Morphology, taxonomy and distribution of *Diphyonyx* gen. n., a lineage of geophilid centipedes with unusually shaped claws (Chilopoda: Geophilidae)

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**Abstract.** A new genus *Diphyonyx* is proposed here for a previously unrecognised lineage of geophilid centipedes. It is distinct from other geophilids in its unique combination of morphological characters, including the peculiar shape of the pretarsus of the legs on the anterior part of the trunk. The type species *D. conjungens* (Verhoeff, 1898), comb. n., is redescribed in detail and its geographical distribution updated (Balkan Peninsula, Anatolia, Crimea). Included in *Diphyonyx* are also *D. sukacevi* (Folkmanová, 1956), comb. n., and *D. garutti* (Folkmanová & Dobroruka, 1960), comb. n., both from southern Russia. *D. garutti* is raised here to species rank.

**INTRODUCTION**

According to the currently most followed systematic arrangement of the geophilomorph centipedes (Chilopoda Geophilomorpha), almost half of the known species in this group belongs to the single family Geophilidae (Minelli, 2006). With more than five hundred described species distributed throughout the world, geophilids represent a taxon only vaguely diagnosed and still in need of being more rigorously circumscribed within a phylogenetic framework.

The internal taxonomic arrangement of the geophilids also appears unsatisfactory. Within the fauna of the Western Palaearctic, where geophilids are highly diverse and most students have concentrated their investigations, the arrangement of species in genera deserves extensive revision: some genera (e.g., *Geophilus* Leach, 1814 and *Brachygeophilus* Bröllemann, 1909) are still used by authors under very broad concepts, that encompass diverse and apparently composite assemblages of species; conversely, other nominal genera (e.g., *Bebekium* Verhoeff, 1941, *Folkmanovius* Dobroruka, 1957 and *Photophilus* Folkmanová, 1928) are monotypic genera whose identity is poorly understood and their taxonomic validity remains to be assessed. Furthermore, many species need to be redescribed, as their morphology is poorly known and sometimes their true identity is unknown or even misunderstood.

Within our ongoing morphological and taxonomic reassessment of Western Palaearctic geophilids and attempts to rearrange species in uniform, putatively natural genera (e.g., Bonato et al., 2006; Bonato & Minelli, in press), we found compelling evidence for the existence of a distinct lineage that has previously not been recognised as a distinct taxon. It differs from all other geophilids in the very peculiar shape of the claws of the walking legs.

After examination of representative specimens and critical evaluation of all published information, we analysed the morphology, taxonomic circumscription and geographical occurrence of this lineage and found that it deserves to be recognised as a distinct genus. This paper provides (i) a taxonomic description of this new genus, (ii) a critical analysis of the included species, (iii) a detailed redescription and illustration of the designated type species, (iv) an analysis and update of the geographical occurrence of the included species, (v) a description of the peculiar structure of the claws of the walking legs of these centipedes.

**MATERIAL AND METHODS**

After examination of large samples of geophilomorphs from private and museum collections, we identified 56 specimens from 40 localities as belonging to the new genus described here, and in particular to the species *Geophilus conjungens* Verhoeff, 1898. Specimens were examined using light microscopy and standard methods for clearing, temporary mounting and dissection of mouth parts of geophilomorphs (Pereira, 2000; Foddai et al., 2002). Leg claws of a representative specimen were examined using Environmental Scanning Electron Microscopy (XL30 Philips).

Even though we did not examine the type material of all relevant taxa, we tried to locate and examine that necessary for assessing morphological features and taxonomic status.

For the analysis of geographical distribution, all published and new localities and their current names were identified by browsing the Geographic Names Data Base of N.G.I.A. (http://gnswww.nga.mil/geonames/GNS).

Abbreviations for repositories: AM – collection of A. Minelli, Dipartimento di Biologia, Università di Padova, Italy; ZMUC – Zoological Museum, University of Copenhagen, Denmark; MCSN – Museo Civico di Storia Naturale, Genova, Italy; MZ – collection of Marzio Zapparoli, Dipartimento di Protezione delle Piane, Università della Tuscia, Viterbo, Italy; NA – Istituto di
RESULTS

Genus Diphonyx gen. n.
(Figs 1–10)

Type species. Geophilus conjungens Verhoeff, 1898.

Diagnosis. Geophilids with clypeus lacking finely areolate areas; labral side-parts partially distinct from the clypeus, bearing slender projections; first maxillae with two pairs of lappets; telopodites of the second maxillae with a pair of anterior tubercles and complete chitin-lines; forcipular tarsungulum crenulated, with a small basal tubercle; trunk sterna without pores; on the legs of an anterior part of the trunk, claws swollen, the anterior spur of each claw enlarged into an elongate projection; sternum of the last leg-bearing segment wider than long; most coxal glands opening through a single pouch on the lateral margin of the sternum; telopodites of the last pair of legs slender in females, moderately swollen and densely hairy in males, provided with pointed claws.

Differences with respect to other genera. Table 1 gives the main diagnostic characters differentiating Diphonyx from all other genera tentatively recognised by us in the uniform subgroup of Geophilidae, to which Diphonyx belongs (see legend of Table 1). Contrasting Diphonyx with the two nominal genera to which the species of Geophilus have been hitherto referred, in both Geophilus Leach, 1814 [type species G. electricus (Linnaeus, 1758)] and Brachygeophilus Brölemann, 1909 [type species B. truncorum (Berggäewe & Meiner, 1866); considered by different authors either a synonym of Geophilus or a distinct genus] the anterior margin of the forcipular coxosternum has no tubercles and the coxal glands open through separate pores; furthermore, in Brachygeophilus the chitin-lines are incomplete.

Etymology. From the Ancient Greek “diphyës” (= of double nature) and “ónyx, ónychos” (= claw); referring to the bipartite shape of the pretarsus of the legs on the anterior part of the trunk, and a posterior isolated pore in addition to the anterior porouch on each coxopleuron.

Diagnostic characters of the Diphonyx species are presented in Table 2.

Type material. Syntypes: 2 specimens: 1♂, 32 mm long, with 67 pairs of legs, from “Cilicien” (= Cilicia, Turkey), in the Museum für Naturkunde, Berlin, microslide 3386a; 1♀, 55 mm long, with 71 pairs of legs, from “Kleinasiens” (= Anatolia, Turkey), in the Museum für Naturkunde, Berlin, microslide 3386 (Verhoeff, 1898; Moritz & Fischer, 1979).

Worth noting is that Verhoeff (1898: 350) states that his description of G. conjungens is based only on the two specimens listed above, but in the same paper refers 1♂ and 5♀ from “Cilicien” to this species (Verhoeff, 1898: 360). Also worth noting is that one specimen labelled “Paratyroid” from “Kleinasiens”, is preserved in the Zoologisches Museum Hamburg (Weidner, 1960).

Type locality. Both syntypes are most probably from Cilicia (Turkey), but the precise localities are unknown.

Material examined. Localities are listed by country and administrative unit, in alphabetic order, and are mapped in Fig. 11; the number of leg-bearing segments is given in parentheses for each specimen, whenever known; bibliographic references are given for localities already recorded in the literature; abbreviations for repositories are listed under “Material and Methods”.

Greece. Nomos Imathias: Geraki, 1♀ (73), 5.vi.1983 G. Etoni Igt, AM; Lekanis Mts, near Kavala, 1500 m, 1♀ (73), 4.vi.1983 G. Etoni Igt, AM. Nomos Piraio: Asklepiion, Kos island, 2♀ (75, 75), 23.iii.1989 M.A. Bologna Igt, MZ (Zapparoli, 1994); Menetai, Karpathos island, 1 ex., v.1933, NA (Zapparoli, 1994); Profitis Ilias, direction Salakos, Ródos island, 600 m, 1 ex., M. Zapparoli Igt, MZ (Zapparoli, 2002).

Turkey. Ayfon Ilt: Karkas Dağ, S Karadilli, NW Eğdir Gölü, 1400 m, 1♀ (77), 3.v.1995 H. Enghoff, M. Frater & H. Read Igt, ZMUC. Agri Ilt: 5 km E Tutak, 1600–1700 m, 1♂ (77), 22.v.1988 P.A. Audisio Igt, MZ. Antalya Ilt: Gullukdağı-Termessos National Park, ca. 25 km NW Antalya, 900 m, 1♂ (75), 5.v.1995 H. Enghoff, M. Frater & H. Read Igt, ZMUC; İrmasen Geçidi, 1430–1525 m, 4♀ (all 75), 28.iv.1982 M. Zapparoli Igt, MZ; Korkuteli, 1♀ (75), 28.iv.1973 M. Di Raro Igt, MZ. Aydın Ilt: Nazilli-Beydağ, 700 m, 1♀ (73), 6.v.1995 H. Enghoff, M. Frater & H. Read Igt, ZMUC; Bursa Ilt: Lake of Bêysehir, Is. Haci Akif, 1♀ (77) and 1 ex., 24.iv.1973 P. Brignoli Igt, MZ. Bilecik Ilt: Muratdere, 800 m, 1♀ (81), 10.v.1991 M.A. Bologna Igt, MZ. Bursa Ilt: 12–15 km N Bursa, 200 m, 1♂ (77), 12.v.1991 M. Zapparoli Igt, MZ; Keles-Egen, between Bursa and Tavşanti, 1100 m, 2♂ (71, 71), 2.v.1995 H. Enghoff, M. Frater & H. Read
Fig. 1–5. *Diphyonyx conjungens* (Verhoeff, 1898), ♀, 33 mm long, from Geraki, Thrace, Greece; light microscope photographs after clearing in lactophenol; all photographs taken from the underside. 1 – forcipular segment; 2 – labrum and maxillary complex; 3 – anterior margin of the forcipular coxosternum; 4 – left forcipular tarsungulum; 5 – left coxopleuron.
Bodrum, 1♀ (73), 3.xi.1919 R. Varriale lgt, MCSN. Mus Ilı: Buglan Geçidi, E slope, 1500–1600 m, 1♂ (73), 24.v.1988 M. Zapparoli lgt, MZ. Ordu Ilı: Gaga Gölü, near Camas, 60 m, 1♂ (67) and 1♀ (69), 13.v.1987 A. Vigna Taglianti lgt, MZ. Sivas Ilı: Mazikaran Geçidi, 1800 m, 2♂ (75, 79) and 1♀ (81), 6.v.1993 M. Zapparoli lgt, MZ. Tokat Ilı: Dumanli Ormani, 1500–1700 m, 1♀ (79), 12/13.vii.1976 G.M. Carpaneto lgt, MZ; 3 km N Zile, 1190 m, 1♂ (75), 7.v.1993 M. Zapparoli lgt, MZ. Yozgat Ilı: Cayozu, 30 km N Sarikaya, 1100 m, 1♀ (79), 8.v.1991 M. Zapparoli lgt, MZ.

Ukraine. A. R. Krym: Yalta, 1♂ (73), 1907 L. Jägerskiöld lgt, NHMW (Attems, 1929).

Description. Based on an adult female, 33 mm long, with 73 leg-bearing segments, from Geraki (Greece, Thrace) (see above, under “Material examined”). See also Figs 1–10.

General features. Body slender, slightly narrowing anteriorly, more attenuated towards the posterior tip. Colour (preserved in ethanol) almost uniform, dark yellow.

Cephalic capsule. Cephalic plate sub-rectangular, the lateral margins evidently convex, ca. 1.1 times as long as wide. Frontal line not evident. Dorsal setae arranged approximately in five transverse rows. Clypeus: uniformly areolate, without finely areolate areas; a pair of transversally elongated, not-areolate areas along the labral margin; three pairs of setae on the anterior part, close to the median line. Labrum: margin slightly angled medially,

Figs 6–8. *Diphyonyx conjunctions* (Verhoeff, 1898), ♀, 33 mm long, from Geraki, Thrace, Greece; line drawings from the underside. 6 – labrum and maxillary complex; 7 – forcipular segment; 8 – last leg-bearing segment and terminal segments.
projecting backwards; a row of slender filaments and 1–2 tubercles at the mid-point (Figs 2, 6).

Antennae. Each antenna slender, ca. 3 times as long as the head. Articles slightly, gradually narrowing and shortening from article II, which is ca. 1.2 times as long as wide, to article XIII, which is ca. 0.9 times as long as wide. Article XIV sub-ovoid, ca. 2.1 times as long as wide. Setae gradually more dense and shorter from the basal articles to the distal ones. Apical sensilla ca. 12 µm long, spear-like, slender, narrowing quite abruptly from about the mid-length. Club-like sensilla ca. 10 µm long, only on article XIV, grouped on the distal parts of both the internal and external sides. Three longitudinal rows of propioceptive spine-like sensilla at the bases of articles: 3–4 sensilla in each row on articles II–V, 2–3 sensilla in each row on articles VII–IX, 1–2 sensilla in each row on articles XI–XIV; rows lacking on articles VI, X and XIV, where only a single, dorsal sensillum is present.

Mandible. A single pectinate lamella.

Maxillae I (Figs 2, 6). Coxosternum entire. Medial projections sub-triangular, longer than wide. Telopodite ca. 1.3 times as long as the medial projection, composed of two articles; tip rounded, covered with fine scales. Two pairs of lateral lappets, covered with scales, on the anterior corners of the coxosternum and basal articles of the telopodites, respectively.

Maxillae II (Figs 2, 6). Coxosternum entire, the anterior margin widely concave. Telopodite composed of three articles, gradually narrowing towards the tip; claw simple, pointed, slightly curved.

Forcipular segment (Figs 1, 7). Tergum subtrapezoid, the lateral margins evidently converging anteriorly, ca. 2.3 times as wide as long. Exposed part of the coxosternum ca. 1.4 times as wide as long; a pair of dark, stout tubercles on the anterior margin (Fig. 3); coxo-pleural sutures entirely ventral and strongly converging posteriorly; chitin-lines well marked, reaching the coxyles anteriorly. Basal article of the forcipule approximately as long as wide, the internal side shorter than the external side, without tubercles, only with two shallow bulges. Middle articles of the forcipule distinct, without tubercles, each only with a shallow bulge. Tarsungulum abruptly narrowing near the base, the distal part uniformly curved and narrowing; a basal, small tubercle; internal margin evidently crenulated (Fig. 4).

Leg-bearing segments. Tergum I wider than the subsequent one, the lateral margins slightly converging posteriorly; pretergum not exposed. Sternum I rounded anteriorly. Sterna from II to penultimate sub-rectangular; setae of various sizes, the longest arranged in two transverse rows; no trace of a “carphophagus” socket on the anterior margin, nor of a backward projection (condyle) on the posterior margin; no sternal pores. On the most anterior and most posterior segments, legs slender and claws slender, slightly curved and bearing two basal, tiny spines (spurs), one anterior to the other. From segment I to about XV, legs become gradually more swollen, the claws gradually larger, more swollen at the base and more evidently curved; the anterior spur becomes thicker and more elongate, and extends beyond the tip of the claw (Figs 9–10). From about segment XXV to about segment XXXV, legs, claws and spurs become gradually similar to those on the most anterior segments. Last leg-bearing segment (Fig. 8). Pretergum ca. 3.5 times as wide as long, without apparent sutures on its dorso-lateral sides. Tergum ca. 1.1 times as wide as long, the lateral margins evidently convex and converging posteriorly, the posterior margin truncate. Sternum ca. 1.5 times as wide as long, the posterior margin evidently rounded. Coxal glands grouped on the anterior part of each coxopleuron, most of them opening through a longitudinally elongate pouch, on the ventral side of the coxopleuron, close to the lateral margin of the sternum; the most posterior gland opening through an independent, large pore on the posterior part of the ventral side of the coxopleuron; no pores opening on the dorsal side (Fig. 5). Telopodite ca. 1.6 times as long and slightly more swollen than the preceding one; all articles covered with long, scattered setae; ventral side of the most basal articles covered with short, dense setae. Claw well developed, curved and pointed, with only one basal, postero-ventral, tiny spur.
### TABLE 1. Main diagnostic characters differentiating *Diphyonyx* gen. n. from all other genera tentatively recognised in the subgroup of Geophilidae to which *Diphyonyx* belongs. Genera in this subgroup have only slightly elongated head and forcipules, coxosternum of the second maxillae without chitinised ridges, sutures between forcipular coxosternum and pleurites evidently converging posteriorly, forcipular tergum not evidently narrower than the subsequent tergum. This subgroup corresponds roughly to the Geophilinae sensu Attems (1929), but also includes probably some genera originally placed in the poorly diagnosed family Sogonidae (see Crabill, 1961, 1968). Only genera considered valid in ChiloBase (Minelli, 2006) are included. Character states are for the type species only and, therefore, do not encompass the variation within each genus, as the circumscription of some genera remains uncertain.

| Genus                        | Type species                | Finely areolate areas on elyptes | Labrum mid-part | Anterior tubercles on forcipular coxosternum | Basal tubercle on forcipular tar-sungulum | Internal margin of forcipular tar-sungulum | “Carpophagus” sockets | Sternal pores | Anterior spur of legs on anterior trunk | Openings of coxal glands | Claw on last pair of legs |
|------------------------------|-----------------------------|----------------------------------|-----------------|---------------------------------------------|------------------------------------------|-------------------------------------------|-----------------------|--------------|---------------------------------------|---------------------------|-------------------------|
| *Diphyonyx* gen. n.         | *Geophilus conjungens*      | absent                           | tubercles       | complete                                    | present                                  | crenulated                                 | absent                | elongate     | one pouch                             | two pouches               | pointed                |
| *Abatons* Chamberlin, 1965   | *Abatorus allredi* Chamberlin, 1965 | absent?                          | tubercles       | complete                                    | absent                                   | ?                                         | absent?               | small?       | two pouches                           | small?                   | pointed                |
| *Acanthogeophilus* Minelli, 1982 | *Acanthogeophilus dentiger* Minelli, 1982 | absent                           | tubercles       | incomplete                                  | absent                                   | smooth                                    | absent                | smooth       | two pouches                           | rounded tubercle, with spines | pointed                |
| *Arenophils* Chamberlin, 1912 | *Geophilus alternatus unstar Chamberlin, 1909* | absent                           | tubercles       | incomplete                                  | absent                                   | smooth                                    | absent                | smooth       | two pouches                           | two pouches               | pointed                |
| *Bebekium* Verhoeff, 1941    | *Bebekium mirabile* Verhoeff, 1941 | absent                           | bare            | absent?                                     | absent                                   | ?                                         | ?                     | small?       | independent pores                     | tiny bristle              |                        |
| *Caliphils* Chamberlin, 1941 | *Caliphilus alakmedans* Chamberlin, 1941 | ?                               | tubercles       | incomplete                                  | absent                                   | ?                                         | ?                     | small?       | independent pores                     | a few pouches             | absent                  |
| *Clinopodes* C.L. Koch, 1847 | *Clinopodes flavids* C.L. Koch, 1847 | absent                           | skinder projections | complete                                  | present                                  | smooth                                    | absent                | small?       | independent pores                     | small?                   | pointed                |
| *Confilona* Chamberlin, 1941 | *Confilona sonigos Chamberlin, 1941* | ?                               | tubercles       | poorly developed                            | absent                                   | ?                                         | present               | small?       | independent pores                     | one pouch                 | pointed                |
| *Dysmosophilus* Verhoeff, 1938 | *Nhoxophils longisimus Verhoeff, 1938* | present                          | tubercles       | incomplete                                  | absent                                   | smooth                                    | absent                | small?       | two pouches                           | two pouches               | pointed                |
| *Dysmus* Chamberlin, 1944    | *Dysmus orites* Chamberlin, 1944 | absent                           | tubercles       | incomplete                                  | absent                                   | ?                                         | present               | small?       | independent pores                     | one pouch                 | pointed                |
| *Eremorus* Chamberlin, 1963  | *Eremorus becki* Chamberlin, 1963 | absent                           | tubercles       | (on plates)                                 | absent                                   | ?                                         | absent                | small?       | two pouches                           | one pouch                 | pointed                |
| *Eritihphils* Cook, 1899     | *Eritihphils neopum* Cook, 1899 | absent                           | tubercles       | ?                                          | absent                                   | ?                                         | present               | small?       | independent pores                     | tiny tubercle             |                        |
| *Eusygoophils* Verhoeff, 1899 | *Geophilus multistiliger* Verhoeff, 1899 | absent                           | tubercles       | not evident                                 | absent                                   | smooth                                    | absent                | small?       | one pore or pouch                     | absenct                  |                        |
| *Folkmanovius* Dobronruga, 1957 | *Folkmanovius paralelus Dobronruga, 1957* | absent                           | skinder projections | incomplete                                  | present                                  | smooth                                    | absent                | small?       | independent pores                     |                        |                        |
| *Galiiophils* Ribaut & Brölemann, 1927 | *Galiiophils beatonis Ribaut & Brölemann, 1927* | absent                          | tubercles       | complete                                    | absent                                   | crenulated                                | absent                | small?       | independent pores                     |                        |                        |
| *Geophilus* Leach, 1814      | *Sclopendera electrica* Limaeus, 1758 | absent                           | tubercles       | complete                                    | absent                                   | smooth                                    | present               | transversally elongate, posterior area | small?                   | pointed                |
| Genus | Type species | Finely areolar areas on Clypeus | Labrum Mid-part | Chitin-lines | Anterior tubercles on forcipular coxosternum | Basal tubercle on forcipular tar-sungulum | Internal margin of forcipular tar-sungulum | “Carpophagus” sockets | Sternal pores | Anterior spur of legs on anterior trunk | Openings of coxal glands | Claw on last pair of legs |
|-------|--------------|--------------------------------|-----------------|-------------|---------------------------------------------|--------------------------------------------|-------------------------------------------|----------------------|-----------------|------------------------------------------|--------------------------|-------------------------|
| Gospina Chamberlin, 1940 | Gospina hexata Chamberlin, 1940 | ? | ? | complete | absent | absent | ? | ? | transversally elongate, posterior area | small? | one pouch | rounded tubercle, with spines |
| Harmostela Chamberlin, 1941 | Harmostela hespera Chamberlin, 1941 | ? | tubercles | ? | absent? | present | ? | ? | absent | small? | two pores or pouches | long peg |
| Kurdistanius Verhoeff, 1941 | Kurdistanius kosswigii Verhoeff, 1941 | ? | tubercles | complete | absent | ? | ? | absent? | small? | independent pores | ? |
| Nannocrix Chamberlin, 1918 | Nannocrix porethus Chamberlin, 1918 | ? | ? | complete | absent | absent | ? | ? | absent? | small? | independent pores? | tiny tubercle |
| Nanhogeophilus Lewis, Jones & Keay, 1988 | Nanhogeophilus turki Lewis, Jones & Keay, 1988 | absent | tubercles | incomplete | absent | present | smooth | absent | small | one pouch | pointed |
| Photophilus Folkmanová, 1929 | Photophilus grisaeus Folkmanová, 1928 | absent? | tubercles | complete | absent | present | smooth | present | small | two-three pores or pouches | pointed |
| Plesurogeophilus Verhoeff, 1901 | Geophilus mediterraneus Meinert, 1870 | absent | slender projections (sometimes tubercles) | complete | absent | smooth | absent | rounded, posterior area | small | independent pores | absent |
| Serrona Chamberlin, 1941 | Serrona kernensis Chamberlin, 1941 | ? | tubercles | ? | absent | present | crenulated | ? | absent | small? | two pores or pouches | ? |
| Sogona Chamberlin, 1912 | Sogona minima Chamberlin, 1912 | ? | slender projections? | complete | absent | absent | ? | present | transversally elongate, posterior area | small? | two pouches | absent |
| Stenotaenia C.L. Koch, 1847 | Geophilus linearius C.L. Koch, 1835 | absent | slender projections | complete | absent | absent | smooth | absent | sub-ovoid, posterior area | small | two pouches | pointed |
| Synthophilus Chamberlin, 1946 | Synthophilus boreus Chamberlin, 1946 | absent? | tubercles | absent | absent | present | ? | ? | absent | small | independent pores | pointed |
| Tampiya Chamberlin, 1912 | Tampiya pylorus Chamberlin, 1912 | ? | tubercles | complete | present | absent | smooth? | ? | absent? | small? | independent pores | pointed |
| Taschkentia Verhoeff, 1930 | Taschkentia armata Verhoeff, 1930 | absent | tubercles | incomplete | absent? | present | smooth | absent? | different areas | small? | independent pores | pointed |
| Timpina Chamberlin, 1912 | Timpina texana Chamberlin, 1912 | ? | slender projections | complete? | absent | absent | smooth? | absent? | transversally elongate, posterior area | small? | one pouch | absent |
| Tuoba Chamberlin, 1920 | Tuoba cucicoe Chamberlin, 1920 | absent | tubercles | complete | absent | present | smooth | present | small | one pouch | pointed |
| Zygona Chamberlin, 1960 | Zygona duplex Chamberlin, 1960 | absent? | tubercles | ? | absent | absent | ? | absent? | small | two pouches | pointed |
Terminal segments (Fig. 8). Genital sternum inflated; gonopodal lamina uniformly curved, without an apparent median notch or sinuosity.

Last leg-bearing segment and terminal segments in the male (based on two adult males, 35 and 36 mm long, respectively, both with 75 leg-bearing segments, from the pass between Cankiri and Iltgaz, Anatolia, Turkey; see above, under “Material examined”). Telopodites of the last pair shorter than in the female and moderately swollen. Claws of the last pair relatively thin and about three times shorter than in the female (occasionally much smaller, as observed in 3 adult males out of 15 examined). Gonopodes biarticulate and well separated, a sub-conic medial projection between the gonopodes.

Geographical distribution. *D. conjungens* is recorded in the Balkan Peninsula between Macedonia and Thrace, throughout the entire Anatolia from the western coast and southern Sporades islands to the most eastern part of Turkish Armenia, northwards to the Pontic mountains and southwards to the Tauric mountains, and also in Crimea. See Fig. 11.

After the original record and description from Cilicia (Verhoeff, 1898), the same author recorded *D. conjungens* from Küçük Çekmece (Turkey, Istanbul Ili) (Verhoeff, 1941) and from Adana (Turkey, Adana Ili) (two specimens preserved in the Zoologisches Staatsammlung München, J. Spelda, pers. comm.; unpubl. record). The species is cited also from Crimea by Attems (1929). More recently, it was recorded from the islands of Kos, Karpathos and Ródos (Zapparoli 1994, 2002) and from different localities in Anatolia (Zapparoli, 1999; Misirlioglu, 2003).

*D. conjungens* is recorded here for the first time from the Balkan Peninsula, as well as other localities throughout Anatolia; furthermore, we confirm Attems’s record from Crimea after examination of the voucher specimen from Yalta (preserved in the Naturhistorisches Museum Wien, NHMV6507).

Variation in segment number. 69–81 leg-bearing segments recorded in females (n = 38), 67–79 leg-bearing segments

| Character                              | *D. conjungens* | *D. sukacevi* | *D. garutti* |
|----------------------------------------|-----------------|---------------|--------------|
| mid-part of labrum                     | 1–2 stout tubercles and 2–4 slender filaments | tubercles absent; 5–7 slender filaments | tubercles absent; 2–4 slender filaments |
| condyles between anterior trunk sterna | not evident     | evident       | evident      |
| single, isolated pore on each coxopleuron | present        | absent        | present      |
recorded in males (n = 15) (Fig. 12). No apparent geographic variation in segment number.

**Diphyonyx sukacevi** (Folkmanová, 1956) comb. n.

*Brachygeophilus sukacevi* Folkmanová, 1956: 1635 (original description), figs (1) 4–6.

*Brachygeophilus sukacevi* sukacevi: Folkmanová & Dobroruka, 1960: 1813.

*Brachygeophilus sukacevi*: Titova, 1969: 165.

**Diagnosis.** A *Diphyonyx* species with ca. 5–7 slender filaments but without tubercles on the labrum, with evident condyles between the sterna of the anterior part of the trunk, and without any isolated pores in addition to the anterior pouch on each coxopleuron.

Diagnosis is based on the original description only (Folkmanová, 1956).

Diagnostic characters of the *Diphyonyx* species are presented in Table 2.

**Type material.** Syntypes: 31 specimens: 6♀, 2♂, 23 juveniles, up to 45 mm long, with 65–81 pairs of legs (Folkmanová, 1956); repository unknown. The type material probably no longer exists.

Based on published information (Folkmanová, 1956), the specimens of the type series were given by M.S. Ghiharov (Laboratory of Soil Zoology of the Institute of Animal Morphology, USSR Academy of Sciences) to B. Folkmanová (at that time, at the Faculty of Science of the Masaryk University in Brno). At present, however, no specimen recognisable as belonging to such material is preserved in the Institute of Animal Morphology, Moscow, nor in the Zoological Museum of Moscow University where part of the collections of the former institute was transferred (A. Shielyko, pers. comm.), nor even in the Masaryk University in Brno, Czech Republic (K. Tajorovský, pers. comm.); further, specimens retained in the personal collection of L.J. Dobroruka are possibly lost (K. Tajorovský and I. Tuf, pers. comm.).

**Type localities.** All syntypes are from two localities: Erivanskaya, Tuapsinsk region, Chelepsinsk forest (Russia, Krasnodar Oblast); Imeni Frunze forest management unit (Russia, Rostov Oblast). The localities were given as “stanitsa Ehrivansikaia; Tuapsinskij rayon, Chelepsinskoe lesnichestvo” and “Manyutschki leszhov”, respectively (Folkmanová, 1956).

**Geographical distribution.** *D. sukacevi* is known from the most western part of the Caucasian range, north of the Black Sea, and from the Manyč valley, north of the Caucasus. See Fig. 11.

After the original description from two localities (Folkmanová, 1956), *D. sukacevi* has not been recorded again. Despite our examination of samples of geophilomorphs collected from both eastern Anatolia and the Caucasus, we have not found any specimen referable to this species.

**Variation in segment number.** 65–81 leg-bearing segments recorded (n = 31, including both males and females; Folkmanová, 1956).

**Diphyonyx garutti** (Folkmanová & Dobroruka, 1960) comb. n., stat. n.

*Brachygeophilus sukacevi* garutti Folkmanová & Dobroruka, 1960: 1813 (original description).

**Diagnosis.** A *Diphyonyx* species with ca. 2–4 slender filaments but without tubercles on the labrum, with evident condyles between the sterna of the anterior part of the trunk, and a posterior isolated pore in addition to the anterior pouch on each coxopleuron.

Diagnosis is based on the original description only (Folkmanová & Dobroruka, 1960).

Diagnostic characters of the *Diphyonyx* species are presented in Table 2.

**Type material.** Syntypes: 23 specimens: sex, body length and segment number unknown (Folkmanová & Dobroruka, 1960); repository unknown. The type material probably no longer exists.

Based on published information (Folkmanová & Dobroruka, 1960), the specimens of the type series were given by M.S. Ghiharov (Laboratory of Soil Zoology of the Institute of Animal Morphology, USSR Academy of Sciences) to B. Folkmanová and his student L.J. Dobroruka (at that time, at the Faculty of Science of the Masaryk University in Brno) and were deposited in the personal collection of L.J. Dobroruka. At present, however, specimens retained by L.J. Dobroruka are possibly lost (K. Tajorovský and I. Tuf, pers. comm.), whereas no specimen recognisable as belonging to this material is preserved in the Institute of Animal Morphology, Moscow, nor in Zoological Museum of Moscow University, where part of the collections of the former institute was transferred (A. Shielyko, pers. comm.), nor even in the Masaryk University in Brno, Czech Republic (K. Tajorovský, pers. comm.).

**Type locality.** All syntypes are from a locality between Goryachy Klyuch, Azov, Gendzhik and Mikhailovsky Pereval (Russia, Krasnodar Oblast). The locality was given as “mezhdju Goryachim Klyuchom, stanitsej Azovskoj, Gendzhikom i Mikhailovskim perevalom” (Folkmanová & Dobroruka, 1960).

**Geographical distribution.** *D. garutti* is known from the most western part of the Caucasian range, north of the Black Sea. See Fig. 11.

After the original description from the type locality (Folkmanová & Dobroruka, 1960), *D. garutti* has not been recorded again. An examination of samples of geophilomorphs collected from both eastern Anatolia and the Caucasus did not find any specimens referable to this species.

**Variation in segment number.** Unknown.

**DISCUSSION**

**Taxonomy**

When Verhoeff (1898) described *Geophilus conjungens*, he provided an incomplete account of its morphology. In particular, he completely omitted to describe the unusual shape of the claws. This is not surprising, however, as the walking legs were usually not seen to be of
diagnostic value in the systematics of geophilomorphs (but see Attems, 1959). Verhoeff did not discuss explicitly the taxonomic position of *G. conjungens* and referred the species to the large and ill-defined genus *Geophilus* Leach, 1814. Even though the species was recorded again (Attems, 1929; Verhoeff, 1941; Zapparoli, 1994, 1999, 2002; Misirlioglu, 2003), these contributions did not provide a better understanding of its morphology and taxonomic position. *G. conjungens* was either kept in *Geophilus*, according to the traditional broad concept of this genus, or moved to *Brachygeophilus*, a composite assemblage of geophilid species based mainly on the shared absence of sternal pores, most probably a homoplastic trait (Turcato et al., 1995; Foddai & Minelli, 2000).

*Brachygeophilus sukacevi* and its subspecies *garutti* are described in two rather obscure papers written in Russian (Folkmanová, 1956; Folkmanová & Dobroruka, 1960). No other specimens were subsequently referred to these taxa, which were almost completely ignored in the subsequent literature, so that their taxonomic position remained to be assessed. Indeed, Folkmanová (1956) commented on the similarity between *B. sukacevi* and *G. conjungens* and contrasted the two species in a comparative table. To date, however, these two species have not been recognised explicitly as taxonomically related.

After evaluating and integrating all the published information and evidence obtained by examination of representative specimens, it was found that *conjungens*, *sukacevi* and *garutti* are closely related taxa and deserve to be regarded as members of a distinct genus. They share a combination of morphological traits, which is unique to geophilid genera, including all nominal genera of uncertain identity. Among these traits are the general shape and pattern of tubercles on the forcipules and forcipular coxosternum, some features of the trunk sterna, the shape of the claws of the walking legs and the arrangement of coxal glands. A phylogenetic analysis is beyond the scope of this paper and its effectiveness would be limited by the inadequate knowledge available on some geophilid genera. However, *conjungens*, *sukacevi* and *garutti* constitute most probably a monophyletic group, as they share a unique, highly derived shape of claw. Other possible synapomorphies, which are found also in other lineages of geophilids but most probably originated independently, are the evident crenulation of the forcipular tarsungula, the lack of sternal pores and the aggregation of most coxal glands into a common pouch. Our proposal to give this lineage genus status is consistent with current practice in geophilomorph taxonomy, as it is based on characters that are usually given a highly diagnostic value at the genus level. Even though the phyletic position of this lineage relative to other geophilid genera is uncertain, no evidence points to a close relationship of *conjungens*, *sukacevi* and *garutti* with the type species of either *Geophilus* or *Brachygeophilus*, and therefore their inclusion in these two genera appear unjustified. Instead, distinguishing *Diphyonyx* from both *Geophilus* and *Brachygeophilus* contributes to a more appropriate circumscription of these two currently composite genera.

We assessed the morphology and geographical distribution of *D. conjungens* by examination of representative specimens from a wide region spanning from Greek Macedonia to Turkish Armenia. All these specimens were confidently placed in the single species *D. conjungens* as they all have the morphological traits described by Verhoeff (1898) as diagnostic for *G. conjungens*, but not the putative differential characters described by Folkmanová (1956) and Folkmanová & Dobroruka (1960) for either *B. sukacevi* or *B. sukacevi garutti*. In contrast, our taxonomic evaluation of both *D. sukacevi* and *D. garutti* is based on published accounts, because we were not able to locate the type specimens of these taxa (see remarks under “Type material” of both taxa), nor other specimens referable to them.

Putative differential characters between the three taxa *conjungens*, *sukacevi*, and *garutti* are the presence and number of tubercules and slender projections on the labrum, the presence vs. absence of evident condyles between the sterna on the anterior part of the trunk, and the presence vs. absence of an isolated coxal pore in addition to the common pouch (see Table 2). Worth noting is that Folkmanová (1956), relying on Verhoeff’s description of *G. conjungens*, cites the presence of two pairs of lappets on the first maxillae and the peculiar shape of the claws as distinguishing his *B. sukacevi* from *G. conjungens*; however, Verhoeff’s account is inaccurate on these points, as both traits in *D. conjungens* correspond to those described in *B. sukacevi*. Even though the actual morphological difference between *B. sukacevi*, *B. sukacevi garutti* and *G. conjungens* remains to be assessed, the available information appears to indicate that *B. sukacevi* and *B. sukacevi garutti* are taxonomically distinct from *G. conjungens*. Furthermore, even though *garutti* was originally described as a subspecies of *sukacevi* and this treatment was never disputed, *garutti* is given species rank here because (i) there is no evidence that *garutti* is more closely related to *sukacevi* than to *conjungens*, and (ii) the two putative subspecies were originally described from very close localities, only a few dozen kilometres apart, within a region lacking any apparent biogeographical barriers, so that an intraspecific differentiation appears unlikely.

Twelve other nominal species of geophilids, from either Anatolia or the western part of North America, are described under *Brachygeophilus* (Chamberlin, 1938, 1941, 1952). They are *B. anonyx* Chamberlin, 1941, *B. delotus* Chamberlin, 1941, *B. erzurumensis* Chamberlin, 1952, *B. eudontus* Chamberlin, 1952, *B. honozus* Chamberlin, 1952, *B. leionyx* Chamberlin, 1938, *B. mandsus* Chamberlin, 1952, *B. oregonus* Chamberlin, 1941, *B. orientis* Chamberlin, 1952, *B. simoporus* Chamberlin, 1952, *B. transitus* Chamberlin, 1941 and *B. yavapainus* Chamberlin, 1941. The original assignment of these species to *Brachygeophilus* was mainly based on the lack of sternal pores, a character shared with the type species *B. truncorum*; however, the true identity and taxonomic position of
these species remains to be assessed. After evaluation of all published information and examination of the type material of some of these species from Turkey (B. erzurumensis, B. eudontus, B. mundus; preserved at the National Museum of Natural History, Washington), it was concluded that none of these species should be included in Diphyonyx, even though the taxonomic position of most of them remains uncertain.

Morphology of the leg claws

In Diphyonyx, the shape of the pretarsus of the walking legs varies greatly along the trunk and, in particular, is highly modified in a series of about a dozen pairs of legs on the anterior half of the trunk. The shape of all other pairs conforms to that usually present along the whole trunk of other geophilids: the pretarsus bears a single claw, which is relatively slender and only slightly curved; two needle-like, straight spurs (also called accessory spines or parungues) emerge from the claw, on the ventral side, close to the basal articulation of the pretarsus, one anterior to the other; both spurs are evidently narrower and shorter than the claw and are similar to each other. Unlike in other geophilids, however, in Diphyonyx the shape of the pretarsus changes gradually but dramatically from both the most anterior and posterior segments towards those on the anterior half of the trunk: the claw increases in size, becoming more swollen and more evidently curved; the anterior spur becomes an approximately cylindrical projection, only slightly tapering, with rounded tip, and extends beyond the tip of the claw; the posterior spur, however, remains relatively small.

This peculiar shape and pattern of variation in the claws is most probably present in all specimens of all species of Diphyonyx of both sexes, and not only in adults but juveniles as well. Even though not previously described for D. conjungens, we found it in all 56 specimens examined of both sexes and different sizes. As for D. sukacevi and D. garutti, it was reported by Folkmanová (1956) in all of 31 specimens of Brachygeophilus sukacevi, and Folkmanová & Dobroruka (1960) in all of 23 specimens of Brachygeophilus sukacevi garutti.

The function of these peculiar claws remains unknown. We refrain from speculation, pending observations on living specimens and information on the ecology of Diphyonyx. Worth noting is that early records suggest D. conjungens is a littoral species (Verhoeff, 1941), but it was subsequently recorded at many inland sites, up to 1800 m (see above, under “Material examined”).

Even though a slight variation in the size and some minor morphological features of the walking legs along the trunk is common in geophilids, the highly derived shape of the claws observed in Diphyonyx is unprecedented in the family. Worth noting, however, is that a similar pattern of longitudinal variation, with a similar modified morphology of the claws, is documented for two other lineages of geophilomorphs, both of uncertain phylogenetic position but obviously only distantly related to Diphyonyx. One of these lineages comprises Neogeophilus Silvestri, 1918 and Evallogeophilus Silvestri, 1918, two strictly related genera traditionally recognised as belonging to a distinct family Neogeophilidae, which includes four species found only in Central America (Silvestri, 1918; Crabill, 1961, 1969). The other lineage comprises the single genus Eucratonyx Pocock, 1898, which is variously classified in distinct family Eucratonychidae or within the Gonibregmatidae, and includes two species found only in South-Eastern Asia (Pocock, 1891, 1898; Ribaut, 1912; Attems, 1914; Silvestri, 1919). In both these lineages, as in Diphyonyx, there is a longitudinal gradient in the overall enlargement of the claws and the hypertrophic growth of the anterior spur, with the centre in a sub-anterior region of the trunk. Worth noting is that the similarity between the claws of B. sukacevi and those of neogeophilids and Eucratonyx was noted by Folkmanová (1956), and Crabill (1969) proposed the term “fibulunguis” for this kind of biramous pretarsus. The modified pretarsi of the neogeophilids and Eucratonyx, however, differ from those of Diphyonyx in the overall shape of the additional projection and other features of the claw. The function of these pretarsi in Diphyonyx remains obscure, even though Crabill (1961, 1969) speculated that they function as anchoring devices in locomotion. In addition to these two lineages, where the pretarsi have been examined and illustrated in detail, modified claws were detected by Crabill (1961, 1969) in a few other genera, namely the himantariid Bothriogaster Selivanov, 1879, the schendylid Pectiniunguis Bollman, 1889 and the gonibregmatid Sagophagus Chamberlin, 1912, but their actual shape has not been described in detail.

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REFERENCES

ATTEMS C. 1903: Synopsis der Geophiliden. Zool. Jb. Syst. 18: 155–302.

ATTEMS C. 1914: Die indo-australischen Myriopoden. Arch. Naturg. (A) 80: 1–398.

ATTEMS C. 1929: Myriapoda I: Geophilomorpha. Das Tierreich 52. De Gruyter, Berlin and Leipzig, 388 pp.

ATTEMS C. 1947: Neue Geophilomorpha des Wiener Museums. Ann. Naturhist. Mus. Wien 55: 50–149.
