription); 1947: 120 (in key). *Clinopodes abbreviatus*: Matic, 1972: 65 (in key), 95 (redescription). **Syn. nov.**

*Type locality*: 'Mte. Faito' = Monte Faito, in the Sorrento Peninsula (Italy).

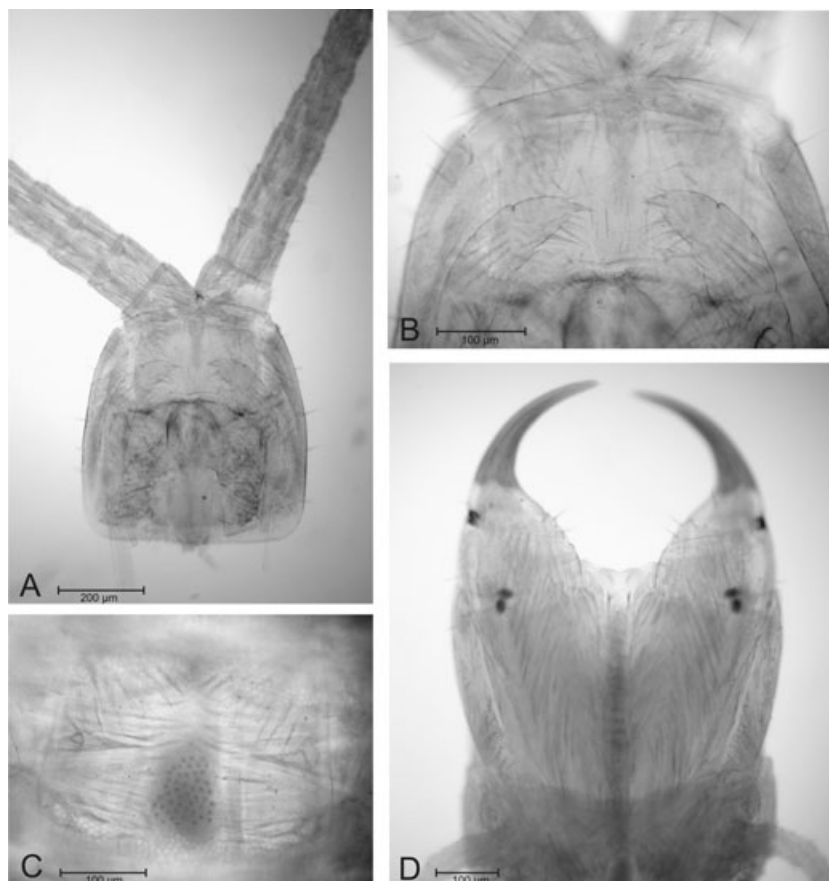
*Type material*: Holotype, female, 22-mm long; held in the Naturhistorisches Museum, Vienna, NHMW6101 (V. Stagl, pers. comm.).

*Diagnosis*: A *Stenotaenia* species of intermediate body size (total length reaching at least 3.5 cm); c. 53–67 leg-bearing segments; labrum either with or without a single tubercle; first maxillae with distinct lappets on the coxosternum, and with small lappets on the telopodites; chitin lines of the forcipular coxosternum

reaching the anterior condyles; anterior margin of the forcipular coxosternum angulated; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, longer than wide, and placed on the posterior half of each sternum; each coxopleuron with one anterior and one posterior pouch with pores (see also Table 3).

*Taxonomic history*: The original description of this species was quite incomplete, so its true identity remained uncertain and no other specimens were referred to it. The holotype was redescribed and illustrated in detail by Lewis (1994), who, however, regarded it as a juvenile of *G. linearis*.

*Assignment to Stenotaenia*: It is assigned confidently to *Stenotaenia* (**comb. nov.**), based on the redescription of the holotype by Lewis (1994) (Table 2), as well as on our own examination of other representative specimens from most of the known range of the species (Fig. 6). *Stenotaenia sorrentina* shares all major diagnostic characters of the genus, including



**Figure 6.** Microscopic images of a female specimen of *Stenotaenia sorrentina* (Attems, 1903) from Palmarola Island (Italy: Tyrrhenian Sea) (23-mm long, with 61 leg-bearing segments; 3-IV-1966 Consiglio lg, collection A. Minelli): (a) head, ventral; (b) clypeus and maxillary complex, ventral; (c) sternum of leg-bearing segment X; (d) forcipular segment, ventral.

the shape of the labrum, the features of the maxillary complex and the mandibles, the general structure of the forcipular segment, the pattern of the sternal pore areas and of the coxal pores, and features of the legs of the last pair.

**Validity:** It is considered here a distinct species, as it can be distinguished from other species occurring in the same region, at least in body size and in the range of variation of trunk segment number (Table 3). Actually, many authors identified representative specimens of *S. sorrentina* as *S. linearis*, based on a larger concept of this latter species, and Lewis (1994) indeed synonymized it explicitly under *S. linearis* (Lewis, 1994). However, our comparative observation of representative material revealed differences in body size and in the range of variation of segment number, correlated with geographical distribution, even though further investigations are required to assess the specific identity of most populations from the Liguria region, which are morphologically somehow intermediate in the putative diagnostic traits. Furthermore, the distinction between *S. sorrentina* and other nominal species in the Balkan Peninsula, namely *S. antecribellata* and *S. cribelliger*, have to be considered provisional, pending critical evaluation of the putative diagnostic traits.

#### Remarks on synonyms

*Geophilus forcicularius* Fanzago, 1881. *Geophilus forcicularius* was described by Fanzago (1881b) from a series of specimens of both sexes from near Sassari, in Sardinia (Fanzago, 1881a), but it was largely ignored by subsequent authors (e.g. Attems, 1929a). Berlese (1903) listed it as a synonym of *Henia vesuviana* (Newport, 1845), without any comment, whereas Minelli (1983b) suggested it could be a synonym of *Geophilus carpophagus*. The original description does not contain many of the most useful diagnostic characters, but the combination of the given characters (mainly, quite short antennae and legs of the last pair, presence of a claw on the last legs, and sexual difference in the width of the last telopodites) suggests that *G. forcicularius* most probably represents a *Stenotaenia* species. It is worth noting that Fanzago (1881b) explicitly recognized that *G. forcicularius* resembled *S. linearis*, stressing that the two species were different in the shape of the antennae and the relative elongation of the legs of the last pair, but these putative differences are not obvious from the descriptions provided by the author (Fanzago, 1881a, b). Conversely, the characters described do not agree with any other geophilomorph species known to occur in Sardinia. In particular, the legs of the last pair in male *H. vesuviana* are not provided with an evident claw, and

are so swollen that they cannot be curved, evidently, as described in male *G. forcicularius*. The antennae of *G. carpophagus* are significantly more elongated than those observed in specimens of *G. forcicularius* representative of both sexes and different in size. A revision of published faunistic records (Minelli, 1983b) and our direct examination of specimens from Sardinia together suggest that *S. romana* and *S. sorrentina* are the only known species of *Stenotaenia* occurring on the island. We are confident in recognizing *G. forcicularius* as a synonym of *S. sorrentina*, as *S. sorrentina* is the only species compatible with the few characters described for *G. forcicularius*, including the limited elongation of the antennae, the lack of tubercles on the forcipules, the dimorphic shape of the last pair of legs, and the presence of an evident claw in the last legs of both sexes. It is worth noting that *S. sorrentina* is also known to occur in the area from which *G. forcicularius* was described. Even though *G. forcicularius* is the senior name, we do not think that it would be advisable to resurrect this almost neglected name as the valid name for this taxon, especially because of the residual uncertainty arising from both the lack of the original material and the poor quality of the original description. As the conditions for the reversal of precedence (ICZN: art. 23.9) are not met, the matter has been referred to the International Commission on Zoological Nomenclature for a ruling under the plenary power (Bonato & Minelli, 2007).

*Geophilus linearis abbreviatus* Verhoeff, 1925. *Geophilus linearis abbreviatus* was described by Verhoeff (1925) from two specimens, one from the locality 'Corpo di Cava' in the Sorrento Peninsula, and the other from Ferrania in Liguria. Some authors did not accept this taxon as distinct from *G. linearis* (e.g. Lewis, 1994), but most of them accepted it as either a subspecies or a distinct species, and even identified other representative specimens mainly from the Italian Peninsula, the Dinarids, and the Carpathians (e.g. Verhoeff, 1937b, 1943a; Matic, 1972; Minelli & Zapparoli, 1985, 1992; Kos, 1995, 1996; Kos & Praprotnik, 2000). Through direct examination of the holotype of *G. sorrentinus*, Lewis (1994) demonstrated the morphological identity between *G. sorrentinus* and *G. linearis abbreviatus*, but he considered both names as junior synonyms of *G. linearis*. As *G. sorrentinus* is recognized here as the distinct species *S. sorrentina*, *G. linearis abbreviatus* has to be synonymized under *S. sorrentina*. Apart from the morphological consistency among the type specimens, it is worth noting the geographical closeness between one of the localities of the syntypes of *G. linearis abbreviatus* and the type locality of *G. sorrentinus* in the Sorrento Peninsula.



**Distribution:** Populations reliably referred to *S. sorrentina* occur through most of the Italian Peninsula, from the Maritime and Ligurian Alps to Gargano and Calabria, and also from Elba and some minor islands such as Ponza, Palmarola, Zannone, Ventotene, Capri, and Ischia (Verhoeff, 1931, 1940, 1942, 1943a; Matic & Darabantu, 1969), as well as Sardinia. Records of specimens with 59–63 leg-bearing segments from the eastern part of Sicily (Silvestri, 1897; under *G. linearis*) should most probably be referred to *S. sorrentina*. Conversely, published records for *G. abbreviatus* from other regions, mainly in the Balkan Peninsula (Verhoeff, 1937b; Matic, 1972; Kos, 1995; Kos & Praprotnik, 2000), need to be reassessed, given the uncertain taxonomic relations between *S. sorrentina* and other nominal *Stenotaenia* species from the same general area, namely *S. antecribellata* and *S. cribelliger*. Specimens from Corsica with 63–69 leg-bearing segments (Léger & Duboscq, 1903; new locality, see Appendix) may belong to *S. sorrentina*, but further investigation is needed.

*STENOTAENIA STURANYI* (ATTEMS, 1903)

*Insigniporus sturanyi* Attems, 1903: 270 (original description), figs 21–22; 1929a: 208 (redescription), figs 181–182. Kanellis, 1959: 37 (in key).

**Type locality:** ‘Gnevgheli, Macedonien’ = Gevgelija (Republic of Macedonia).

**Type material:** Holotype, female, 70-mm long; held in the Naturhistorisches Museum, Vienna, NHMW327 (V. Stagl, pers. comm.).

**Diagnosis:** A *Stenotaenia* species of very large body size (total length overreaching at least 7.5 cm); c. 105–115 leg-bearing segments; labrum with a pair of tubercles; first maxillae with distinct lappets on both the coxosternum and the telopodites; chitin lines of the forcipular coxosternum reaching the anterior condyles; anterior margin of the forcipular coxosternum angulated; forcipular intermediate articles distinct; sternal pore areas in the anterior part of the trunk oval, with a median restriction both anteriorly and posteriorly, and placed on the posterior half of each sternum; each coxopleuron with one anterior and one posterior pouch with pores (see also Table 3).

**Taxonomic history:** After the original description by Attems (1903), other specimens were identified by Zapparoli (2002) and by Simaiakis *et al.* (2004). However, the taxonomic position of *I. sturanyi* remained uncertain, and its original combination was never questioned (Kanellis, 1959; Kos, 1992; Stoev, 1997).

**Assignment to *Stenotaenia*:** It is assigned confidently to *Stenotaenia* (**comb. nov.**), based on the original description and illustrations (Table 2), as well as on our study of other specimens obviously belonging to this species (Figs 3, 7). *I. sturanyi* shares a combination of characters that are diagnostic of *Stenotaenia*, including the shape of the labrum and of the maxillary complex, the features of the forcipular segment, the pattern and longitudinal variation of the sternal pore areas, the shape of the sternum of the last leg-bearing segments, the arrangement of the coxal pores, and the shape of the legs of the last pair. Actually, the coxosternum of the second maxillae was described and illustrated as provided, with an evident median sulcus, but our direct examination of representative specimens demonstrated that the coxosternum is undivided, as is typical of *Stenotaenia* and all other geophilids.

**Validity:** It is recognized here as a very distinct species, differing from all other known species of *Stenotaenia* mainly for the larger body size, the higher number of trunk segments, and the peculiar shape of pore areas on the anterior sterna (Table 3).

**Distribution:** The species occurs in the region between Macedonia and the Chalcidic Peninsula (Attems, 1903; Zapparoli, 2002; new locality, see Appendix) (Fig. 3). It was also recorded from Crete, but without evidence supporting the identification (Simaiakis *et al.*, 2004).

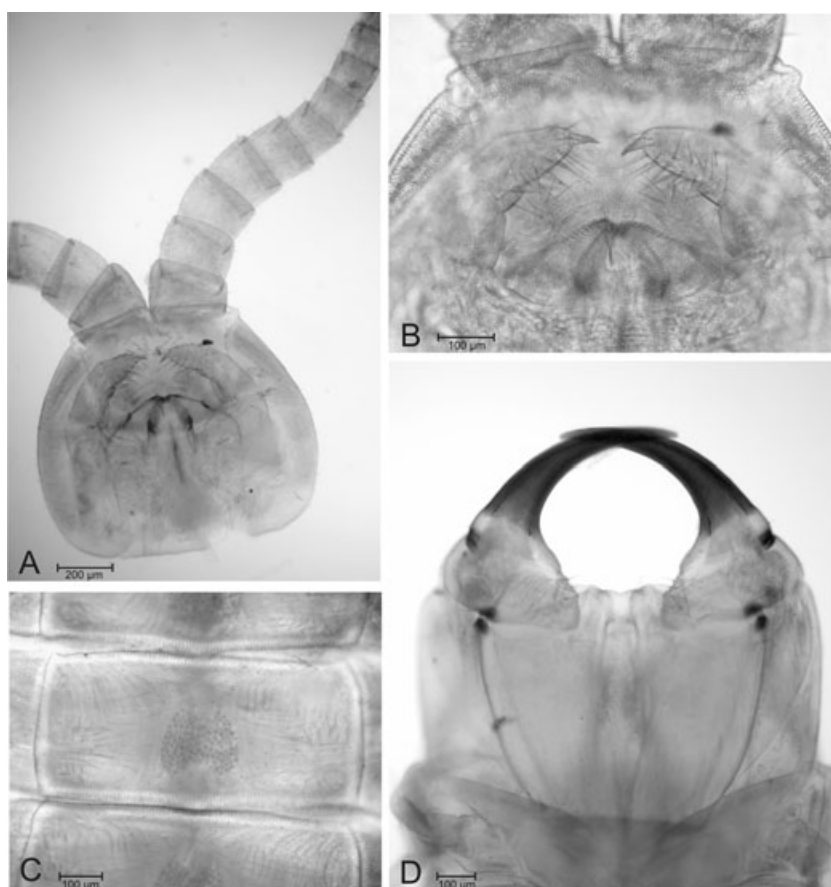
## DISCUSSION

### THE GENUS *STENOTAENIA*

Our taxonomic revision is a contribution to the better understanding of the diversity of geophilomorph centipedes in the western Palaearctic. Indeed, the taxonomic and nomenclatural frame currently available is still largely affected by inconsistencies and redundancies, obviously complicating any effort to assess the actual biotic richness, as well as to analyse evolutionary and biogeographical patterns.

The circumscription of *Stenotaenia* proposed here is based on the recognition of the consistent occurrence of a well-defined combination of morphological characters, encompassing different parts of the body, including the mouth parts, the forcipules, the sternal glands, and the last leg-bearing segment (Table 1; Fig. 1). Even though an adequate phylogenetic analysis would be hindered today by the inadequate level of knowledge of many other relevant geophilid taxa, we can say that the following shared characters are most probably synapomorphies of *Stenotaenia*: the shape of the labral margin (slightly projecting backwards into





**Figure 7.** Microscopic images of a female specimen of *Stenotaenia sturanyi* (Attems, 1903) from Xiropotamos near Drama (Greece: Macedonia) (58-mm long, with 111 leg-bearing segments; 10-IV-1993, Beron lg, collection Natn. Mus. Nat. Hist., Bulgarian Acad. Sci., Sofia): (a) head, ventral; (b) clypeus and maxillary complex, ventral; (c) sternum of leg-bearing segment X; (d) forcipular segment, ventral.

a medial, obtuse angle), the shape of the forcipules (the basal and the two intermediate articles relatively short, internal margins of the forcipules and the coxosternum without any tubercle), and the pattern of the sternal pores (arranged into a rounded to oval, medioposterior area on the anteriormost and posteriormost segments of the trunk, in two paired areas on the intermediate segments). This group of species is treated here as a distinct genus, as it can be unambiguously distinguished from all other known genera through a unique, strongly conserved combination of traits. This treatment is also consistent with the traditional, current practice in geophilid taxonomy, which assigns most of these traits a high diagnostic value at the genus level.

Out of the nominal taxa included here in *Stenotaenia*, some were already recognized as somehow related to each other. In particular, Verhoeff (1901, 1902–25, 1924a, 1934a, b) proposed the name *Onychopodogaster*, either as an informal taxonomic assemblage, or as a subgenus of *Geophilus*, to group

*abbreviatus*, *antecribellatus*, *asiaeaminoris*, *cribelliger*, *fimbriatus*, *linearis*, *naxius*, and *palaestinus* together. Attems (1929a) independently recognized the affinities of *frenum*, *albanensis*, and *palaestinus*, and assigned them to the poorly understood genus *Simophilus*. More recently, Minelli (1992) suspected strict affinities between *linearis*, *abbreviatus*, and *romanus*. Instead, the identity and relationships of other nominal species remained unclear or even misunderstood, as for *acuneli*, *bosporanus*, *caldarium*, *giljarovi*, and *sturanyi*. New genera or subgenera were introduced and maintained for some of these taxa (*Bithyniphilus*, *Insigniporus*, *Notadenophilus*, *Schizopleres*, *Simophilus*, and *Euronesogeophilus*), whereas the best-known species were included by most authors into already established genera, most often *Geophilus* and *Clinopodes*, but also to *Nesogeophilus* (which is a synonym of *Tuoba*), *Pachymerium*, and even *Himantarium*. Actually, geophilid genera such as *Geophilus*, *Clinopodes*, *Pachymerium*, and *Tuoba* can be diagnosed unambiguously in respect to

*Stenotaenia* (Table 1; Fig. 1), whereas *Himantarium* is now regarded as belonging to another family (Himantariidae).

We recognized confidently nine genus-group nominal taxa and 27 species-group nominal taxa as belonging to *Stenotaenia*. Minor doubts remain only for *Geophilus forficularius* Fanzago, 1881, because its original description is very incomplete, and we could not locate the type material (if still extant).

In addition, *Geophilus ungviculatus* Daday, 1889, a nominal species described from Patras (Greece), but still of uncertain identity (Daday, 1889b; Attems, 1929a; Kanellis, 1959; Stoev, 1997; Zapparoli, 2002), could actually be referred to *Stenotaenia*, as suggested by features of the labrum, the forcipules, the sternum of the last leg-bearing segment, and the last telopodites. However, according to the original description, the arrangement of the sternal pore areas, and of the coxal pores, is unusual for a species of *Stenotaenia*. Therefore, we refrain from provisionally recognizing *G. ungviculatus* as belonging to this genus.

Two other species have been occasionally suggested to be closely related to *G. linearis*, but their original descriptions document unambiguously that they do not belong to *Stenotaenia*. *Geophilus hartmeyer* Attems, 1911, described from a few localities in Australia, was considered similar to *G. linearis* since its original description (Attems, 1911), but it was later recognized as belonging to the genus *Tuoba*, as a synonym of either *Tuoba laticeps* (Pocock, 1891) or *Tuoba sydneyensis* (Pocock, 1891) (Crabill, 1962, 1968; Jones, 1998). *Geophilus aragonicus* Daday, 1889, described from the region of Aragon in the Iberian peninsula, was considered to be a junior synonym of *G. linearis* by Verhoeff (1931), but its identity remained uncertain; according to the original description (Daday, 1889b) it clearly departs from *Stenotaenia*, as the sternal pores are arranged in transverse bands and only one pouch is present on each coxopleuron.

Outside the western Palaearctic, several, poorly known other species of *Geophilus* and allied genera have been described so far, mainly from North America. However, based on the original accounts, none of them may be recognized as belonging to *Stenotaenia*. As far as we know, only the northern American *Mycotheres* (*Nemopleura*) *vittatus* Rafinesque, 1820, currently known as *Geophilus vittatus* (Rafinesque, 1820) (with some synonyms; Hoffman & Crabill, 1953; Crabill, 1954), resembles *Stenotaenia* in some characters, such as the general shape of the forcipules and the arrangement of coxal pores. However, *G. vittatus* departs from *Stenotaenia* in other highly diagnostic traits, such as the arrangement of the sternal pores in transverse areas, and in the

presence of other unusual features, e.g. dark dorsal patches on the trunk (Crabill, 1954).

#### GEOGRAPHICAL DISTRIBUTION

The genus *Stenotaenia* is distributed within a limited part of the western Palaearctic (Fig. 2). It is well documented in the central part of continental Europe, the Mediterranean part of mainland France, Corsica, Sardinia, the Italian Peninsula, Sicily, part of the African Atlas chain, the Balkan Peninsula, the Aegean islands, Crete, Anatolia, western Caucasus, and the coastal region of the eastern Mediterranean Sea. Towards the north, only scattered records are known from central and southern parts of Great Britain and the Baltic area, mainly from synanthropic sites, and therefore possibly result from recent introduction by humans. Towards the south-west, *Stenotaenia* is apparently absent from the whole of the Pyrenees, as well as from Iberia and the Balearic Islands, despite of the relatively high research efforts carried out in those areas (Verhoeff, 1924b; Brölemann, 1930; Machado, 1946, 1953; Attems, 1952; Barace & Herrera, 1980; Salinas, 1990; Serra & Ascaso, 1990; Serra, Vicente & Mateos, 1996; García & Serra, 2000, 2003). It is worth noting that Attems (1926) cited *Onychopodogaster* generically for the Balearic Islands, but actually he almost surely was referring to *Tuoba poseidonis* (Verhoeff, 1901), a well-known species that had been erroneously assigned to *Onychopodogaster* by Brölemann (1909b). Towards the east, *Stenotaenia* reaches the Carpathian range and the regions around the Black Sea, the most eastern records being from the eastern part of the Pontic area. No records are available from the internal regions of Ukraine and Russia, and from most of the Caucasus, but investigations in those areas have been very limited so far. Towards the south, *Stenotaenia* reaches Palestine, whereas there is no record for Cyprus.

#### SPECIES DIVERSITY

The species-level taxonomic arrangement proposed here is founded on a critical reassessment of all of the available information, as well as on comparative examination of representative specimens from throughout the range of the genus. However, it must be considered as only a preliminary arrangement, as the actual specific diversity within *Stenotaenia* remains understood only in part.

Some species are indeed very distinct and recognizable, as is the case of *S. frenum*, *S. romana*, and *S. sturanyi*, and we were able to contribute to the understanding of their morphology and geographical occurrence. Conversely, most species are treated here

as valid only provisionally, pending more thorough investigations that could add to the understanding of their actual identity and their relations. This is particularly the case for *S. antecribellata*, *S. asiaemisoris*, *S. bosporana*, *S. cribelliger*, *S. palpiger*, and *S. giljarovi*.

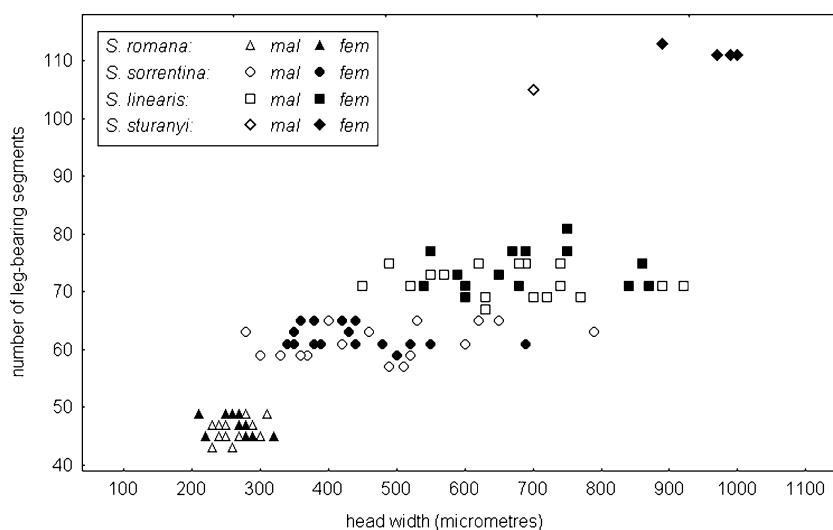
Our revision of the actual diversity of *Stenotaenia* species was more effective for the western part of the range of the genus, approximately west of the Adriatic Sea. Here, extensive sampling and detailed published accounts allowed us to obtain a more satisfactory taxonomic, nomenclatural, and distributional synthesis. Major questions, however, remain: above all, regarding the taxonomic distinction and geographical limits between *S. linearis* and *S. sorrentina*, in a possible transitional area encompassing the western Alps and the nearby Mediterranean coastal regions. The arrangement proposed here is admittedly incomplete and provisional for the eastern part of the range of *Stenotaenia*, east of the Adriatic Sea, where sampling was less intense, where many nominal taxa were described inadequately, and where different authors followed different taxonomic opinions.

A thorough reassessment of the internal taxonomy of *Stenotaenia* will require testing the putative diagnostic value attributed by authors to some minor characters, such as the presence and the number of tubercles on the labrum and the size of the maxillary lappets, through the evaluation of intraspecific variation.

#### DIVERSITY OF BODY SIZE AND SEGMENTAL STRUCTURE

Our morphological comparison revealed a consistent invariance in most of the anatomical traits in *Stenotaenia*, encompassing different parts of the body. However, despite the conservative body shape, species differ conspicuously both in the maximum size, reached by fully grown specimens, and in the number of trunk segments, which is invariant during postembryonic growth, as in all geophilomorphs. The extreme conditions are represented by *S. romana*, which is less than 2-cm long at full growth with as few as 43 leg-bearing segments in some specimens, and by *S. sturanyi*, reaching almost 8 cm in length, with up to 115 leg-bearing segments. As for the number of segments, in spite of a wide overall range of variation (72 segments), intraspecific variation is very limited, even in those species for which large numbers of specimens have been examined (Table 3): ranges of variation observed for each sex were from six segments (in many dozen females of *S. romana*) to 14 segments (in 15 males of *S. frenum*; estimates for *S. linearis* and *S. sorrentina* are similar, but distinguishing between these two species is problematic).

Comparing the species of *Stenotaenia*, we found that the number of leg-bearing segments correlates significantly with the maximum head width (Fig. 8) (Spearman correlation: for males  $R = 0.83$ ,  $t = 10.8$ ,  $P < 0.000$ ; for females  $R = 0.88$ ,  $t = 14.0$ ,  $P < 0.000$ ),



**Figure 8.** Relationship between the adult body size, as measured by the maximum width of the head, and the number of leg-bearing segments in different species of *Stenotaenia*. We considered only specimens with fully developed gonopods, and only species for which at least five adults were available. Distinction between *Stenotaenia sorrentina* and *Stenotaenia linearis* is only tentative for some specimens, as it is based on a conventional threshold in the number of leg-bearing segments (see Table 3, and remarks under *S. sorrentina*).

revealing that the number of segments, which is fixed since hatching is associated with the maximum body size reached after growth.

The extent of variation of both body size and segment number in *Stenotaenia* is unusual in respect to all other recognized genus-level groups, not only within geophilomorph centipedes, but also within myriapods as a whole. As a rule, even in higher taxa where the segment number is very different between different genera, variation is very limited between closely related species included in a single genus. As far as is known, only two genera of geophilomorphs surpass *Stenotaenia* in the extent of variation of segment number, coupled with a comparable variation of body size, namely *Henia* Koch, 1847, ranging from 43 leg-bearing segments and less than 2-cm long in *Henia brevis* (Silvestri, 1896) to 153 leg-bearing segments and up to 15-cm long in *Henia devia* (Koch, 1847), and *Ribautia* Brölemann, 1909, ranging from 43 leg-bearing segments and less than 2-cm long in *Ribautia coarctata* Ribaut, 1923 to 125 leg-bearing segments and up to 7.5-cm long in *Ribautia taeniata* Ribaut, 1923 (Attems, 1929a). However, each of these genera encompasses a more diversified assemblage of species, and the two extreme species of *Henia* cited above are actually separated in two distinct subgenera (Minelli, 1982). The genus *Notiphilides* Latzel, 1880 has a range of variation in the segment number comparable with that of *Stenotaenia* (from 85 to 151 leg-bearing segments; Attems, 1929a), but this is not matched by a significant variation in body size. As for the relation between body size and segment number, preliminary analyses suggest that this may be common to other lineages and to geophilomorphs as a whole (Foddai *et al.*, 2003), but it has not been documented so far to the same extent as in *Stenotaenia*.

Therefore, interspecific comparison in *Stenotaenia* offers evidence of an extensive and concerted evolution of body size and segmental structure. This evolutionary pattern, together with the putative underlying developmental constraints, may contribute to the on-going research on the morphogenetic mechanisms, still inadequately understood, involved in the segmentation of the trunk of arthropods.

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## APPENDIX

Specimens of *Stenotaenia* examined.

For each specimen (in alcohol), the approximate body length and number of leg-bearing segments (lp) are given in parentheses. Specimens belong to the following collections: AM, A. Minelli, Univ. Padova; BAS, National Museum of Natural History, Bulgarian Academy of Sciences, Sofia; MAM, Zoological Museum Amsterdam; MBG, Museo Civico di Scienze Naturali 'E. Caffi', Bergamo; MVR, Museo civico di Storia naturale di Verona; RSI, Romanian Speleological Institute, Cluj-Napoca and Bucharest.

*Stenotaenia* cf. *antecribellata* (Verhoeff, 1898)

Bjelašnica, near Sarajevo (Bosnia-Herzegovina): 1♂ (37 mm, 61 lp), 25-X-1983 Etonti lg, AM.

Mt Ucka (Croatia: Istria): 1♂ (25 mm, 61 lp), 9-VIII-1973 Daccordi lg, MVR.

Kavala Lekanis (Greece: Macedonia region): 1♀ (21 mm, 63 lp), 4-VI-1983 Etonti lg, AM.

Mt Pangeon (Greece: Macedonia region): 1♂ (24 mm, 61 lp), 30-V-1983 Etonti lg, AM.

Klenoec (Macedonia): 1♂ (21 mm, 55 lp), 22-V-1954 Jeekel lg, MAM.

*Stenotaenia frenum* (Meinert, 1870)

Baie de Tamanart (Algeria): 1♀ (28 mm, 81 lp), 7-XI-1984 collector unknown, AM.

Ski kDa (Algeria): 1 juvenile (15 mm, 75 lp), 8-IV-1977 collector unknown, AM.

7-km west of Tamera (Tunisia): 1♀ (28 mm, 89 lp), date and collector unknown, AM.

Locality unknown (Tunisia): 1♂ (21 mm, 87 lp), 28-II-1981 Omodeo lg, AM.

Massif de l'Edough (Tunisia): 1♂ (33 mm, 85 lp), 22-X-1984 collector unknown, AM.

11 km south of Ain Drahan (Tunisia): 1♂ (31 mm, 91 lp), 30-IV-1983 Omodeo lg, AM.

*Stenotaenia linearis* (Koch, 1835)

Appiano (Italy: Alto Adige): 1♀ (34 mm, 77 lp), 16-IV-1978 Copello lg, AM.

Punta Manara (Italy: Liguria): 1♀ (31 mm, 73 lp), 27-II-1977 Cassulo lg, AM.

M. Saccarello (Italy: Liguria): 1♀ (43 mm, 77 lp), 10-VII-1980 Zapparoli lg, AM.



S. Marino di Struppa (Italy: Liguria): 1♀ (34 mm, 69 lp), 24-III-1985 Gardini lg, AM.  
 Varazze (Italy: Liguria): 1♀ (35 mm, 71 lp), 20-I-1977 Bernabò lg, AM.  
 Clibbio (Italy: Lombardia): 1♂ (22 mm, 71 lp), 6-V-1979 Osella lg, MVR.  
 Clusone (Italy: Lombardia): 1♂ (39 mm, 75 lp), 21-IV-1979 collector unknown, MVR.  
 Morbegno (Italy: Lombardia): 4♂ (24, 31, 32, 39 mm; 69, 69, 69, 71 lp), 2♀ (21, 26 mm; 73 lp), 6-V-1979, Omodeo & Bonifazi lg, AM.  
 Oltre il Colle, Val Brembana (Italy: Lombardia): 1♂ (30 mm, 67 lp), 10-V-1964 Osella lg, MVR.  
 Pasturo (Italy: Lombardia): 1♀ (25 mm, 77 lp), 23-IX-1987 Valle, Pandolfi & Quirli lg, MBG.  
 Sacco, Val Gerola (Italy: Lombardia): 1♀ (29 mm, 71 lp), 5-V-1979 Omodeo & Bonifazi lg, AM.  
 Servetta-Forcola (Italy: Lombardia): 1♂ (23 mm, 71 lp), 5-V-1979 Omodeo & Bonifazi lg, AM.  
 Brusasco (Italy: Piemonte): 1♀ (29 mm, 71 lp), 2-IV-1972 Osella lg, MVR.  
 Grazzano Badoglio (Italy: Piemonte): 1♂ (32 mm, 69 lp), 1-X-1982 Torti lg, AM.  
 Locana (Italy: Piemonte): 1♀ (46 mm, 75 lp), 26-IV-1980 Bianchi & Moretti lg, MBG.  
 Montecastello (Italy: Piemonte): 2♂ (32, 35 mm; 71 lp), 27-X-1978 Torti lg, AM.  
 Pian Traversagn (Italy: Piemonte): 1♀ (48 mm, 71 lp), 1-VII-1977 Vigna lg, AM.  
 Piedicavallo (Italy: Piemonte): 1♀ (41 mm, 71 lp), 26-VI-1979 Riese lg, AM.  
 Viozene (Italy: Piemonte): 1♀ (37 mm, 77 lp) 9-VII-1980 Zapparoli lg, AM.  
 Avesa (Italy: Veneto): 1♂ (38 mm, 75 lp), 3-III-1978 Osella lg, MVR.  
 Ca' degli Oppi (Italy: Veneto): 1♂ (23 mm, 75 lp), 1♀ (33 mm, 77 lp), 1977 Sette lg, MVR.  
 Cologna Veneta (Italy: Veneto): 4♂ (27, 27, 31, 33 mm; 73, 73, 75, 75 lp), 1♀ (30 mm, 77 lp), 8-X-1978/21-X-1979 Gioco lg, MVR.  
 F. Bacchiglione (Italy: Veneto): 1♂ (25 mm, 75 lp), date unknown Omodeo lg, AM.  
 Foza (Italy: Veneto): 1♀ (35 mm, 81 lp), 29-IV-1991 Zanon lg, AM.

*Stenotaenia cf. linearis* (Koch, 1835)

Biokovo (Croatia: Dalmatia): 1♀ (22 mm, 73 lp), 27-X-1983 Etonti lg, AM.  
 Kelkit-Erzincan (Turkey): 1♂ (30 mm, 79 lp), 1♀ (24 mm, 85 lp), 21-VI-1975 Osella lg, MVR.

*Stenotaenia cf. palaestina* (Verhoeff, 1925)

Nes Harim (Israel): 1♀ (12 mm, 69 lp), 10-IV-1993 Negrea lg, RSI.

*Stenotaenia cf. rhodopensis* (Kaczmarek, 1970)

Bistritsa, Vitosha Mts (Bulgaria): 2♀ (16, 30 mm; 63 lp), 9-IV-1998 Lapeva-Gjonova lg, BAS.

*Stenotaenia romana* (Silvestri, 1895)

Gavi, near Alessandria (Italy: Piemonte): 1♀ (13 mm, 47 lp), 6-X-1982 Torti lg, AM.  
 Capriata d'Orba (Italy: Liguria): 1♀ (10 mm, 45 lp), 28-X-1968 Torti lg, AM.  
 Isola del Cantone, near Genova (Italy: Liguria): 2♂ (11, 12 mm; 45 lp), 3♀ (9, 12, 12, 12 mm; 45, 45, 45, 47 lp), 5-XI-1978) Gardini lg, AM.  
 M. Fasce, near Genova (Italy: Liguria): 1♂ (10 mm, 43 lp), 3♀ (10, 11, 12 mm; 45 lp), 23-XI-1975/30-I-1976 Briganti lg, AM.  
 S. Bernardino, near Finale Ligure (Italy: Liguria): 1♂ (12 mm, 45 lp), 1♀ (12 mm, 47 lp), 24-III-1974 Gardini lg, AM.  
 S. Martino di Struppa (Italy: Liguria): 1♀ (11 mm, 47 lp), 24-III-1985 Gardini lg, AM.  
 Val Graveglia, near Genova (Italy: Liguria): 1♂ (10 mm, 45 lp), 1♀ (9 mm, 45 lp), 1-II-1976 Gardini lg, AM.  
 Codolo (Italy: Toscana): 8♂ (9, 11, 9, 9, 10, 11, 12, 12 mm; 43, 43, 45, 45, 45, 45, 45 lp), 3♀ (9, 14, 14 mm; 45 lp), 7-II-1976 Briganti lg, AM.  
 Legri (Italy: Toscana): 4♂ (13, 14, 17, 13 mm; 47, 47, 47, 49 lp); 6♀ (15, 11, 12, 17, 17, 17 mm; 47, 49, 49, 49, 49, 49 lp), 2-III-1978 Magrini lg, AM.  
 Trequanda (Italy: Toscana): 1♂ (11 mm, 47 lp), XII-2002 Petrioli lg, AM.  
 Seprevisa (Italy: Lazio): 1♀ (11 mm, 47 lp), 5-I-2003 Petrioli lg, AM.  
 Olbia (Italy: Sardinia): 1♂ (12 mm, 47 lp), 6-V-1980 Omodeo lg, AM.  
 M. Rusta (Italy: Colli Euganei): 4♂ (9, 11, 11, 12 mm, 47 lp), 2♀ (12 mm, 49 lp), 16-IV-2000 Bonato, AM.

*Stenotaenia sorrentina* (Attems, 1903)

Spigno Monferrato (Italy: Piemonte): 1♂ (19 mm, 59 lp), 1♀ (20 mm, 61 lp), 22-IV-1980 Zoia lg, AM.  
 Cisano sul Neva (Italy: Liguria): 1♂ (16 mm, 63 lp), 24-VII-1980 Gardini & Zoia lg, AM.  
 Finale Ligure (Italy: Liguria): 2♀ (17, 19 mm; 65 lp), 7-XII-1975 Gardini lg, AM.  
 Santuario di Savona (Italy: Liguria): 1♀ (19 mm, 63 lp), 1-X-1959 Jeekel lg, MAM.  
 M. Fasce (Italy: Liguria): 1♂ (13 mm, 65 lp), 30-I-1976 Gardini lg, AM.  
 Bovecchio-Cavallina (Italy: Toscana): 1♂ (30 mm, 65 lp), 20-X-1978 Magrini lg, AM.  
 Legri (Italy: Toscana): 1♂ (26 mm, 65 lp), 2-III-1978 Magrini lg, AM.  
 Vallombrosa (Italy: Toscana): 1♂ (19 mm, 63 lp) 9-XII-1959 Jeekel lg, MAM.  
 M. Pigno (Italy: Marche): 1♂ (42 mm, 63 lp), 9-XI-1979 Briganti lg, AM.

- Palmarola Island (Italy: Tyrrhenian Sea): 1♂ (15 mm, 59 lp), 1♀ (23 mm, 61 lp), 3-IV-1966 Consiglio lg, AM.
- Palmarola Island (Italy: Tyrrhenian Sea): 4♀ (14, 16, 20, 20 mm, 61 lp), 14-XI-1966 Argano & Cottarelli lg, AM.
- Ponza (Italy: Tyrrhenian Sea): 1♂ (13 mm; 59 lp), 23-II-1968 Vigna lg, AM.
- Ponza (Italy: Tyrrhenian Sea): 1♂ (24 mm, 59 lp), 28-I-1960 Argano lg, AM.
- Ventotene (Italy: Tyrrhenian Sea): 1♀ (21 mm, 61 lp), 12-III-1967 Cottarelli lg, AM.
- Zannone (Italy: Tyrrhenian Sea): 1♀ (21 mm, 61 lp), 28-III-1966 Sbordonì lg, AM.
- Zannone (Italy: Tyrrhenian Sea): 1♂ (17 mm, 61 lp), 28-I-1966 Argano & Vigna lg, AM.
- Roma, Jenne (Italy: Lazio): 1♂ (24 mm, 61 lp), 14-XI-1971 Sbordonì lg, AM.
- Roma, Villa Paganini (Italy: Lazio): 1♀ (16 mm, 65 lp), 9-XI-1978 Zapparoli lg, AM.
- Vallonina (Italy: Lazio): 1♀ (32 mm, 61 lp), 19-XI-1969 collector unknown, AM.
- M. Prena (Italy: Abruzzo): 1♀ (16 mm, 65 lp), 27-V-1979 Nicolai lg, AM.
- M. Tranquillo (Italy: Abruzzo): 1♀ (19 mm, 63 lp), 20-VII-1973 Vigna lg, AM.
- M. Viglio (Italy: Abruzzo): 1♂ (35 mm, 61 lp), 7-VIII-1974, Pace lg, MVR.
- Alatri (Italy: Lazio): 1♂ (18 mm, 57 lp), 24-VI-1973 Pace lg, MVR.
- Circeo (Italy: Lazio): 2♀ (15, 17 mm; 63, 65 lp), 31-X-1968 collector unknown, AM.
- M. Semprevise (Italy: Lazio): 1♂ (23 mm, 57 lp), 26-X-1969 Brignoli lg, AM.
- M. Caruso (Italy: Molise): 1♀ (20 mm, 59 lp), 13-VII-1975 Pace lg, MVR.
- Portici (Italy: Campania): 1♂ (17 mm, 61 lp), date unknown Cavanna lg, AM.
- S. Antonio (Italy: Sardinia): 2♂ (17, 20 mm; 59, 61 lp), 3♀ (11, 17, 16 mm; 61, 61, 63 lp), 27-III-1977 collector unknown, AM.
- Punta Balestreri (Italy: Sardinia): 1♂ (26 mm, 61 lp), 30-III-1972 Brignoli lg, AM.
- Stenotaenia cf. sorrentina* (Attems, 1903)
- Ruisseau de Lonca (France: Corsica): 2♂ (12, 13 mm; 69 lp), 25-IV-2003 Bonato lg, AM.
- Stenotaenia sturanyi* (Attems, 1903)
- Xiropotamos, near Drama (Greece: Macedonia region): 1♂ (42 mm, 105 lp), 4♀ (58, 70, 77, 57 mm; 111, 111, 111, 113 lp), 10-IV-1993) Beron lg, BAS.