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**ONTOGENY, PHYLOGENY AND CHEMOECOLOGY OF PARENTAL
CARE IN SOME GEOPHILOMORPH CENTIPEDES (CHILOPODA:
GEOPHILOMORPHA)**

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**ONTOGENETSKA, FILOGENETSKA I HEMOEKOLOŠKA OBELEŽJA
BRIGE O POTOMSTVU KOD NEKIH GEOFILOMORFNIH
STONOGA (CHILOPODA: GEOPHILOMORPHA)**

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CONTENTS

| | Page |
|---|------|
| Abstract | 1 |
| Sažetak | 2 |
| Chapter 1. Introduction | 3 |
| Chapter 2. Materials and Methods | 11 |
| Experimental animals | 11 |
| Behavioural and comparative morphological analyses | 14 |
| Chemical analyses | 15 |
| Chapter 3. <i>Geophilus serbicus</i> Stojanović, Mitić and Antić, 2019 — new species | 17 |
| Chapter 4. Parental care in seven geophilomorph centipedes from Serbia | 27 |
| Chapter 5. Early development of <i>Geophilus serbicus</i> | 30 |
| Embryonic phase | 30 |
| Embryoid phase | 33 |
| Adolescens phase | 34 |
| Chapter 6. Chemistry of the defensive secretion of <i>Geophilus serbicus</i> | 37 |
| Chapter 7. Discussion | 38 |
| Chapter 8. Conclusions | 47 |
| Bibliography | 49 |

ABSTRACT

Parental care is a character that shows enormous diversity both within and between different animal taxa and is an important topic in evolutionary biology and behavioural ecology. In centipedes (Chilopoda), parental care includes relatively simple forms of care such as egg attendance and offspring attendance. As in most geophilomorphs, the females of *Geophilus serbicus* Stojanović, Mitić and Antić in Stojanović et al, 2019; *Henia illyrica* (Meinert, 1870); *Pleurogeophilus herzegowinensis* (Verhoeff, 1901); *Stenotaenia linearis* (C. L. Koch, 1835); *Stenotaenia rhodopensis* (Kaczmarek, 1970); *Strigamia herzegowinensis* (Verhoeff, 1935); and *Schendyla carniolensis* Verhoeff, 1902 are wrapped around the eggs or juveniles and have at least part of the trunk in an S-curve. Most of the trunk is orientated so that the dorsal side faces the brood and the ventral side faces outwards. This observation confirms the basal division of the Geophilomorpha into Placodesmata (to which only the family Mecistocephalidae belongs) and Adesmata, which corresponds to the anatomical differences between these groups, especially with regard to the absence or presence of ventral pores — the openings of the ventral glands. The dichloromethane extracts of the ventral gland secretion of *G. serbicus* contain three volatile compounds: benzaldehyde, methyl 2-phenylacetate and benzoyl cyanide. A species new to science (*G. serbicus*), the description of which is part of this dissertation, is clearly distinguished from its congeners by a unique combination of morphological characters. The early development of *G. serbicus* can be divided into three phases: embryonic (eight embryonic stadia), early postembryonic or embryoid (stadia proembryoid I, II and III, peripatoid and foetus) and adolescens (stadium adolescens I).

Key words: parental care, centipedes (Chilopoda), egg attendance, offspring attendance, *Geophilus serbicus*, early development, phylogeny, chemical defence.

Scientific field: Biology

Scientific subfield: Developmental biology of animals

S A Ž E T A K

Briga o potomstvu je ponašajni karakter koji pokazuje ogromnu raznovrsnost unutar i između različitih životinjskih taksona i predstavlja važnu temu u evolucionoj biologiji i ponašajnoj ekologiji. Kod stonoga iz klase Chilopoda, briga o potomstvu obuhvata relativno jednostavne oblike ponašanja kao što su briga o jajima i briga o mladima. Kao i kod većine geofilomorfa, ženke vrsta *Geophilus serbicus* Stojanović, Mitić i Antić u Stojanović et al., 2019; *Henia illyrica* (Meinert, 1870); *Pleurogeophilus herzegowinensis* (Verhoeff, 1901); *Stenotaenia linearis* (C. L. Koch, 1835); *Stenotaenia rhodopensis* (Kaczmarek, 1970); *Strigamia herzegowinensis* (Verhoeff, 1935); i *Schendyla carniolensis* Verhoeff, 1902 su sklupčane oko jaja ili mladih tako da im je bar deo trupa u obliku slova „S”. Najveći deo trupa je dorzalnom stranom okrenut ka leglu, a ventralnom stranom ka spolja. Ovo zapažanje potvrđuje bazalnu podelu Geophilomorpha na Placodesmata (obuhvata samo porodicu Mecistocephalidae) i Adesmata, što odgovara anatomskim razlikama između ovih grupa, posebno u pogledu odsustva ili prisustva ventralnih pora — otvora ventralnih žlezda. Dihlormetanski ekstrakt sekreta ventralnih žlezda vrste *G. serbicus* sadrži tri isparljiva jedinjenja: benzaldehid, metil 2-fenilacetat i benzoil cijanid. Nova vrsta za nauku (*G. serbicus*), čiji je opis deo ove disertacije, od bliskih srodnika se razlikuje po jedinstvenoj kombinaciji morfoloških karaktera. Rano razviće vrste *G. serbicus* može se podeliti u tri faze: embrionalnu (osam embrionalnih stadijuma), ranu postembrionalnu ili embrioidnu (stadijumi proembrioid I, II i III, peripatoid i fetus) i adolescens fazu (stadijum adolescens I).

Ključne reči: briga o potomstvu, Chilopoda, briga o jajima, briga o mladima, *Geophilus serbicus*, rano razviće, filogenija, hemijska odbrana.

Naučna oblast: biologija

Uža naučna oblast: biologija razvića životinja

CHAPTER 1. INTRODUCTION

Parental care is a character that shows enormous diversity both within and between different animal taxa and is an important topic in evolutionary biology and behavioural ecology (Trivers, 1972; Wilson, 1975; Clutton-Brock, 1991; Godfray, 1991, 1995; Westneat and Sherman, 1993; Mock and Parker, 1997; Martin, 2004; Smiseth et al., 2012; Smiseth, 2018; Fusco and Minelli, 2019). It can be defined as any parental trait that enhances the fitness of a parent's offspring and that seems likely to have originated and/or to be currently maintained for this function (Clutton-Brock, 1991; Smiseth et al., 2012; Smiseth, 2018; Fusco and Minelli, 2019). The simplest and probably most widespread form of care consists of the females supplying the eggs with additional nutrients over and above those required for successful fertilisation (Simmons and Parker, 1989; Williams, 1994; Heeb et al., 1998; Royle et al., 1999; Fox and Czesak, 2000; Hilker and Meiners, 2002; Ang et al., 2008; Boulinier and Staszewski, 2008; Groothuis and Schwabl, 2008; Smiseth et al., 2012; Smiseth, 2018). This can be illustrated using the example of the females of the seed beetle *Stator limbatus* (Horn, 1873) adjust the egg size to the environmental conditions in order to enhance the survival of the larvae after hatching (Smiseth, 2018). At the other extreme end, the parents of some mammals continue to care for their offspring even after they have reached adulthood. This form of care is extremely rare, but occurs in bonobos, where females support their adult male offspring in competition with rival males, thus enhancing their son's social status and mating success (Clutton-Brock, 1991; Surbeck et al., 2011; Smiseth et al., 2012; Smiseth, 2018). Between these two extremes, there are many other ways in which parents can enhance the fitness of their offspring (Melber and Schmidt, 1975; Smith, 1976; Hinton, 1977; Scot, 1980; Blumer, 1982; Forester, 1984; Diesel, 1989; Clutton-Brock, 1991; Smiseth et al., 2003, 2012; Field, 2005; Seibel et al., 2005; Blackburn, 2006; Rozen et al., 2008; Requena et al., 2009; Refsnider and Janzen, 2010; Kudo et al., 2011; Smiseth, 2018).

The terminology used to describe the diversity of parental care can sometimes be confusing, as alternative schemes are used for different taxa and the same form of care may go by different names in different taxonomic groups (Blumer, 1979; Clutton-Brock, 1991; Crump, 1995; Smiseth et al., 2012). Smiseth and associates (2012) have provided a general description of the basic forms of care observed in all animals in chronological order during the development of the offspring. The most common and phylogenetically most widespread form of postfertilisation parental care in various groups of invertebrates, fish and amphibians is egg attendance, which takes place in species where the parents remain with the eggs at a fixed location, usually the oviposition site. This form of care is often associated with behaviours directed towards specific threats, such as egg guarding (directed at predators or oophagic conspecifics), egg fanning (to prevent hypoxia) and egg cleaning (directed at fungal pathogens) (Melber and Schmidt, 1975; Hinton, 1977; Blumer, 1982; Forester, 1984; Crump, 1995; Green and McCormick, 2005; Costa, 2006; Requena et al., 2009; Kudo et al., 2011; Smiseth et al., 2012; Smiseth, 2018). On the other hand, egg brooding is a non-behavioural form of parental care in which the parents carry the eggs after laying either externally (parent's back) or internally (specialized pouches or parent's mouth) (Oppenheimer, 1970; Smith, 1976; Duellman and Maness, 1980; Seibel et al., 2005; Smiseth et al., 2012; Smiseth, 2018). Similarly, offspring attendance occurs in species where the parents stay with the young after hatching at a fixed location or escorting the offspring as they move around (Kok et al., 1989; Tallamy and Denno, 1981; Rozen et al., 2008; Smiseth et al., 2012; Smiseth, 2018), whereas offspring

brooding implies the carrying of young after hatching or birth, either externally or internally (Oppenheimer, 1970; Low, 1978; Tyler et al., 1983; Adiyodi and Adiyodi, 1989; Altmann and Samuels, 1992; Crump, 1995; Shaffer and Formanowicz, 1996; Smiseth et al., 2012; Smiseth, 2018). Egg and offspring brooding could offer some advantages over egg and offspring attendance to parents breeding in variable environments, as brooding allows parents to move more freely while caring for the eggs (Clutton-Brock, 1991; Smiseth et al., 2012; Smiseth, 2018).

Relatively little is known about why different taxa or species have evolved specific forms of care. This may reflect differences in the ecological conditions of a particular species and the specific hazards for the offspring (Weyrauch, 1927; Wilson, 1975; Smith, 1976; Tallamy, 1984; Tallamy and Wood, 1986; Wyatt, 1986; Armstrong and Shelton, 1990; Clutton-Brock, 1991; Filippi-Tsukamoto et al., 1995; Kohno, 1997; Nalepa and Bell, 1997; Lin et al., 2004; Mank et al., 2005; Suzuki et al., 2005; Estévez and Ribeiro, 2011; Gardner and Smiseth, 2011; Smiseth et al., 2012; Wong et al., 2013; Smiseth, 2018). For instance, selection might favor different forms of parental care when offspring are exposed to a high risk of predation (and/or drying and pathogen infections) as opposed to a high risk of starvation. In addition, the evolution of different forms of care in different species may also reflect differences in life histories and the presence of pre-existing characters that can be modified by selection into parental care (Smiseth et al., 2012). Thus, the risk of predation may favour parental care only if the parents are able to defend their offspring against predators, and it may be due to behaviours that males or females use to guard a territory or a partner (Clutton-Brock, 1991; Smiseth et al., 2012; Wong et al., 2013; Smiseth, 2018).

The extent to which females and males contribute to parental care after laying or birth varies both between and within higher animal taxa. As a rule, females are more involved in care than males (Maynard Smith, 1977; Clutton-Brock, 1991; Kokko and Jennionis, 2003, 2008; McDowall, 2003; Cockburn, 2006; Buzatto and Machado, 2009; Smiseth et al., 2012; Wong et al., 2013; Smiseth, 2018; Fusco and Minelli, 2019). In the vast majority of mammals, for instance, the females provide food in the form of milk and defend the young against predators after birth, while the males make no contribution whatsoever (Gittleman and Thompson, 1988; Hayssen, 1993; Vorbach et al., 2006; Balshine, 2012; Smiseth et al., 2012). Likewise in arthropods that take care of eggs or young in some way, it is usually only the female that provides care (Tallamy, 2001; Bonato and Minelli, 2002; Costa, 2006; Nazareth and Machado, 2010; Smiseth et al., 2012; Trumbo, 2012; Wong et al., 2013). However, there are also exceptions to this pattern. Firstly, it is relatively common in both fish and amphibians for only the males to care for eggs (Blumer, 1979; Gross and Sargent, 1985; Crump, 1996; Schulte et al., 2020; Vági et al., 2022). In sticklebacks, for instance, the males provide care by building nests and fanning the eggs to supply additional oxygen, and in African bullfrogs the males dig channels to adjacent pools to prevent the pool with their tadpoles from drying out. Secondly, in the vast majority of bird species, both parents work together to care for their joint offspring. In addition to these broad patterns, there are also differences in the involvement of males and females in care within individual taxa. Thus, although care patterns show a strong phylogenetic signal, they can change evolutionarily under the appropriate conditions (Smiseth et al., 2012; Smiseth, 2018).

Why is female-only care more common than male-only care? One possible explanation for this predominance could be found in anisogamy — the fact that females produce larger gametes than males (Trivers, 1972; Smiseth, 2018), but Kokko and Jennions (2008) suggested that anisogamy alone is not

sufficient to promote the evolution of sex role divergence and female-only parental care. On the other hand, Fromhage and Jennions (2016) suggested that biparental care is replaced by uniparental female or male care due to genetic drift or small differences in the costs or benefits of care. The same authors also predicted that strong sperm competition and/or strong sexual selection in males favours female-only care (Fromhage and Jennions, 2016). Male-only care is thus much rarer than female-only care (but see Smith, 1976; Blumer, 1979; Tallamy, 2001; Beal and Tallamy, 2006; Nazareth and Machado, 2010; Vági et al., 2022), and its evolution may be accompanied by the evolution of characters that ensure paternity, such as mate guarding and frequent copulation, ensuring that the benefits of caring are almost as high for males as for females (Trivers, 1972; Smiseth, 2018).

In the arthropod subphylum Myriapoda, parental care has been recorded in centipedes (class Chilopoda) and millipedes (class Diplopoda) (Minelli, 2011; Minelli and Michalik, 2015). Centipedes and millipedes are familiar arthropods, easily distinguished from all other terrestrial invertebrates by a specific body regionalisation, a body divided into just two tagmata, the cephalon and the long, homonomous and many-segmented trunk arranged with many pairs of articulated legs. Myriapods are gonochoristic and oviparous, although parthenogenesis occurs in several families of millipedes and in some centipedes, pauropods and symphylans. Many myriapods rely on indirect copulation and insemination (Brusca et al., 2016). In millipedes, egg-laying begins two weeks after copulation and can continue for several months (Banerjee, 1973; Snider, 1981; Dhaenens and VandenSpiegel, 2006). The eggs of most glomerids are protected in individual chambers made by the mother with faeces and/or soil particles (Tabacaru, 1963; Dohle, 1992). In spirobolids and at least some spirostreptids, the eggs are also protected by individual earthy capsules (Aouti, 1980; Nguyen Duy-Jacquemin, 1992). Nematophoran millipedes have spinnerets and use the silky secretion to produce egg chambers. The females of Chordeumatida use the secretion of their silk glands to produce a kind of loose cocoon that isolates the eggs from direct contact with the substrate like an air-filled cushion. The females of many polydesmidans use soil material passed through their gut, together with fecal pellets, to build a kind of earthy bell in which their often numerous eggs are protected; in some species, the chamber is provided with a ventilation chimney (Minelli and Michalik, 2015). However, many other polydesmidans lay their eggs loosely in the soil (Eaton, 1943; Murakami, 1966; Toye, 1967). In *Polydesmus angustus* Latzel, 1884, the female remains near the ‘bell’ until the young hatch and repairs any damage. True parental care is limited to the Colobognatha (Minelli and Michalik, 2015; Moritz et al., 2023). For example, the female of *Polyzonium germanicum* Brandt, 1837 remains curled up around the eggs until hatching, secreting a repellent substance that probably also acts as a biocide and prevents the eggs from rotting. Maternal brood care has also been observed in other Polyzoniida, Platydesmida and Polydesmida (Rimsky-Korsakow, 1895; Verhoeff, 1926–32; Silvestri, 1949; Murakami, 1962; Minelli, 1981; Enghoff, 1984). Paternal brood care has been observed in the andrognathid genus *Brachycybe* Wood, 1864 (Murakami, 1962; Gardner, 1975; Kudo et al., 2011; Wong et al., 2020) and *Yamasinaium noduligerum* Verhoeff, 1939 (Kudo et al., 2009), as well as in the pyrgodesmid genus *Cryptocorypha* Attems, 1907 (Kudo et al., 2014).

In centipedes, parental care includes relatively simple forms of care, especially in the basal groups. After fertilisation, the females of Scutigermorpha and Lithobiomorpha (i.e., the centipedes with the most obvious anamorphic postembryonic development) lay a number of eggs, one by one, without additional care for eggs after covering them with a secretion that cements the soil particles together

(Minelli, 2011). In the house centipede, *Scutigera coleoptrata* (Linnaeus, 1758), the egg covered by soil particles is eventually dropped into a crevice (Dohle, 1970), but sometimes simply abandoned on the surface or clustered into a ‘nest’ that eventually contains 7–10 eggs (Knoll, 1974). In the common stone centipede, *Lithobius forficatus* (Linnaeus, 1758), the female holds the egg between the genital valves for a long time and turns it constantly (Brocher, 1930). In the meantime, she retrieves fine-grained material from the substrate with the gonopods, which is finally glued to the surface of the egg, probably with the help of a secretion. After an hour of this behaviour, the egg is completely camouflaged, but the actual egg-laying does not take place until two or three hours later. In the meantime, the female remains inactive and continues to hold the egg. The soil capsule concealing the egg is almost spherical in *L. forficatus*, whereas in *Lithobius piceus* L. Koch, 1862 it is flattened like a poached egg (Demange, 1956). In the absence of guarding mother to protect them, the newly hatched Scutigermorpha and Lithobiomorpha must be active and able to feed and breathe through their tracheae, although the number of articulated trunk segments and appendages is still incomplete (Minelli, 2011). The adult number of segments and accompanying appendages is achieved through a series of moults of the first several early stadia (called anamorphs) during the anamorphic phase of postembryonic development (Stojanović et al., 2023).

Evolutionary transitions to more complex behaviours include attendance of eggs and offspring in *Craterostigmus* Pocock, 1902 (which hatches from the egg as a 12-legged stadium and acquires the adult number of 15 pairs of legs in the subsequent stadium), Scolopendromorpha and Geophilomorpha, with the latter two orders almost universally united in a group named Epimorpha due to their strictly epimorphic mode of development, i.e., having a fixed number of segments during the postembryonic development (Fernández et al., 2014). These centipedes lay all their eggs in a single clutch, inside a brood cavity in soil, decaying logs or under bark. The females then spend weeks in guarding, grooming and moistening clutches of eggs, hatchlings (which are still embryoid and rely on residual yolk from the anterior part of the body) and juveniles until they reach a sufficiently advanced stadium of development to fend for themselves (Minelli, 2011). The females of these groups are sensitive to disturbance while caring for the eggs and hatchlings, and they always react either by abandoning the brood, which then invariably perishes from desiccation or fungal infestation, or by devouring the eggs and hatchlings (filial cannibalism) (Brunhuber, 1970; Siriwt et al., 2014; Cabanillas et al., 2019). Two alternative postures are observed here: in *Craterostigmus* and all Scolopendromorpha in which guarding females have been observed, the mother rolls her body around the mass of eggs, hatchlings or young and presents her ventral surface to them (Manton, 1965; Brunhuber, 1970; Mitić et al., 2012, 2016, 2023; Siriwt et al., 2014; Vega Román et al., 2018), whereas in Geophilomorpha the opposite posture is generally observed (Bonato and Minelli, 2002; Chipman et al., 2004; Edgecombe et al., 2010; Knoflach, 2010; Mitić et al., 2010, 2016; Mitić, 2012; Stojanović et al., 2020a). Significantly, such behaviour is a valuable character for the phylogenetics and systematics of centipedes (Dohle, 1985; Bonato and Minelli, 2002; Edgecombe and Giribet, 2004; Fernández et al., 2014).

Egg-laying and guarding in geophilomorphs and scolopendromorphs of temperate regions takes place during the summer (Verhoeff, 1902–25; Palmén and Rantala, 1954; Weil, 1958; Vaitilingham, 1960; Lewis, 1959, 1961a, 1962; Minelli, 2011; Mitić, 2012; Stojanović, 2016). The minimum attending period that has been established to date is 18 days in *Scolopendra heros* Girard, 1853 (Iorio, 2003). Fecundity is not easy to determine in anamorphic centipedes, as their eggs are laid individually over a long period of time. In the laboratory, females of *S. coleoptrata* usually lay four eggs (but up to 20) per

day, with the highest number of 151 eggs recorded during the entire season (Knoll, 1974). A maximum of 30–40 eggs per season has been recorded for *Lithobius mutabilis* L. Koch, 1862 (Albert, 1983; Voigtländer, 2007), but the fecundity of larger lithobiomorphs may be higher. In some *Lithobius* Leach, 1814 species from temperate regions, eggs are laid in several periods during the year (Voigtländer, 2000).

In the epimorphic centipedes, the annual production of eggs is limited to one batch, the size of which can be easily determined. In the Scolopendromorpha, the numbers range from only 7–9 eggs in *Cryptops hyalinus* Hay, 1821 (Cornwell, 1934; Johnson, 1952) to 15–30 eggs in *Otostigmus tibialis* Brölemann, 1902 and *Scolopocryptops ferrugineus* (Linnaeus, 1767) (Bücherl, 1971), 15–23 eggs in *Scolopendra* Linnaeus, 1758 (Heymons, 1901), 25 in *Dinocryptops miersi* (Newport, 1845) (Machado and Chagas-Junior, 2002), 26 in *Ethmostigmus trigonopodus* (Leach, 1817) (Iorio and Ythier, 2007), 4–41 eggs in *Cryptops parisi* Brolemann, 1920 (Stojanović, 2016), up to 40 in *Cormocephalus multispinus* (Kraepelin, 1903) (Lawrence, 1947), 18–48 in *Cryptops schubarti* Bücherl, 1953 (Machado and Chagas-Junior, 2002), 15–58 in *Otostigmus scabricauda* (Humbert and Saussure, 1870) (Bücherl, 1971; Siritwut et al., 2014; Machado, 2000), 49–65 eggs in *Scolopocryptops sexspinosus* Say, 1821 (Auerbach, 1951) and up to 86 eggs in *Scolopendra morsitans* Linnaeus, 1758 (Lewis, 1970). Up to 47 eggs were found in broods of *Geophilus flavus* (De Geer, 1778) (Weil, 1958); 20–55 in those of *Pachymerium ferrugineum* (C. L. Koch, 1835) (Palmén and Rantala, 1954) and 13–87 in *Clinopodes flavidus* C. L. Koch, 1847 (Mitić et al., 2010; Mitić, 2012). On the other hand, the recorded brood size of *Craterostigmus tasmanianus* Pocock, 1902 ranges from 44–77 eggs (Mesibov, 1995).

Centipedes have the simplest kind of development — a direct development, with the juveniles hatching as 'miniature adults', although often with fewer body segments. On the other hand, indirect development, whether in echinoderms, insects or amphibians, is more complex in that the route to the adults takes what might be thought of as a 'detour' via immature stadia that are radically different from the adult as opposed to miniature versions of it (Arthur, 2011). In the class Chilopoda, two different developmental patterns are distinguished: anamorphosis (i.e. hemianamorphosis) and epimorphosis. Anamorphic centipedes (the orders Scutigleromorpha, Lithobiomorpha and Craterostigmomorpha) are characterised by an incomplete number of trunk segments in the specimens after hatching and the lack of extended care for their eggs and young (with the exception of two recent species of the order Craterostigmomorpha) (Edgecombe and Giribet, 2007). In contrast, Epimorpha (Scolopendromorpha and Geophilomorpha) form all segments during embryogenesis and hatch with the segment number of the adult. Eggs, hatchlings and early juveniles are surrounded by the mother's body and are absolutely dependent on her protection (Radl, 1992). The early development of Epimorpha comprises the brood-dependent developmental period, which can be divided into three phases: embryonic, embryoid and late postembryonic (Brena, 2014; Stojanović et al., 2015, 2020a). The largest and most significant developmental changes that lead to an adult-like appearance take place in the embryonic phase (Scholtz and Wolff, 2013). During this period, the fertilised egg is transformed in the chorion and undergoes cleavage, peripheral migration, gastrulation, segmentation and organogenesis, which leads to the establishment of the longitudinal body axis and the development of the individual body structures and segments. The end of the embryonic phase is marked by hatching (Brena and Akam, 2012). The following embryoid phase represents an extension of the embryonic phase outside the chorion (Brena 2014). This author recognised five embryonic stadia (proembryoid I, II and III; peripatoid; and foetus) in the development of the geophilomorph *Strigamia maritima* (Leach, 1817). The following stadium

(adolescens I) begins under attending conditions, but its extension as a brood-independent stadium is significantly longer (Lewis, 1959, 1961a; Stojanović, 2016; Stojanović et al., 2020b).

The number of publications dealing with the early development of the Chilopoda is not particularly large. From the earliest works (published in the second half of the nineteenth century) to the present day, studies on the earliest part of centipede development are mostly based on detailed descriptions of the developmental mechanism in individual species. Published reports on the embryogenesis of epimorphic centipede exist for the orders Scolopendromorpha (Heymons, 1901; Ivanov, 1940; Dawydoff, 1956; Whittington et al., 1991; Sakuma and Machida, 2002, 2004, 2005; Stojanović et al., 2015) and Geophilomorpha (Metschnikoff, 1875; Sograff, 1882; Chipman et al., 2004; Brena and Akam, 2012). Most significant reviews of centipede embryology are based on Heymons' (1901) description of the embryos of *Scolopendra*. Brena and Akam (2012) gave the best description of geophilomorph embryonic development using *S. maritima*. They recognised eight pre-hatching stadia and hatching as an intermediate stadium. Detailed descriptions of brood-dependent postembryonic development are only available for some epimorphic species. In the order Geophilomorpha (as well as in the study of embryonic development), *S. maritima* is again the most frequently studied model organism (Brena, 2014; Lewis, 1959, 1961a; Økland, 1984; Horneland and Meidell, 1986; Vedel et al., 2008, 2009, 2010; Vedel and Arthur, 2009). The first detailed description of the embryoid development of Geophilomorpha was published on *Dicellyphilus carniolensis* (Koch, 1847), where terms such as 'peripatoid' and 'foetus' were used for the first time (Verhoeff, 1902–1925). Since then, these terms have been widely accepted and used for geophilomorphs (e.g. Weil, 1958; Lewis, 1959, 1961a; Mitić et al., 2010; Mitić, 2012).

As can be seen from the above, the embryonic and early postembryonic development of Geophilomorpha has only been studied in very few species. With the exception of *S. maritima*, whose early development has been described in detail using specimens under natural and laboratory conditions, we have only fragmentary information about this part of development in all other cases. This means that it is difficult to compare different taxa of this order with each other. The species *S. maritima* has become a model organism mainly thanks to the collection of large samples from one population (localities known from England and Scotland; see Lewis, 1959, 1961a; Chipman, et al. 2004; Brena and Akam, 2012). In the case of other species of Geophilomorpha, the small number of collected females with broods per species means a low probability of the presence of all developmental stadia among the collected broods and the inability to document all early development.

Invertebrates, especially arthropods, synthesise an incredible variety of secondary metabolites in their exocrine glands (e.g. Blum, 1981, 1987, 2009; Pasteels and Gregoire, 1983; Pawlik, 1993; Berenbaum, 1995; Eisner et al., 2004; Zagrobelny et al., 2008, 2018; Clucas, 2010; Vujisić et al., 2013; Dettner, 2015; Shear, 2015; Brückner et al., 2017). Many of these compounds are unique natural products whose known distribution in arthropods is often limited to a few species (Blum, 1981). These chemicals probably contributed to the dominance of arthropods, which account for about 81.5 % of all living animal species described to date (Meinwald and Eisner, 1995; Brusca et al., 2016). Within myriapods, millipedes synthesise alkaloids, quinones, phenols and cyanogenic compounds (Eisner et al., 1978; Ōmura et al., 2002; Makarov et al., 2010, 2011, 2012, 2017; Vujisić et al., 2011; Makarov, 2015; Shear, 2015; Stanković et al., 2016; Bodner et al., 2024), while centipedes are known to produce lethal venom consisting of protein and non-protein compounds (Undheim and King, 2011) in aggregated epidermal

glands located in the forcipules (maxillipedes) (Rosenberg et al., 2011; von Byern et al., 2017). Most geophilomorph centipedes studied so far also produce cyanogenic and non-cyanogenic compounds and release them together with a viscous proteinaceous secretion from the ventral glands (Schildknecht et al., 1968; Jones et al., 1976; Vujisić et al., 2013; Mitić et al., 2024), which consist of numerous glandular units that open on the ventral surface via a pore within a clearly defined pore field (Turcato and Minelli, 1990; Turcato et al., 1995; Rosenberg et al., 2011; von Byern et al., 2017). In *Himantarium gabrielis* (Linnaeus, 1767), the defensive secretion consists of hydrogen cyanide (HCN), benzaldehyde, benzoyl cyanide, benzyl nitrile, mandelonitrile, mandelonitrile benzoate, 3,7,6O-trimethylguanidine (himantarine), farnesyl 2,3-dihydrofarnesoate, farnesyl farnesoate and one major protein with a molecular weight of 55 kDa (Vujisić et al., 2013), while in *C. flavidus* it contains eight compounds: 2-methylpentanoic acid, benzaldehyde, benzoyl cyanide, 2-methyl branched C-9 carboxylic acid (tentatively identified as 2-methyloctanoic acid), methyl 2-phenylacetate, benzoic acid, mandelonitrile, HCN and four major proteins with a molecular weight of 150, 66.2, 59 and 55 kDa (Mitić et al., 2024). *Henia vesuviana* (Newport, 1845) is currently the only geophilomorph species known to contain only proteinaceous glue in its ventral gland secretions (Hopkin and Gaywood, 1987; Hopkin et al., 1990). The defensive secretions have also been reported in the lithobiomorph centipede *L. forficatus*, associated with telopodal glandular organs from the posterior legs (Schendel et al., 2024), as well as in the undescribed scolopendromorph *Asanada* Meinert, 1886 from Sri Lanka (HCN, an unknown carbonyl compound and protein), associated with unicellular glands distributed over the legs and the entire body (from the second to the last body segment) (Maschwitz et al., 1979).

In this study we present a new species of the genus *Geophilus* Leach, 1814 from eastern Serbia. The genus *Geophilus* is one of the largest and best known centipede groups in the family Geophilidae with about 140 species, most of which are distributed in the Northern Hemisphere (Bonato et al., 2016). However, it must be emphasised that the taxonomic relationships between the species are still unclear and many of the nominal species are insufficiently known in terms of their morphology and deserve confirmation of their validity, so that even the monophyly of the genus is called into question. Crabill (1954) designated the genus *Geophilus* as ‘one of the hallmarks of the Holarctic Chilopoda’, whose representatives can be found in almost any habitat suitable for geophilomorph centipedes. According to a revision of the Geophilomorpha in Europe (Bonato and Minelli, 2014), in which a recently described species was added (Stoev et al., 2015), the total number of European *Geophilus* species known to date was 50. Here we also present the first evidence of parental care in seven geophilomorph centipedes from Serbia: *Geophilus serbicus* Stojanović, Mitić and Antić, 2019; *Henia illyrica* (Meinert, 1870); *Pleurogeophilus herzegowinensis* (Verhoeff, 1901); *Stenotaenia linearis* (C. L. Koch, 1835); *Stenotaenia rhodopensis* (Kaczmarek, 1970); *Strigamia herzegowinensis* (Verhoeff, 1935); and *Schendyla carniolensis* Verhoeff, 1902. In addition, we describe all brood-dependent stadia of *G. serbicus*, based on a large sample from a single population. For each stadium, we give a brief morphological description, as well as meristic and morphometric values for important body characters. We also provide comparative data for some external morphological characters between young and their mothers in *S. rhodopensis* to clarify changes in taxonomic characters during early postembryonic development and discuss factors that have favoured the evolution of parental care in centipedes. Finally, in this study we asked: What is the chemical composition of the secretion of the endemic *G. serbicus*?

The results of this dissertation were presented in the articles Mitić et al. (2016), Stojanović et al. (2019, 2020a) and Gedged et al. (2024), the last of which has been accepted for publication but not yet published.

CHAPTER 2. MATERIALS AND METHODS

Experimental animals

The holotype male of *G. serbicus* (IZB ChG001) was collected on 20 July 2013 in Babin Zub (Stara Planina Mountains) in eastern Serbia (43°22.262'N; 22°36.532'E) (Fig. 1), at an altitude of about 1580 m, under stone, *Fagetum moesiace montanum*, D. Stojanović, I. Stojanović and K. Stojanović legit. Two paratype males (IZB ChG002 and IZB ChG003) and four paratype females (IZB ChG004–IZB ChG007) of *G. serbicus* were also collected in Babin Zub: one male and one female were collected under stones on 21 June 2013, *Fagetum moesiace montanum*, D. Stojanović and K. Stojanović legit, while one male and three females were collected on 20 July 2013 under stones, *Fagetum moesiace montanum*, D. Stojanović, I. Stojanović and K. Stojanović legit.

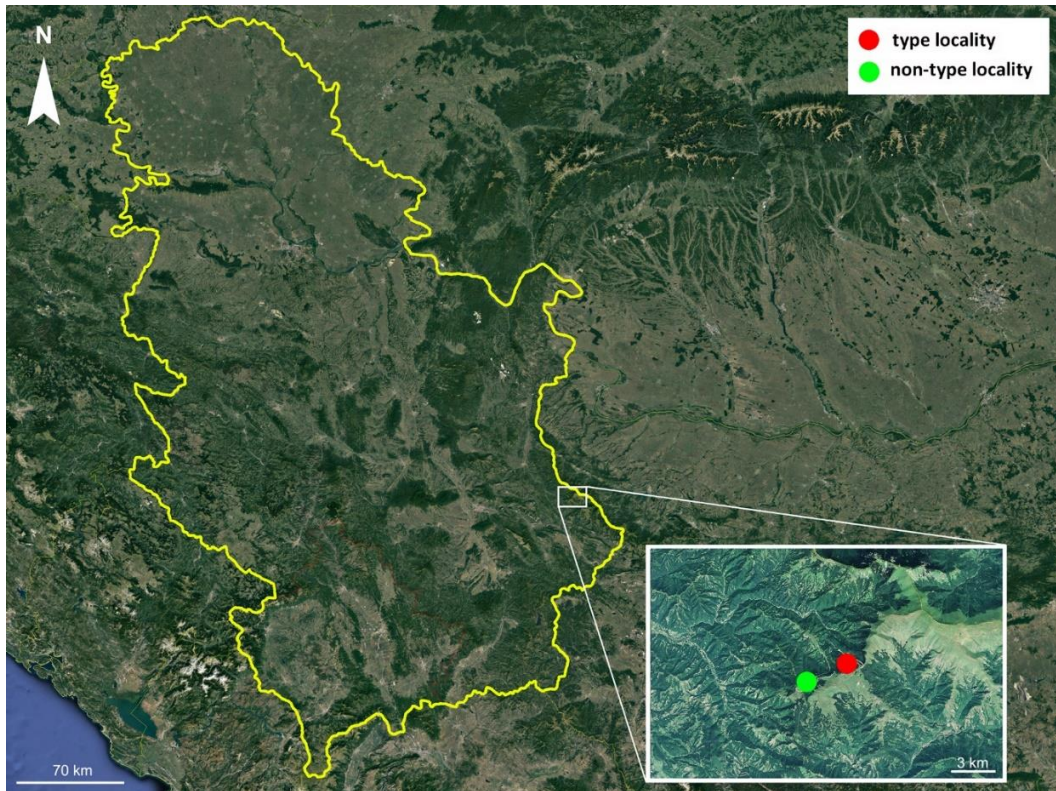


Fig. 1. Type and non-type localities of *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 sp. nov. in the Stara Planina Mountains in eastern Serbia.

Additional non-type material of *G. serbicus*, 23 males (nine specimens in the last adolescens stadium) and 93 females (of which 82 females with brood, nine without brood and only four adolescens specimens) (IZB ChG008–IZB ChG123) were collected in Babin Zub (Stara Planina Mountains), *Fagetum moesiace montanum*, in leaf litter, under stones and rotten stumps: two males, eight females, 21 June 2013, D. Stojanović and K. Stojanović legit; five males, 15 females, 6 July 2013, D. Stojanović, I. Stojanović and I. Stojanović legit; five males, 16 females, 20 July 2013, D. Stojanović, I. Stojanović and K. Stojanović legit; four males, 15 females, 3 August 2013, D. Stojanović, K. Stojanović, A. Petrović

and J. Petrović *legit*; four males, 17 females, 16 August 2013, D. Stojanović, I. Stojanović and K. Stojanović *legit*; three males, 11 females, 10 July 2014, D. Stojanović, N. Zukanović and D. Antić *legit*; and 11 females, 15 June 2016., D. Stojanović, D. Antić and S. Makarov *legit*. Two more females (IZB ChG124 and IZB ChG125) were collected on 19 June 2013 in Jabučko Ravnište (Stara Planina Mountains) (43°21.724'N; 22°35.008'E), at an altitude of about 1490 m, under stones, *Fagetum moesiace montanum*, D. Stojanović, K. Stojanović, M. Kučinić and M. Živić *legit*. The non-type material is only used to obtain data on the variability of the number of leg-bearing segments, the number of coxal pores on the coxopleura of the ultimate leg-bearing segments and the total length of the specimens.

Furthermore, two broods of *H. illyrica* (Kulina, Mt Medvednik, western Serbia, 7 August 2011; 44°12.554'N; 19°39.471'E) (Fig. 2A), six broods of *P. herzegowinensis* (Kulina, Mt Medvednik, western Serbia, 11–13 August 2011; 44°12.550'N; 19°39.460'E), one brood of *S. linearis* (Jabučko Ravnište, Stara Planina Mountains, eastern Serbia, 19 June 2013; 43°21.437'N; 22°34.598E), nine broods of *S. rhodopensis* (Babin Zub, Stara Planina Mountains, eastern Serbia, mid-June to mid-August, 2013–2016; 43°22.262'N; 22°36.532'E) (Fig. 3B), one brood of *S. herzegowinensis* (Samokovska Reka, Mt Kopaonik, southern Serbia, 8 July 2012; 43°18.225'N; 20°47.401'E) (Fig. 2B) and eight broods of *S. carniolensis* (Mt Medvednik, western Serbia, 6–11 August 2011; 44°13.212'N; 19°39.321'E) were sampled by D. Stojanović and D. Antić in a phase of the breeding season chosen to maximise the probability of collecting broods.

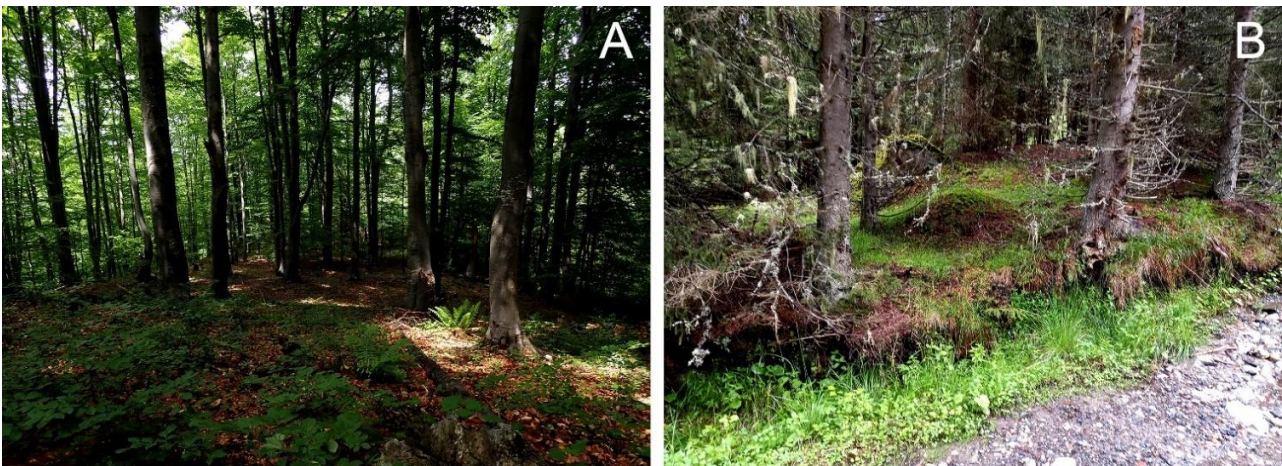


Fig. 2. Other collecting localities. A — Kulina, Mt Medvednik, the locality of *Henia illyrica* (Meinert, 1870), *Pleurogeophilus herzegowinensis* (Verhoeff, 1901) and *Schendyla carniolensis* Verhoeff, 1902; B — Samokovska Reka, Mt Kopaonik, the locality of *Strigamia herzegowinensis* (Verhoeff, 1935). Photographs by D. Antić and D. Stojanović.

The collected specimens were analysed using light microscopy and standard methods for clearing, temporary mounting and dissecting the mouthparts of geophilomorph centipedes (Foddai et al., 2002). The identification of *P. herzegowinensis* is based on the diagnostic characters of Verhoeff (1901) and Attems (1959) as well as on the type specimen (Fig. 4) from the slide collection of the Naturkundemuseum Berlin. The identification of *S. rhodopensis* (Fig. 5) was based on the diagnostic characters given by Kaczmarek (1970), Dányi (2010) and Bonato et al. (2014). In addition, identification of *S. herzegowinensis* is based on the diagnostic characters displayed by Verhoeff (1935), Dobroruka

(1977) and Bonato et al. (2012). The photographs of the egg and foetus stadium and the sterna were taken using a Nikon DS-Fi2 camera with a Nikon DS-L3 camera controller attached to a Nikon SMZ 1270 binocular stereomicroscope, and with a Canon PowerShot A80 digital camera connected to an Axioscope 40 microscope. Individual broods were preserved in labelled plastic vials with 70% ethanol. The material is deposited in the collection of the Institute of Zoology of the University of Belgrade – Faculty of Biology (IZB collection).

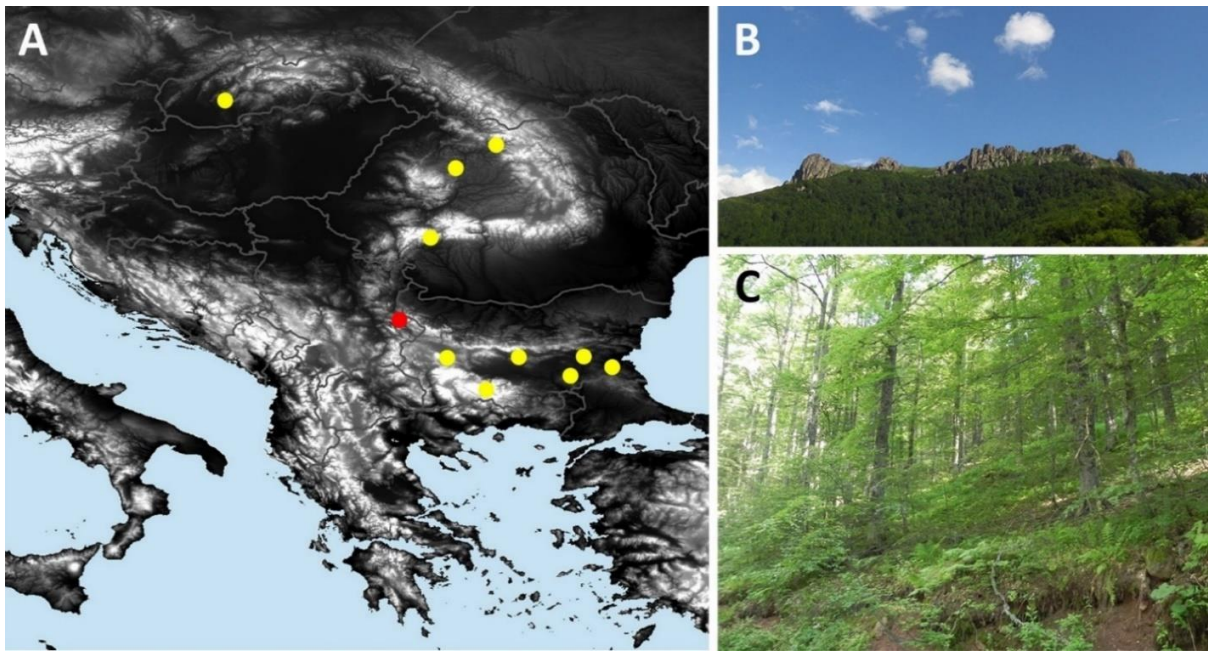


Fig. 3. Geography and ecology of *Stenotaenia rhodopensis* (Kaczmarek, 1970). A — Distribution in Slovakia, Romania, Bulgaria (yellow dots) and Serbia (red dot); B — Mountain peak Babin Zub on the Stara Planina Mountains; C — The sampling site, old mountain beech forests (*Fagetum moesiacaе montanum*). Photographs by D. Stojanović.



Fig. 4. The type specimen of *Pleurogeophilus herzegowinensis* (Verhoeff, 1901) from the slide collection of the Naturkundemuseum Berlin. A, C — dorsal habitus; B, D — ventral habitus. Photograph by B. Mitić.

Behavioural and comparative morphological analyses

Each collected brood and each specimen of the examined geophilomorphs is preserved in a single labelled plastic vial containing 70% ethanol. In the field and before conservation, the females and offspring were photographed and some of their behavioural characters (such as the position of the female's body in relation to the offspring, the conditions under which the females leave their brood, and the type and frequency of the hatchlings' movements) were recorded. The material was analysed using a Nikon SMZ 745T binocular stereomicroscope. For a more detailed description of some faintly visible structures in *G. serbicus* (mouthparts, carpophagus structures, ventral pore fields, genital structures, etc.) we immersed the specimens of the type material in 10% KOH (for 2–3 days). All soft tissue was then removed and the chitin structures were clearly recognisable. We then mounted whole specimens or their dissected parts in glycerol for temporary microscope slides and observations with a Carl Zeiss Axioscope 40 microscope. Images of the specimens and some body parts were taken with a Nikon DS-Fi2 camera with a Nikon DS-L3 camera controller connected to a Nikon SMZ 1270 binocular stereomicroscope and with a Canon PowerShot A80 digital camera connected to an Axioscope 40 microscope. The drawings of *G. serbicus* were created from the images using a computer monitor. The measurement of the samples was carried out using a Carl Zeiss Stemi 2000-C binocular stereomicroscope with an AxioCam MRc camera and integrated Axio Vs40 software packages. Focal stacking for some of the images was performed using Zerene Stacker software. The distribution map was created using Google Earth Pro (version 7.3.2.5776) and Adobe Photoshop CS6. The final images were processed with Adobe Photoshop CS6.

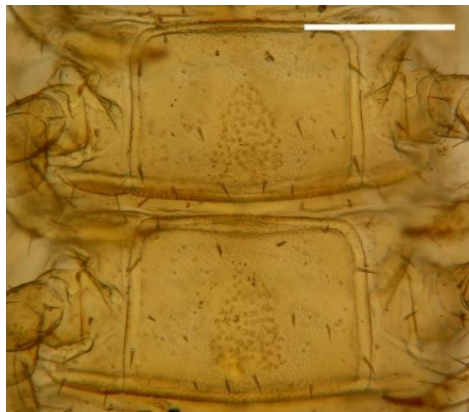


Fig. 5. The subtriangular ventral pore fields 6 and 7 of *Stenotaenia rhodopensis* (Kaczmarek, 1970). Scale bar: 2 mm.

The descriptions of the external morphological structures follow the terminology proposed by Bonato et al. (2010). The categorisation of antennal sensilla follows the terminology recommended by Ernst et al. (2009). To identify morphologically similar species for comparative purposes, we used the open-access web application ChiloKey to identify European geophilomorph centipedes (Bonato et al. 2014). For the same purpose, we analysed a type specimen of *Geophilus pusillifrater* Verhoeff, 1898 from the Naturkundemuseum Berlin (inventory number ZMB 13541; Nb. 1460 coll. Verhoeff; see Moritz and Fischer, 1979). For the separation of the developmental stadia of *S. rhodopensis*, we follow the same

characters previously used to distinguish the embryonic and postembryonic stadia of *G. serbicus* (Stojanović et al., 2020a) and *S. maritima* (Brena and Akam, 2012; Brena, 2014). Fecundity was calculated on the basis of the number of eggs or young found in the broods.

Chemical analyses

Five males and five females of *G. serbicus* were soaked in 2 ml dichloromethane (DCM) for 2 minutes and then analysed using an Agilent 7890A GC system equipped with an 5975C inert XL EI/CI mass selective detector (MSD) and a flame ionisation detector (FID) connected by capillary flow technology 2-way splitter. For all experiments, a non-polar 30 m long capillary column HP-5 MS (Agilent Technologies, Santa Clara, USA) with an internal diameter of 0.25 mm and a stationary phase film with a thickness of 0.25 μm was used. The samples were injected in the most sensitive splitless mode. The injection volume was 1 μl and the injector temperature was 250 $^{\circ}\text{C}$. The linear velocity of the carrier gas (He) was 31 cm/s at 60 $^{\circ}\text{C}$ (constant pressure mode), while the oven temperature was programmed linearly in a range of 60–315 $^{\circ}\text{C}$ at a rate of 3 $^{\circ}\text{C}/\text{min}$. The temperature of the transfer line was 315 $^{\circ}\text{C}$ and the temperature of the FID was 300 $^{\circ}\text{C}$. The electron ionisation mass spectra (EI-MS) were acquired with an ionisation energy of 70 eV and in the mass spectral range m/z 40-550. The temperature of the ion source was 230 $^{\circ}\text{C}$ and the quadrupole temperature was 150 $^{\circ}\text{C}$.



Fig. 6. Laboratory for GC and GC-MS analysis at Center for Instrumental Analysis of the Faculty of Chemistry – University of Belgrade and the Centre of Chemistry – Institute of Chemistry, Technology and Metallurgy, National Institute of the Republic of Serbia, University of Belgrade. Photograph by L. Vujisić.

The identification of the compounds was based on the comparison of their electron ionisation mass spectra (EI-MS) obtained from GC-MS total ion chromatograms of DCM extracts with computerised mass spectra libraries (Wiley 7 and NIST 17) and comparison with previously identified cyanogenic compounds in millipedes and centipedes (e.g. Makarov et al., 2010, 2012; Makarov, 2015; Vujisić et al., 2013; Mitić et al., 2024). NIST MS Search Software Version 2.3 and AMDIS 32 Deconvolution and Identification Software Version 2.73 (both NIST, Gaithersburg, MD, USA) were used to identify the compounds. The relative mass percentages of the identified compounds were calculated based on the corresponding GC-FID peak areas.

CHAPTER 3. *GEOPHILUS SERBICUS* STOJANOVIĆ, MITIĆ & ANTIĆ, 2019 — NEW SPECIES

Etymology — The name is an adjective referring to the country from which the type locality originates.

Diagnosis — The new species is clearly distinguished from its congeners by a unique combination of characters: small body size (less than 20 mm in adults); 41–47 pairs of legs; cephalic plate ca. 1.1–1.2 times longer than wide; antennae ca. 3.1–4.5 times as long as the head; lappets present on the first maxillary coxosternite and the basal telopodite; the pretarsus of the second maxillae apparently tapers gradually to a pointed tip, without spines or filaments; the forcipular coxosternite is ca. 1.1–1.2 times wider than long, with an anterior margin without denticles and with chitin lines pointing laterally to the condyles; basal denticles present only on the tarsungulum, all other forcipular telopodite articles without denticles; clypeus without distinct clypeal area; ventral pore fields present in all metasternites (from first to penultimate), undivided only in the anterior region of the body (up to ca. metasternites 12–13), all other metasternites with divided pore fields; carpophagus pit inconspicuous; 3–7 (usually 4–5) coxal organs, all ventral, distinct and opening separately, most of them close to the margin of the ultimate metasternite, also a single one isolated posteriorly; apical claws of walking legs long, with two accessory spines, ultimate pretarsi short, curved and without spines; anal pores present. *Geophilus serbicus* sp. nov. can be clearly distinguished from the other Western Palaearctic *Geophilus* species with a similar number of leg-bearing segments by a number of characters shown in Tab. 1 and in the following discussion.

Description — Holotype male, 41 pairs of legs, body length about 17 mm, maximum body width 0.68 mm. Paratype males with 43 and 45 pairs of legs, body length 14 mm, maximum body width 0.68 mm. Each of the four paratype females with 45 pairs of legs, body length 16.6–18 mm, and width 0.59–0.68 mm.

Colouration — From whitish-yellow to pale yellow, with slightly darker colouration of the head, mouthparts, forcipular segment and walking and ultimate legs (Fig. 7A). Distal parts of the forcipular tarsungulum reddish brown.

Antennae — Elongate, about 3.1–4.5 (usually 3.5) times longer than the cephalic plate (in specimens from ethanol, untreated with KOH). The basal article as long as wide; all other antennal articles longer than wide (Fig. 8A). Terminal article is about 1.5 times longer than the penultimate article. There is no difference between dorsal and ventral chaetotaxy. All antennal articles with sensilla trichodea, their density is higher in the distal half of the antennae. In addition, the terminal article with sensilla basiconica (in adult specimens of both sexes) is present opposite each other on the internal and external margins (Fig. 8B). In the holotype of the male, the left and right antennae have 14 and 12 internal and nine and 11 external sensilla basiconica, respectively. Apex of terminal antennomeres completely rounded, without any recession on the surface.

Cephalic plate — Longer than wide (length/width holotype 1.16:1; paratype males 1.11:1; paratype females 1.17:1, 1.14:1, 1.15:1 and 1.18:1). Maximum cephalic plate length and width in a holotype 0.57 mm and 0.49 mm; in paratype males length 0.51–0.52 mm, width 0.46–0.47 mm; in paratype females length 0.52–0.64 mm, width 0.44–0.56 mm. Posterior margin almost straight, laterally slightly rounded. Without sutures or paramedian sulci. Chaetotaxy as in Fig. 7C.

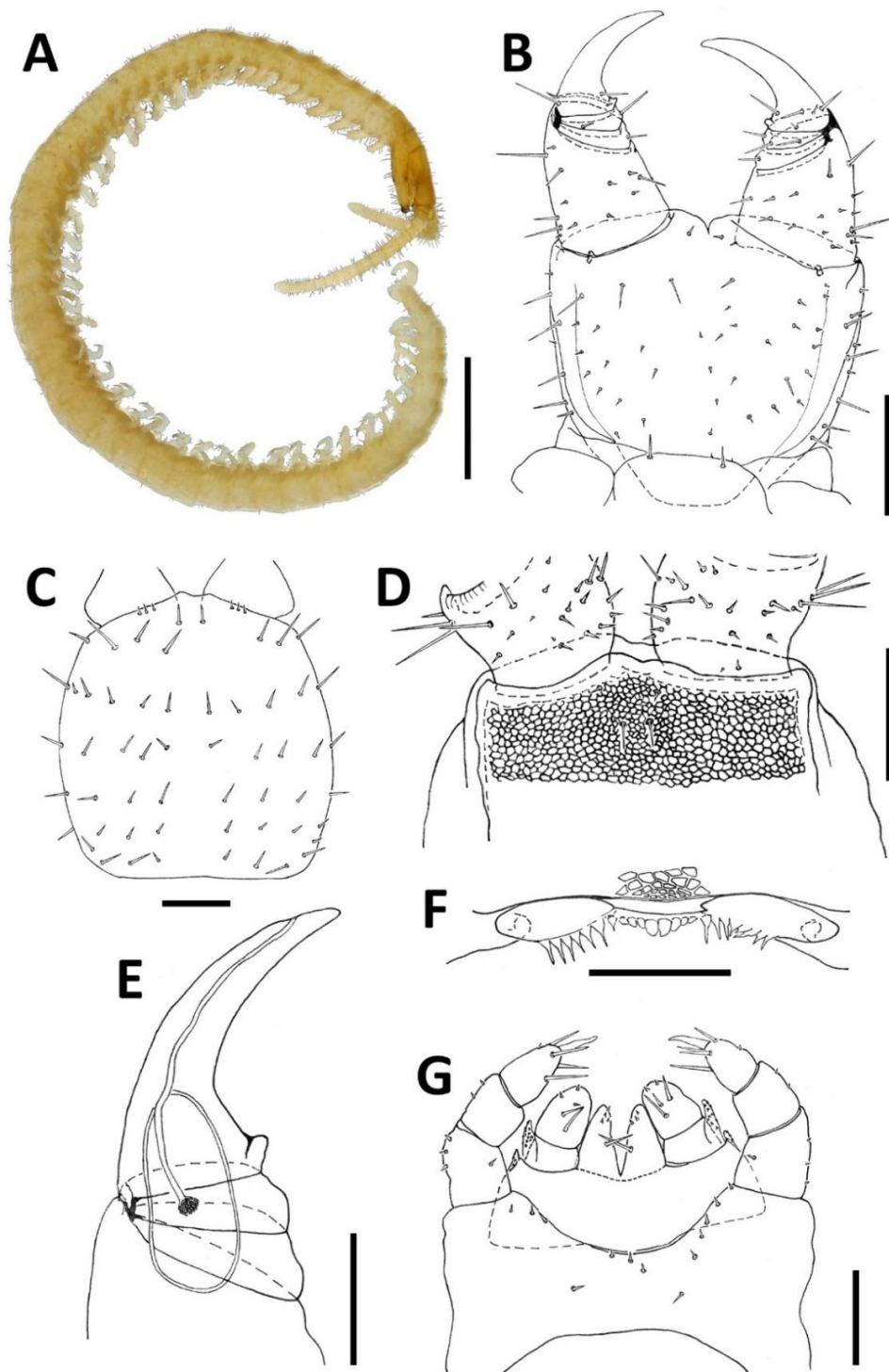


Fig. 7. *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 sp. nov.: A — Paratype male, adult (IZB ChG002); B, D, F — Holotype male, adult (IZB ChG001); C — Paratype male, adult (IZB ChG003); E — Paratype female, adult (IZB ChG007); G — Paratype female, adult (IZB ChG005). A — Habitus, lateral view; B — Forcipular segment, ventral view; C — Cephalic plate, dorsal view; D — Clypeus and basal antennomeres, ventral view; E — Venom apparatus of right forcipular telopodite, ventral view; F — Labrum, ventral view; G — First and second maxillae, ventral view. Scale bars: 1 mm (A); 0.3 mm (B–D); 0.2 mm (E–G).

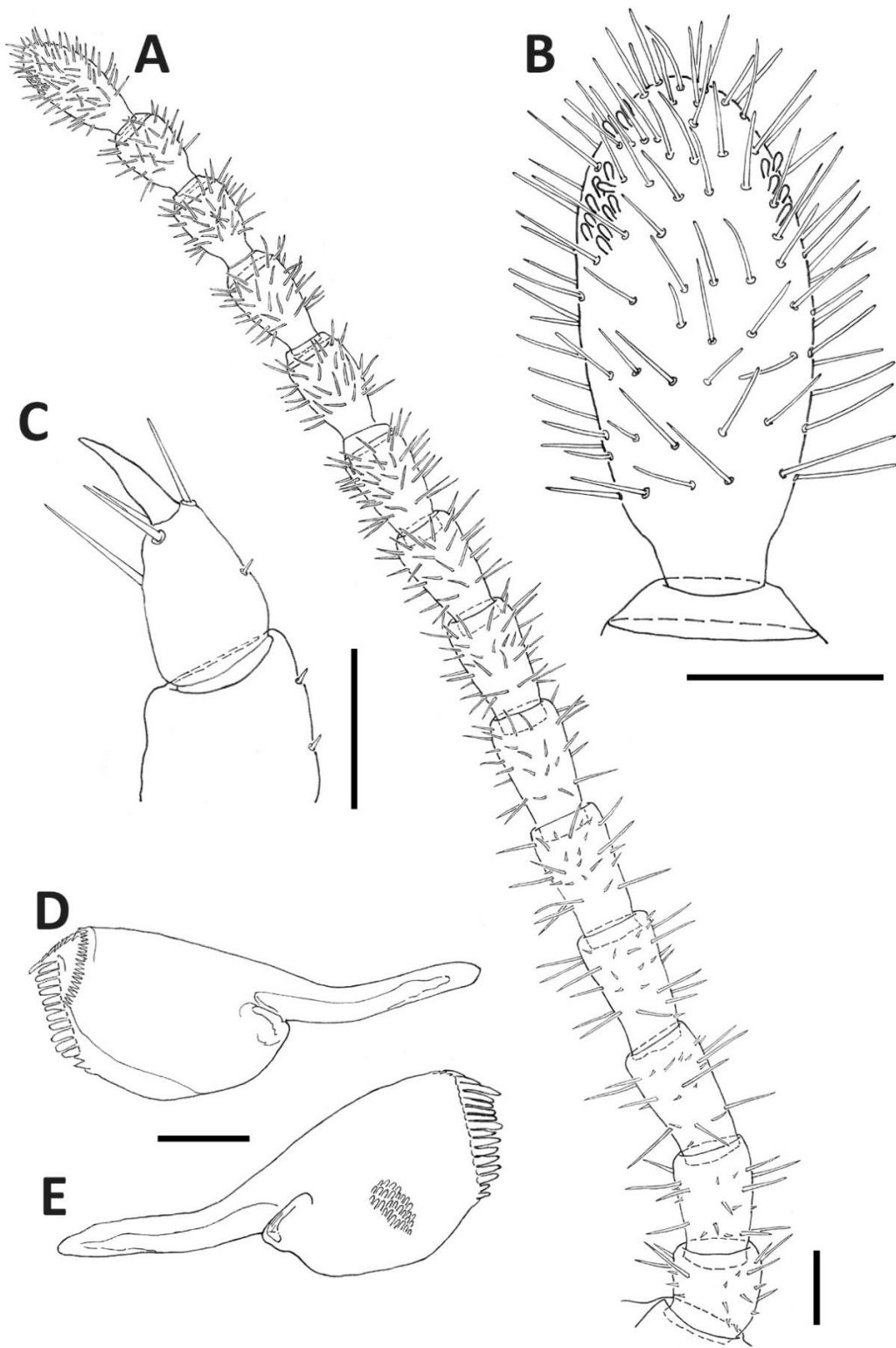


Fig. 8. *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 sp. nov.: A, B — Holotype male, adult (IZB ChG001); C-E — Paratype female, adult (IZB ChG005). A — Right antenna, ventral view; B — Terminal article of right antenna, ventral view; C — Apex of left second maxillary telopodite, ventral view; D — Right mandible, dorsal view; E — Right mandible, ventral view. Scale bars: 0.3 mm (A); 0.2 mm (B); 0.1 mm (C-E).

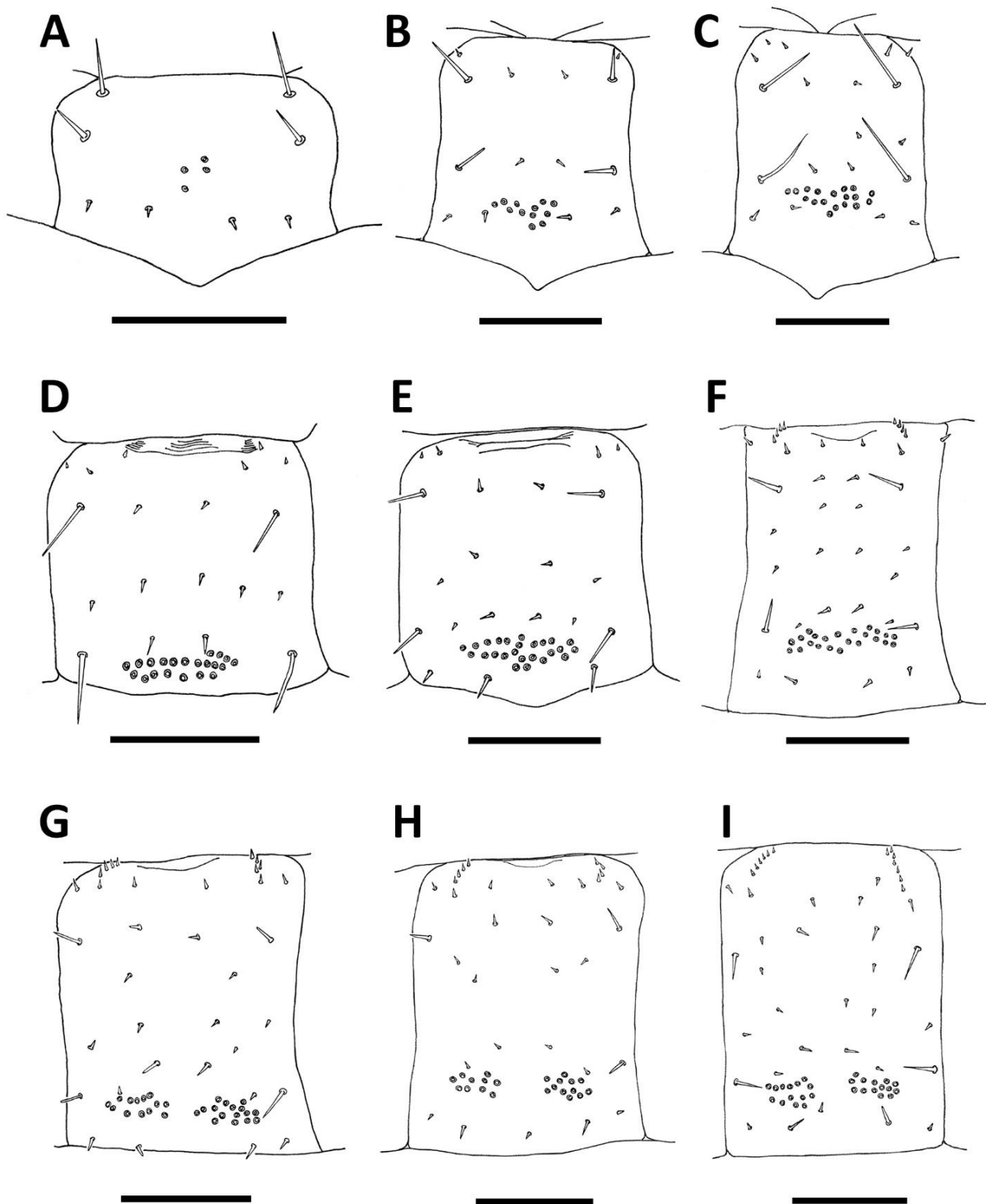


Fig. 9. *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 sp. nov.: holotype male, adult (IZB ChG001). A — Metasternite 1; B — Metasternite 2; C — Metasternite 3; D — Metasternite 7; E — Metasternite 8; F — Metasternite 12; G — Metasternite 13; H — Metasternite 14; I — Metasternite 15. Scale bars: 0.3 mm.

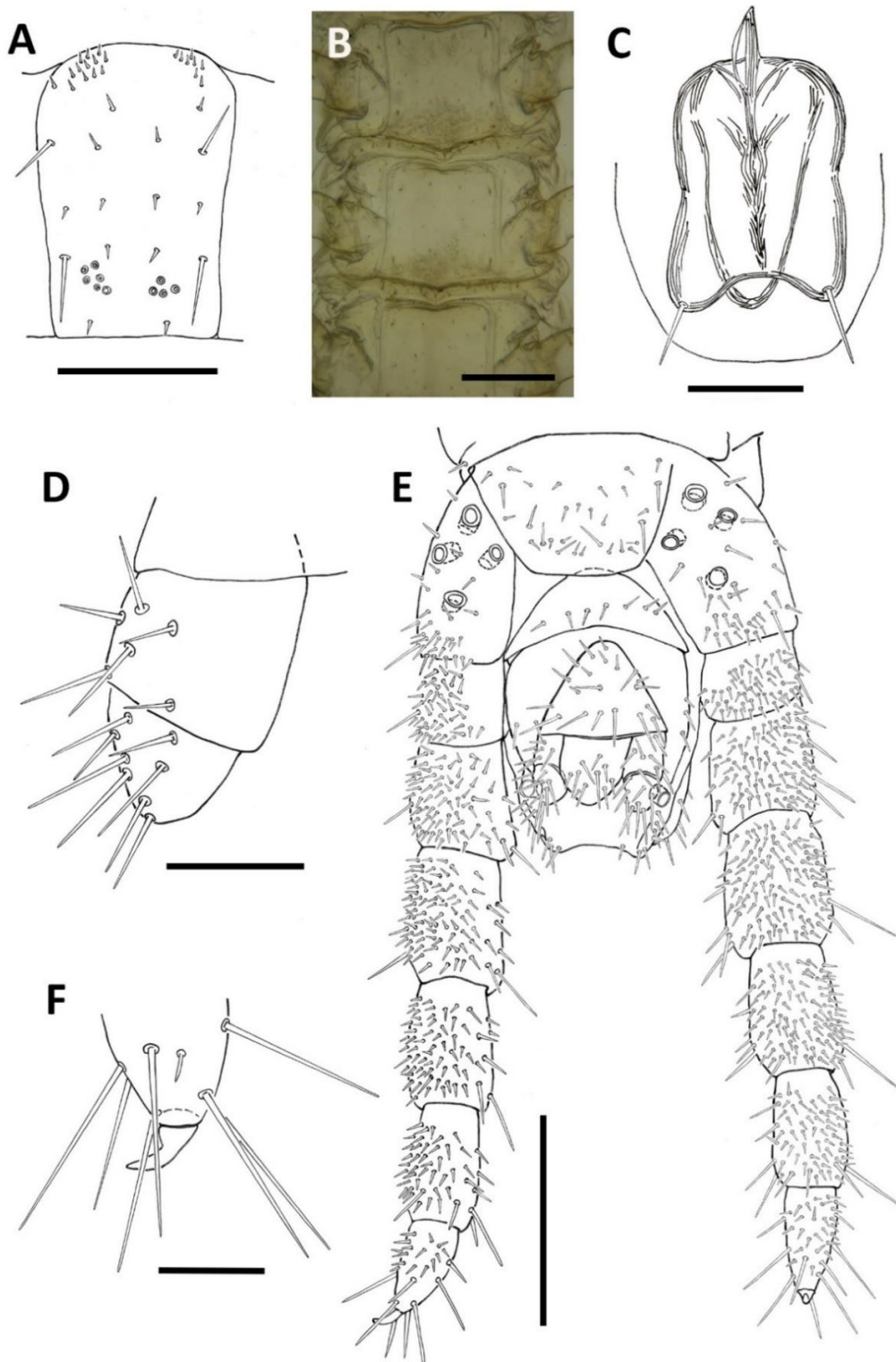


Fig. 10. *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 sp. nov.: A, C-F — Holotype male, adult (IZB ChG001); B — Paratype female, adult (IZB ChG006). A — Metasternite 40; B — Metasternites 7–9; C — Penis, ventral view; D — Right gonopod, ventral view; E — Ultimate leg-bearing segment and postpedal segments, ventral view; F — Pretarsus of right ultimate leg, ventral view. Scale bars: 0.5 mm (E); 0.3 mm (A, B); 0.1 mm (C, D, F).

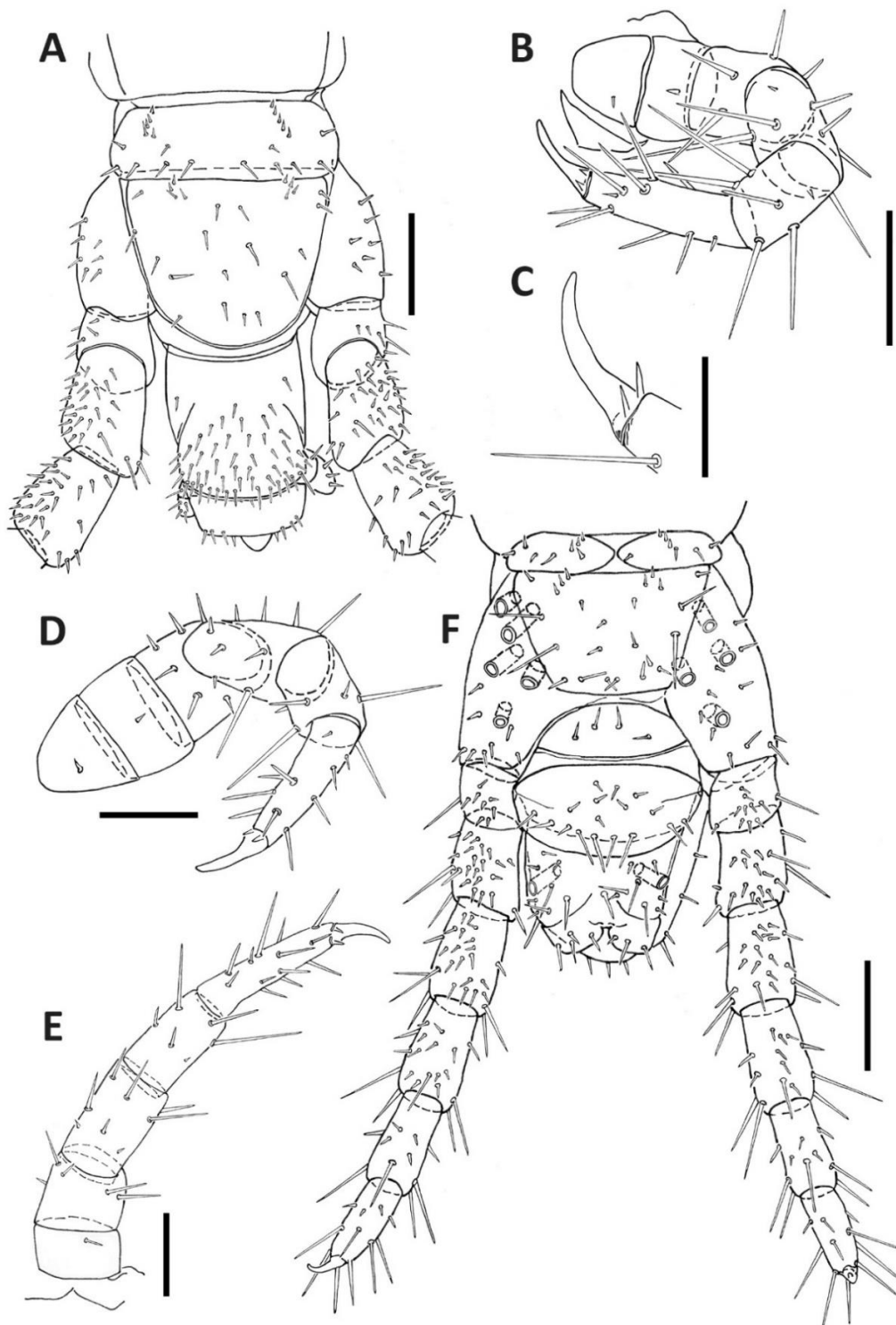


Fig. 11. *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 sp. nov.: A — Paratype male, adult (IZB ChG003); B-E — Holotype male, adult (IZB ChG001); F — Paratype female, adult (IZB ChG004). A. Ultimate leg-bearing segment and postpedal segments, dorsal view; B — Left walking leg 1, anteroventral view; C — Claw of left walking leg 1, anteroventral view; D — Left walking leg 14, anteroventral view; E — Left walking leg 34, anteroventral view; F — Ultimate leg-bearing segment and postpedal segments, ventral view. Scale bars: 0.3 mm (A, F); 0.2 mm (B, D, E); 0.1 mm (C).

Clypeus — Without clypeal area (Fig. 7D). Surface clearly reticulated, with three pairs of setae, of which the postantennary and intermediate pairs are slightly larger, the posterior pair smaller (2/2/2; uniform in all type specimens).

Labrum — Lateral and intermediate parts distinct. Intermediate part well developed, with eight symmetrically arranged tubercles, the two central ones significantly larger. Lateral parts with 7–8 bristles (Fig. 7F).

Mandible — Shape of the mandibles as in Fig. 8D and 8E. The slightly sclerotised pectinate lamella with ca. 15 hyaline teeth. Ventral ridge not expanded, continuous with pectinate lamella (Fig. 8D). Condyle moderately chitinised.

First maxillae — (Fig. 7G): Coxosternite undivided, without setae, with a small lappet on lateral margin. Telopodital lappets well developed and almost twice as long as the coxosternal ones. The ratio of their length is similar to that of the distal and basal articles of the first maxillary telopodite. The distal telopodital article is apically rounded, with 2–3 long setae and 3–4 small sensilla. Basal telopodital articles without setae. Coxal projections subtriangular, well developed, each with a long mesal seta and 3–4 short sensilla distally.

Second maxillae — Coxosternite undivided, without medial sutura or inner and foraminal processes; isthmus well sclerotised, indistinct statumina; anterior margin concave, with three groups of short setae (3–5 per group) distributed along the border, and two separate paramedial setae (Fig. 7G). Telopodite poorly setose. Terminal article distally with four long, sclerotised setae (Figs. 7G and 8C). Pretarsus well developed, moderately elongate, about half the length of the terminal article, apparently gradually tapering into a pointed tip, without spines or filaments (Fig. 8C).

Forcipular segment — Forcipular tergite distinctly narrowing anteriorly. Forcipular coxosternite wider than long (width/length 1.1–1.3:1; usually 1.2:1), slightly wider than the cephalic plate. Maximum forcipular coxosternite width in a holotype 0.53 mm, in paratype males 0.51–0.52 mm and in paratype females 0.46–0.57 mm. Anterior margin of coxosternite slightly concave and without denticles (Fig. 7B). Coxopleural sutures clearly diverging forwardly; chitin- lines present, pointing laterally to the condyles but not reaching them. Tarsungulum with almost straight basal denticle; without denticle-like projections along the slender and moderately curved apical peak (Fig. 7E). Trochanteroprefemur, femur and tibia without denticles. The calyx of poison gland cluster-associated, with an almost straight duct opening externally near the apical end of the tarsungulum (Fig. 7E). Chaetotaxy of the forcipular coxosternite and telopodites as in Fig. 7B.

Trunk — Pore-fields present on all leg-bearing segments except metasternite of the ultimate leg-bearing segment. In the anterior half of the trunk, pore-fields are located in the posterior half, but near the middle of the metasternites (metasternites 1–7 in the holotype male, 1–12 in the paratype female). On all other metasternites, pore-fields closer to the posterior margin. Fields undivided on metasternites 1–12 in holotype male (metasternites 1–13 in one paratype female; IZB ChG007). The rest of the leg-bearing segments with divided fields. Number of sternal pores in holotype male as follows: metasternite 1 (4 pores), 2 (12), 3 (18), 4 (19), 5 (23), 6 (23), 7 (21), 8 (22), 9 (26), 10 (33), 11 (28), 12 (30), 13 (29: left 16/right 13), 14 (22: 12/10), 15 (28: 14/14), 16 (22: 12/10), 17 (20: 9/11), 18 (22: 9/13), 19 (18: 10/8), 20 (14: 8/6), 21 (15: 7/8), 22 (17: 8/9), 23 (17: 8/9), 24 (13: 5/8), 25 (15: 9/6), 26 (18: 11/7), 27 (18: 9/9), 28 (14: 5/9), 29 (14: 8/6), 30 (13: 5/8), 31 (17: 9/8), 32 (19: 10/9), 33 (18: 9/9), 34 (19: 10/9), 35 (15:

7/8), 36 (26: 14/12), 37 (21: 10/11), 38 (20: 9/11), 39 (15: 8/7) and metasternite 40 (10: 4/6). Number of sternal pores in the paratype female (IZB ChG007) as follows: 1 (4), 2 (8), 3 (16), 4 (16), 5 (18), 6 (17), 7 (16), 8 (18), 9 (22), 10 (21), 11 (21), 12 (21), 13 (19), 14 (19: left 10/right 9), 15 (17: 9/8), 16 (14: 8/6), 17 (11: 3/8), 18 (12: 6/6), 19 (12: 6/6), 20 (12: 6/6), 21 (11: 7/4), 22 (10: 7/3), 23 (10: 5/5), 24 (7: 4/3), 25 (11: 5/6), 26 (7: 4/3), 27 (12: 6/6), 28 (9: 4/5), 29 (6: 3/3), 30 (14: 6/8), 31 (11: 4/7), 32 (10: 6/4), 33 (8: 4/4), 34 (10: 4/6), 35 (8: 4/4), 36 (11: 5/6), 37 (13: 6/7), 38 (14: 6/8), 39 (10: 4/6), 40 (11: 5/6), 41 (13: 8/5), 42 (12: 4/8), 43 (11: 7/4) and metasternite 44 (5: 2/3). Without distinct carpophagus pits, only a small median plateau in the anterior part of the trunk: metasternites 7–14 in the holotype male (Fig. 9D–9H) and metasternites 4–12 in the paratype female (Fig. 10B). Chaetotaxy, shape of the pore fields and their relative size on selected metasternites are shown in Figs. 8 and 9A.

Walking legs — Chaetotaxy similar over the entire body length. Distribution and relative size of setae as in Figs 11B, 11D and 11E. Apical claws curved, with two short accessory spines ventrobasally (Fig. 11C).

Ultimate leg-bearing segment — Metasternite ca. 1.1–1.4 times wider than long (usually 1.2), trapezoidal, ultimate presternite medially divided (Fig. 11F). Coxopleuron slightly swollen, laterally rounded, ventrally with numerous small setae on distal ventral margin, a few larger setae present on remaining surface. Each coxopleuron with 3–7 (usually 4–5) coxal organs opening separately on ventral surface; no ventral pits with multiple coxal organs; no dorsal pores or pits. In all specimens collected, one coxal pore is displaced with a more posterior position and one more laterally; other coxal organs open close to the metasternite margin (Figs 10E and 11F). In both sexes, the ultimate legs are much longer than the penultimate ones and consist of six articles. The ultimate legs of the females are slender, those of the males somewhat thicker (Figs 10E and 11F). The ventral surface is much more setose in the males than in the females (Fig. 10A and 11E). The dorsal surface of the same pair of legs in males also has a significantly lower density of setae than the ventral surface of the same specimen (Fig. 11A). Apical claws are curved and shorter than in the walking legs, without accessory spines (Fig. 10F).

Postpedal segments — Intermediate sternite in males with several setae arranged along the concave posterior margin (Fig. 10E). The posterior margin in females is more convex (Fig. 11F). The first genital sternite in males triangular, with many setae distributed almost evenly over the surface (Fig. 10E). Male gonopods biarticulate, separated at base, with setae distributed mostly on outer sides of articles; basal article with ca. six setae, apical article with ca. eight setae (Fig. 10D). Penis as in Fig. 10C. The second genital sternite has a rounded posterior margin. First genital sternite in females ellipsoid, with several short central setae and longer setae on posterior margin (Fig. 11F). Female gonopods in a single lamina. Anal pores present in both sexes (Figs 10E and 11F).

Intraspecific variation — Overall, the type specimens and the additional non-type specimens show a variability between 41 and 45 pairs of legs in the males and between 45 and 47 pairs of legs in the females. All specimens of the entire sample have a body length of less than 20 mm (the largest female collected is about 18.6 mm long). The morphological differences between adult males and females consist in the different morphology of the genital segments and the ultimate legs as well as in minor differences in size (slightly higher length values in females) and in the ratio between antennae/cephalic plate length [ca. 3.5 (3.1–4.5) in females and ca. 3.7 (3.2–4.5) in males]. The measurement of the specimens resulted in average values of 12.98 mm (min. 9.64 mm; max. 16.7 mm) for males and 13.26 mm (min. 11.54 mm; max. 16.58 mm) for non-attending females. The average body length of attending

females is 13.55 mm (the recorded extreme values are: min. 8.92 mm and max. 18.56 mm). There are some differences in colour nuances between the more yellowish attending females and the more whitish females caught as free-living specimens.

Apart from the small differences in body size [average values of 11.07 (min. 10.65 mm; max. 11.94 mm) for young females and 11.06 mm (min. 8.53 mm; max. 12.71 mm) for young males] and antennae/cephalic plate length ratio [ca. 3.2 (3.1–3.7) for females and ca. 3.5 (3.2–4) for males], the juvenile specimens collected (all from the last adolescens stadium) show similar values to the adults in all other proportions: Cephalic plate length/width (ca. 1.1–1.2), forcipular coxosternite width/length (ca. 1.1–1.2) and ultimate leg-bearing segment metasternite maximum width/length (ca. 1.1–1.4). The number and arrangement of the coxal pores is also similar (each coxopleuron has four or five pores).

Tab. 1. Comparison between *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 sp. nov. and all other European *Geophilus* species with similar pairs of legs. Data presented from Bonato et al. (2014), original descriptions and available redescriptions.

| Species | <i>G. serbicus</i> sp. nov. | <i>G. aenariensis</i> Verhoeff, 1942 | <i>G. alpinus</i> Meinert, 1870 | <i>G. nesiotis</i> Attems, 1903 |
|---|---|--------------------------------------|---|------------------------------------|
| Body length (mm) | < 19 | ≤ 22 | ≤ 52 (mostly 15–35) | 16 |
| Pairs of legs | ♂ 41–45; ♀ 45–47 | ♂ 47; ♀ 51 | 43–63 ♂♀ | 41–43 ♂♀ |
| Antennae/cephalic plate length | Ca. 3.5 | ? | Ca. 3 | ? |
| Cephalic plate length/width | Ca. 1.1–1.2 | ? | Ca. 1 | Ca. 1 |
| Labrum: lateral part: bristles (presence) | Yes | No | Yes | Yes |
| Carpophagus pit distinct (absence) | No | Yes | Yes | Yes |
| First maxillae: lappets (presence) | Yes | ? | Yes | No |
| Second maxillae: pretarsus (shape) | Elongated, pointed | Small, curved, apically pointed | Stout tubercle with 1–2 apical tips | Subconic, curved, apically pointed |
| Posterior part of the trunk: pore-fields (presence) | Yes | ? | Yes | No |
| Coxal pores in each coxopleuron (number) | 3–7 (usually 4–5) | 3–5 (usually 4) | 5–10 | 5–10 |
| Isolated coxal pore in each coxopleuron (presence/position) | Yes, same size as other pores, near the middle of the coxopleuron | No | Yes, same size as other pores, near the posterior margin of the coxopleuron | No |
| Anal pores (presence) | Yes | No | Yes | Yes |
| Ultimate legs: pretarsus | Curved, without accessory spines | ? | Curved, without accessory spines | Curved, without accessory spines |
| Distribution | Central Balkan Peninsula | Southern Apennine Peninsula | Widespread European species | Crete (Greece) |

Tab. 1. Continued

| Species | <i>G. oligopus</i> (Attems, 1895) | <i>G. pellekanus</i> Attems, 1903 | <i>G. pusillifrater</i> Verhoeff, 1898 | <i>G. pygmaeus</i> Latzel, 1880 |
|---|--------------------------------------|--------------------------------------|--|--|
| Body length (mm) | ≤ 18 | 16 | ≤ 13 | < 20 |
| Pairs of legs | 37–39 ♂♀ | 45 ? | ♂ 39–41; ♀ 43 | ♂ 41–45, ♀ 43–47 |
| Antennae/cephalic plate length | Ca. 3.5–4 | ? | Ca. 3.4 | Ca. 2 |
| Cephalic plate length/width | Ca. 0.8–0.9 | Ca. 1 | Ca. 1.3 | Ca. 1.1 |
| Labrum: lateral part: bristles (presence) | Yes | Yes | Yes | Yes |
| Carpophagus pit distinct (presence) | Yes | Yes | No | Yes |
| First maxillae: lappets (presence) | No | No | No | Yes |
| Second maxillae: pretarsus (shape) | Stout tubercle with 1–2 apical tips | Subconic, curved, apically pointed | Elongated, pointed | Elongated, small dorsal bulge |
| Posterior part of the trunk: pore-fields (presence) | No | No | Yes | No |
| Coxal pores in each coxopleuron (number) | 2–7 | 5–10 | 3–5 | 3–4 |
| Isolated coxal pore in each coxopleuron (presence/position) | No | No | Yes, smaller, near the middle of the coxopleuron | Yes, smaller, near the middle of the coxopleuron |
| Anal pores (presence) | Yes | No | Yes | Yes |
| Ultimate legs: pretarsus | Curved, without accessory spines | Curved, without accessory spines | Curved, pointed to a stout tubercle | Curved, two accessory spines |
| Distribution | Alps, Dinarides, Carpathians | Corfu (Greece) | Armorican Massif, British Isles, Dinarides | Alps |

CHAPTER 4. PARENTAL CARE IN SEVEN GEOPHILOMORPH CENTIPEDES FROM SERBIA

The brood chambers of the centipedes *G. serbicus*, *H. illyrica*, *P. herzegowinensis*, *S. linearis*, *S. herzegowinensis* and *S. carniolensis* were cavities in the soil, the volume of which was largely taken up by the geophilomorphs. When found, the adult females were curled around the eggs or young and had at least part of the trunk in an S-curve, as is common in other Geophilomorpha. The largest part of the trunk was directed with the dorsal side towards the brood (Fig. 12A-F).

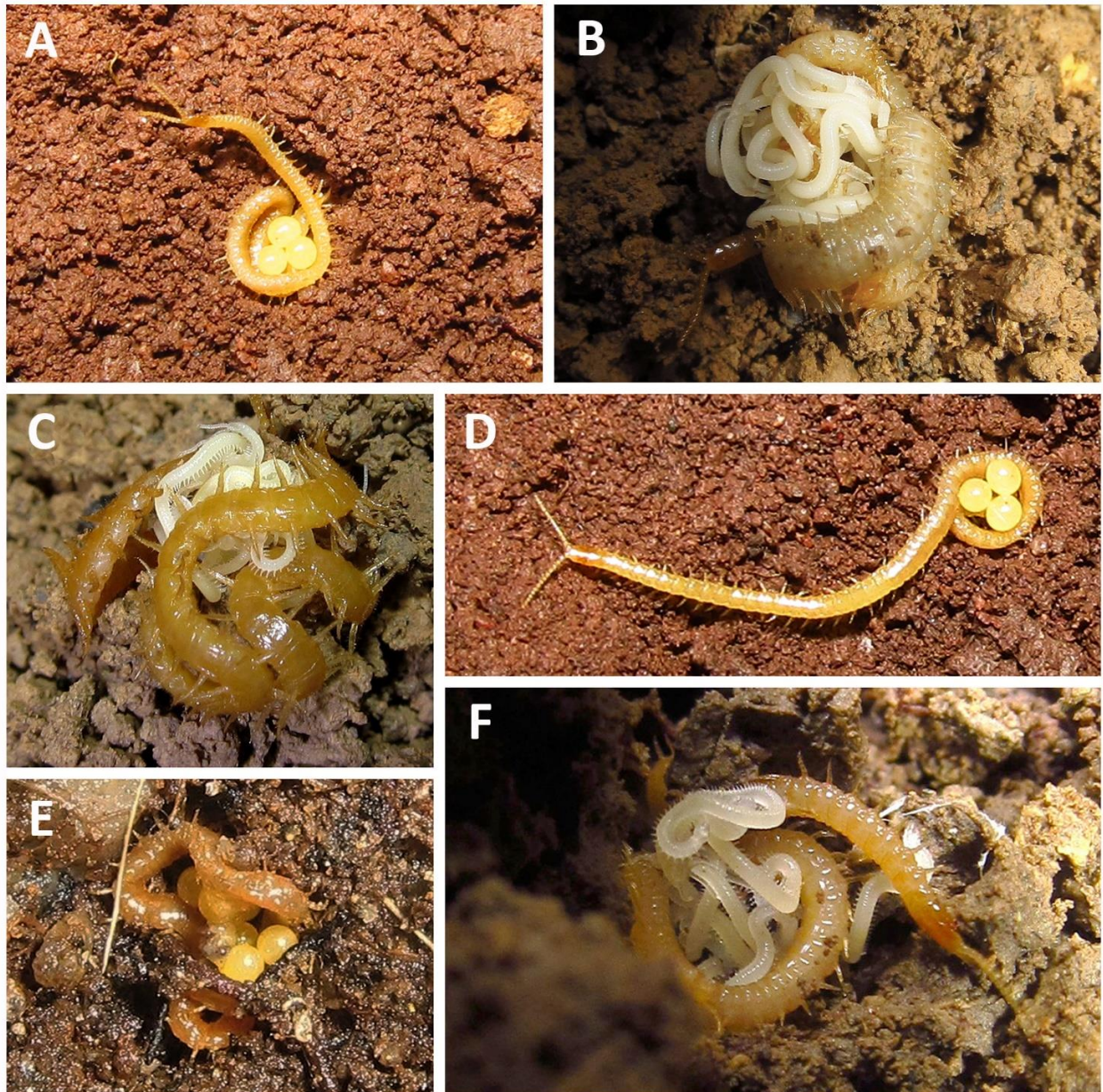


Fig. 12. Guarding females of *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 (A), *Henia illyrica* (Meinert, 1870) (B), *Pleurogeophilus herzegowinensis* (Verhoeff, 1901) (C), *Stenotaenia linearis* (C. L. Koch, 1835) (D), *Strigamia herzegowinensis* (Verhoeff, 1935) (E) and *Schendyla carniolensis* Verhoeff, 1902 (F). At this stadia, young centipedes are unable to fend for themselves when attacked. Photographs by D. Stojanović and D. Antić.

The embryonic and early postembryonic stadia from the broods of *G. serbicus*, *H. illyrica*, *P. herzegowinensis*, *S. linearis*, *S. herzegowinensis* and *S. carniolensis* were almost without exception in the same phase of development (Fig. 12A-F), which indicates that the eggs are laid in a relatively short period of time. As in other geophilomorphs, a female rolls around the eggs she has laid and remains in this position until they have developed into the adolescens I stadium. Interestingly, *G. serbicus* occurs in large numbers; in this respect the species is unusual, as geophilomorphs from other habitats are generally not caught in large numbers. The high density that obtains in the population of *G. serbicus* makes this species particularly suitable for life history studies.

Adult females of *S. rhodopensis*, body length 12.99–17.18 mm (mean, 15.30 mm; n = 9), with a mass of eggs or young, were observed under stones. All females had their ventral surface facing outwards and their dorsal surface in contact with the broods (Fig. 13A). When disturbed, the female moved slightly away from the original position, but the terga remained in contact with the brood and the sterna were exposed outwards while the head waved with open forcipules. If the disturbance persisted, the female abandoned her brood. Clutch sizes vary from 2 to 4 (mean, 3.33; n = 9). The eggs are spherical and have a diameter of 0.79–1.22 mm (mean, 1.05 mm; n = 26). The shell (chorion) is yellow in colour, translucent and elastic (Fig 13B). The foetus stadium is capable of “writhing” movements and begins to be slightly compressed dorso-ventrally; it is yellowish-cream in color and 6.35–8.40 mm long (mean, 7.52 mm; n = 4). The antennae are fully segmented and directed forwards. This stadium tends to contract and bring the head close to the posterior end of the animal; all legs are developed and the forcipules are stretched forwards (Fig 13C). The first small setae appear, although they are only clearly visible on appendages (antennae and legs). The last leg-bearing and genital segments are clearly separated, but not yet fully developed. Therefore, sex determination is not possible at this postembryonic stadium.



Fig. 13. *Stenotaenia rhodopensis* (Kaczmarek, 1970). A — female guarding the mass of eggs *in situ*; B — embryonic stadium; C — foetus stadium. Scale bars: 1 mm. Photograph by D. Stojanović.

The species *P. herzegowinensis*, *S. rhodopensis* and *S. herzegowinensis* do not appear to have been previously recorded from Serbia. All three species have so far only been found in one locality each, namely on Mt Medvednik, in the Stara Planina Mountains and on Mt Kopaonik.

CHAPTER 5. EARLY DEVELOPMENT OF *GEOPHILUS SERBICUS*

We have used all available externally visible morphological characters to differentiate the early developmental stadia of *G. serbicus*. The division into three phases (embryonic, early postembryonic or embryoid and late postembryonic or postembryoid) is based on the most conspicuous characters, such as the presence/absence of a chorion and the degree of similarity to adults in habitus.

Embryonic phase

The embryonic phase begins with egg laying and brood construction. The end of this phase is characterised by the rupture of the chorion. Between these two events, the embryos undergo a series of transformations that lead to the formation of the longitudinal axis of the body and the appearance of segments and appendages. The eggs of *G. serbicus* have a circular to moderately oval shape and are whitish to slightly yellowish in colour. In presenting the size of the eggs of earlier stadia, we have taken into account the longer (length) and shorter (width) of the egg axis, measured between the two opposite edges of the chorion. When measuring egg length in later stadia, we used the axis that runs between the parallel orientated anterior and posterior halves of the embryo. In total, we analysed 255 embryos, which were divided into eight pre-hatching stadia (Tab. 2; Fig. 14A-K).

The first embryonic stadium comprises the process of cleavage in the centre of the eggs and the migration of the divided cells to the surface (Fig. 14A-C). At the beginning of this stadium, the central mass with the nucleus of the zygote divides into large blastomeres. Between the central mass and the peripheral elastic chorion is a space filled with extracellular medium (Fig. 14A). In the last part of the stadium, the central mass expands towards the chorion (Fig. 14B, C). The stadium is completed when the entire interior of the egg is filled. The cell divisions continue on the surface and produce the first blastoderm.

The second embryonic stadium is characterised by a uniform layer (early blastoderm) that covers the entire surface of the egg (Fig. 14C). Subsequent events lead to an increase in the number of cells at the periphery of the egg and the formation of the first morphologically recognisable structure (the cephalic condensation) on one side of the egg (Fig. 14D).

The pivotal event in the third embryonic stadium is the appearance of terminal segments within the cephalic condensation of the not yet differentiated embryo (Fig. 14E). The appearance of this structure marks the beginning of the segmentation process.

The addition of trunk segments is the main feature of this stadium. Starting from the already formed terminal segments, the segmentation rungs (future trunk segments) appear one after the other in the anterior half of the body (Fig. 14F).

In the fifth embryonic developmental stadium, new segments are created in the posterior part of the body. Except for the terminal segments (the last trunk segment and the postpedal segments), all other trunk segments are visible at this stadium. The end of the stadium is characterised by the induction of a dent (the future flexure channel) on about half of the future ventral surface (the segmentation rungs plate) (Fig. 14G).

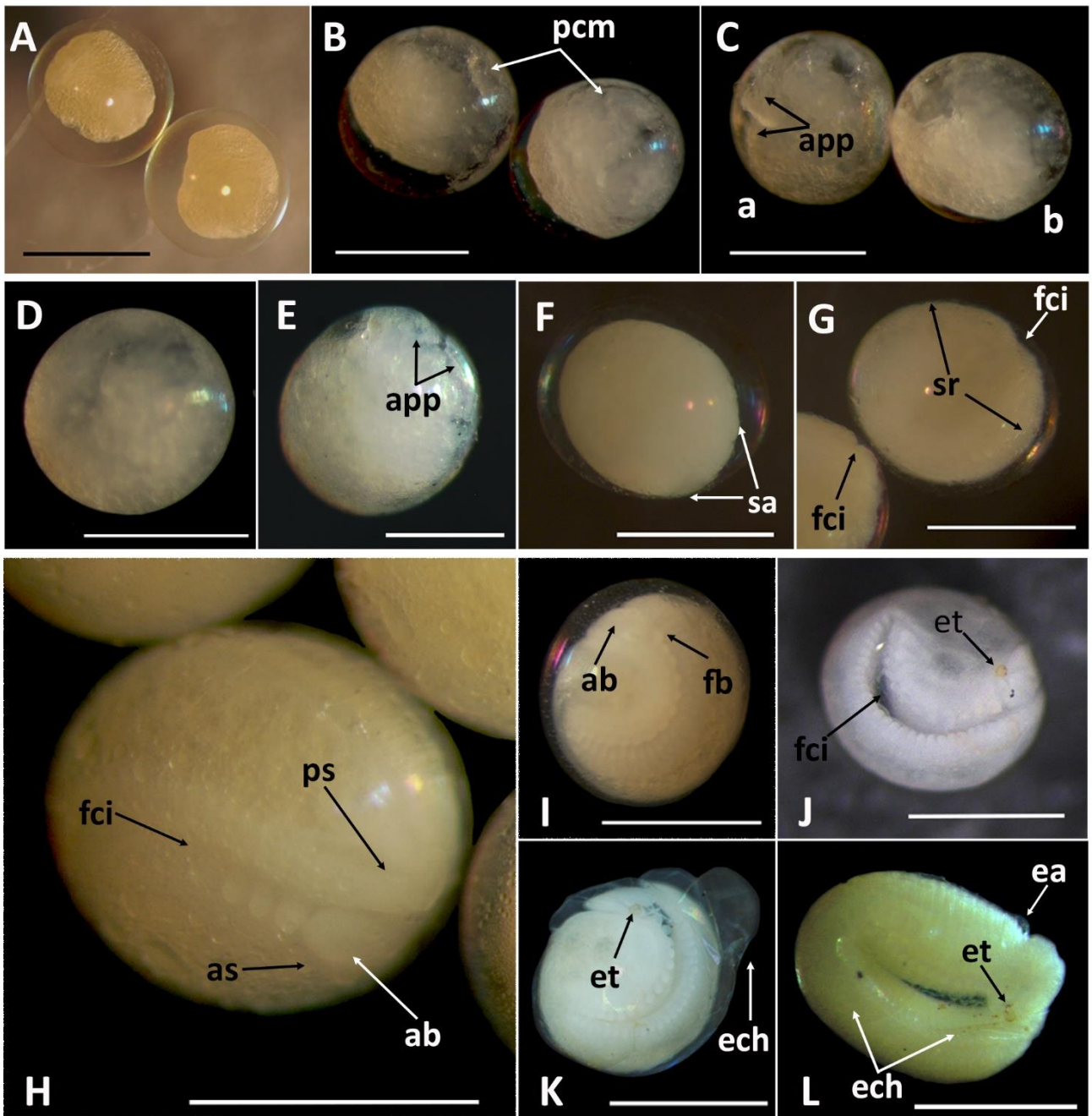


Fig. 14. Embryonic stadia of *Geophilus serbicus* Stojanović, Mitić and Antić, 2019. Stadium 1 — cleavage and peripheral migration: early cleavage (A), late cleavage and peripheral cell migration (B), cell migration completed (C); stadium 2 — blastoderm formation (D), cephalic condensation (E); stadium 3 — early phase of segmentation and appearance of anterior and posterior segments (F); stadium 4 — addition of trunk segments (G); stadium 5 — late segmentation and start of spreading (I); stadium 6 — embryo spreading (J); stadium 7 — pre-apolysis stadium (K); stadium 8 — embryo half apolysis, hatching: chorion cracking (L), embryo stretching and first moulting (M). Abbreviations: antennal bud (ab), anterior-posterior polarisation (app), anterior side (as), exuvia apolysis (ea), excluded chorion (ech), egg tooth (et), forcipular bud (fb), flexure channel induction (fci), peripheral cell migration (pcm), posterior side (ps), segmentation appearance (sa) and segmentation rungs (sr). Scale bar: 0.5 mm.

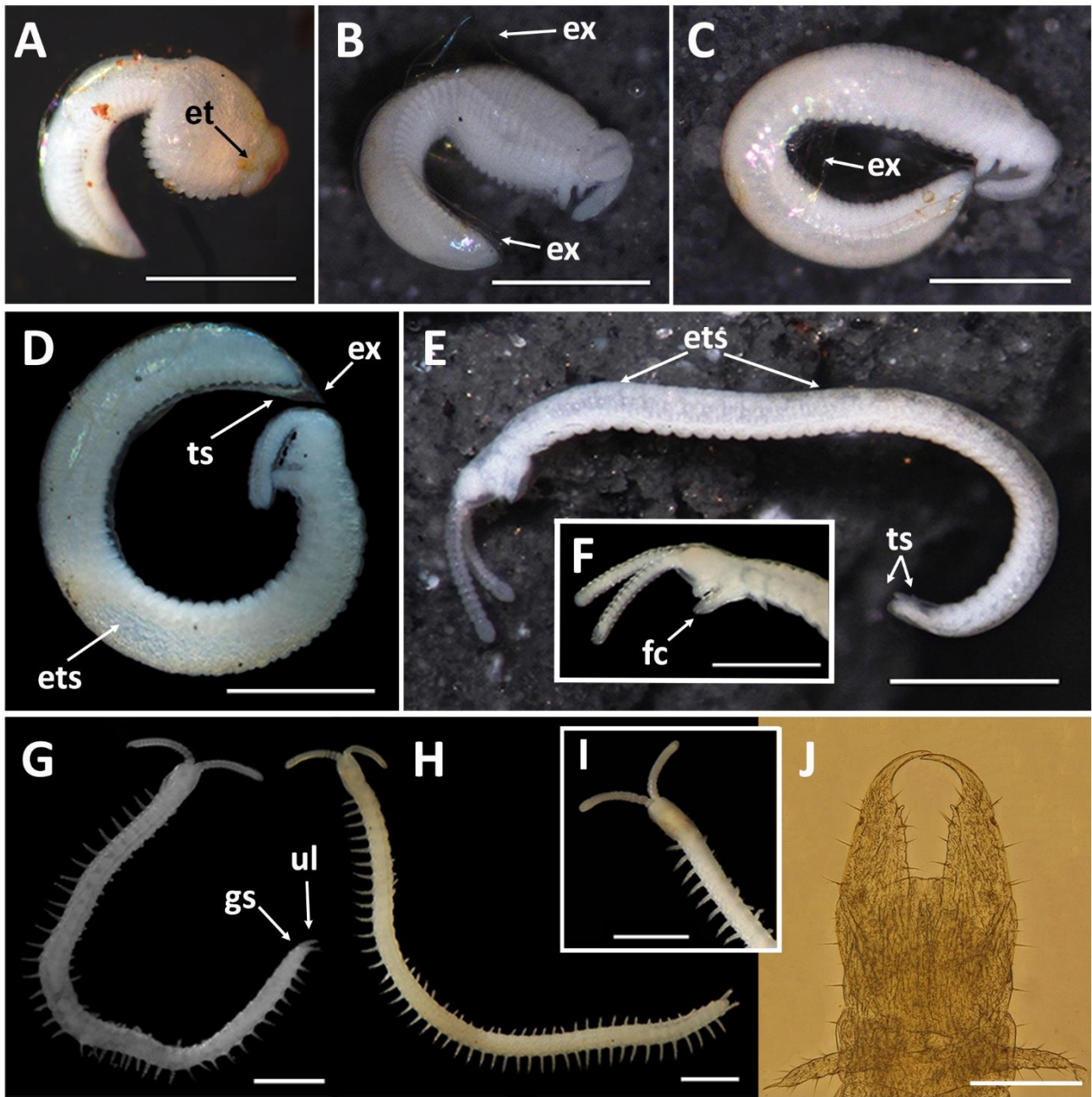


Fig. 15. Embryoid development and first adolescens stadium of *Geophilus serbicus* Stojanović, Mitić and Antić, 2019. Proembryoid stadia: proembryoid I (A), II (B) and III (C) stadia. Peripatoid stadium (D). Foetus stadium: foetus habitus (E), foetus cephalic capsule (F) (lateral view). Adolescens I stadium: male habitus (G), female habitus (H), cephalic capsule of adolescens I (dorsal view) (I), forcipular segment of adolescens I, male (ventral view) (J). Abbreviations: egg tooth (et), embryonic tissue (ets), exuvia (ex), forcipule (fc), genital segment (gs), terminal segments (ts), ultimate legs (ul). Scale bars: 0.5 mm (A-I), 0.2 mm (J).

Recognisable as a shallow dent in the previous stadium, the initiated flexure progresses significantly during the sixth stadium and forms a flexure channel between the ventral surface of the anterior and posterior half (Fig. 14H). During this stadium of development, the flexure channel lies in one plane. This channel deepens due to a retracting wave transmitted through the segmentation front.

The progression of the flexure process leads to a reversal of the embryonic axis. The segmentation rungs plate, which was previously located on the egg surface, now moves into the interior of the egg. The reverse process takes place with the embryonic mass containing the yolk, which was previously located inside the egg. Unsegmented antennae, two maxillae and forcipular appendages are clearly visible apically on the anterior half of the embryo's body (Fig. 14H). The appendages of the trunk segments are only visible as limb buds. The anterior and posterior halves are adjacent to each other.

The dorso-ventral flexure process is completed in the seventh embryonic stadium. A lateral view shows the symmetrical appearance of the embryo while the flexure channel is in a plate (stadium 6; Fig. 14H) and the disruption of this morphological organisation with the dorsal bending of the posterior half of the same channel (stadium 7; Fig. 14I). The opposite anterior and posterior halves are in close proximity. Antennae and mouthparts are clearly distinguishable and extend faster than the limb buds, but still without segmentation. Except for the last two leg-bearing segments, all others are clearly recognisable. The egg tooth is still not visible.

The eighth embryonic stadium represents the end of embryonic development. This stadium can be described as the final preparation for hatching. The development of many of the previously described features of the embryo progresses under the chorion (Fig. 14J). For the first time it is possible to clearly recognise the boundaries of the head of the specimen. The segmentation of the antennae is just recognisable and the egg tooth (a small protuberance at the base of the second maxilla) has become visible as a darkening. On the posterior end, the last two leg-bearing segments are forming. At this stadium, the anterior and posterior halves move away from each other, spreading the flexure channel (Fig. 14J). Cracking of the chorion indicates the end of this stadium and of the entire embryonic phase.

The embryoid specimens use the egg tooth to break through the surface of the chorion, marking the beginning of the stadium (Fig. 14K). Subsequent events ensure emergence from the eggshell (Fig. 14L). The hatched specimens of *G. serbicus* are characterised by a conspicuous elongation process towards the end of the stadium.

Embryoid phase

The embryoid phase is a series of transitional stadia between embryo and juvenile. A total of five embryoid stadia are distinguished: three proembryoid stadia (I, II and III), a peripatoid stadium and a foetus stadium. Each individual stadium is separated from the next by a moult. An overview of the characters of the embryoid stadia can be found in Tab. 2.

We use the term 'proembryoid' for the first three stadia after hatching, which are characterised by a whitish colouration, the horseshoe shape of the body, an unclear body segmentation and undifferentiated genital and last leg-bearing segments. The only type of movement observed in specimens at this developmental period is a slight contraction of the entire body. Significant body growth is observed from the first to the third proembryoid stadium. The body length almost doubles during this period (see Tab. 2).

The first embryoid stadium is easily recognised by the appearance of the anterior half of the body (Fig. 15A). After hatching, the ventral side of the anterior half retains the same expanded shape as in the seventh and eighth embryonic stadia (Fig. 14J, K). The anterior side is shorter than the posterior side due to compression and has an almost circular shape. All body appendages are only recognisable as

undifferentiated buds. The trunk segmentation is visible in all body segments except the terminal posterior segments. At the end of the stadium, one of the most recognisable embryonic structures of centipedes, the egg tooth, disappears with the first (pro) embryoid moult.

Proembryoid II is a short-term stadium characterised by the process of extension of the entire body, especially the anterior half, and the increase in the overall length of the body (Fig. 15B; Tab. 2). The process of trunk segmentation is ongoing. Antennae and mouthparts are barely elongated and not segmented. The remains of the exuvia are recorded at the end of the stadium.

The third proembryoid stadium is characterised by the continuation of all previously initiated developmental processes (Fig. 15C). The length of the body and all body appendages increases. For the first time in the development of *G. serbicus*, the segmentation of the antennae becomes visible, but only slightly. No progress can yet be seen in the segmentation of the other appendages. The anterior half of the body is elongated and almost cylindrical. The end of the stadium is characterised by the third proembryoid moult.

The most recognisable character of the peripatoid stadium is the circular curvature of the cylindrical body (Fig. 15D). The body trunk has a circular shape in cross-section. Many developmental processes are already advanced. The segmentation process is still limited and can only be recognised on the body surface and on some elongated, downward-pointing antennae. The last leg-bearing segment and the post pedal segments are externally distinct for the first time, but morphologically incompletely differentiated. The forcipular segment and the trunk legs are not segmented. The penultimate embryoid moult is recorded at the end of the stadium.

The last embryoid stadium was the most frequently encountered brood-dependent stadium of *G. serbicus* in the sample. In this stadium, a continuous change in the appearance of the body — from spirally banded to falciform to fully unfolded — was observed, together with changes in shape from initially cylindrical to the onset of dorsoventral flattening (Fig. 15E). Compared to the previous stadium, the development of all body appendages is advanced. The antennae are fully segmented and directed forwards (Fig. 15F). The forcipular apparatus and trunk legs are also segmented, but do not yet have apical claws (Fig. 15F). The trunk legs elongate, initially from the anterior half. This elongation process is transferred to the posterior half like a kind of elongation wave. The last leg-bearing and genital segments are clearly separated, but not yet fully developed. Therefore, sex determination is not yet possible at this stadium. The last embryoid moult is recorded at this stadium. When examining the behaviour of the specimens in the brood, intensive writhing was the only type of movement observed.

Adolescens phase

In this phase there is only one attending stadium (adolescens I), which is both the last attending stadium and the first brood-independent stadium (Fig. 15G-J). All morphological structures are already developed, the segmentation of the body and all appendages as well as the process of dorso-ventral flattening are completed, and the differentiation of the last leg-bearing segment, the ultimate legs and the genital segment is finished. The colouration changes from whitish (at the beginning of the stadium) to pale yellowish (later), especially on the head, trunk legs and posterior end (Fig. 15G-I). Specimens in this stadium are completely mobile. Species identification and sex determination are conditionally possible for the first time at this stadium. Forcipular segment with clearly recognisable, taxonomically

important features such as coxopleural sutures, chitinous lines and basal denticles on the tarsungulum (Fig. 15J). The poison glands and the associated ducts are morphologically differentiated. The characters of the mouthparts are also important for species identification. Both pairs of lappets (coxosternal and telopodital) on the first maxillae and the pretarsus of the second maxillae are clearly recognisable. The pore fields on the metasternites of the trunk are not yet visible. Sex determination is only possible on the basis of the appearance of the postpedal segments. Males are easily recognised by the shape of the first and second genital sternites, the somewhat shorter biarticulate gonopods and the clearly visible penis; females by the gonopods in a single lamina. The shape and setation of the terminal legs are still not particularly informative for distinguishing the sexes. On each coxopleuron one coxal pore displaced posteriorly and one near the ultimate metasternite margin. Anal pores are already present in both sexes. Significantly, adolescens I is the second most common stadium in the entire sample.

Tab. 2. Summary of character changes during the brood-dependent postembryonic stadia of *Geophilus serbicus* Stojanović, Mitić and Antić, 2019.

| Stadium | Body shape | Average (\pm S.D.) body length (extremes in mm) | Antennae | Forcipular segment | Trunk legs |
|-----------------|---|--|--|---------------------------------------|---|
| Proembryoid I | Horseshoe; anterior half much higher, longer than posterior | 1.50 mm (\pm 0.01) (min 1.34; max 1.68) | Oval, non segmented; downwardly oriented | Rudiments; non segmented | Limbless |
| Proembryoid II | Horseshoe; equal height and length of anterior and posterior halves | 1.92 mm (\pm 0.08) (min 1.76; max 2.00) | Oval, some elongated, non segmented; downwardly oriented | Some elongated; non segmented | Appearance of limb buds |
| Proembryoid III | Horseshoe with folding of posterior half | 2.86 mm (\pm 0.16) (min 2.50; max 3.18) | Elongated, initiation of segmentation; downwardly oriented | Elongated; non segmented | Appearance of limb buds |
| Peripatoid | Annular with folding of posterior half into spiral shape | 3.59 mm (\pm 0.13) (min 2.57; max 5.45) | Final shape, segmented; downwardly oriented | Elongated; initiation of segmentation | Barely elongated; non segmented |
| Foetus | Spiral-falciform-unfolding (during stadium) with cylindrical shape to initiation of dorsoventral flattening | 4.05 mm (\pm 0.03) (min 2.32; max 5.36) | Final shape; forwardly oriented | Segmented; without apical claws | Segmented; initial lengthening from anterior half |
| Adolescens I | Unfolding, dorsoventral flattening | 4.94 mm (\pm 0.06) (min 3.06; max 5.93) | Final shape; laterally oriented | Complete developed | Complete developed |

Tab. 2. Continued

| Stadium | Last leg-bearing segment | Postpedal segment | Egg tooth | Colouration | Moulting at the end of the stadium | Movements |
|-----------------|---|---|-----------|----------------------|------------------------------------|--------------------|
| Proembryoid I | Limbless | Undifferentiated; short | + | Whitish | + | – |
| Proembryoid II | Barely elongated; non segmented | Undifferentiated; extended | – | Whitish | + | Mild contractions |
| Proembryoid III | Barely elongated; non segmented | Undifferentiated; extended | – | Whitish | + | Mild contractions |
| Peripatoid | Appearance of limb buds; initiation of segmentation | Appearance of a single genital segment | – | Whitish | + | Writhing |
| Foetus | Limbs segmented; still incompletely developed | Elongation of genital segment; still incompletely developed | – | Whitish | + | Intensive writhing |
| Adolescens I | Complete developed | External complete developed | – | Whitish to yellowish | – (in brood) | Walking |

CHAPTER 6. CHEMISTRY OF THE DEFENSIVE SECRETION OF *GEOPHILUS SERBICUS*

As is well known to myriapodologists, geophilomorph centipedes tend to release a cyanogenic secretion when disturbed. The ventral glands of *G. serbicus*, like those of other adesmatan geophilomorphs, are composed of numerous glandular modules that discharge their secretion into the cuticle via a separate pore opening; their openings are visible as well-defined ventral pore fields. The DCM extracts of the ventral gland secretion of *G. serbicus* contained three volatile compounds: the major components were benzaldehyde (65.4 %) and methyl 2-phenylacetate (30.1 %), while the minor component was benzoyl cyanide (4.5 %) (Fig. 16; Tab. 3). Of these chemical compounds, benzaldehyde and benzoyl cyanide are involved in cyanogenesis. Furthermore, no significant sexual difference was found in the amounts of the components in the species studied.

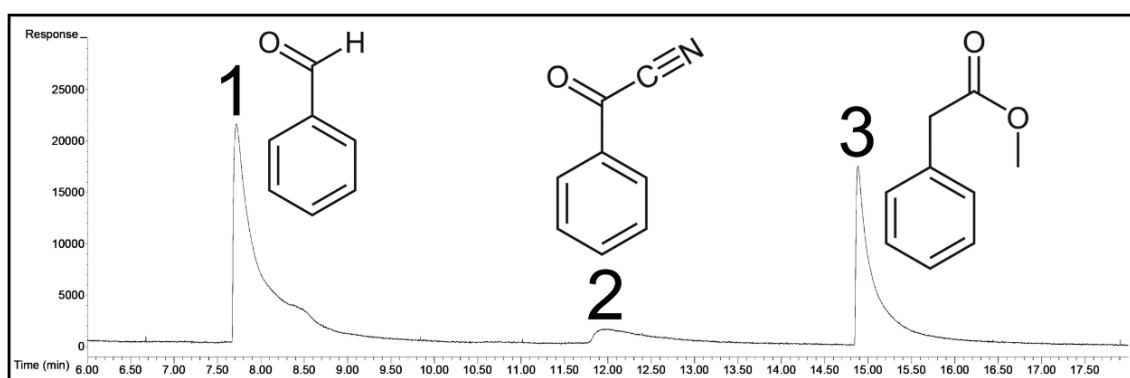


Fig. 16. GC-FID chromatogram of the DCM extract of the defensive secretion of *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 with structures of the identified compounds.

Tab. 3. The chemical composition of the defensive secretion of *Geophilus serbicus* Stojanović, Mitić and Antić, 2019 by GC-FID and GC-MS (percentages calculated from GC-FID peak areas).

| Peak | t _r (min) | Compound | Relative abundance (%) |
|------|----------------------|------------------------|------------------------|
| 1 | 7.72 | Benzaldehyde | 65.4 |
| 2 | 11.94 | Benzoyl cyanide | 4.5 |
| 3 | 14.88 | Methyl 2-phenylacetate | 30.1 |

CHAPTER 7. DISCUSSION

Our knowledge of the composition of the European fauna is often described as good compared to other areas. This is certainly true for many arthropod groups, but hardly for the geophilomorph centipedes, for which a consistent taxonomic and nomenclatural framework for the European fauna is still lacking (Bonato and Minelli, 2014). After the worldwide compendium by Attems (1929a), many taxonomic novelties were introduced. Regional monographs were produced only for a few countries (Brolemann, 1930 for France; Eason, 1964 and Barber, 2009 for the British Isles; Matic, 1972 for Romania; Stoev, 2002 for Bulgaria; Andersson et al., 2005 for Sweden), but only checklists were produced for other countries or regions (Foddai et al., 1995 for Italy; Stoev, 1997 for the Balkans; Wytwer, 1997 for Poland; Berg, 1999 for the Netherlands; Lock, 2000 for Belgium; Mitić, 2001, 2002, 2005 and Mitić and Tomić, 2002 for Serbia; Tajovský, 2001 for the Czech Republic; Andersson et al., 2008 for the Nordic countries; Geoffroy and Iorio, 2009 for France). However, all these contributions differed largely in the taxonomy and nomenclature used (Bonato and Minelli, 2014).

The genus *Geophilus* represents one of the most diverse geophilomorph centipede groups in Europe (Bonato and Minelli, 2014). After reviewing the available data for all *Geophilus* species known from the western Palaearctic (the western Euro-Siberian region, the Mediterranean basin, North Africa and western Asia), we have here described a new species that clearly differs from the other congeners by a unique combination of the previously presented morphological characters.

Geophilus serbicus sp. nov. shares many similarities in most morphological characters with other European species of this genus. The greatest overlap of characters is found in several species with an approximately equal or similar number of leg-bearing segments, such as: *G. aenariensis* Verhoeff, 1942; *G. impressus* C. L. Koch, 1847 (cited in Stojanović et al., 2019 as *G. alpinus* Meinert, 1870); *G. nesiotetes* Attems, 1903; *G. oligopus* (Attems, 1895); *G. pellekanus* Attems, 1903; *G. pusillifrater* Verhoeff, 1898 and *G. pygmaeus* Latzel, 1880. But besides the similarities, there are also some important morphological differences that distinguish *G. serbicus* sp. nov. from each of the above species individually.

Due to the presence of an isolated posterior coxal pore on each coxopleuron, *G. serbicus* sp. nov. resembles the morphologically diverse *G. impressus*, widely known mainly through its junior synonym *G. alpinus* (Case 3673; see Bonato and Minelli, 2015, and ICZN, 2020). Considering that *G. impressus* is a widespread European species with a large number of taxa recognised (more or less justified or not) as junior synonyms (see Bonato et al. 2016), this species shows a large morphological variability in certain taxonomically important characters. For example, when all literature data are considered, the number of leg-bearing segments varies from 41 to 63 (Popovici, 2020). Therefore, we had to check the range of variability of the individual characters and compare them with *G. serbicus*. The appearance of the pretarsus of the second maxillae and the carpophagus structures are considered to be the most appropriate characters to distinguish these two species (pretarsus as a stout tubercle with one or two apical tips and conspicuous carpophagus pits in *G. impressus*). In addition to these easily recognisable characters, there are some other, less conspicuous differences, such as the somewhat less pronounced proximity of the above-mentioned isolated pore to the posterior margin in *G. serbicus* sp. nov., differences in the setation on the clypeus, the appearance of the labrum and the first maxillae, etc. However, most of the differences can be absorbed in the great morphological variability of the species *G. impressus* (as already mentioned, part of this variability is reflected in the description of many junior

synonyms; e.g. Attems, 1895; Verhoeff, 1928, 1938; Bagnall, 1935; Koren, 1986; Christian, 1996; Popovici, 2020).

Problems in the comparison between species caused by insufficiently known morphology can be clearly illustrated by the example of *G. aenariensis* from the southern Italian peninsula. Verhoeff (1942, 1943) listed several characters of this species that may be helpful in distinguishing it from *G. serbicus* sp. nov., such as: the absence of bristles on the lateral parts of the labrum, the small but pointed pretarsus of the second maxillae, the absence of anal pores and the specific arrangement of the coxal pores. Unfortunately, the lack of description of other characters makes a more precise comparison impossible.

Two little known endemic species from Greece — *G. nesiotis* (from Crete) and *G. pellekanus* (from Corfu) — differ from each other in the absence of anal pores in *G. pellekanus*. They represent biogeographically and morphologically interesting species for comparison with *G. serbicus* sp. nov. The main differences between the two Greek species and *G. serbicus* sp. nov. are the absence of both pairs of lappets on the coxosternite of the first maxillae, the small pretarsus of the second maxillae, the absence of pore fields on the posterior part of the trunk and the absence of an isolated posterior coxal pore (Attems, 1929a).

Dányi (2007) provided a detailed re-description of *G. oligopus*, a species with an Alpine-Dinaric distribution. The following morphological characters can be used to distinguish *G. serbicus* sp. nov. from *G. oligopus*: a smaller number of leg-bearing segments reported in the literature (37–39), differences in the labrum, the presence of spear-like sensillae on the terminal article of the antennae, the absence of lappets on the first maxillae and a small pretarsus of the second maxillae, which presents as a stout tubercle with one or two apical tips. All other features show a considerable overlap between these two species.

The main differences between *G. serbicus* sp. nov. and *G. pusillifrater* are the absence of lappets on the first maxillae and some different features of the labrum in *G. pusillifrater*. The most striking similarities are the inconspicuous carpophagus pits and the presence of 3–5 coxal pores, with the isolated pore located more posteriorly on the coxopleura. The original description of *G. pusillifrater* was based on a juvenile specimen collected near Mostar in Bosnia and Herzegovina (Verhoeff, 1898). Later, this species was also recorded from Great Britain and France (Lewis, 1961b; Iorio, 2006). The type specimen deposited in the Naturkundemuseum Berlin (Inv. Nom. ZMB 13541) is not particularly informative due to the poor condition of the microscopic plate. Only the cephalic plate with the antennae and the maxillary complex are preserved in good condition. In addition, the posterior third of the trunk with only a single walking leg without pretarsus and the apical part of the one separated walking leg (tarsus and pretarsus) are partially preserved. Unfortunately, the complete forcipular segment, the labrum, the remaining parts of the trunk, the ultimate legs and the ventral part of the ultimate leg-bearing segment as well as the postpedal segments are missing. However, a direct examination of the remains of the holotype of *G. pusillifrater* provides us with some new and confirmed some already known information useful in distinguishing these two species, such as: the dimensions of the cephalic plate (about 1.2 times longer than wide) and the antennae (about 3.4 times longer than cephalic plate), as well as the absence of the two pairs of lappets on the first maxillae. The other characters observed that are similar to *G. serbicus* sp. nov. are: clypeus without a distinct clypeal area, elongate and apically pointed second maxillary pretarsus, walking legs with a long, curved pretarsus with two accessory spines and the presence of the pore fields in the posterior part of the trunk. All other taxonomically important characters are not

conspicuous. Furthermore, it is not possible to confirm the body size, sex and arrangement of the coxal pores given by Verhoeff (1898) for *G. pusillifrater*. Judging by the appearance of the specimen, the holotype is most probably at the adolescens developmental stadium. To verify the differences in the early developmental stadia, we dissected several adolescent specimens of *G. serbicus* sp. nov. from the brood and found that both pairs of lappets (coxosternal and telopodital) are already fully developed at this stadium.

The redescription of *G. pygmaeus* by Peretti and Bonato (2016) provides sufficient information that is useful for a comparison. The most striking differences from *G. serbicus* sp. nov. are the much shorter antennae (about twice as long as the cephalic plate), the presence of a small dorsal bulge near the tip of the pretarsus of the second maxillae, pore fields only in the anterior part of the trunk, ultimate pretarsi ventrally with two accessory spines, and an isolated coxal pore that is smaller and positioned more anteriorly in relation to the posteriormost remaining pores. Other characters of these two species are similar. On the basis of all these considerations, we believe that the description of our specimens as a new species is justified. The Balkan Peninsula is considered a potential centre of diversity for European centipedes (Stoev, 1997; Simaiakis and Strona 2014). For this reason, the discovery of new species of an insufficiently known animal group such as the geophilomorph centipedes is by no means surprising. Ecologically, *G. serbicus* sp. nov. inhabits the leaf litter and surface layers of the soil in mountain beech forests (at altitudes of about 1500 metres above sea level). For the time being, the new species can be designated as a local endemic of the Stara Planina Mountains and Serbia, although there is a good chance that it also occurs in the same mountain range on the other side of the Bulgarian border, in which case it would have the status of a Balkan endemic.

A basal split of the Geophilomorpha into Placodesmata (= Mecistocephalidae) and Adesmata (all other geophilomorphs), which has been recognised in many studies (Verhoeff, 1902–25; Foddai and Minelli, 2000; Edgecombe and Giribet, 2004), corresponds to the anatomical differences between these groups, especially with regard to the absence or presence of the ventral pores — openings of the ventral glands. Ventral pores are observed in members of all Adesmata families with the exception of the small tropical American family Neogeophilidae, although there are repeated apparent secondary losses within different families. In contrast, ventral pores are absent in the Mecistocephalidae, apart from doubtfully homologous structures present only in the males of most species of the genus *Tygarrup* Chamberlin, 1914 (Turcato et al., 1995). The observations that egg and/or offspring attendance in *G. serbicus*, *H. illyrica*, *P. herzegowinensis*, *S. linearis*, *S. rhodopensis*, *S. herzegowinensis* and *S. carniolensis* follows the pattern of all Adesmata (the female guards the brood with sterna facing outwards) (Chipman et al., 2004; Mitić et al., 2010, 2012, 2016; Stojanović et al., 2020; Gedged et al., 2024) and not that of the mecistocephalid *Dicellogophilus carniolensis* (C. L. Koch, 1847), all Scolopendromorpha and the genus *Craterostigma* (guarding with the terga facing outwards) (Manton, 1965; Bonato and Minelli, 2002; Mitić et al., 2012, 2016, 2023; Siritwut et al., 2014; Stojanović, 2016; Vega Román et al., 2018) is behavioural evidence for the hypothesis of the Placodesmata-Adesmata division. However, the guarding behaviour documented in another mecistocephalid species, *Mecistocephalus togensis* (Cook, 1896) (Edgecombe et al., 2010), shows that at least some mecistocephalids guard their brood with the ventral side facing outwards, as in Adesmata. This variability between different mecistocephalids suggests that guarding posture may be more subject to homoplasy (convergence or reversal) than previously thought. Within the clade of centipedes with prolonged parental care (= Phylactometria), the female position with

outward-facing terga is plesiomorphic, and the opposite position with outward-facing sterna is an apomorphy that appeared early within the Adesmata (Bonato and Minelli, 2002; Edgecombe et al., 2010). According to the alternative Amalpighiata hypothesis, in which Lithobiomorpha and not *Craterostigmus* is the sister group of Epimorpha, it is assumed that maternal care is homoplastic. It is either a general feature of Pleurostigmophora (which includes all living centipede orders except Scutigermorpha) that was secondarily modified (lost, reversed or otherwise altered) in Lithobiomorpha, or it was convergently shared by *Craterostigmus* and Epimorpha (Fernández et al., 2014).

We have confirmed here that in all geophilomorphs from temperate regions for which adequate data are available (Verhoeff, 1902–25; Palmén and Rantala, 1954; Weil 1958; Bonato and Minelli, 2002; Mitić et al., 2010, 2012, 2016, 2023; Stojanović et al., 2020), egg-laying and attending the eggs and offspring usually take place in the summer months. Weil (1958) has reported that the time of egg and offspring attendance in *G. flavus* and *S. linearis* lasts until October and November, respectively, but these data were based on laboratory observations. The egg-laying and attending period is much shorter in the littoral species *S. maritima*, and Lewis (1961) has suggested that this may be necessary to prevent the eggs and young from being exposed to immersion by the high autumn tides. In large parts of Europe, most centipedes are perennial. They are characterised by a low reproductive potential, a long life span and a high intraspecific variability in terms of duration and number of developmental stadia. Almost all European centipedes are such equilibrium species or so-called ‘k-strategists’ (Voigtländer, 2011). Considering that the average clutch sizes of Geophilomorpha vary between ten (*G. serbicus*) (Stojanović et al., 2020) and 39 (*Geophilus rubens* Say, 1821) (Lewis, 1981), the fecundity of the studied species is very low, probably due to the small body size of the females, as is the case for most insects (Honěk, 1993). Our results are also in line with previous studies (Brena, 2014; Stojanović et al., 2020), according to which there is a developmental gradient along the antero-posterior axis during this phase of postembryonic development, with the last segments being less developed. The adult structures/organs in *S. rhodopensis* are not yet fully developed and foetus relies exclusively on the yolk.

What factors have promoted parental care in centipedes? Parental care is considered a prime example of an altruistic character that has evolved to enhance the fitness of the recipients of care (offspring) at the expense of the donor of care (parents). The costs of decreased parental reproductive success associated with parental care must be outweighed by the indirect benefits of the parents in the form of increased fitness of the offspring (Clutton-Brock, 1991; Smiseth et al., 2012; Wong et al., 2013; Smiseth, 2018). Although the few empirical studies on parental care in epimorphic centipedes provide good evidence for its current benefits, almost nothing is known about the evolutionary origins of care (Mitić et al., 2017). Ecological factors such as harsh environments, ephemeral food sources or predation pressure in combination with life history or social interactions are generally accepted as evolutionary drivers of parental care (Wong et al., 2013). In agreement with previous studies (Manton, 1965; Brunhuber, 1970; Bonato and Minelli, 2002; Chipman et al., 2004; Edgecombe et al., 2010; Knoflach, 2010; Mitić et al., 2010, 2012, 2016; Siriwtut et al., 2014; Vega Román et al., 2018; Stojanović, 2016; Stojanović et al., 2020), we have demonstrated that in Epimorpha not only the egg clutch is cared for until hatching, but also the early postembryonic stadia, which are very incomplete and show only restricted movements (if any), remain under the protection of the mother. Several studies have shown that if the attending mothers are disturbed or irritated beyond a certain level, they react by either devouring the eggs or abandoning the brood to their fate. In the latter case, the eggs or young soon die

due to natural enemies (predators, cannibalistic conspecifics and pathogens) or harsh environmental conditions (desiccation) (Lawrence, 1947; Auerbach, 1951; Palmén and Rantala, 1954; Brunhuber, 1970; Radl, 1992; Cabanillas et al., 2019). Such forms of care probably emerge from relatively simple ancestral forms of care — once egg attendance has evolved, it could evolve into offspring attendance by simply delaying the time of parental desertion (Smiseth et al., 2012; Smiseth, 2018).

The morphologically supported tree recognises a fundamental division of the Chilopoda into Notostigmophora (composed of the single order Scutigermorpha) and Pleurostigmophora, which groups the other four living orders (Pocock, 1902; Verhoeff, 1902–25). Pleurostigmophora is further divided into Lithobiomorpha and a putative clade that groups the remaining three orders; this group is called Phylactometria and is based on the common behavior of maternal care for the eggs and hatchlings. Phylactometria consists of the relictual *Craterostigma*, Scolopendromorpha and Geophilomorpha, whereby the latter two orders are almost universally united in a group called Epimorpha (Edgecombe and Giribet, 2004). The genus *Craterostigma* has a single anamorphic stadium in its life cycle; it hatches from the egg as a 12-legged stadium and acquires the adult number of 15 leg-pairs — the plesiomorphic number of legs in Chilopoda — in the following stadium (Manton, 1965). This is in contrast to numerous anamorphic stadia in the orders Scutigermorpha and Lithobiomorpha, which hatch with 4 or 6–8 leg pairs respectively and add more and more segments until they reach the definitive 15 leg pairs (e.g. Verhoeff, 1902–25, 1905; Murakami, 1956a, 1956b, 1958, 1959a, 1959b, 1960, 1961a, 1961b, 1963; Andersson, 1976, 1979, 1984; Daas et al., 1996; Serra and Miquel, 1996; Voigtländer, 2007; Stojanović et al., 2023). The Phylactometria hypothesis has generally regarded the “reduced hemianamorphosis” of *Craterostigma* as a transitional stadium in the evolution of complete epimorphosis in Epimorpha (Fernández et al., 2014), where the evolutionary change in developmental timing (i.e. the acceleration of segment formation) has led to the ‘embryonalisation’ of the originally postembryonic stadia which would risk an early death without parental care (Arthur, 2011). The ancestral state of Chilopoda is to have no parental care, which has evolved later in evolutionary history in the stem-group of Phylactometria.

The early development of *G. serbicus* can be described according to a ‘three-phase model’, similar to *S. maritima* and *C. parisi* (Brena, 2014; Stojanović et al., 2015, 2016). The proposed developmental model envisages the existence of an embryonic, an embryoid and an adolescens phase under brood conditions. The first two phases are obligatorily linked to the mother. This may help to ensure that the offspring receive optimal humidity and are protected from bacterial and fungal infections and, to a certain extent, from soil predators (Brunhuber, 1970; Radl, 1992; Mitić et al., 2024). Finally, the last attending stadium or adolescens I stadium is ready to leave the mother. This stadium is also the first juvenile stadium with adult appearance and exists significantly longer than a brood-independent stadium (Lewis, 1959, 1961a; Stojanović, 2016).

Every single stadium of the overall brood-dependent development of *G. serbicus* overlapped with the same developmental period of the best-studied geophilomorph species, *S. maritima* (Lewis, 1959, 1961a; Chipman et al., 2004; Chipman and Stollewerk, 2006; Brena and Akam, 2012; Brena, 2014). The total number of stadia and the same processes per stadia are identical in both species, with small differences in certain details. One of these differences is in the dynamics of cell migration during the earliest embryonic stadia. In our case, cell migration from the centre of the egg to its periphery does not show such a pronounced radial movement as has been shown in *S. maritima* (Brena and Akam, 2012). Figure 14B shows that the peripheral migration in *G. serbicus* exhibits a certain polarity in the filling of

the egg volume. The colouration of the eggs is also different in these two species. In *S. maritima* the eggs have a distinctly yellowish colour from the beginning of embryonic development, whereas in *G. serbicus* they tend to be more whitish. Due to the pellucid chorion in *G. serbicus*, all morphological features of the embryos are visible through the membrane without dechoriation. This is the main reason why it was not necessary to remove the chorion from the surface of the embryo. In contrast, the description of the embryonic development of *S. maritima* was largely based on the characters of dechorionated embryos (Brena and Akam, 2012).

The development of the embryos within a brood is not synchronised, as can be seen in the case of the hatching stadium. Hatching was only observed in five specimens from different broods (Tab. 2). This indicates that this transitional stadium between embryonic and postembryonic development is the shortest during the entire early development of *G. serbicus*. After hatching, the egg teeth become unusable and are thrown out with the first embryoid exuviae at the end of the proembryoid I stadium. Brena and Akam (2012) suggested that these exuviae in *S. maritima* remain attached to the posterior end of the specimens until the peripatoid stadium. A similar situation can also be observed in some peripatoids (Fig. 15D).

The traditional concept of the developmental pattern of Epimorpha is defined with almost dogmatic certainty as epimorphosis. This interpretation implies that specimens have the final number of trunk segments immediately after hatching. Some earlier studies suggest that the number of segments increases slightly during postembryonic development in certain geophilomorph species (Johnson, 1952; Misioch, 1978). Several later studies failed to confirm such a claim and sought additional evidence (Minelli, 1985; Horneland and Meidell, 1986). According to Brena (2014), the embryoid part of postembryonic development can be interpreted as an extension of embryonic development. Brena emphasised that the appearance of this stadium may have significance for the evolution to epimorphic from anamorphic developmental patterns, as it “completes itself without completely losing the postembryonic segmentation activity”. In the case of the early development of *G. serbicus*, one can agree with such claims, considering that segmentation of the last leg-bearing segment and the postpedal segments is completed in the late stadia of embryoid development (at the peripatoid and foetus stadia; Fig. 15D, E).

The last attending stadium (adolescens I) is the first morphologically fully developed stadium. Many authors agree that adolescens I stadium can be considered the first juvenile stadium of centipedes (e.g. Brena, 2014; Lewis, 1959, 1961a; Mitić et al., 2010; Mitić, 2012). At this stadium, thanks to the degree of differentiation of the individual morphological structures, it is possible for the first time in the developmental history of *G. serbicus* to conditionally make a precise species identification and sex determination. Most of the taxonomically important characters are clearly visible for the first time in stadium adolescens I, e.g. the coxopleural sutures, the chitin lines and the basal denticles on the tarsungulum (all on the forcipular segment; see Fig. 15J), coxosternal and telopodital lappets on the first maxillae and the pretarsus of the second maxillae, the presence of a coxopleural pore on each coxopleuron and one near the margin of the last metasternite, which is displaced further posteriorly, and the presence of anal pores. However, some of the characters important for species identification, such as the pore fields on the metasternites of the trunk, are still not recognisable. Sexual dimorphism is also only recognisable for the first time at this stadium on the basis of some characters of the postpedal segments. In many geophilomorph species, sex determination is possible on the basis of the number of

leg pairs (Lewis, 1981). The number of leg pairs in *G. serbicus* is already recognisable in the peripatoid and foetus stadia, but this character is not as reliable in determining the sex of this species. According to the original description by Stojanović et al. (2019), there is a certain percentage of overlap in the number of leg pairs between mature males and females in the population. Sexual dimorphism in the studied species is more strongly expressed in certain features of the terminal legs and genital segments, with the second group of characters being clearly recognisable for the first time in the last attending stadium. The most clearly recognisable characters between the sexes in *G. serbicus* are the presence of biarticulate gonopods and penis in males and gonopods in a single lamina in females. The differences in the shape of the first and second genital sternites can also be helpful in sex determination (as already shown in adult specimens by Stojanović et al. 2019). The ultimate legs of adolescens I attending specimens are still without differences between the sexes in shape and chaetotaxy. Upon leaving the brood and mother, the adolescens I stadium becomes a free-living stadium and the early development of *G. serbicus* is complete.

As already mentioned, in temperate regions, Epimorpha guards in summer (Verhoeff, 1902–1925; Palmén and Rantala, 1954; Weil, 1958; Lewis, 1959, 1961a). The duration of early development and the length of the attending period vary between species. Brunhuber (1970) estimates the attending period at 50 to 60 days for *Cormocephalus westwoodi* Newport, 1844, while the same period is estimated at 54 days for *Scolopendra cingulata* Latreille, 1829 (Radl, 1992) and around 70 days for *C. parisi* (Stojanović et al. 2015). Iorio (2003) recorded an unusual minimum brooding period of only 18 days for *S. heros* in captivity. In Geophilomorpha species, the duration of attending can be longer, but differences in this reproductive character have also been found within species. In a natural population of *Strigamia maritima* from southern England, Lewis (1961) estimated the duration of early development to be about eight weeks. In a population of the same species from the west coast of Norway, this period lasted about two months (Økland, 1984). In *S. maritima*, the transition from egg laying to the appearance of stadium adolescens I takes almost 90 days under laboratory conditions. This period can be divided into 49 days for the time from oviposition to hatching (Brena and Akam, 2012) and 40 days for the embryoid phase until the appearance of adolescens I stadium (Brena, 2014). The duration of the first postembryoid stadium in the brood is not known. The shorter duration of early development in natural populations is explained by the variable temperature values in the habitat (Brena, 2014). The attending period of *G. serbicus* from the Babin Zub, which was analysed in the present study, is estimated at around 60 to 70 days (Tab. 2). At least half of this time is the duration of embryonic development.

In this dissertation we have confirmed that cyanogenesis is almost universally present in the geophilomorph centipedes (see Schildknecht et al., 1968; Jones et al., 1976; Vujisić et al., 2013; Mitić et al., 2024); the only known exception to date is the genus *Henia* C. L. Koch, 1847 (see Hopkin and Gaywood, 1987; Hopkin et al., 1990), which is often found curled up in a defensive ball (Barber, 2008), in the absence of a powerful chemical defence. The presumed precursor of HCN in *G. serbicus* is benzoyl cyanide, while benzaldehyde is probably formed by the degradation of mandelonitrile, as is the case in most cyanogenic centipedes and millipedes (Jones et al., 1976; Mori et al., 1994; Taira et al., 2003; Eisner et al., 2005; Zagrobelny et al., 2008; Vujisić et al., 2013; Shear, 2015; Mitić et al., 2024). It is known that benzoyl cyanide inhibits mycelial growth and spore germination (Roncadori et al., 1985), so that the ventral secretion of *G. serbicus* could also serve as a defence against noxious fungi. The DCM extract of the studied species also contained a non-cyanogenic compound, methyl 2-phenylacetate, which is a

known component of the pheromone of the leaf-cutting ant *Atta sexdens* (Linnaeus, 1758) (Cross et al., 1979) and the ventral secretion of *C. flavidus* (Mitić et al., 2024). However, the role of this compound in the ventral secretion of *G. serbicus* and *C. flavidus* is still unknown. Pheromone signals, which are emitted by individuals to affect the behavior or physiology of conspecifics, play a pivotal role for numerous arthropods (Karlson and Lüscher, 1959; Karlson and Butenandt, 1959; Ryan, 1966; Butler, 1967; Free and Simpson, 1968; Regnier and Law, 1968; Atema and Engstrom, 1971; Blum and Brand, 1972; Shorey, 1973; Dunham, 1978; Gleeson, 1980; Attygalle and Morgan, 1985; Jackson and Morgan, 1993; Howse et al., 1998; Winston and Slessor, 1998; Keeling et al., 2003; Morgan, 2004, 2009; Schulz, 2013; Fleischer and Krieger, 2018). They trigger and control various critical processes such as mating, reproduction, aggregation, and alarming as well as the division of labor in eusocial insects (Fleischer and Krieger, 2018). However, pheromones have never been identified in centipedes (and millipedes), with the exception of the coxal pheromone of *L. forficatus* (Littlewood and Blower, 1987; Littlewood, 1988), and further analyses need to be carried out to prove this hypothesis.

Schildknecht et al. (1968), Jones et al. (1976), Vujisić et al. (2013) and Mitić et al. (2024) identified thirteen compounds in the ventral secretions of the geophilomorph centipedes — cyanogenic compounds, alkaloids, branched long-chain esters, branched acids and phenylacetate esters. Some of these compounds are unique or rare in nature. For example, in the himantariid *H. gabrielis*, farnesyl 2,3-dihydrofarnesoate was a new compound, whereas himantarine and farnesyl farnesoate were not known to be natural products (Vujisić et al., 2013). Although the defensive chemistry of the families Dignathodontidae, Geophilidae, Himantariidae and Linotaeniidae has been studied for a few species (Schildknecht et al., 1968; Jones et al., 1976; Hopkin et al., 1990; Vujisić et al., 2013; Mitić et al., 2024), the chemistry of all other geophilomorph groups is still completely unexplored. We hope that the specificity of the chemical composition of the defensive secretion will serve to some extent as a criterion for chemotaxonomy and that the analysis of more species will help to clarify the phylogenetic relationships within the Geophilomorpha.

Last but not least, three geophilomorph centipedes analysed in this study — *P. herzegowinensis*, *S. rhodopensis* and *S. herzegowinensis* — have not yet been reported from Serbia (Mitić, 2001, 2002, 2005; Mitić and Tomić, 2002). *P. herzegowinensis* is a species whose actual taxonomic value is still uncertain, as its morphology is poorly known (Bonato and Minelli, 2014); the type locality is Konjsko in Bosnia and Herzegovina (Verhoeff, 1901; Moritz and Fischer, 1979; Bonato et al., 2016). On the other hand, *S. rhodopensis* is closely related to *S. antecribellata* (Verhoeff, 1898) and *S. cribelliger* (Verhoeff, 1898), from which it differs by the first maxillary lappets (present in *S. rhodopensis*, absent in the other two species) and by the shape of the ventral pore fields (sub-triangular in *S. rhodopensis*, trapezoidal-oval in *S. antecribellata* and oval-elongated in *S. cribelliger*) (Kaczmarek, 1970; Dányi, 2010). Our results confirm that *S. rhodopensis* is a montane species distributed in the Carpathians and the Balkans. In addition, the name *S. herzegowinensis* was first introduced by Verhoeff (1901) as a “nomen nudum” for a variety of *Scolioptanes acuminatus crassipes* and then listed by Attems (1903) as a variety “*hercegovinensis*” of *Scolioptanes crassipes*. However, it was only later, by Verhoeff (1935), validly described as a species of *Scolioptanes* Bergsøe & Meinert, 1866. It was assigned to *Strigamia* Gray in Jones, 1843 by Dobroruka (1977). No other specimens were known, but the validity of the species has never questioned. *S. herzegowinensis* is known from a single locality in the Dinarides (Plasa near Jablanica, Bosnia and Herzegovina) (Verhoeff, 1935; Bonato et al., 2012, 2016). Significantly, the

centipede fauna of Serbia, based on critically revised literature data (Attems, 1929b, 1959; Folkmanová, 1935; Vučković, 1956; Matic, 1957; Matic and Dărăbanțu, 1968; Pujin, 1973; Kos, 1992; Stoev, 1997; Mitić, 2001, 2002, 2005; Mitić and Tomić, 2002; Mitić et al., 2003, 2012; Stojanović et al., 2019; Stojanović, 2024), is represented by a total of 70 species (one Scutigermorpha, 36 Lithobiomorpha, five Scolopendromorpha and 28 Geophilomorpha).

CHAPTER 8. CONCLUSIONS

Despite a considerable increase in research efforts in recent decades, centipedes (Chilopoda) are still an insufficiently known group of arthropods. In this study we analysed ontogenetic, phylogenetic and chemoeological characteristics of parental care in seven geophilomorph centipedes from Serbia. One of these species was *G. serbicus*, a new species for science described here, which was found near the peak of Babin Zub in the Stara Planina Mountains. Despite the similarity to some *Geophilus* species, the newly described taxon differs in a number of morphological characters, which indicates a great diversity of the centipede fauna in this part of the Balkan Peninsula. Parental care is a purely descriptive term that does not take into account the costs incurred by parents in providing care. We have confirmed that female-only parental care in geophilomorph centipedes enables the development of eggs and juveniles under suitable conditions and increases their chances of survival; it includes both prenatal behaviour, such as egg attendance and postnatal care, such as offspring attendance. Furthermore, the terminology used to describe diversity in parental care can sometimes be confusing, as alternative schemes are used for different taxa and the same form of care may go by different names in different taxonomic groups. In these myriapods we have thus for the first time clearly emphasised the difference between the terms ‘attendance’ and ‘brooding’, the latter of which was traditionally used in myriapodology. The importance of parental care in evolutionary biology has only been recognised relatively recently — the evolution of parental care represents an important step in the evolution of sociality, as it leads to the formation of family groups that form a bridge to more complex forms of social structures. In centipedes, maternal care is a derived (apomorphic) character restricted to *Craterostigma* (with the suppressed anamorphosis) and Epimorpha, in which heterochronic change has led to embryonalisation of early postembryonic stadia that would risk early death without offspring attendance. We strongly believe that in centipedes, ecological factors such as harsh environments and predation pressure combined with life history have promoted parental care. However, further experimental studies and phylogenetic analyses are needed that combine the potential effects of a species’ ecology and life history on the evolution of parental care. We also showed that females of Geophilomorpha wrap themselves around the eggs or young during prolonged parental care, keeping at least part of the trunk in an S-curve. At the same time, most of their trunk was orientated so that the dorsal side faced the brood and the ventral side faced outwards. Such behaviour confirms the basal division of the Geophilomorpha into Placodesmata (i.e. family Mecistocephalidae) and Adesmata, which corresponds to the anatomical differences between these groups, especially with regard to the absence or presence of the openings of the ventral glands. As in *S. maritima* and probably in all other geophilomorph centipedes, the early development of *G. serbicus* consists of an embryonic, an early postembryonic (embryoid) and a adolescens phase, based on the presence or absence of a chorion and the degree of similarity to the adult habitus. The data presented in this dissertation confirm that the embryoid phase of postembryonic development of geophilomorphs may represent an extension of embryonic development that could correlate with the evolution of epimorphic development from an anamorphic ancestor. Significantly, three of the species analysed, including *S. rhodopensis*, have not yet been reported from Serbia, whose fauna is currently represented by a total of 70 species. Although we have found only three volatile compounds in the ventral gland secretion of *G. serbicus*, and the secretion of a relatively small number of geophilomorph species in few families has been studied to date, these centipedes should continue to be excellent candidates for secondary metabolite

studies, not only in the search for molecules new to science or geophilomorphs, but also in the expectation that more data will lead to chemotaxonomic and phylogenetic information in the future.

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Biography

Amna Gedged was born in 1981 in Bani Walid, Libya. Amna received her Bachelor's degree in biology from the University of Macerata, Libya in 2002, where she worked as a teaching assistant in the Biology Department. She received a scholarship from the Libyan Ministry of Higher Education to obtain her master's and PhD degrees abroad. Amna completed her master's degree at the University of Belgrade – Faculty of Biology in 2012 and the following year enrolled in a PhD programme at the University of Belgrade – Faculty of Biology, module Developmental Biology of Animals. To date, she has published four articles in peer-reviewed journals and two conference abstracts.

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Broj indeksa: B3051/2013

Izjavljujem da je doktorska disertacija pod nazivom „Ontogenetska, filogenetska i hemoekološka obeležja brige o potomstvu kod nekih geofilomorfnih stonoga (Chilopoda: Geophilomorpha)“, *engl.* „Ontogeny, phylogeny and chemoecology of parental care in some geophilomorph centipedes (Chilopoda: Geophilomorpha)“

- rezultat sopstvenog istraživačkog rada;
- da disertacija u celini ni u delovima nije bila predložena za sticanje druge diplome prema studijskim programima drugih visokoškolskih ustanova;
- da su rezultati korektno navedeni;
- da nisam kršila autorska prava i koristila intelektualnu svojinu drugih lica.

U Beogradu, 5.8.2024. godine

Potpis autora



Izjava o istovetnosti štampane i elektronske verzije doktorskog rada

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Studijski program: biologija

Naslov rada: „Ontogenetska, filogenetska i hemoekološka obeležja brige o potomstvu kod nekih geofilomorfnih stonoga (Chilopoda: Geophilomorpha)“, *engl.* „Ontogeny, phylogeny and chemoeecology of parental care in some geophilomorph centipedes (Chilopoda: Geophilomorpha)“

Mentori: prof. dr Bojan Mitić i prof. dr Vladimir Tomić

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