

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

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Key words. Chilopoda, Geophilomorpha, Geophilidae, *Diphyonyx*, new genus, *Diphyonyx conjungens*, morphology, taxonomy, geographical distribution

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* Brölemann, 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 on 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 Piante, Università della Tuscia, Viterbo, Italy; NA – Istituto di

RESULTS

Genus *Diphyonyx* 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 simple, pointed claws; forcipular coxosternum 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 *Diphyonyx* from all other genera tentatively recognised by us in the uniform subgroup of Geophilidae, to which *Diphyonyx* belongs (see legend of Table 1). Contrasting *Diphyonyx* with the two nominal genera to which the species of *Diphyonyx* have been hitherto referred, in both *Geophilus* Leach, 1814 [type species *G. electricus* (Linnaeus, 1758)] and *Brachygeophilus* Brölemann, 1909 [type species *B. truncorum* (Bergsøe & Meinert, 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 “diphyés” (= 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. The gender of *Diphyonyx* is masculine, as “ónyx, ónychos” is a masculine noun.

Included species. *Diphyonyx conjungens* (Verhoeff, 1898) [from *Geophilus*]; *Diphyonyx sukacevi* (Folkmanová, 1956) [from *Brachygeophilus*]; *Diphyonyx garutti* (Folkmanová & Dobroruka, 1960) [from *Brachygeophilus*]

Diphyonyx conjungens (Verhoeff, 1898) comb. n.

(Figs 1–10)

Geophilus (*Geophilus*) *conjungens* Verhoeff, 1898: 344 (key), 350 (original description), 360, figs 13–15. Attems, 1903: 219 (key), 224.

Brachygeophilus conjungens: Attems, 1929: 190 (key), 191 (description; new locality); 1947: 122 (key). Folkmanová, 1956: 1636. Zapparoli, 1993: 91, 95; 1994: 21 (new localities).

Geophilus conjungens: Verhoeff, 1940: 25; 1945: 329, 334. Weidner, 1960: 62. Moritz & Fischer, 1979: 340. Stoev,

1997: 103. Zapparoli, 1999: 134, 144 (new localities); 2002: 101 (new locality). Misirlioglu, 2003: 40 (new locality).

Geophilus (*Brachygeophilus*) *conjungens*: Verhoeff, 1941: 91 (new locality), 108.

Geophilus coniungens (sic): Chamberlin, 1952: 186.

Brachygeophilus coniungens (sic): Chamberlin, 1952: 200, 201.

Diagnosis. A *Diphyonyx* species up to 6 cm long, with a few stout tubercles on the mid-part of the labrum, slender filaments on both side-parts of the labrum, no 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.

Diagnostic characters of the *Diphyonyx* 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, microscope slide 3386a; 1♀, 55 mm long, with 71 pairs of legs, from “Kleinasien” (= Anatolia, Turkey), in the Museum für Naturkunde, Berlin, microscope slide 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 “Paratypoid”, from “Kleinasien”, is preserved in the Zoologisches Museum Hamburg (Weidner, 1960).

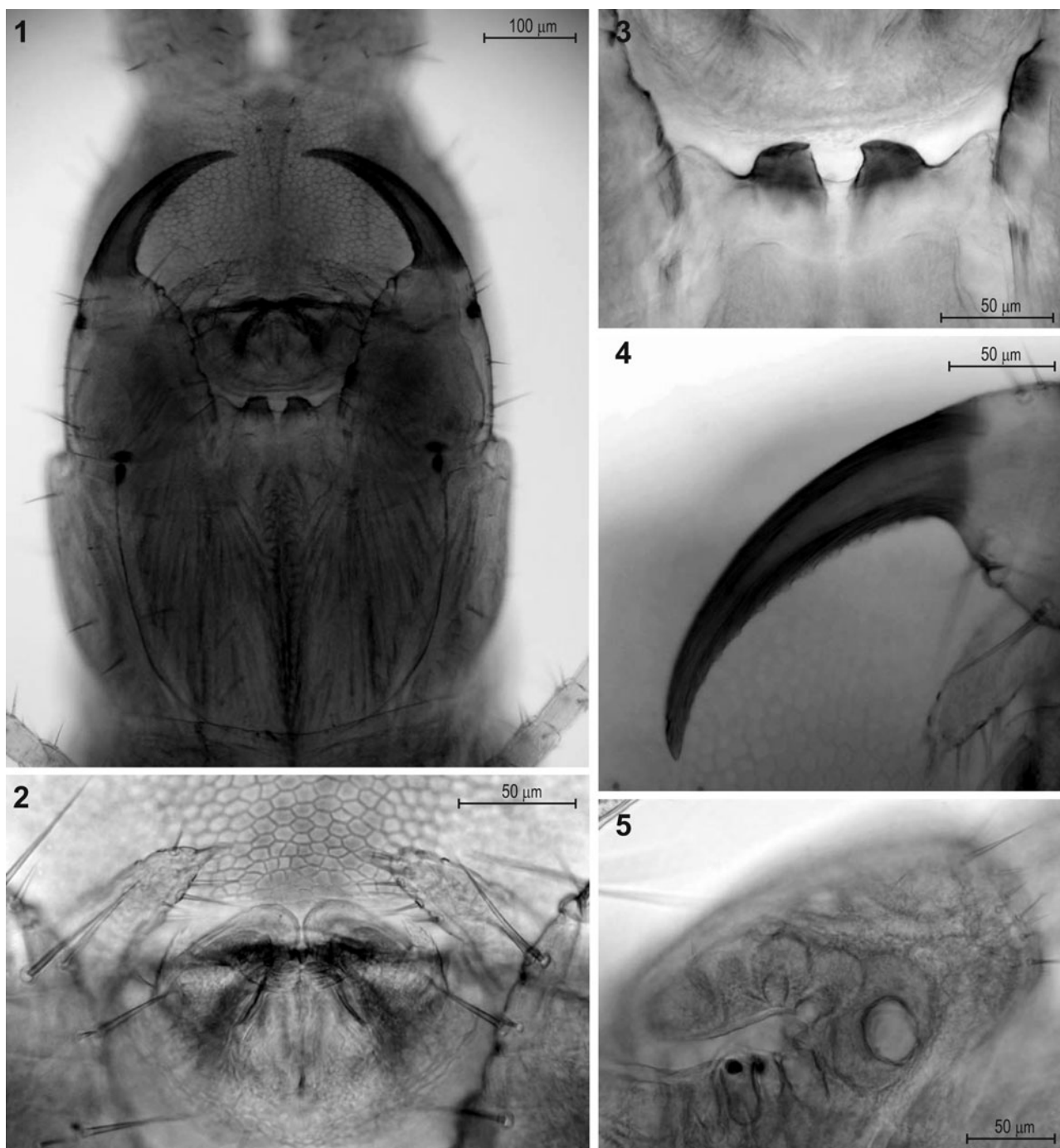
Type locality. Both syntypes are most probably from Cilicia (Turkey), but the precise localities are unknown.

Worth noting is that the type locality is given as “Cilicien, Kleinasien” by Verhoeff (1898) and the labels associated with the two syntypes indicate “Cilicien” and “Kleinasien”, respectively (Moritz & Fischer, 1979).

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. Etonti lgt, AM; Lekanis Mts, near Kavala, 1500 m, 1♀ (73), 4.vi.1983 G. Etonti lgt, AM. Nomos Piraïos: Asklepion, Kos island, 2♀ (75, 75), 23.iii.1989 M.A. Bologna lgt, 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 lgt, MZ (Zapparoli, 2002).

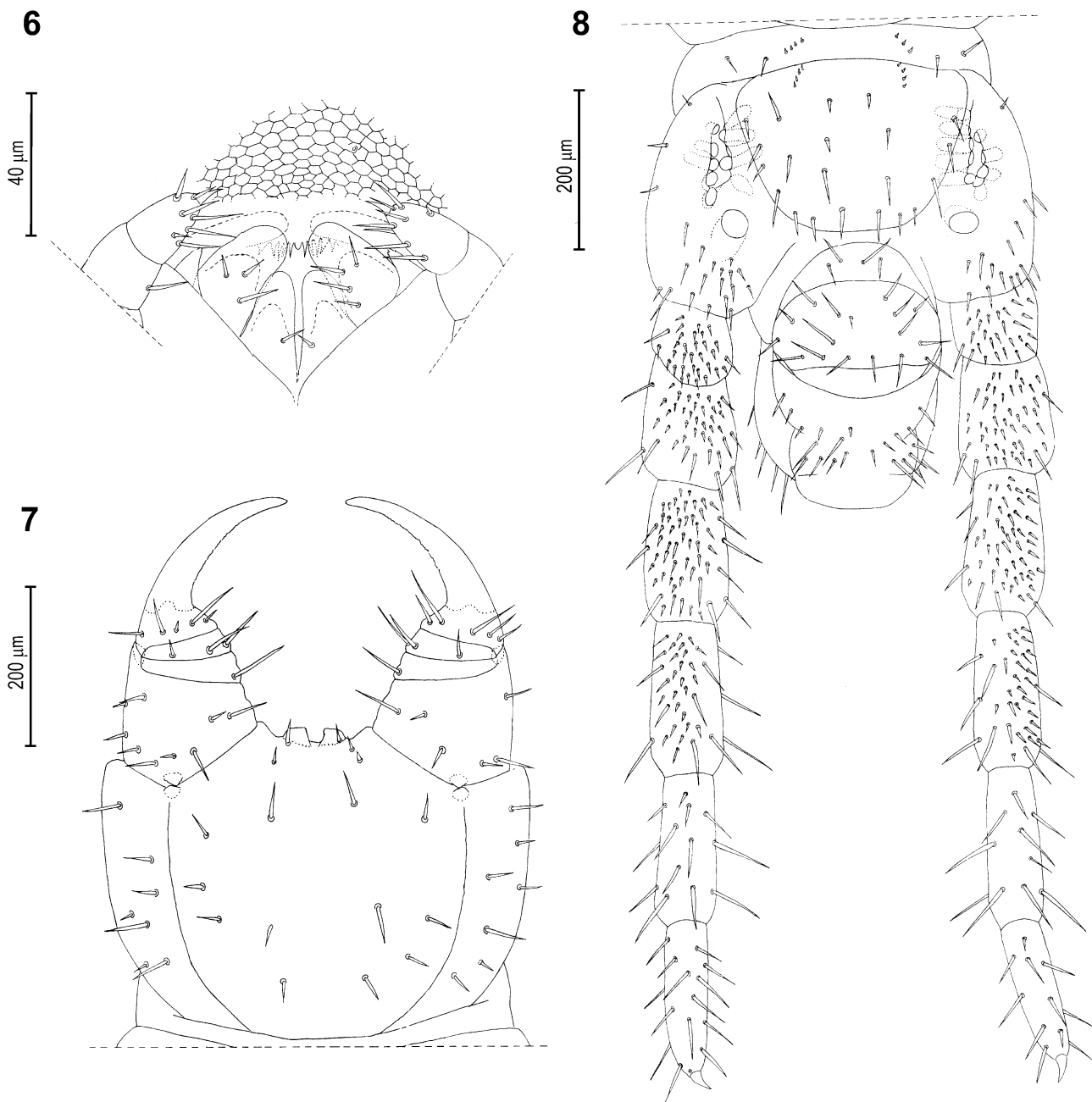
Turkey. Afyon Ili: Karakus Dağ, S Karaadilli, NW Eğridir Gölü, 1400 m, 1♀ (77), 3.v.1995 H. Enghoff, M. Frater & H. Read lgt, ZMUC. Agri Ili: 5 km E Tutak, 1600–1700 m, 1♀ (77), 22.v.1988 P.A. Audisio lgt, MZ. Antalya Ili: Gullukdağı-Termessos National Park, ca. 25 km NW Antalya, 900 m, 1♀ (75), 5.v.1995 H. Enghoff, M. Frater & H. Read lgt, ZMUC; İrmasan Geçidi, 1430–1525 m, 4♀ (all 75), 28.iv.1982 M. Zapparoli lgt, MZ; Korkuteli, 1♀ (75), 28.iv.1973 M. Di Rao lgt, MZ. Aydın Ili: Nazilli-Beydağ, 700 m, 1♀ (73), 6.v.1995 H. Enghoff, M. Frater & H. Read lgt, ZMUC. Balıkesir Ili: near Havran, 50 km from Balıkesir, 450 m, 2 exx., 23.iv.1982 A. Vigna Taglianti lgt, MZ. Beyşehir Ili: Lake of Beyşehir, Is. Hacı Akif, 1♀ (77) and 1 ex., 24.iv.1973 P. Brignoli lgt, MZ. Bilecik Ili: Muratdere, 800 m, 1♀ (81), 10.v.1991 M.A. Bologna lgt, MZ. Bursa Ili: 12–15 km N Bursa, 200 m, 1♀ (77), 12.v.1991 M. Zapparoli lgt, MZ; Keles-Egen, between Bursa and Tavşanlı, 1100 m, 2♂ (71, 71), 2.v.1995 H. Enghoff, M. Frater & H. Read



Figs 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.

lgt, ZMUC; Uludağ, 1350 m, 1♂ (71) and 1♀ (79), 11.v.1991 M. Zapparoli lgt, MZ; Uludağ, main road, 1300 m, 1♀ (79), 1/2.V.1995 H. Enghoff, M. Frater & H. Read lgt, ZMUC. Canakkale Ili: near Ayvacik, 350 m, 2♀ (71, 71), 23.iv.1982 M.A. Bologna lgt, MZ; Troya, 100 m, 1♀ (79), 3.v.1991 M. Zapparoli lgt, MZ. Cankiri Ili: Pass between Cankiri and Ilgtaz, 1300 m, 2♂ (75, 75) and 2♀ (75, 81), 3.v.1987 M. Zapparoli lgt, MZ. Denizli Ili: Honaz Dağ, W slope, 1500–1650 m, 1♂ (67), 5.v.1991 M. Zapparoli lgt, MZ. Eskisehir Ili: Eskisehir, near Porsuk Dam, 1♀ (79), 15.iv.2001, M. Karakaya lgt, MZ (Misirlioglu, 2003). Giresun Ili: near Canakci, 80 m, 1♂ (67) and 1♀ (71), 6.v.1987 M. Zapparoli lgt, MZ. Gumushane Ili:

Tersundagi Geçidi, S slope, 1500 m, 1♂ (75), 19.vi.1992 M. Zapparoli lgt, MZ; Zigana Geçidi, S slope, 1700 m, 1♀ (75), 19.vi.1992 M. Zapparoli lgt, MZ. Icel (= Mersin) Ili: above Arslankoy, 1700–1800 m, 1♀ (75), 17.v.1988 M. Zapparoli lgt, MZ; near Camliyayla, 1000–1200 m, 1♂ (67), 16.v.1988 M. Zapparoli lgt, MZ. Izmir Ili: Bergama-Yukaribey, 100 m, 1♀ (73), 8.v.1995 H. Enghoff, M. Frater & H. Read lgt, ZMUC; Bergama-Yukaribey, 650 m, 1♀ (73) 8.v.1995 H. Enghoff, M. Frater & H. Read lgt, ZMUC. Malatya Ili: 15 km S Balaban, near Malatya, 1800 m, 1♀ (81), 6.v.1983 M.A. Bologna lgt, MZ. Mugla Ili: between Korkuteli and Kemer, 32 km from Kemer, 1200 m, 1♀ (75), 30.iv.1982 M.A. Bologna lgt, MZ;



Figs 6–8. *Diphonyx conjungens* (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.

Bodrum, 1 ♀ (73), 3.xi.1919 R. Varriale lgt, MCSN. Mus Ili: Buglan Geçidi, E slope, 1500–1600 m, 1 ♀ (73), 24.v.1988 M. Zapparoli lgt, MZ. Ordu Ili: Gaga Gölü, near Camas, 60 m, 1 ♂ (67) and 1 ♀ (69), 13.v.1987 A. Vigna Taglianti lgt, MZ. Sivas Ili: Mazikaran Geçidi, 1800 m, 2 ♂ (75, 79) and 1 ♀ (81), 6.v.1993 M. Zapparoli lgt, MZ. Tokat Ili: 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 Ili: Cayozu, 30 km N Sarikaya, 1100 m, 1 ♀ (79), 8.v.1991 M. Zapparoli lgt, MZ.

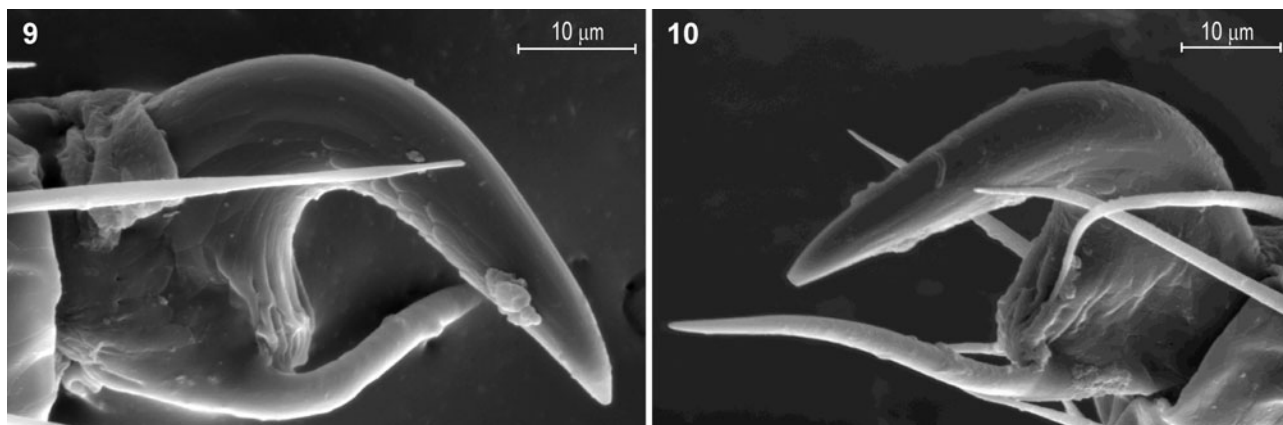
Ukraine. A. R. Krym: Yalta, 1 ♂ (73), 1907 L. Jägerskiöld lgt, NHMW (Attems, 1929).

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 9–10. *Diphyonyx conjungens* (Verhoeff, 1898), ♀, 33 mm long, from Geraki, Thrace, Greece; Environmental Scanning Electron Microscope (XL30 Philips, 15.0 kV) micrographs. 9 – claw of the left leg of the X leg-bearing segment, anterior side; 10 – claw of the right leg of the XXI leg-bearing segment, anterior side.

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 proprioceptive 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–XIII; 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); coxopleural sutures entirely ventral and strongly converging posteriorly; chitin-lines well marked, reaching the condyles 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. Intermediate 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 clypeus	Labrum mid-part	Chitin-lines	Anterior tubercles on forcipular coxosternum	Basal tubercle on forcipular coxosternum	Internal margin of forcipular tarsungulum	"Carpophagus" sockets	Sternal pores	Anterior spur of legs on anterior trunk	Openings of coxal glands	Claw on last pair of legs
<i>Diphyonyx</i> gen. n.	<i>Geophilus conjungens</i> Verhoeff, 1898	absent	tubercles	complete	present	present	crenulated	absent	absent	elongate	one pouch	pointed
<i>Abatorius</i> Chamberlin, 1965	<i>Abatorius allredii</i> Chamberlin, 1965	absent?	tubercles	complete	absent	absent	?	absent?	transversally elongate, posterior area	small?	two pouches	pointed
<i>Acanthogeophilus</i> Minelli, 1982	<i>Acanthogeophilus dentifer</i> Minelli, 1982	absent	tubercles	incomplete	absent	present	smooth	absent	transversally elongate, posterior area	small	independent pores	pointed
<i>Arenophilus</i> Chamberlin, 1912	<i>Geophilus attenuatus unaster</i> Chamberlin, 1909	absent	tubercles	incomplete	absent	present	smooth	absent	sub-ovoid, posterior area	small	two pouches	rounded tubercle, with spines
<i>Bebekium</i> Verhoeff, 1941	<i>Bebekium mirabile</i> Verhoeff, 1941	absent	bare	absent?	absent	absent	smooth	absent?	absent	small?	two pouches	pointed
<i>Caliphilus</i> Chamberlin, 1941	<i>Caliphilus alamedamus</i> Chamberlin, 1941	?	tubercles	incomplete	absent	absent	?	?	transversally elongate, posterior area	small?	independent pores	tiny bristle
<i>Clinopodes</i> C.L. Koch, 1847	<i>Clinopodes flavidus</i> C.L. Koch, 1847	absent	slender projections	complete	present	absent	smooth	absent	transversally elongate, posterior area	small	a few pouches	absent
<i>Condylona</i> Chamberlin, 1941	<i>Condylona sontipes</i> Chamberlin, 1941	?	tubercles	poorly developed	absent	absent	?	present	absent	small?	independent pores	pointed
<i>Dyodesmophilus</i> Verhoeff, 1938	<i>Nesogeophilus longissimus</i> Verhoeff, 1938	present	tubercles	incomplete	absent	absent	smooth	absent?	transversally elongate, posterior area	small?	two pouches	pointed
<i>Dysmesus</i> Chamberlin, 1944	<i>Dysmesus orites</i> Chamberlin, 1944	absent?	tubercles	incomplete	absent	present	?	absent?	absent	small?	independent pores	pointed
<i>Eremorius</i> Chamberlin, 1963	<i>Eremorius becki</i> Chamberlin, 1963	absent	tubercles (on plates)	incomplete	absent	absent	?	absent	absent	small?	one pouch	pointed
<i>Eriothophilus</i> Cook, 1899	<i>Eriothophilus neopus</i> Cook, 1899	absent	tubercles	?	absent	absent	?	present	transversally elongate, posterior area	small?	two pouches	pointed
<i>Eurygeophilus</i> Verhoeff, 1899	<i>Geophilus multistitiger</i> Verhoeff, 1899	absent	tubercles	not evident	absent	absent	smooth	absent	transversally elongate, posterior area	small	independent pores	pointed
<i>Folkmanovius</i> Dobronrka, 1957	<i>Folkmanovius paralielus</i> Dobronrka, 1957	absent	slender projections	incomplete	present	present	smooth	absent?	transversally elongate, posterior area	small?	one pore or pouch	tiny tubercle
<i>Galliophilus</i> Ribaut & Brölemann, 1927	<i>Galliophilus beatensis</i> Ribaut & Brölemann, 1927	absent	tubercles	complete	absent	present	crenulated	absent	absent	small	independent pores	absent
<i>Geophilus</i> Leach, 1814	<i>Scolopendra electrica</i> Linnaeus, 1758	absent	tubercles	complete	absent	present	smooth	present	transversally elongate, posterior area	small	independent pores	pointed

TABLE 1 continued.

Genus	Type species	Finely areolate areas on clypeus	Labrum mid-part	Chitin-lines	Anterior tubercles on forficular coxosternum	Basal tubercle on forficular tarsungulum	Internal margin of forficular tarsungulum	"Carpophagus" sockets	Sternal pores	Anterior spur of legs on anterior trunk	Openings of coxal glands	Claw on last pair of legs
<i>Gospina</i> Chamberlin, 1940	<i>Gospina bexara</i> Chamberlin, 1940	?	?	complete	absent	absent	?	?	transversally elongate, posterior area	small?	one pouch	rounded tubercle, with spines
<i>Harmostela</i> Chamberlin, 1941	<i>Harmostela hespera</i> Chamberlin, 1941	?	tubercles	?	absent?	present	?	?	absent	small?	two pores or pouches	long peg
<i>Kurdistanius</i> Verhoeff, 1941	<i>Kurdistanius kosswigii</i> Verhoeff, 1941	?	tubercles	complete	absent	?	?	absent?	transversally elongate, posterior area	small?	independent pores	?
<i>Nannocrix</i> Chamberlin, 1918	<i>Nannocrix porethus</i> Chamberlin, 1918	?	?	complete	absent	absent	?	absent?	two rounded, anterior areas; transversally elongate, posterior area	small?	independent pores?	tiny tubercle
<i>Nothogeophilus</i> Lewis, Jones & Keay, 1988	<i>Nothogeophilus turki</i> Lewis, Jones & Keay, 1988	absent	tubercles	incomplete	absent	present	smooth	absent	transversally elongate, posterior area	small	one pouch	pointed
<i>Photophilus</i> Folkmanová, 1929	<i>Photophilus griseus</i> Folkmanová, 1928	absent?	tubercles	complete	absent	present	smooth	present	transversally elongate, posterior area	small	two-three pores or pouches	pointed
<i>Pleurogeophilus</i> Verhoeff, 1901	<i>Geophilus mediterraneus</i> Meinert, 1870	absent	slender projections (sometimes tubercles)	complete	absent	absent	smooth	absent	rounded, posterior area	small	independent pores	absent
<i>Serrona</i> Chamberlin, 1941	<i>Serrona kerneris</i> Chamberlin, 1941	?	tubercles	?	absent	present	crenulated	?	absent	small?	two pores or pouches	?
<i>Sogona</i> Chamberlin, 1912	<i>Sogona minima</i> Chamberlin, 1912	?	slender projections?	complete	absent	absent	?	present	transversally elongate, posterior area	small?	two pouches	absent
<i>Stenotaenia</i> C.L. Koch, 1847	<i>Geophilus linearis</i> C.L. Koch, 1835	absent	slender projections	complete	absent	absent	smooth	absent	sub-ovoid, posterior area	small	two pouches	pointed
<i>Synthophilus</i> Chamberlin, 1946	<i>Synthophilus boreus</i> Chamberlin, 1946	absent?	tubercles	absent	absent	present	?	?	absent	small?	independent pores	pointed
<i>Tampiya</i> Chamberlin, 1912	<i>Tampiya pylorus</i> Chamberlin, 1912	?	tubercles	complete	present	absent	smooth?	?	absent?	small?	independent pores	stout
<i>Taschkentia</i> Verhoeff, 1930	<i>Taschkentia armata</i> Verhoeff, 1930	absent	tubercles	incomplete	absent?	present	smooth	absent?	different areas	small?	independent pores	pointed
<i>Timpina</i> Chamberlin, 1912	<i>Timpina texana</i> Chamberlin, 1912	?	slender projections	complete?	absent	absent	smooth?	absent?	transversally elongate, posterior area	small?	one pouch	absent
<i>Tuoba</i> Chamberlin, 1920	<i>Tuoba curiceps</i> Chamberlin, 1920	absent	tubercles	complete	absent	present	smooth	present	transversally elongate, posterior area	small	one pouch	pointed
<i>Zygona</i> Chamberlin, 1960	<i>Zygona duplex</i> Chamberlin, 1960	absent?	tubercles	?	absent	absent	?	absent?	absent	small?	two pouches	pointed

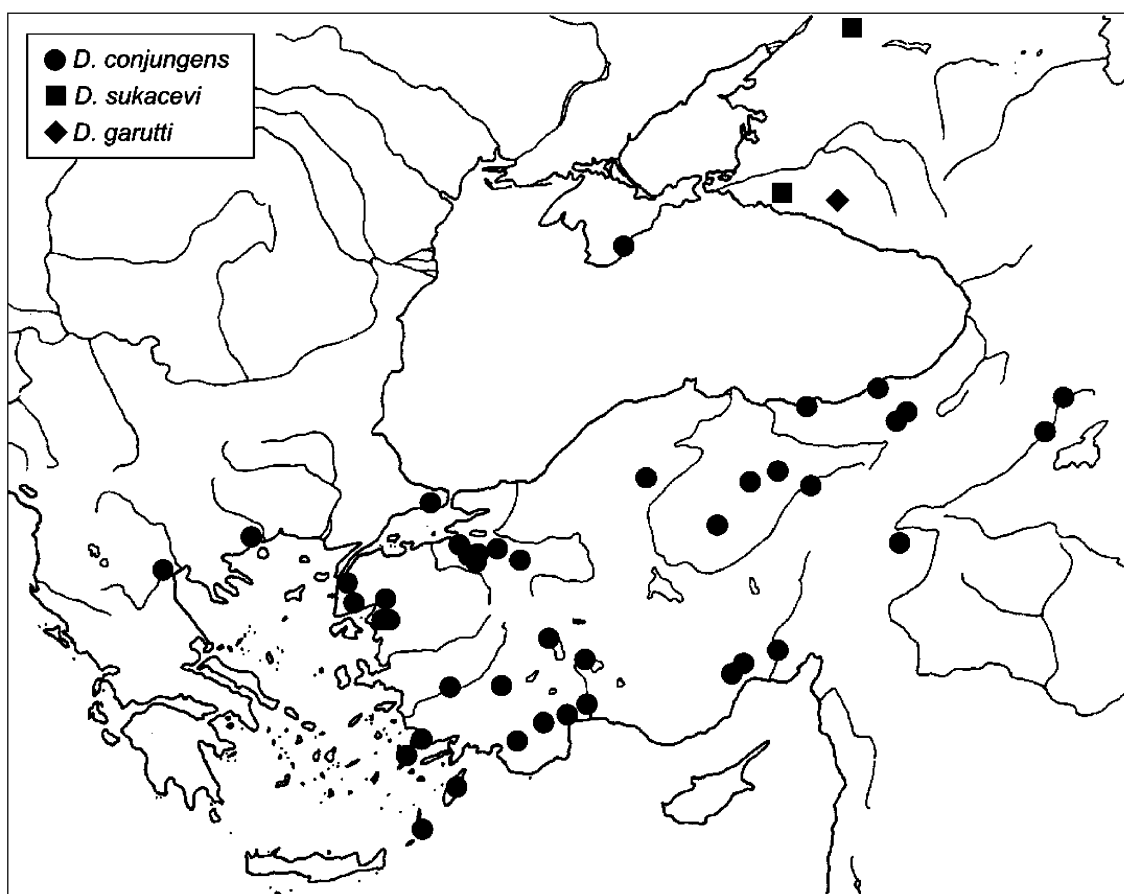


Fig. 11. Geographical distribution of the species of *Diphyonyx*.

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 Iltaz, 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, İstanbul İli) (Verhoeff, 1941) and from Adana (Turkey, Adana İli) (two specimens preserved in the Zoologisches Staatssammlung 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

TABLE 2. Putative diagnostic characters of the species included here in *Diphyonyx*. Data for *D. sukacevi* and *D. garutti* are based on the original descriptions.

Character	<i>D. conjungens</i>	<i>D. sukacevi</i>	<i>D. garutti</i>
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. Ghilarov (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. Shileyko, pers. comm.), nor even in the Masaryk University in Brno, Czech Republic (K. Tajovský, pers. comm.); further, specimens retained in the personal collection of L.J. Dobroruka are possibly lost (K. Tajovský and I. Tuf, pers. comm.).

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

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

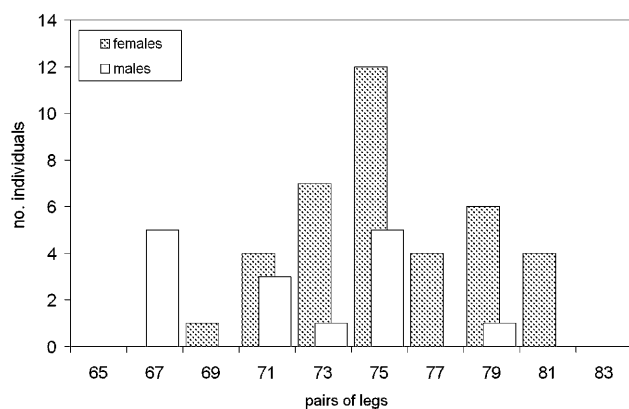


Fig. 12. Number of leg-bearing segments in *Diphyonyx conjugens* (Verhoeff, 1898), based on both published and unpublished data ($n = 53$).

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. Ghilarov (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. Tajovský 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. Shileyko, pers. comm.), nor even in the Masaryk University in Brno, Czech Republic (K. Tajovský, pers. comm.).

Type locality. All syntypes are from a locality between Goryachiy Klyuch, Azov, Gelendzhik and Mikhaylovskiy Pereval (Russia, Krasnodar Oblast). The locality was given as “mezhdú Goryachim Klyuchom, stanitsej Azovskoj, Gelendzhikom i Mikhajlovskim perevalom” (Folkmanová & Dobroruka, 1960).

Geographical distribution. *D. garutti* is known from the most western part of the Caucasus 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 conjugens*, 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 spreading 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 tubercles 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. mundus* 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 phyletic 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* Seliwanov, 1879, the schendylid *Pectiniunguis* Bollman, 1889 and the gonibregmatid *Sogophagus* Chamberlin, 1912, but their actual shape has not been described in detail.

ACKNOWLEDGEMENTS. We are grateful to J. Coddington and D. De Roche (National Museum of Natural History, Smithsonian Institution, Washington), H. Enghoff (ZMUC), R. Poggi (MCSN) and V. Stagl (NHMW) for allowing us to study specimens preserved in museum collections. We also thanks P.A. Audisio and A. Vigna Taglianti (Department of Animal and Human Biology, University "La Sapienza", Rome), M.A. Bologna, P. Brignoli and G.M. Carpaneto (Department of Biology, University of Roma Tre, Rome), M. Di Rao (Department of Biology, University of Tor Vergata, Rome), G. Etonti (Mestre, Italy) and K. Thaler † (Institute of Zoology and Limnology, University of Innsbruck, Innsbruck) for providing us with specimens. We are grateful to S.I. Golovatch (Institute for Problems of Ecology and Evolution, Russian Academy of Sciences, Moscow), A.A. Shileiko (Zoological Museum, Lomonosov State University, Moscow), J. Spelda (Bavarian State Collection of Zoology, Munich), K. Tajovský (Institute of Soil Biology, Biology Centre, Academy of Sciences of the Czech Republic, České Budějovice) and I. Tuf (Department of Ecology and Environmental Sciences, Palacký University, Olomouc) for sharing precious information about the repositories of type specimens or interpretation of Russian papers. We also thank M. Uliana for commenting on the manuscript.

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Received September 14, 2007; revised and accepted December 18, 2007