Graellsia, 79(1): e180
enero-junio 2023
ISSN-L: 0367-5041
https://doi.org/10.3989/graellsia.2023.v79.347

HABITAT, AGGREGATIONS AND POSTEMBRYONIC DEVELOPMENT OF THE SIPHONOCRYPTID MILLIPEDE *HIRUDICRYPTUS CANARIENSIS* (LOKSA, 1967) IN THE LAUREL FOREST OF TENERIFE (DIPLOPODA: SIPHONOCRYPTIDA)

Leif Moritz[1,4,*], Thomas Wesener[2] & Benjamin Wipfler[3]

[1,2,3] Zoologisches Forschungsmuseum Alexander Koenig, Leibniz Institute for the Study of Biodiversity Change (LIB),
Adenauerallee 160, 53113 Bonn, Germany.
[2] Email: t.wesener@leibniz-lib.de – ORCID iD: https://orcid.org/0000-0002-2028-3541
[3] Email: Benjamin.Wipfler@leibniz-lib.de – ORCID iD: https://orcid.org/0000-0002-2367-6789

[4] Institute of Evolutionary Biology and Ecology, University of Bonn, An der Immenburg 1, 53121 Bonn, Germany.

[*] Corresponding author: moritz.leif@gmail.com – ORCID iD: https://orcid.org/0000-0002-6028-5189

ABSTRACT

Millipedes (Diplopoda) are detritivores, which mostly live hidden within the soil and leaf litter, and for most species only little is known about their biology. This is especially true for the enigmatic Colobognatha, such as *Hirudicryptus canariensis*, a siphonocryptid millipede which is endemic to the laurel forests of Macaronesia. So far, no one reported observations of a living Siphonocryptida. Here we present observations of living specimens in the Anaga Mountains on Tenerife, Canary Islands (Spain) as well as data on their postembryonic development based on observations of 296 specimens, including data from the literature. On Tenerife *Hirudicryptus canariensis* was exclusively found on and under the bark of the heather *Erica platycodon* at elevations of 630–870 m. *Hirudicryptus canariensis* formed aggregations of juvenile and mature individuals with several hundred individuals per tree and can be considered as 'transient subsocial'. *Hirudicryptus canariensis* hatches with 6 tergites and 7 leg pairs (stadium I), lacking an apodous tergite, and subsequent stadia always have a single apparently apodous tergite, although a varying number of podous tergites is added. Therefore, podous tergites can develop de novo without an apodous precursor. The number of leg pairs is always odd, and immature gonopods (modifications of leg 9 and 10 in males) occur first in individuals of stadium III with 15 tergites and 23 leg pairs. Gonopods are fully developed in stadium IV. The postembryonic development is partly reflected in the color pattern. For future identification of *H. canariensis*, we provide first barcode data (CO1) of the species and the first molecular data of a member of the Siphonocryptida.

Key words: Anaga Mountains, Canary Islands, endemism, *Erica platycodon*, Macaronesia, social.

RESUMEN

Hábitat, agregaciones y desarrollo postembrionario del milpiés *Hirudicryptus canariensis* (Loksa, 1967) en el bosque de laurisilva de Tenerife (Diplopoda: Siphonocryptida)

Los milpiés (Diplopoda) son detritívoros que viven generalmente ocultos dentro del suelo y la hojarasca, y en la mayoría de las especies poco se conoce sobre su biología. Esto es especialmente cierto en el caso de los enigmáticos Colobognatha, como *Hirudicryptus canariensis*, un milpiés sifonócriptido endémico de los bosques de laurisilva de la Macaronesia. Hasta ahora, nadie ha reportado observaciones de un Siphonocryptida vivo. Aquí presentamos observaciones de ejemplares vivos en el macizo de Anaga en Tenerife, Islas Canarias (España), así como también datos sobre su desarrollo postembrionario basados en observaciones de 296 ejemplares, incluyendo datos de la literatura. En Tenerife *Hirudicryptus canariensis* se encontró exclusivamente sobre y bajo la corteza del brezo *Erica platycodon* a elevaciones de 630-870 m. *Hirudicryptus canariensis* forma agregaciones de individuos juveniles y maduros con varios cientos de ejemplares por árbol y puede considerarse como 'temporalmente subsocial. *H. canariensis* eclosiona con 6 terguitos y 7 pares de patas (estadio I), careciendo de un terguito ápodo, y en los estadios posteriores siempre tiene un único terguito aparentemente ápodo, aunque se añade un número variable de terguitos con patas. Por lo tanto, estos últimos pueden desarrollarse de nuevo sin un precursor ápodo. El número de pares de patas es siempre impar, y los gonópodos inmaduros (modificaciones de los pares de patas 9 y 10 en los machos) aparecen inicialmente en individuos del estadio III con 15 terguitos y 23 pares de patas. Los gonópodos están completamente desarrollados en el estadio IV. El desarrollo postembrionario se refleja en parte en el patrón de color. Para futuras identificaciones de *H. canariensis*, proporcionamos los primeros datos de la secuencia genética (CO1) de la especie y los primeros datos moleculares de un miembro de los Siphonocryptida.

Palabras clave: endemismo, *Erica platycodon,* Islas Canarias, Macaronesia, Macizo de Anaga, social.

Recibido/*Received*: 14/03/2022; **Aceptado/*Accepted***: 14/09/2022; **Publicado en línea/*Published online***: 16/05/2023

Cómo citar este artículo/*Citation*: Moritz, L., Wesener. T. & Wipfler, B. 2023. Habitat, aggregations and postembryonic development of the siphonocryptid millipede *Hirudicryptus canariensis* (Loksa, 1967) in the laurel forest of Tenerife (Diplopoda: Siphonocryptida). *Graellsia*, 79(1): e180. https://doi.org/10.3989/graellsia.2023.v79.347

Introduction

Millipedes (Diplopoda) play a fundamental role in terrestrial ecosystems as detritivores and soil forming organisms (Golovatch & Kime, 2009; Joly *et al.*, 2020), and are often adapted to certain microclimates, and biotic and abiotic factors (David, 2015). For example, the hygrophilous colobognathan millipedes, which contain the millipede species with the highest number of legs (Marek *et al.* 2021), are often found in moist habitats and are vulnerable to desiccation (e.g. Cook & Loomis, 1928; Wegensteiner, 1982; Golovatch *et al.*, 2015). The Colobognatha comprise the four taxa Platydesmida, Siphonophorida, Polyzoniida and Siphonocryptida (Blanke & Wesener, 2014), and are probably one of the least studied and most neglected millipede groups with regard to their taxonomy (Brewer *et al.*, 2012; Read & Enghoff, 2018), biology and morphology (Manton, 1961; Hoffman, 1980; Read & Enghoff, 2009; Shorter *et al.*, 2018). They share highly derived mouthparts, which are siphon-like in some groups (Manton, 1961) and used to feed on liquid food (Moritz *et al.*, 2021, 2022). Colobognatha might feed on fungi, algae, or bacterially degraded substances (Lewis, 1984; Dunger, 1993; Macias *et al.*, 2019). The biology of this group is largely unknown, and observations of living animals are rare, as many species have not been collected nor observed since their initial discovery. However, some colobognathan species are reported to exhibit subsocial or colonial behavior like brood care, even male brood care, and the formation of aggregations with individuals of overlapping generations (e.g. Murakami, 1962a; Gardner, 1974; Enghoff, 1984; Lewis, 1984; Wong *et al.*, 2020). Only few studies focus on the postembryonic development of Colobognatha (Murakami 1962a, 1962b, 1963; David & Couret, 1983; Enghoff *et al.*, 1993; Wong *et al.*, 2020), but available data suggest that the Colobognatha differ from most other Diplopoda by hatching with more than three leg pairs (Enghoff *et al.*, 1993; Blanke & Wesener, 2014). Postembryonic stadia in millipedes extend between two molts (Enghoff *et al.*, 1993; Minelli, 2015), and in rare cases the color pattern of a millipede can reflect the course of anamorphosis; i.e. the number of tergites added between subsequent stadia (Enghoff, 2011). Studies on the anamorphosis (the addition of segments and legs) of millipedes do not only give an insight into their biology but also allow conclusions concerning the evolution and phylogeny of millipedes (Enghoff *et al.*, 1993).

Siphonocryptid millipedes are considered to represent an independent order (Shelley, 2003), but were previously treated as a family or suborder of the Polyzoniida (e.g. Hoffman, 1977; Enghoff & Golovatch, 1995; Arndt *et al.*, 2008). The group comprises 7 known species (Enghoff *et al.*, 2015) in two genera (*Hirudicryptus* Enghoff & Golovatch, 1995, *Siphonocryptus* Pocock, 1894), which makes it the second most species-poor millipede order after the Siphoniulida (Sierwald & Bond, 2007; Liu *et al.* 2017). Despite their few species, Siphonocryptida show a very unusual distribution pattern. They occur in Sumatra (*Siphonocryptus compactus* Pocock, 1894), Malaysia (*Siphonocryptus latior* Enghoff & Golovatch, 1995; *Siphonocryptus zigzag* Enghoff, 2010), Taiwan (*Hirudicryptus taiwanensis* Korsós, Enghoff & Chang, 2008), Nepal (*Hirudicryptus quintelementum* Korsós, Geoffroy & Mauriès, 2009), Georgia and Russia (*Hirudicryptus abchasicus* Golovatch, Evsyukow & Reip, 2015), and on the Macaronesian islands (*Hirudicryptus canariensis* (Loksa, 1967)). Siphonocryptida probably had a wider distribution in the past and the today observed relict distribution might be due to extinction linked to changes in climate and vegetation (Korsós *et al.*, 2009; Golovatch *et al.*, 2015). The phylogenetic position of the Siphonocryptida within the Colobognatha remains unresolved (e.g. Blanke & Wesener, 2014), not the least because not a single genetic sequence is available, and their biology and internal anatomy remains largely *terra incognita*. The siphonocryptid species *Hirudicryptus canariensis*, which is endemic to Macaronesia, measures up to 10 mm in length and 1 mm in width and has a flattened body with lateral paraterga and a minute cone shaped head. The species was re-described in detail by Enghoff & Golovatch (1995) and the first data on its post-embryonic development was presented by Enghoff *et al.* (1993) and Enghoff & Golovatch (1995).

Hirudicryptus canariensis is restricted to the volcanic islands Madeira, La Gomera and Tenerife (Loksa, 1967; Enghoff, 1992; Enghoff & Golovatch, 1995; Vicente & Enghoff, 1999), where it can only be found in the Laurisilva, evergreen laurel subtropical cloud-forests. Around 20 million years ago laurel forests could also be found in Southern Europe and Northern Africa. However, the laurel forest largely disappeared in the Mediterranean due to climatic changes in the Quaternary period, and it only persisted on the Macaronesian islands as a relic (Morales *et al.*, 1996; Fernández-Palacios *et al.*, 2011). On Tenerife, laurel forests occur in the Anaga Mountains in the east, the Monte del Agua in the west, and in small patches between those areas in the north of the island (de Nascimento *et al.*, 2009; González-Montelongo & Pérez-Vargas, 2019). The evergreen Laurisilva on Tenerife is formed by ca. 20 tree species, of which many are Canarian endemics, and which vary in their composition according to the prevalent environmental conditions (Morales *et al.*, 1996). For example, the heath *Erica platycodon* (Webb & Berthel.) Rivas-Mart. & al. is part of the ridge-crest evergreen laurel forest ecosystem, which occurs at year-round cloudy and windy ridges with the highest precipitation (del Arco Aguilar *et al.*, 2010).

Here we present observations of the biology, habitat, and postembryonic development of *Hirudicryptus canariensis* in the Anaga-mountains of Tenerife (Canary Islands, Spain). Furthermore, we provide the first barcode data (CO1) for the order Siphonocryptida, which will aid in future identification.

Material and methods

Collecting and observation

Hirudicryptus canariensis was observed and collected on Tenerife (Canary Islands, Spain) in the laurel forest (Laurisilva) of the Anaga mountains in October 2019 at 9 localities (Table 1, Fig. 1a). The GPS-coordinates and elevation of each locality was recorded with the mobile-app maps.me (accessible via https://maps.me/). For the publication localities were numbered from west to east, and locality numbers differ from those originally used when collecting. A distribution map (Fig. 1a) was generated in Q-GIS 3.8 Zanzibar (QGIS Development Team 2019). Living specimens were observed and photographed in the field with an Olympus TG-5 digital camera equipped with an Olympus LG-1 light guide. Specimens from each locality were fixed in 95% ethanol and investigated with a Discovery.V12 stereomicroscope (Zeiss) to count the number of tergites and leg pairs, and to note the absence or presence of gonopods. This data has been combined with available data from the literature (Enghoff *et al.*, 1993) to a total of 296 specimens (Table 2). Specimens with less than 15 tergites were counted as juveniles of uncertain sex, specimens with 15 tergites or more were counted as females if gonopods were absent, or as males if gonopods were present (see below). Images of the different stadia were taken with a Keyence VHX2000. Furthermore, the tergite number and color pattern of 107 living specimens was recorded from photographs taken in the field. We did not combine the data from collected animals and animals photographed in the field to avoid artificial duplication of data, as some of the photographed animals might have been collected afterwards. As discussed by Enghoff *et al.* (1993: 107) the Colobognatha do not have completely fused body-rings and the identification of segment or diplosegments can be problematic as the number of dorsal and ventral elements might not correspond to each other. Therefore, we rather refer to the number of tergites and leg-pairs added and to 'podous' and 'apodous tergites' respectively, assuming a legless collum followed by three haplosegments (tergites with a single leg-pair) and a variable number of diplosegments (tergites with two leg-pairs) as done by Enghoff *et al.* (1993: 127-130) for Colobognatha. All data this study is based on, including additional photographs and tables, are deposited on Zenodo (https://doi.org/10.5281/zenodo.6353889).

Scanning electron microscopy (SEM)

Scanning electron microscopy (SEM) was used to examine the number of ommatidia and antennomeres, as well as sexual characters (pseudopenes and gonopods). For SEM specimens were dehydrated in an ascending ethanol series and critical point dried with a Leica EM CPD 300. The specimens were mounted to SEM-stubs using conductive tape and sputtered with gold (ca 35 nm) using the Cressington Sputter Coater 108auto. SEM-images were obtained with a Zeiss Sigma 300 VP scanning electron microscope at the ZFMK. Here the number of antennomeres includes the apical disc (carrying the sensory cones) which is traditionally interpreted as 8th antennomere (e.g. Verhoeff, 1928: 788; Enghoff, 1990). For a discussion see Koch (2015).

Barcoding (CO1)

DNA was extracted from two individual, one from locality 4 (ZFMK-MYR08837; ON007316) and one from locality 9 (ZFMK-MYR08838; ON007317). Following Spanish ABS bylaw 124/2017 of 24 February (Real Decreto 124/2017, de 24 de febrero, relativo al acceso a los recursos genéticos procedentes de taxones silvestres y al control de la utilización) access authorization for the utilization of genetic resources is not needed for exclusively taxonomic purposes (Capitoli I, Articolo 3.2) as defined in Capitoli I, Articolo 2.3 (https://www.miteco.gob.es/en/biodiversidad/temas/recursos-geneticos/protocolo-de-nagoya/FAQ_Autorizaciones.aspx). For DNA extraction, muscle tissue from legs and

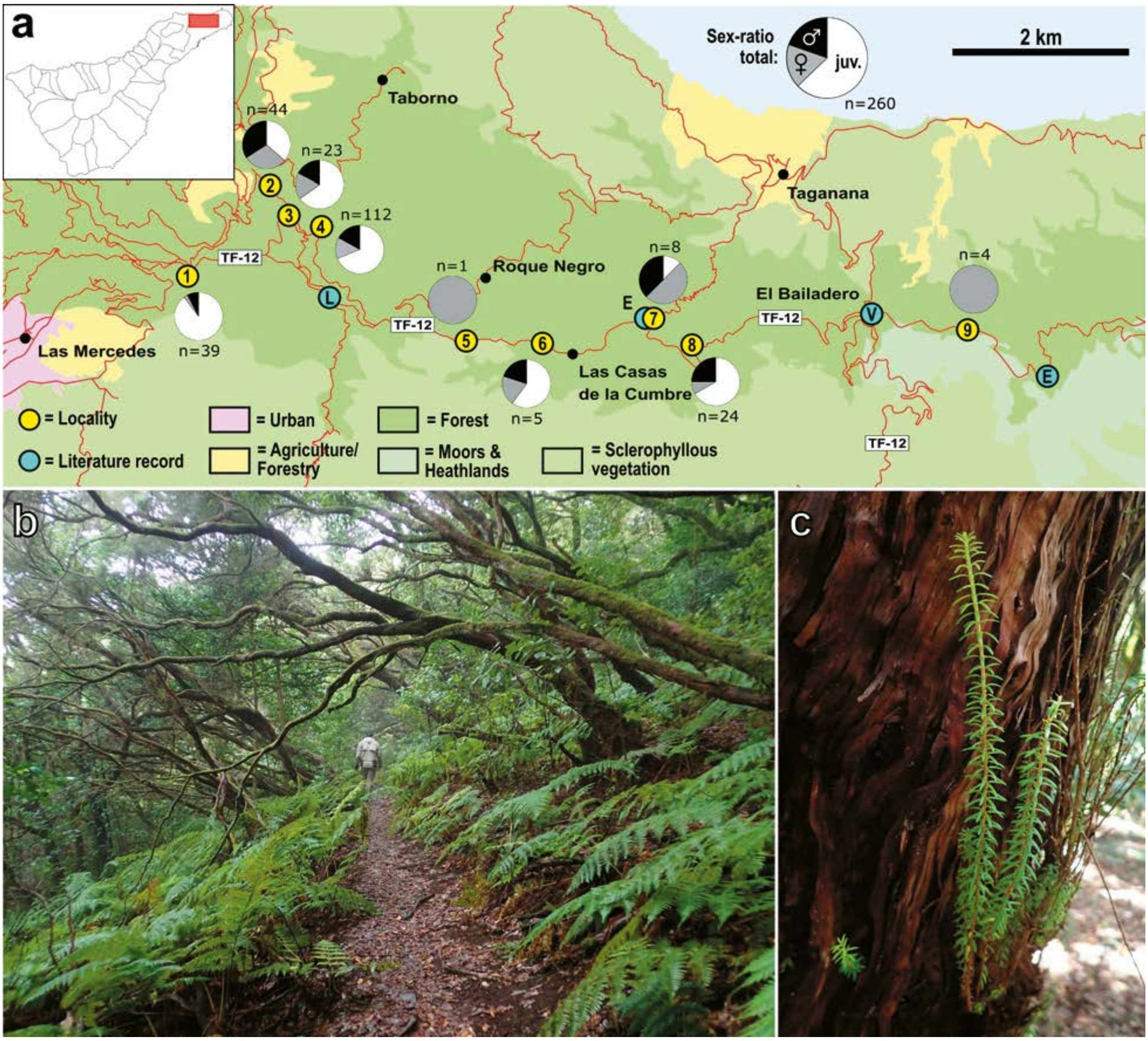


Fig. 1.– Distribution and habitat of *Hirudicryptus canariensis* (Loksa, 1967). **a** Distribution of *H. canariensis* in the Anaga mountains. Pie-charts indicate relative abundance of females (grey), males (black) and juveniles of undetermined sex with less than 15 tergites (white). Numbers refer to localities in Table 1; L = Loksa (1967); E = Enghoff & Golovatch (1995); V = Vicente & Enghoff (1999); n = number of individuals examined. (Map modified from Corine Land Cover (CLC) 2006 (© European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)) **b & c** The typical habitat of *H. canariensis*: Humid laurel forest on the slopes of the Anaga mountains (**b**), on and underneath the bark of the Macaronesian endemic *Erica platycodon* (**c**).

Fig. 1.– Distribución y hábitat de *Hirudicryptus canariensis* (Loksa, 1967). **a** Distribución de *H. canariensis* en el macizo de Anaga. Los gráficos circulares indican la abundancia relativa de hembras (gris), machos (negro) y juveniles de sexo indeterminado con menos de 15 terguitos (blanco). Los números se refieren a las localidades de la Tabla 1; L = Loksa (1967); E = Enghoff & Golovatch (1995); V = Vicente & Enghoff (1999); n = número de individuos examinados. (Mapa modificado a partir de Corine Land Cover (CLC) 2006 (© Unión Europea, Copernicus Land Monitoring Service 2018, Agencia Europea de Medio Ambiente (AEMA)) **b & c** Hábitat típico de *H. canariensis*: Bosque húmedo de laurisilva en las laderas del macizo de Anaga (**b**), sobre y bajo la corteza del endémico *Erica platycodon* de Macaronesia (**c**).

body segments was used. A fragment of the cytochrome c oxidase subunit I (CO1) mitochondrial gene was amplified with the primers HCO2198-JJ and LCO1490-JJ (Astrin & Stüben, 2008) and sequenced as outlined in previous studies (e.g. Wesener, 2015). BLAST searches (Altschul *et al.*, 1990) were used to check the sequences for contaminations. Sequences were translated into amino acids to rule out the accidental amplification of pseudogenes. New sequences were uploaded to Genbank (see Table 4). Sequences were aligned by hand in Bioedit (Hall 1999). Distance analysis was performed in Mega 6 (Tamura *et al.*, 2013) using the uncorrected p-distance model for a total of two sequences with 683 positions. Variation among sites was modeled with gamma distribution with shape parameter = 1. Included were the 1st+2nd+3rd codon positions.

Results

HABITAT AND AGGREGATIONS

We found *Hirudicryptus canariensis* exclusively on the heath *Erica platycodon* in the Anaga mountains at elevations between 630 and 870 m (Table 1, Fig. 1a). The animals occurred only in humid places on the lower part of the trees, on or under its bark, or under moss growing on its trunk (Fig. 1b, c). Those habitats were also inhabited by julidan millipedes (Julidae and Blaniulidae), Collembola, and nymphs of *Aneurus* cf. *tagasastei* Enderlein, 1931 (Heteroptera: Aradidae). Sifted soil samples taken adjacent to the trees and sampled with Winkler extraction did not include any specimens of *H. canariensis*.

Hirudicryptus canariensis mostly occurred in accumulations of juveniles in different stadia and adults (Fig. 2a–c), although at some localities only single (5) or few individuals (6, 7, 9), mainly adults, have been found. Larger individuals were often encountered coiled, with their head and collum stuck underneath the lateral paraterga of their mid-body (Fig. 2d, e). At several localities (1, 2, 3, 4 & 8) *H. canariensis* was found in large numbers (Fig. 2a, b), in some spots counting several hundred individuals (e.g. 2 & 4). Overall, most of the individuals found were juveniles of undetermined sex (63%), while males (19%) and females (18%) were nearly equally abundant. The highest proportion of juveniles of undetermined sex (90%) was found at locality 1 (Fig. 1a).

Disturbance of aggregations led to a flight response by adults and juveniles, but no defense fluid was secreted. Removal of juveniles did not lead to any response by mature individuals in their surroundings. TW observed in March 2012 an adult

Table 1.– Localities of *Hirudicryptus canariensis* (Loksa, 1967) in the Anaga Mountains on Tenerife (Canary Islands, Spain). Abbreviations: Loc = locality number, Lat =latitude in decimal degree, Long = longitude in decimal degree, Elev = elevation in meter above sea level.

Tabla 1.– Localidades de *Hirudicryptus canariensis* (Loksa, 1967) en el macizo de Anaga en Tenerife (Islas Canarias, España). Abreviaturas: Loc = número de localidad, Lat = latitud en grado decimales, Long = longitud en grados decimales, Elev = elevación en metros sobre el nivel del mar.

ZFMK-MYR	Loc	Locality	Lat (DG)	Long (DG)	Elev (m)	Date	Habitat
08910	**1**	Cruz del Carmen, both sides of street	28.530435	-16.280268	870	07.x.2019	Laurisilva, on and under bark of *E. platycodon* on slope. North slope
08911	**2**	Street between TF12 and Rio	28.542069	-16.274008	806	07.x.2019	Laurisilva, on and under bark of *E. platycodon* on side and at slope under street. North slope
08914	**3**	TF12, between street to pico de ingles and street to Rio	28.539815	-16.271059	890	13.x.2019	Laurisilva, on and under bark of *E. platycodon*, along slope under street. North slope
08906	**4**	TF12, close to bus stop Cruce de Las Carboneras, hiking path behind house	28.53983	-16.267142	805	6.x.2019	Laurisilva, on and under bark of *E. platycodon*, next to path, ground covered by ferns. North slope
08952 – 08966	**4**	TF12, close to bus stop Cruce de Las Carboneras, hiking path behind house	28.53983	-16.267142	805	10.x.2019	Laurisilva, on and under bark of *E. platycodon*, next to path, ground covered by ferns. North slope
08912	**5**	TF12, between Cruce de Afur and Cruce de Las Carboneras	28.533626	-16.247871	733	07.x.2019	Laurisilva, on and under bark of *E. platycodon* at steep slope (trash and refrigerators). North slope
08913	**6**	Las Casas de la Cumbre	28.53598	-16.23949	773	07.x.2019	Laurisilva, on and under bark of *E. platycodon* at steep slope. North slope
08907	**7**	Casas de la Cumbre, Casas Forestral	28.542008	-16.228718	763	06.x.2019	Laurisilva, on and under bark of *E. platycodon* along hiking path behind Casa Forestral
08908	**8**	TF12, between Casas de la Cumbre and El Bailadero	28.540909	-16.193475	709	06.x.2019	Laurisilva, on and under bark of *E. platycodon.* South slope
08909	**9**	El Bailadero, street to Las Bodegas and Lomo de las Casillas	28.551742	-16.193475	637	06.x.2019	Laurisilva, on and under bark of *E. platycodon* along street.

Fig. 2.– *Hirudicryptus canariensis* (Loksa, 1967), photographs of living specimens in the Anaga mountains (Spain, Tenerife). **a & b** Aggregation with individuals of different stadia and sex with 6 to 36 tergites at locality 4. Aggregations can be relatively loose (**a**) or densely packed (**b**). **c** Group of individuals of different stadia. **d** Adult females with 30 and 39 tergites at locality 9, showing the typical coiled position, with the head underneath paraterga of the mid-body. **e** Single female individual with 47 tergites at locality 6.

Fig. 2.– *Hirudicryptus canariensis* (Loksa, 1967), fotografías de ejemplares vivos en el macizo de Anaga (España, Tenerife). **a & b** Agregación con individuos de diferentes estadios y sexo con 6 a 36 terguitos en la localidad 4. Las agregaciones pueden ser relativamente sueltas (**a**) o densamente empaquetadas (**b**). **c** Grupo de individuos de diferentes estadios. **d** Hembras adultas con 30 y 39 terguitos en la localidad 9, mostrando la típica posición enroscada, con la cabeza debajo de la paraterga de la parte media del cuerpo. **e** Único individuo femenino con 47 terguitos en la localidad 6.

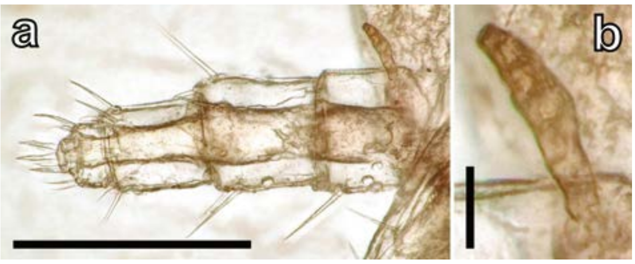


Fig. 3.– Parasitic fungus on the antenna of a *Hirudicryptus canariensis* juvenile (stadium I). **a** Overview of antenna. **b** Detail of fungi. Scale: a = 100 µm; b = 10 µm.

Fig. 3.– Hongo parásito en la antena de un juvenil de *Hirudicryptus canariensis* (estadio I). **a** Vista general de las antenas. **b** Detalle del hongo. Escala: a = 100 µm; b = 10 µm.

individual of uncertain sex coiling around an egg clutch at locality 7.

In one juvenile specimen with six tergites a fungus was observed growing on the basal article of one antenna (Fig. 3).

Postembryonic development

The specimens with the lowest number of tergites had six tergites and seven leg pairs and lacked apodous tergites and coxal sacks (Fig. 4a); those were the most abundant individuals (Table 2). Individuals with six tergites had a single pair of ommatidia, and five antennomeres (Fig. 5a) including the apical disc. Ozopores were present on tergites 5 and 6 (Fig. 4a). The next larger individuals counted ten tergites and 13 leg pairs (Table 2).

Individuals with more than six tergites had a single apodous tergite, coxal sacks from leg-pair 3 onwards (Fig. 4b-d), and two pairs of ommatidia (Fig. 5b-d). The number of antennomeres (including apical disc) increased stepwise from five antennomeres in individuals with six tergites (Fig. 5a), via seven observed in individuals with eleven and 16 tergites (Fig. 5b, c), to a maximum of eight (Fig. 5d) observed in an individuals with 25 tergites (Fig. 5d).

The specimens were white or pale brownish (Figs 2c, 6). In individuals with more than six tergites, a shift from darker to paler colored tergites could be observed. This color pattern was best visible in smaller living individuals (Fig. 6) and less distinct or absent in specimens stored in ethanol (Fig. 7) and in larger individuals. A shift from darker to paler coloration occurred behind tergite six (Figs 6, 7a-d) and behind tergite 10–14 (Figs 6, 7e-h) as well as in

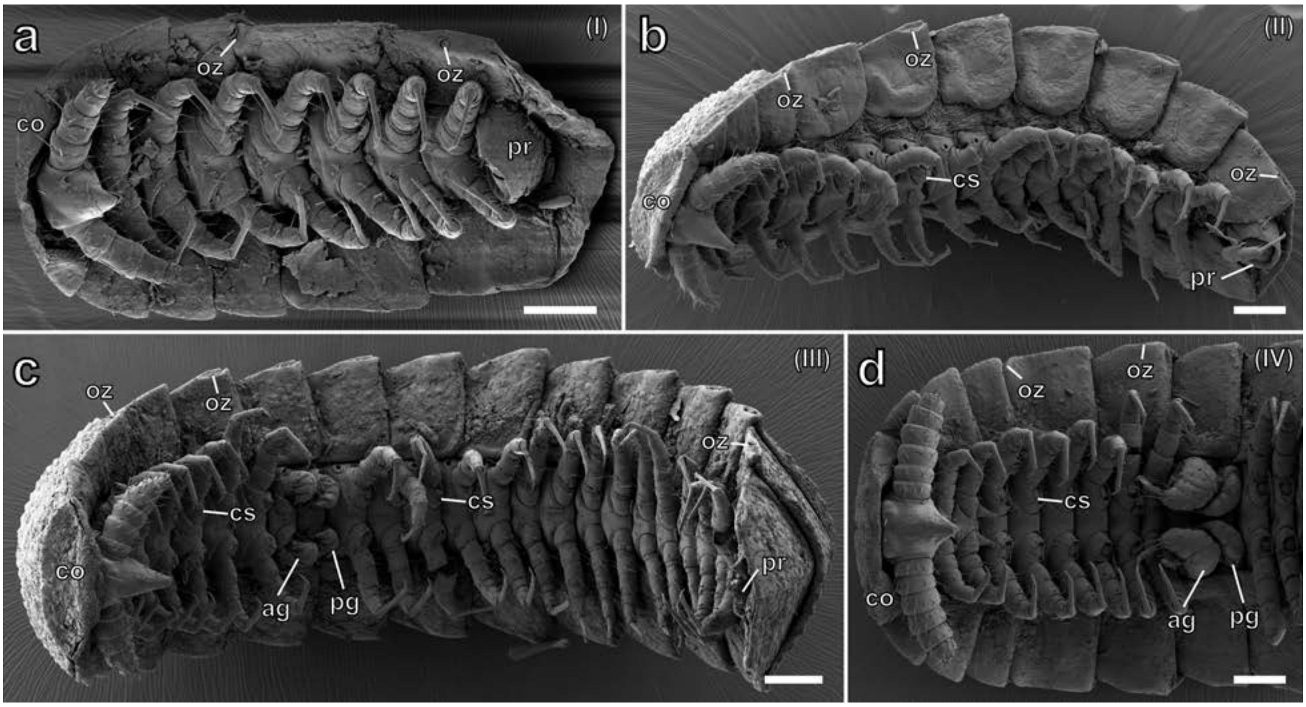


Fig. 4.– *Hirudicryptus canariensis* (Loksa, 1967), scanning electron micrographs. **a** Juvenile, stadium I with 6 tergites and 7 leg pairs, habitus ventral view. **b** Juvenile, stadium II with 11 tergites and 15 leg pairs, habitus, ventral view. **c** Immature male, stadium III with 16 tergites and 25 leg pairs, habitus ventral view. **d** Mature male stadium IV, with 25 tergites and 43 leg pairs, habitus, ventral view. Scale: 100 µm. Abbreviations: ag = anterior gonopod, co = collum, cs = coxal sacks, oz = ozopore, pg = posterior gonopod, pr = preanalring.

Fig. 4.– *Hirudicryptus canariensis* (Loksa, 1967), micrografías electrónicas de barrido. **a** Juvenil, estadio I con 6 terguitos y 7 pares de patas, hábito vista ventral. **b** Juvenil, estadio II con 11 terguitos y 15 pares de patas, hábito vista ventral. **c** Macho inmaduro, estadio III con 16 terguitos y 25 pares de patas, hábito vista ventral. **d** Macho maduro, estadio IV, con 25 terguitos y 43 pares de patas, hábito vista ventral. Escala: 100 µm. Abreviaturas: ag = gonópodo anterior, co = collum, cs = sacos coxales, oz = ozoporo, pg = gonópodo posterior, pr = anillo preanal.

Table 2.– Postembryonic development of *Hirudicryptus canariensis* (Loksa, 1967). Locality numbers in parentheses corresponds to Fig. 1a and Table 1. E = data from Enghoff *et al.* (1993).

Tabla 2.– Desarrollo postembrionario de *Hirudicryptus canariensis* (Loksa, 1967). Los números de localidad en paréntesis corresponden a la Fig. 1a y a la Tabla 1. E = datos de Enghoff *et al.* (1993).

No. tergites	No. legpairs	No. of specimens (Locality)	Total no. of specimens	No. of specimens with gonopods (Locality)
6	7	15(1), 10(2), 9(3), 39(4), 3(8), 7(E)	83	0
10	13	1(1), 4(E)	5	0
11	15	6(1), 2(2), 1(3), 5(4), 1(6), 3(8), 12(E)	30	0
12	17	7(1), 1(2), 14(4), 6(8), 6(E)	34	0
13	19	5(1), 1(2), 3(3), 11(4), 2(6), 1(7), 4(8)	27	0
14	21	1(1), 2(2), 2(3), 8(4), 2(E)	15	0
15	23	1(1), 1(4), 2(8), 1(E)	5	1(8)
16	25	1(1), 3(2), 4(4), 1(E)	9	1(1),2(2),1(4),1(E)
17	27	3(4), 3(8), 3(E)	9	2(4), 3(8), 1(E)
18	29	5(4)	5	3(4)
19	31	2(2), 4(4),1(8)	7	1(2), 3(4), 1(8),
20	33	3(2),1(4),1(8)	5	1(2), 1(4)
21	35	2(2), 1(4)	3	1(4)
22	37	1(2), 1(4)	2	1(4)
23	39	1(1), 1(3), 3(4)	5	1(1), 1(3), 3(4)
24	41	3(2), 1(4), 1(8)	5	3(2), 1(8)
25	43	4(2), 1(7)	5	2(2)
26	45	2(2), 1(3), 1(4), 3(7)	7	2(2), 1(4), 2(7)
27	47	1(2), 1(3), 2(4)	4	1(4)
28	49	1(1),1(2),1(3),1(4)	4	1(1),1(2)
29	51	1(2), 1(4), 1(7)	3	1(7)
30	53	1(2), 1(3), 1(9)	3	1(3)
31	55	1(2), 2(3), 1(4)	4	1(2),1(3)
32	57	1(2), 1(9)	2	1(2)
33	59	2(2),1(3)	3	1(2),1(3)
34	61	1(9)	1	0
35	63	1(4)	1	0
36	65	3(4),1(7)	4	2(4)
38	69	1(4)	1	0
39	71	1(9)	1	0
41	75	1(6)	1	1(6)
47	87	1(6)	1	0
49	91	1(7)	1	0
54	101	1(5)	1	0

some individuals behind tergite 14–22 (Fig. 6). In few individuals such a pattern could also be observed on following tergites (Table 3). Larger individuals of *H. canariensis* were generally darker and did not show such a clear pattern. The color pattern can be used to infer the stadia (see discussion).

Modifications of the coxae of the second leg pair (which carry the gonopores) in both sexes, and of leg pair 9 and 10 (gonopods) in males, could be observed earliest in specimens with 15 tergites and 2 color shifts (stadium III). These structures were fully developed in specimens with 3 color shifts (stadium IV). No changes could be observed in larger individuals (Fig. 8). As the smallest individuals showing sexual modifications counted at least 15 tergites (Table 2) and showed 2 color shifts, all individuals with less than 15 tergites and 2 color shifts were counted as juveniles of undetermined sex, while all individuals with at least 15 tergites and two color shift were counted as males if gonopods were present, or as females if gonopods were absent. In females with two color shifts (stadium III) the second coxae were enlarged and carried a mesal fold (Fig. 8a). In females with 3 (stadium IV) and more color shifts the operculum, and the inner and outer valves of the vulvae were fully developed, and the second sternite showed a median fold (Fig. 8b). In males with two color shifts (stadium III) the developing pseudopenes (gonoapophysis) on the coxae of leg pair 2 were cylindrical and blunt (Fig. 8c), while the fully developed pseudopenes of subsequent stadia were conical and carried an apical incision (Fig. 8d). The immature gonopods (Fig. 8e) mainly differed from the fully developed gonopods (Fig. 8f) by

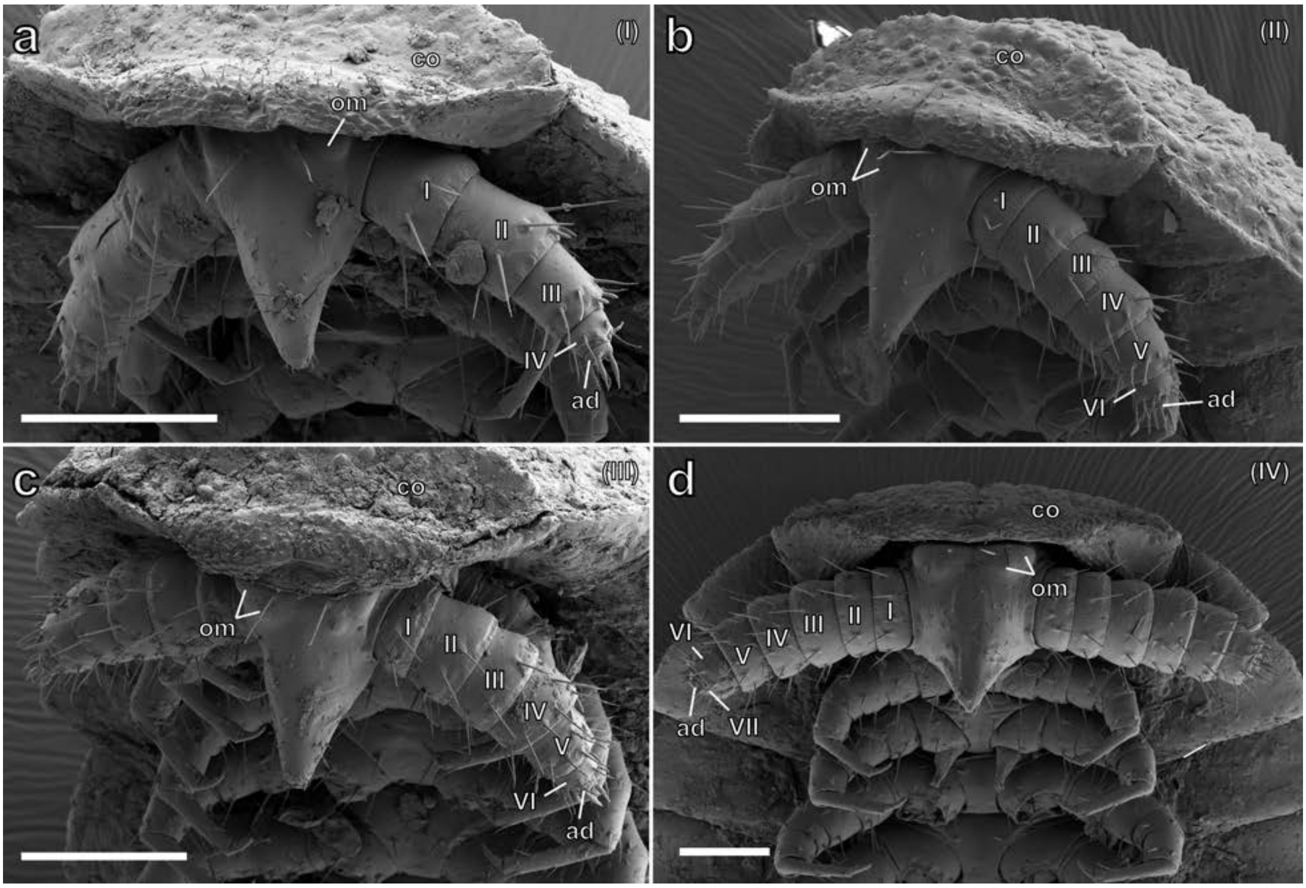


Fig. 5.– *Hirudicryptus canariensis* (Loksa, 1967), somatic characters of the head, scanning electron micrographs. **a** Juvenile, stadium I with 6 tergites and 7 leg pairs, head. **b** Juvenile, stadium II with 11 tergites and 15 leg pairs, head. **c** Immature male, stadium III with 16 tergites and 25 leg pairs, head. **d** Mature male stadium IV, with 25 tergites and 43 leg pairs, head. Scale: 100 µm. Abbreviations: I-VII = antennomere, ad = apical disc/8th antennomere, co = collum, om = ommatidia.

Fig. 5.– *Hirudicryptus canariensis* (Loksa, 1967), caracteres somáticos de la cabeza, micrografías electrónicas de barrido. **a** Juvenil, estadio I con 6 terguitos y 7 pares de patas, cabeza. **b** Juvenil, estadio II con 11 terguitos y 15 pares de patas, cabeza. **c** Macho inmaduro, estadio III con 16 terguitos y 25 pares de patas, cabeza. **d** Macho maduro, estadio IV, con 25 terguitos y 43 pares de patas, cabeza. Escala: 100 µm. Abreviaturas: I-VII = antenómero, ad = disco apical/8° antenómero, co = collum, om = ommatidios.

Table 3.– Color pattern inferred from photographs of 107 living specimens of *Hirudicryptus canariensis* (Loksa, 1967). Numbers indicate behind which tergite the following tergites became paler, number in parenthesis () indicates number of individuals in which this was observed, number in brackets [] indicates in how many individuals this was the maximum number of tergites.

Tabla 3.– Patrón de color inferido a partir de fotografías de 107 ejemplares vivos de *Hirudicryptus canariensis* (Loksa, 1967). Los números indican detrás de cuál terguito los terguitos subsucuentes se volvieron más pálidos, el número entre paréntesis () indica el número de individuos en los que se observó esto, el número entre corchetes [] indica en cuántos individuos éste fue el número máximo de terguitos.

Stadium (No. of color change)	**1st (0)**	**2nd (1)**	**3rd (2)**	**4th (3)**	**5th (4)**	**6th (5)**
Tergite no. (no. of individuals with color change) [no of individuals with maximum tergite no.]	6 (107)	10 (8)[2]	14 (2)[0]	18 (0)[2]	29 (0)[2]	36 (0)[1]
		11 (9)[6]	15 (4)[1]	21 (0)[3]	31 (1)[0]	
		12 (12)[17]	16 (1)[3]	22 (0)[1]	39 (0)[1]	
		13 (7)[30]	17 (4)[7]	23 (0)[2]		
		14 (7)[9]	18 (4)[3]	24 (1)[3]		
			19 (1)[5]	25 (3)[1]		
			20 (1)[2]	27 (0)[1]		
			21 (1)[2]	28 (0)[1]		
			22 (0)[2]			
Total	(107)	(43)[64]	(18)[25]	(4)[14]	(1)[3]	(0)[1]

the shape and size of the flagellate extensions on the apical podomeres. The conspicuous lobe observed on fully developed anterior gonopods, extending beyond the surrounding setae (Fig. 8f), was in the immature gonopod represented by an inconspicuous extension, which was less than 1/3 of the length of the neighboring setae (Fig. 8e). The apical podomere of the posterior gonopod, which extended into a long flagellum and surpasses the anterior gonopod when fully developed (Fig. 8f), was in the immature gonopods a short and thin extension, which had ca. the length of podomere 5 (Fig. 8e). The largest male had 41 tergites and 75 leg pairs (Fig. 7i). The largest individual found was a female with 54 tergites and 101 leg pairs (Figs 6, 7j). The number of leg pairs was always uneven (Table 2).

Barcodes and genetic analyses

The barcoded CO1 fragments (Table 4) included 683 positions. The genetic pairwise distance between the two individuals from locality 4 and 9 was 0.5%

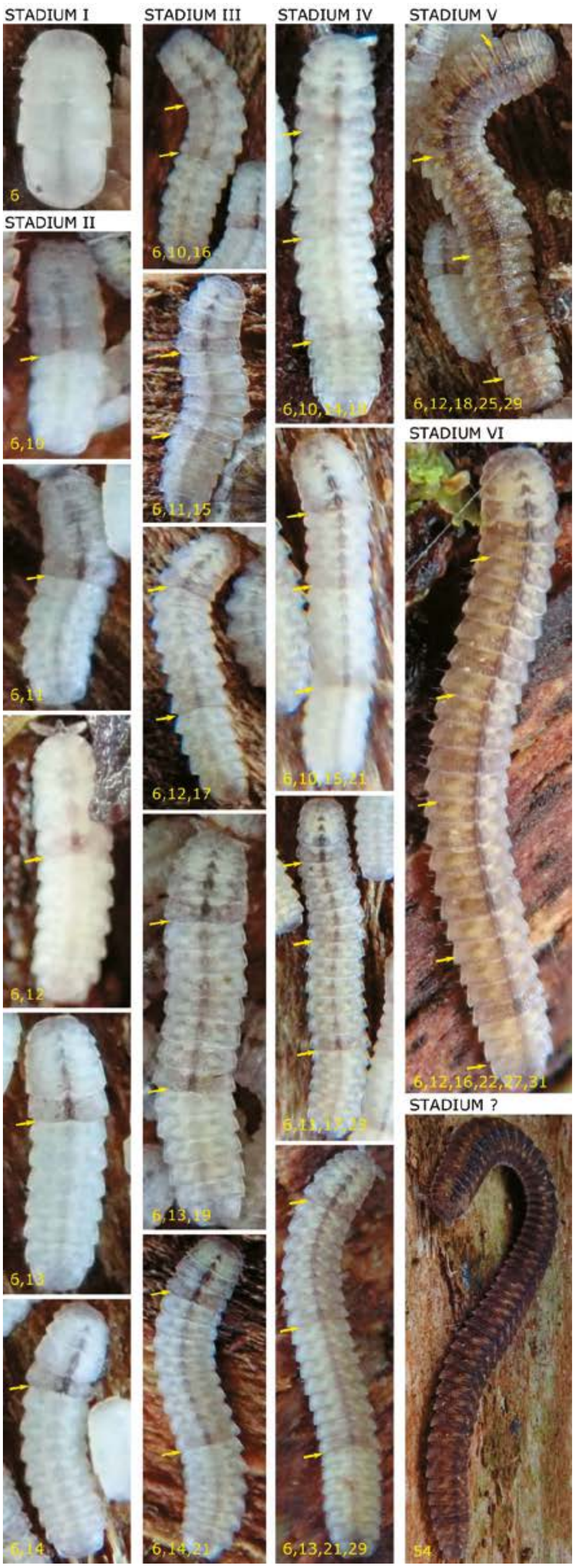


Fig. 6.– Color pattern of *Hirudicryptus canariensis* (Loksa, 1967) during postembryonic development, photographs of living specimens. Yellow arrows and numbers indicate change from darker to paler tergites.

Fig. 6.– Patrón de color de *Hirudicryptus canariensis* (Loksa, 1967) durante el desarrollo postembrionario, fotografías de ejemplares vivos. Las flechas amarillas y los números indican el cambio de los terguitos de más oscuros a más pálidos.

Discussion

Habitat and distribution

Hirudicryptus canariensis seems to be associated to the plant *Erica platycodon* [*Erica scoparia* subsp. *platycodon* (Webb & Berthel.) A.Hansen & G.Kunkel] and humid conditions, as it has only been found on those trees and not in its surrounding in this study. For *H. canariensis* from La Gomera and Madeira we lack information on which plant they occurred (Enghoff & Golovatch, 1995). *Erica platycodon* has the two subspecies *Erica platycodon* subsp. *platycodon*, endemic to the Canary Islands, and *Erica platycodon* subsp. *maderincola* (D.C.McClint.) Rivas Mart. & al., endemic to Madeira (e.g. Rivas-Martinez *et al.*, 1993; Arozena *et al.*, 2008; Fagúndez *et al.*, 2009; POWO, 2022). The close affinity of *H. canariensis* to *Erica platycodon* might be related to the structure of the bark of *Erica platycodon*, which easily peels off and creates abundant crevices. With its small (up to 10 mm in length, ca 1 mm in width) and dorso-ventrally flattened body, *H. canariensis* might be adapted to a subcortical life, as small and flattened bodies are typical for subcortical millipedes (Golovatch & Kime. 2009). However, other siphonocryptids (*Hirudicryptus abchasicus*, *H. taiwanensis*, *H. quintumelementum*, *Siphonocryptus zigzag* and *S. latior*) with a similar habitus are known to inhabit soil and leaf litter (Enghoff & Golovatch, 1995; Korsós *et al.*, 2008, 2009; Enghoff, 2010; Golovatch *et al.*, 2015; Zuev, 2017). On the Canary Islands, *Erica platycodon* is mainly found in the ridge-crest evergreen laurel forests, which occurs at year-round cloudy and windy ridges, where the highest precipitation occurs (del Arco Aguilar *et al.*, 2010). Therefore, the presence of *H. canariensis* on *Erica platycodon* might be related

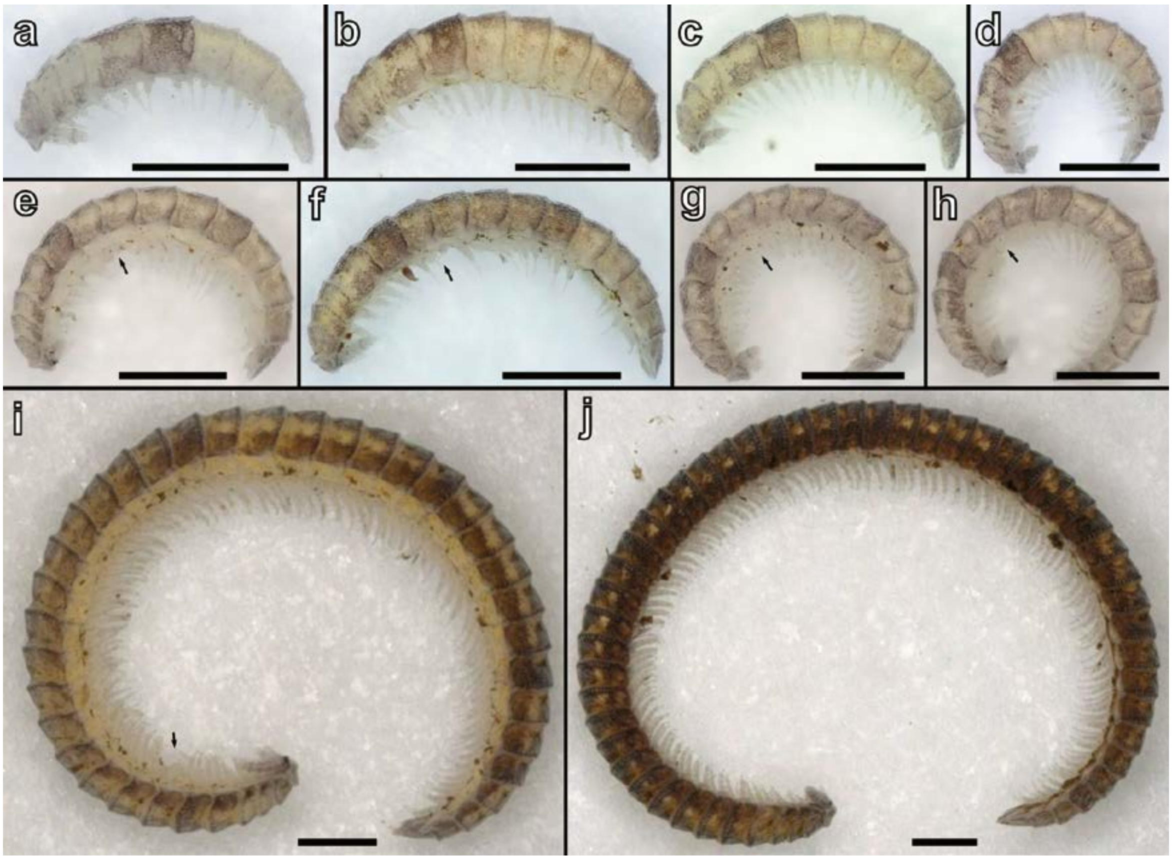


Fig. 7.– Color pattern and tergite number of *Hirudicryptus canariensis* (Loksa, 1967) during postembryonic development, photographs of specimens in ethanol. **a** Juvenile with 10 tergites. **b** juvenile with 12 tergites. **c** Juvenile with 13 tergites. **d** Juvenile with 14 tergites. **e** Smallest male with 15 tergites. **f** Male with 16 tergites. **g** Male with17 tergites. **h** Male with 18 tergites. **i** Largest male with 41 tergites. **j** Largest female with 54 tergites. Scale: 500 µm.

Fig. 7.– Patrón de color y número de terguitos de *Hirudicryptus canariensis* (Loksa, 1967) durante el desarrollo postembrionario, fotografías de ejemplares en etanol. **a** Juvenil con 10 terguitos. **b** Juvenil con 12 terguitos. **c** Juvenil con 13 terguitos. **d** Juvenil con 14 terguitos. **e** Macho más pequeño con 15 terguitos. **f** Macho con 16 terguitos. **g** Macho con 17 terguitos. **h** Macho con 18 terguitos. **i** Macho más grande con 41 terguitos. j Hembra más grande con 54 terguitos. Escala: 500 µm.

Table 4.– Barcode sequence of the CO1-gene of *Hirudicryptus canariensis* (Loksa, 1967) with a total of 683 positions. For localities see Table 1 and Fig. 1a.

Tabla 4.– Secuencia del gen CO1 de *Hirudicryptus canariensis* (Loksa, 1967) con un total de 683 posiciones. Para las localidades, véase la Tabla 1 y la Fig. 1a.

Specimen	Loc	Genbank	Barcode (CO1) sequence
ZFMK-MYR08837	4	ON007316	CATAAAGATATCGGAACAATGTACTTTTTATTTGGTGTCCTAGCTGCCATATTAGGAACTGCATTAAGAATAATTATCCGATCAGAATTAGGTTTAATCGGTGGTCTCATTAACAATGATCAAACATATAACACAATTGTAACAGCCCACGCTTTCATCATAATTTTTTTTGTTGTTATACCAATCATAATAGGTGGTTTTGGAAATTGATTAACCCCCTTTAATGATCGGAGCCCCTGATATAGCCTTCCCACGTTTAAATAATCTTAGTTTTTGATTACTACCTCCATCCCTAACACTTATAATTATATCTATATTTTTAGGGGGTGGTGCAGGAACAGGCTGAACAATCTACCCCCCCACTATCTTCAGCACTAGGACACCCTAGAATCTCAGTAGATTTTGTAATCCTCTCTCTTCACCTAGCAGGAATCTCATCAATTCTAGGATCAATTAATTTCATTACAACAATCATAAATATACGTCCAAAAGAAATAACCATAGAACGAACCCCCTTATTTATTTGATCAGTATTATTAACAGCCCTTCTACTTCTATTGTCTCTACCCATCCTTGCTGGAGCAATCACAATACTCCTTACAGACCGAAATTTTAACACTTCATTTTTTGACCCTGTTGGGGGGGGAGACCCAATTTTATATCAACACCTATTTTGATTCTTTGG
ZFMK-MYR08838	9	ON007317	CATAAAGATATCGGAACAATGTACTTTTTATTTGGTGTCCTAGCTGCCATATTAGGAACTGCATTAAGAATAATTATCCGATCAGAATTAGGTTTAATCGGTGGTCTCATTAACAATGATCAAACATATAACACAATTGTAACAGCCCACGCTTTCATCATAATTTTTTTTGTTGTTATACCAATCATAATAGGTGGTTTTGGAAATTGATTAACCCCCTTTAATGATCGGAGCCCCTGATATAGCCTTCCCACGTTTAAATAATCTTAGTTTTTGATTACTACCTCCATCCCTAACACTTATAATTATATCTATATTTTTAGGGGGTGGTGCAGGAACAGGCTGAACAATCTACCCCCCCACTATCTTCAGCACTAGGACACCCTAGAATCTCAGTAGATTTTGTAATCCTCTCTCTTCACCTAGCAGGAATCTCATCAATTCTAGGATCAATTAATTTCATTACAACAATCATAAATATACGCCCAAAAGAAATAACCATAGAACGAACCCCCTTATTTATTTGATCAGTATTATTAACAGCCCTTCTACTTCTATTGTCTCTACCCATCCTTGCTGGAGCAATCACAATACTCCTTACAGACCGAAATTTTAACACTTCATTTTTTGACCCTGTCGGGGGAGGAGACCCAATTTTATATCAACACCTATTTTGATTCTTTGG

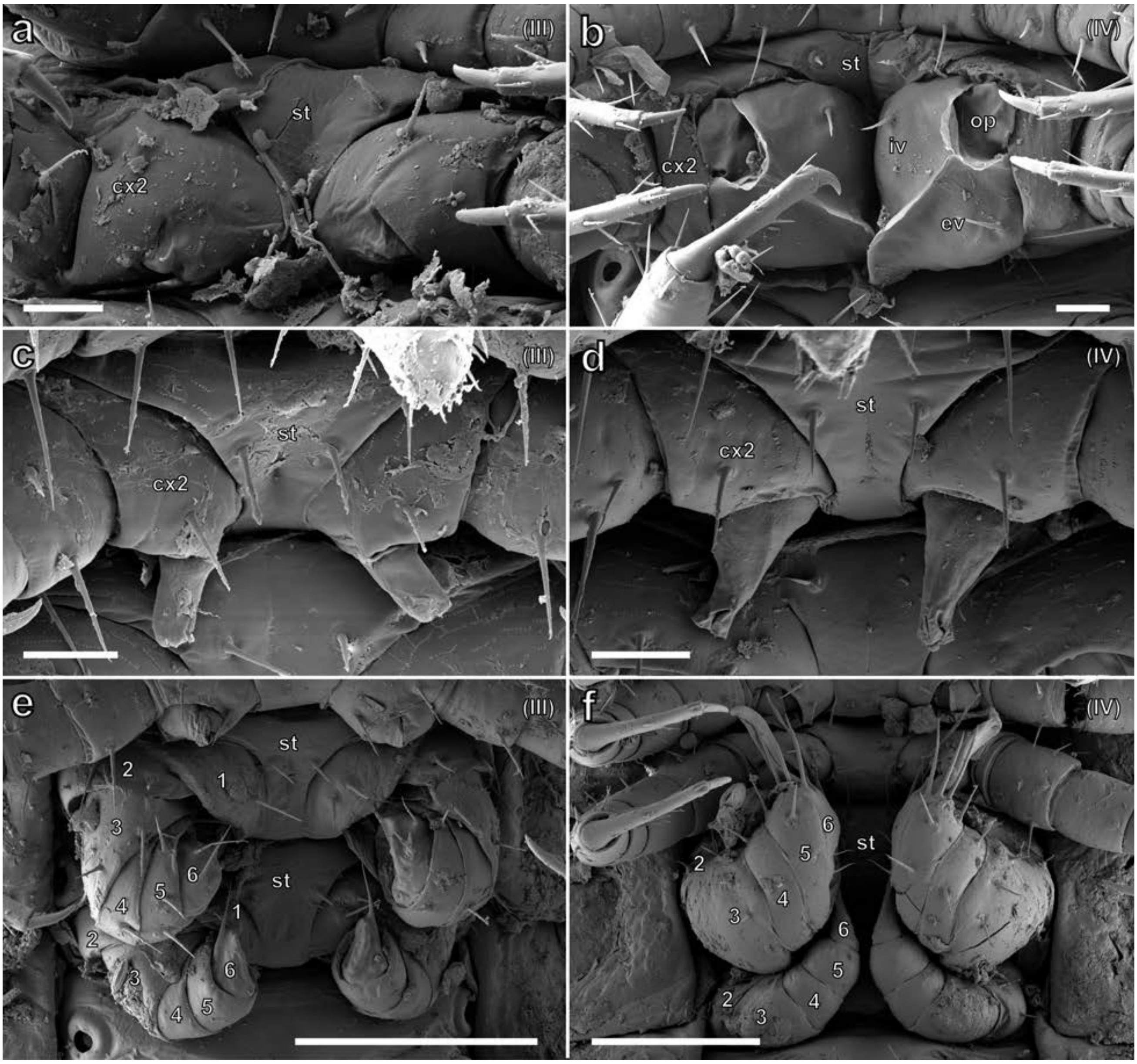


Fig. 8.– *Hirudicryptus canariensis* (Loksa, 1967), female and male sexual characters, scanning electron micrographs. **a** 2nd coxae of immature female, stadium III with 20 tergites and 33 leg pairs. **b** 2nd coxae of mature female, stadium IV with 25 tergites and 43 leg pairs. **c** 2nd coxae of immature male, stadium III with 16 tergites and 25 leg pairs. **d** 2nd coxae of mature male stadium IV, with 25 tergites and 43 leg pairs. **e** Gonopods of immature male, stadium III with 16 tergites and 25 leg pairs. **f** Gonopods of mature male stadium IV, with 25 tergites and 43 leg pairs. Scale: a–d = 20 µm, e, f = 100 µm. Abbreviations: 1-6 = podomere, I-VII = antennomere, cx = coxa, ev = external valve, iv = internal valve, op = operculum, st = sternite.

Fig. 8.– *Hirudicryptus canariensis* (Loksa, 1967), caracteres sexuales femeninos y masculinos, micrografías electrónicas de barrido. **a** Coxas del 2° par de patas de una hembra inmadura, estadio III con 20 terguitos y 33 pares de patas. **b** Coxas del 2° par de patas de una hembra madura, estadio IV con 25 terguitos y 43 pares de patas. **c** Coxas del 2° par de patas de un macho inmaduro, estadio III con 16 terguitos y 25 pares de patas. **d** Coxas del 2° par de patas de un macho maduro, estadio IV, con 25 terguitos y 43 pares de patas. **e** Gonópodos de un macho inmaduro, estadio III con 16 terguitos y 25 pares de patas. **f** Gonópodos de un macho maduro, estadio IV, con 25 terguitos y 43 pares de patas. Escala: a–d = 20 µm, e, f = 100 µm. Abreviaturas: 1-6 = podómero, I-VII = antenómero, cx = coxa, ev = válvula externa, iv = válvula interna, op = opérculo, st = esternito.

to favorable conditions, with high humidity due to precipitation of mist, where *E. platycodon* growth. The distribution of *E. platycodon* (Government of the Canary Islands) matches (with the exception of its presence on El Hierro, where *H. canariensis* is currently unknown) the known distribution of *H. canariensis* on Tenerife, La Gomera and Madeira (Loksa, 1967; Enghoff, 1992; Enghoff & Golovatch, 1995; Vicente & Enghoff, 1999). These laurel forests are a tertiary relict of the subtropical North Thetian forest (del Arco Aguilar *et al.*, 2010) and harbor a great biodiversity with high levels of endemism (e.g.

Machado, 1976; Betzin *et al.*, 2016). The absence of *H. canariensis* on El Hierro is either due to a lack of collecting efforts, or more likely the relatively young age of El Hierro (1.1 Ma) compared to Tenerife (11.5 Ma), La Gomera (12 Ma) (Fernández-Palacios & Whittaker, 2008) and Madeira (5 Ma) (Geldmacher *et al.*, 2000, 2005), and the low dispersal ability of *H. canariensis* compared to the wind-dispersed heathers.

The patchy distribution of the Siphonocryptida is probably the result of extinction events of a once wider Palearctic distribution related to changes in climate and vegetation, as already pointed out by Korsós *et al.* (2008, 2009) and Golovatch *et al.* (2015). Thus, the laurel forests largely disappeared in Europe and only persist in relic habitats on Madeira and the Canary Islands (Fernández-Palacios *et al.*, 2011) alongside *H. canariensis*.

Sociality and aggregations

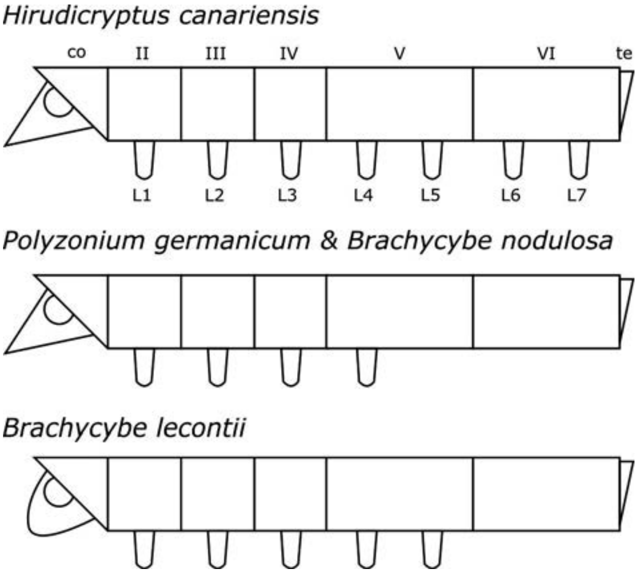
We suggest that *Hirudicryptus canariensis* is social (Costa, 2018) or subsocial (Choe & Crespi, 1997) with parental brood care (see also Blanke & Wesener, 2014; their character 52) and forms aggregations. Yip & Rayor (2014) subdivide subsociality, defining egg-guarding alone as 'transient subsociality' in contrast to 'prolonged subsociality', which is defined as the guarding of juveniles or larvae over some period of time. As only eggs are guarded and disturbance of aggregations of juvenile and mature individuals did not lead to any protective response by the latter, we consider *H. canariensis* as 'transient subsocial'. *Hirudicryptus canariensis* forms aggregations with large numbers of individuals of different stadia, where it is not clear whether this is the result of preferable conditions and availability of food or indicates sociality (i.e. attraction and interaction to each other). Such aggregations of *H. canariensis* have not been reported before and juveniles have been collected singly (Enghoff & Golovatch, 1995). There are reports on social and colonial behavior in other Colobognatha (e.g. Enghoff *et al.*, 2015): Aggregation behavior of individuals of overlapping generations, as well as paternal brood care has been reported for the platydesmids *Brachycybe lecontii* Wood, 1864 (Gardner, 1974; Wong *et al.*, 2020), *Brachycybe nodulosa* (Verhoeff, 1935) (Murakami, 1962a; Kudo *et al.*, 2011) and *Yamasinaium noduligerum* Verhoeff, 1939 (Kudo *et al.*, 2009), while maternal brood care has been reported for the platydesmids *Dolistenus savii* Fanzago, 1874 (Silvestri, 1950) and *Dolistenus humicolus* Verhoeff 1926 (Minelli, 1981), as well as for the polyzoniids *Orsiboe ichigomensis* Attems, 1909 (Murakami, 1962a) and *Polyzonium germanicum* Brandt, 1837 (Rimsky-Korsakow, 1895; Verhoeff, 1928). Therefore, parental care could be a common feature of the Colobognatha but needs further investigations of more taxa. So far brood care has not been reported for Siphonophorida. As in the platydesmidan *Brachycybe nodulosa* (Murakami, 1962a), the ratio of females to males in aggregations of *Hirudicryptus canariensis* is almost 1:1 (Fig. 1a), while a female biased sex ratio has been reported for *Brachycybe lecontii* (Wong *et al.* 2020) and *Pseudodesmus* sp. (Lewis 1984).

Post embryonic development – stadium I

Based on the available material we suggest that *Hirudicryptus canariensis* hatches with six tergites and seven leg pairs (= stadium I). Enghoff *et al.* (1993) and Enghoff & Golovatch (1995) also report the smallest individuals to have six tergites and seven leg pairs but suspect that these might represent stadium II. We argue that these individuals represent stadium I, because no smaller individuals could be found despite extensive sampling, and more importantly, stadium I individuals of other colobognathan taxa (Polyzoniida and Platydesmida) also have six tergites. However, the number of legs (Fig. 8) varies, with six tergites and four leg pairs in *Polyzonium germanicum* and *Brachycybe nodulosa* (Rimsky-Korsakow, 1895; Murakami, 1962b; David & Couret, 1983, 1985; Enghoff *et al.*, 1993), and six tergites and five leg pairs in *Brachycybe lecontii* (Wong *et al.*, 2020) (Fig. 8). Stadium II already has eight or more tergites in Polyzoniida (David & Couret, 1983; Enghoff *et al.*, 1993) and Platydesmida (Murakami, 1963; Wong *et al.*, 2020). We suggest that in stadium I the ultimate tergite, which is apodous in Polyzoniida and Platydesmida (Murakami, 1962b; David & Couret, 1983; Wong *et al.*, 2020), carries two leg pairs in *H. canariensis*, while only in the following stadia the ultimate tergite is apodous, as is the case in the remaining Colobognatha. Thus, podous tergites develop without an apodous precursor between stadium I and stadium II. Other characters supporting that *H. canariensis* with six tergites represent stadium I are (1) the presence of a single pair of ommatidia, (2) antennae consisting of only five antennomeres (including the apical disc), and (3) the absence of coxal sacks. (1) A single pair of ommatidia is also present in stadium I of *Polyzonium germancium*. (2) Only five antennomeres are present in stadium I of *P. germanicum* (Rimsky-Korsakow, 1895), *Brachycybe nodulosa* (Murakami, 1962b) and *Brachycybe lecontii* (Wong *et al.*, 2020: fig. 5), while the following stadia carry more ommatidia (if present) and antennomeres (seven antennomeres in stadium II, eight antennomeres in following stadia (Wong *et al.*, 2020: fig. 5; including apical disc), as is also the case in *H. canariensis*. (3) Coxal sacks, only present in *H. canariensis* with more than six tergites, first appear in *Brachycybe lecontii* in individuals of stadium II (Wong *et al.*, 2020), while for other Colobognatha this state has not been documented.

Post embryonic development – subsequent stadia

In juveniles and younger mature individuals of *Hirudicryptus canariensis*, the more or less regular color pattern corresponds to the total tergite numbers commonly observed in smaller individuals. We suggest that the color pattern can be used to trace the postembryonic development of the earliest stadia, as might be the case in several millipedes like some Platydesmida and the syphonocryptid *Siphonocryptus zigzag* Enghoff, 2010, which show a trans-segmental color pattern (Enghoff, 2011). In *H. canariensis* we observed rather a change in intensity than a well-developed trans-segmental pattern. The anterior six tergites (corresponding to stadium I) are often darker than the following tergites, and juveniles with 6 tergites were common. Subsequent shifts from darker to paler tergites could be observed in several individuals behind tergite 10–14, 14–22 and 18–28, which corresponds to the total numbers of tergites observed in some individuals. Based on the color pattern and the tergite numbers observed, we conclude that the number of color shifts +1 gives the number of the stadium, and that stadium I has 6 tergites and 7 leg pairs, stadium II has 10–14 tergites and 13–21 leg pairs, stadium III has 14–22 tergites and 21–37 leg pairs, and stadium IV has 18–28 tergites and 29–49 leg pairs. This is largely in congruence with the postembryonic development known from the platydesmid *Brachycybe nodulosa*, in which stadium I has 6 tergites, stadium II has 10–14 tergites, stadium 3 has 15–21 tergites and stadium IV has 21–29 tergites (Murakami, 1963: fig. 1). In *H. canariensis* the number of tergites and legs added during molting is irregular and can overlap between individuals of different stadia as is the case in *Polyzonium germanicum* (David & Couret, 1983, 1984) and *Brachycybe* (Murakami, 1963; Wong *et al.*, 2020), and therefore is not reliable for the determination of stadia. In contrast to that, *Hirudisoma latum* (Ribaut, 1908) has a fixed number of tergites and leg pairs per stadium (Brolemann, 1935; Enghoff *et al.*, 1993). In *H. canariensis* there is a strict correspondence between the always odd number of leg pairs (l) and the number of tergites (t), and it can be calculated with the formula $l = 3 + 2(t - 5)$ (the number of haplosegments with a single leg pair is 3, the number of diplosegments with two leg-pairs is $t - 5$, as the collum and the ultimate diplosegment do not carry legs, and the 3 haplosegments have to be excluded). This formula applies for all stadia except for stadium I, which lacks an apodous tergite. In *Polyzonium germanicum* (David & Couret, 1983; Enghoff *et al.*, 1993) and *Brachycybe* (Murakami, 1963; Wong *et al.*, 2020), individuals with the same number of tergites can have a variable numbers of leg pairs, which is always even in *P. germanicum* (David & Couret, 1983). In other Colobognatha there can be several apodous ultimate tergites (e.g. Murakami (1963) and Wong *et al.* (2020) for Platydesmida, David & Couret (1984) for Polyzoniida). In contrast there is always only a single apodous ultimate tergite in *H. canariensis*. This means that in *H. canariensis* several podous tergites can develop de novo without an apodous precursor (or from a single apodous tergite), while in *Polyzonium germanicum* the number of new podous tergites always corresponds to the number of apodous tergites in the previous stadium (David & Couret 1983: table 5). Like the remaining Colobognatha *H. canariensis* develops by euanamorphosis; i.e. segments are added during each molt throughout life (Enghoff *et al.*, 1993; Minelli, 2015).


Hirudicryptus canariensis

Polyzonium germanicum & Brachycybe nodulosa

Brachycybe lecontii

Fig. 9.– Body plan of stadium I juveniles of different Colobognatha. *Polyzonium germanicum* after Rimsky-Korsakow (1895) and David & Couret (1983, 1985), *Brachycybe nodulosa* after Murakami (1962b), *Brachycybe lecontii* after Wong *et al.* (2020).

Fig. 9.– Plan corporal de los juveniles del estadio I de diferentes Colobognatha. *Polyzonium germanicum* según Rimsky-Korsakow (1895) y David & Couret (1983, 1985), *Brachycybe nodulosa* según Murakami (1962b), *Brachycybe lecontii* según Wong *et al.* (2020).

We suggest that in *H. canariensis* the sexual characters of both sexes (vulvae, penes, gonopods) develop gradually via two molts, with not fully developed structures in stadium III (with 2 color shifts), and fully developed structures in stadium IV (with 3 color shifts). In subsequent stadia the external structure of the sexual organs does not change, which is of importance for taxonomic studies, which largely rely on gonopods for species identification. The smallest individuals of *H. canariensis* showing sexual modifications (including immature gonopods) observed in this study had 15 tergites, while the smallest individual reported by Enghoff *et al.* (1993) and Enghoff & Golovatch (1995) had 16 tergites. Our observations correspond to the first appearance of immature gonopods in *Polyzonium germanicum* with 15–21 tergites (David & Couret, 1983), and in *Hirudisoma latum* with 15 tergites (Brolemann, 1935; therein 16 including preanal ring), although these are considered as stadium IV. In *H. canariensis*, fully developed gonopods could be observed in stadium IV, while these appear in stadium V in *P. germanicum* (David & Couret, 1983) and *H. latum* (Brolemann, 1935). In the platydesmidan *Brachycybe nodulosa* males and females can be distinguished from stadia III onwards, suggesting the presence of leg-modifications in this stadium (Murakami, 1963: table 3). In *B. lecontii* immature gonopods first appear in individuals with 24 tergites, corresponding to stadium IV, and are fully developed in individuals with at least 35 tergites, corresponding to stadia V–VII (Wong *et al.* 2020). As the phylogeny of the Colobognatha remains unresolved (e.g. Blanke & Wesener 2014) and the development is only known for very few colobognathan species it remains unknown how these different developmental patterns evolved.

Fungi

The fungus growing on the antennae of a juvenile (stadia I) of *H. canariensis* does not belong to the Laboulbeniales, which are commonly reported from millipedes (e.g. Santamaria *et al.* 2014, 2016; Enghoff & Santamaria 2015), but is one of the less known non-Laboulbenialean fungi associated to millipedes as reported by Enghoff & Reboleira (2017). To our knowledge, this is the first parasitic fungus reported from a colobognathan millipede.

Barcodes and genetic analyses

The genetic distance of 0.5% between the two analyzed specimens of *Hirudicryptus canariensis* is relatively low, as for *Glomeris marginata* (Villers, 1789) intraspecific genetic distances of up to 4.7% are reported (Reip & Wesener, 2018). This high similarity in *H. canariensis* is most likely due to the geographical proximity of the populations with a distance of 7.3 km. Generally, the genetic distance increases with geographical distance, although in some cases *Glomeris marginata* showed 0.0% genetic p-distance between individuals sampled more than 1000 km apart, while larger genetic p-distances of 3% occurred in closer proximity of 9 km (Reip & Wesener, 2018). The moderate genetic distance of 0.5% in the analyzed CO1 fragment supports the view that *H. canariensis* is indeed native to Tenerife and not introduced from another locality. This is further supported by the very specific habitat of the species. Invasive species often show a low genetic diversity due to the founder effect or a higher genetic distance than native populations when multiple introductions occur (e.g. Tsutsui *et al.*, 2000; Allendorf & Lundquist, 2003; Peacock *et al.*, 2009; Estoup & Guillemaud, 2010). Genetic analyses could be used in future studies for a better understanding of the biogeography of *Hirudicryptus canariensis*, as the species is distributed on the volcanic Canary Islands Tenerife and La Gomera, and on the ca. 450 km distant Madeira.

Acknowledgement

We express our gratitude to Prof. del Arco Aguilar from the Departamento de Biologia Vegetal of the Universidad de La Laguna (La Laguna, Santa Cruz de Tenerife, Spain) for the identification of *Erica platycodon* and his advice for finding suitable locations of this plant. We thank the Servicio Administrativo de Medio Ambiente y Seguridad of the Cabildo de Tenerife for granting collection permits for the studied areas. We are grateful to Claudia Etzbauer for DNA extraction and to Juliane Vehof (ZFMK) for obtaining photographs of *H. canariensis* in ethanol (Fig. 7). Furthermore, we thank the hikers and pedestrians, who helped us to orient in the field and pointed us towards interesting spots for observing and collecting. We are grateful to Henrik Enghoff (Natural History Museum of Denmark) for discussions and advice, and the review of this articles, as well as to Sergei Golovatch (Russian Academy of Science) for review of the manuscript and helpful comments. We thank Kerstin Moritz for help in translating Spanish literature and in applying for collecting permits. We thank Antonio Parra Gómez and Kerstin Moritz for help in translating the abstract and captions into Spanish. We are grateful to Brita and Helge Pietsch for accommodation and transportation.

References

Allendorf, F.W. & Lundquist, L.L., 2003. Introduction: population biology, evolution, and control of invasive species. *Conservation Biology*, 17(1): 24-30. https://doi.org/10.1046/j.1523-1739.2003.02365.x

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman D.J., 1990 Basic local alignment search tool. *Journal of Molecular Biology*, 215(3): 403-410. https://doi.org/10.1016/S0022-2836(05)80360-2

del Arco Aguilar, M.J., González-González, R., Garzón-Machado, V. & Pizarro-Hernández, B., 2010. Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity and Conservation*, 19(11): 3089-3140. https://doi.org/10.1007/s10531-010-9881-2

Arndt, E., Enghoff, H. & Spelda, J., 2008. Millipedes (Diplopoda) of the Canarian Islands: checklist and key. *Vieraea*, 36: 1-28. https://doi.org/10.31939/vieraea.2008.36.01

Arozena, M.E., Panareda J.M, & Beltrán, E., 2008. El significado dinámico de los matorrales de *Erica platycodon* en las cumbres del Macizo de Anaga, Tenerife (Islas Canarias, España). *Lazaroa*, 29, 101-115.

Astrin, J.J. & Stüben, P.E., 2008. Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorhynchinae (Coleoptera : Curculionidae). *Invertebrate Systematics*, 22(5): 503-522. https://doi.org/10.1071/IS07057

Attems, C.M.T., 1909. Die Myriopoden der Vega-Expedition. *Arkiv för Zoologi*, 5(3): 1-84. https://doi.org/10.5962/bhl.part.3495

Betzin, A., Thiv, M. & Koch M.A., 2016. Diversity hotspots of the laurel forest on Tenerife, Canary Islands: a phylogeographic study of *Laurus* and *Ixanthus*. *Annals of Botany*, 118(3): 495-510. https://doi.org/10.1093/aob/mcw124

Blanke, A. & Wesener, T., 2014. Revival of forgotten characters and modern imaging techniques help to produce a robust phylogeny of the Diplopoda (Arthropoda, Myriapoda). *Arthropod Structure & Development*, 43(1): 63-75. https://doi.org/10.1016/j.asd.2013.10.003

Brandt, J.F., 1837. Note sur un ordre nouveau de la classe des Myriapodes et sur l'etablissement des sections de cette classe d'animaux en général. *Bulletin Scientifique publié par l'Académie Impériale des Sciences de Saint-Pétersbourg*, 1(23): 178-179.

Brewer, M.S., Sierwald, P. & Bond, J.E., 2012. Millipede taxonomy after 250 years: classification and taxonomic practices in a mega-diverse yet understudied arthropod group. *PLoS One*, 7(5): e37240. https://doi.org/10.1371/journal.pone.0037240

Brolemann, H.W., 1935. Myriapodes Diplopodes (Chilognathes I). *Faune de France*, 29: 1-369.

Choe, J.C. & Crespi, B.J., 1997. *The evolution of social behaviour in insects and arachnids*. Cambridge University Press, Cambridge. 552 pp. https://doi.org/10.1017/CBO9780511721953

Cook, O.F. & Loomis, H.F., 1928. Millipeds of the order Colobognatha, with descriptions of six new genera and type species, from Arizona and California. *Proceedings of the United States National Museum*, 72: 1-26. https://doi.org/10.5479/si.00963801.72-2714.1

Costa, J. T., 2018. The other insect societies: overview and new directions. *Current Opinion in Insect Science*, 28, 40-49. https://doi.org/10.1016/j.cois.2018.04.008

David, J.F., 2015. Diplopoda – Ecology. In: A. Minelli (ed.). *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, 2*. Brill. Leiden: 303-327. https://doi.org/10.1163/9789004188273_013

David, J.F. & Couret, T., 1983. Le développement post-embryonnaire en conditions naturelles de *Polyzonium germanicum* (Brandt)(Diplopoda, Polyzoniida): Les cinq premiers stades. *Bulletin du Muséum national d'histoire naturelle, Section A, Zoologie, biologie et écologie animales*, 5(2): 585-590.

David, J.F. & Couret, T., 1984. La fin du développement post-embryonnaire en conditions naturelles de *Polyzonium germanicum* (Brandt)(Diplopoda, Polyzoniida). *Bulletin du Muséum national d'histoire naturelle, Section A, Zoologie, biologie et écologie animales*, 6(4), 1067-1076.

David, J. F. & Couret, T., 1985. Le cycle biologique du diplopode *Polyzonium germanicum* Brandt, 1831 (Polyzoniida). *Revue d'écologie et de biologie du sol*, 22(3), 367-380.

Dunger, W., 1993. Überklasse Antennata (syn. Tracheata, Atelocerata). In: H.-E. Gruner (ed.). *Lehrbuch der Speziellen Zoologie. Band I. 4. Teil. Arthropoda (ohne Insecta)*. Gustav Fischer. Jena: 1031-1160.

Enderlein, G., 1931. Entomologica Canaria VIII. *Aneurus tagasastei*, eine neue Aradidae. *Zoologischer Anzeiger*, 93: 193-198.

Enghoff, H., 1984. Phylogeny of millipedes - a cladistic analysis. *Journal of Zoological Systematics and Evolutionary Research*, 22(1): 8–26. https://doi.org/10.1111/j.1439-0469.1984.tb00559.x

Enghoff, H., 1990. The ground-plan of chilognathan millipedes. In: A. Minelli (ed.). *Proceeding of the 7th International Congress of Myriapodology*. Brill. Leiden: 1-21.

Enghoff, H., 1992. Macaronesian millipedes (Diplopoda) with emphasis on endemic species swarms on Madeira and the Canary Islands. *Biological Journal of the Linnean Society*, 46(1-2): 153-161. https://doi.org/10.1111/j.1095-8312.1992.tb00857.x

Enghoff, H., 2010. A new strikingly coloured species of *Siphonocryptus*, sixth of its order (Diplopoda: Siphonocryptida). *Zootaxa*, 2681(1): 66-68. https://doi.org/10.11646/zootaxa.2681.1.6

Enghoff, H., 2011. Trans-segmental serial colour patterns in millipedes and their developmental interpretation (Diplopoda). *International Journal of Myriapodology*, 6: 1-27. https://doi.org/10.3897/ijm.6.1949

Enghoff, H., Dohle, W. & Blower, J.G., 1993. Anamorphosis in millipedes (Diplopoda)—the present state of knowledge with some developmental and phylogenetic considerations. *Zoological Journal of the Linnean Society*, 109(2): 103-234. https://doi.org/10.1111/j.1096-3642.1993.tb00305.x

Enghoff, H. & Golovatch, S.I., 1995. A revision of the Siphonocryptidae (Diplopoda, Polyzoniida). *Zoologica Scripta*, 24(1): 29-41. https://doi.org/10.1111/j.1463-6409.1995.tb00473.x

Enghoff, H., Golovatch, S., Short, M., Stoev, P. & Wesener, T., 2015. Diplopoda – taxonomic overview. In: A. Minelli A (ed.). *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, 2*. Brill. Leiden: 363-453. https://doi.org/10.1163/9789004188273_017

Enghoff, H. & Reboleira, A.S.P.S., 2017. Diversity of non-Laboulbenialean fungi on millipedes. *Studies in Fungi*, 2(1):130 –137. https://doi.org/10.5943/sif/2/1/15

Enghoff, H. & Santamaria, S., 2015. Infectious intimacy and contaminated caves – three new species of ectoparasitic fungi (Ascomycota: Laboulbeniales) from blaniulid millipedes (Diplopoda: Julida) and inferences about their transmittal mechanisms. *Organisms Diversity & Evolution*, 15(2): 249-63. https://doi.org/10.1007/s13127-015-0208-8

Estoup, A. & Guillemaud, T., 2010. Reconstructing routes of invasion using genetic data: why, how and so what?. *Molecular Ecology*, 19: 4113-4130. https://doi.org/10.1111/j.1365-294X.2010.04773.x

Fagúndez, J., Juan, R., Fernández, I., Pastor, J., & Izco, J., 2009. Systematic relevance of seed coat anatomy in the European heathers (Ericeae, Ericaceae). *Plant Systematics and Evolution*, 284(1-2): 65-76. https://doi.org/10.1007/s00606-009-0240-2

Fanzago, F., 1874. Sui Chilognati Italiani. *Atti della Società Veneto-Trentina di Scienze Naturali*, 3(2): 233-292.

Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R. & Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests.

Journal of Biogeography, 38(2): 226-246. https://doi.org/10.1111/j.1365-2699.2010.02427.x

Fernández-Palacios, J.M. & Whittaker, R.J., 2008. The Canaries: an important biogeographic meeting place. *Journal of Biogeography*, 35: 379-387. https://doi.org/10.1111/j.1365-2699.2008.01890.x

Gardner, M.R., 1974. Revision of the millipede family Andrognathidae in the Nearctic region. *Memoirs of the Pacific Coast Entomological Society*, 5: 1-61.

Geldmacher, J., van den Bogaard, P., Hoernle, K. & Schmincke, H.U., 2000. The 40Ar/39Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems*, 1(1): 1-26. https://doi.org/10.1029/1999GC000018

Geldmacher, J., Hoernle, K., Bogaard, P., Duggen, S. & Werner, R., 2005. New 40Ar/39Ar age and geochemical data from seamounts in the Canary and Madeira volcanic provinces: support for the mantle plume hypothesis. *Earth and Planetary Science Letters*, 237(1–2): 85-101. https://doi.org/10.1016/j.epsl.2005.04.037

Golovatch, S., Evsyukov, A. & Reip, H.S., 2015. Colobognatha millipedes in the Caucasus (Diplopoda: Polyzoniida, Platydesmida, Siphonocryptida). *Zootaxa*, 3972(2): 250-266. https://doi.org/10.11646/zootaxa.3972.2.6

Golovatch, S.I. & Kime, R.D., 2009. Millipede (Diplopoda) distributions: A review. *Soil Organisms*, 81(3): 565-597.

González-Montelongo, C. & Pérez-Vargas, I., 2019. Looking for a home: Exploring the potential of epiphytic lichens to colonize tree plantations in a Macaronesian laurel forest. *Forest Ecology and Management*, 453: 117541. https://doi.org/10.1016/j.foreco.2019.117541

Government of the Canary Islands. *Biodiversity Data Bank of the Canary Islands* (http://www.biodiversidadcanarias.es/biota). Retrieved 14 March 2022.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Sympsoium*, 41: 95-98.

Hansen, A. & Kunkel, G., 1976. *Erica scoparia* subsp. *platycodon* comb. nova. In: G. Kunkel (ed.). *Gran Canaria, Tenerife y La Gomera: notas floristicas y adiciones*. Cuadernos botanicos canarios 26-27. Las Palmas: 79-80.

Hoffman, R.L., 1977. On the status of *Siphonotus brasiliensis* Brandt, and the diplopod family Siphonotidae (Polyzoniida). *Deutsche Entomologische Zeitschrift*, 24(4–5): 425-431. https://doi.org/10.1002/mmnd.4800240418

Hoffman, R.L., 1980. *Classification of the Diplopoda*. Museum d'Histoire Naturelle. Genève. 237 pp.

Joly, F.X., Coq, S., Coulis, M., David, J.F., Hättenschwiler, S., Mueller, C.W., Prater, I. & Subke, J.A., 2020. Detritivore conversion of litter into faeces accelerates organic matter turnover. *Communications Biology*, 3: 660. https://doi.org/10.1038/s42003-020-01392-4

Koch, M., 2015. Diplopoda – general morphology. In: A. Minelli (ed.). *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, 2*. Brill. Leiden: 7-67. https://doi.org/10.1163/9789004188273_003

Korsós, Z., Enghoff, H. & Chang, H.W., 2008. A most unusual animal distribution pattern: A new siphonocryptid millipede from Taiwan (Diplopoda, Siphonocryptida). *Acta Zoologica Academiae Scientiarum Hungaricae*, 54(2): 151-157.

Korsós, Z., Geoffroy, J.J. & Mauriès, J.P., 2009. The fifth element: reconnection of the disjunct distribution of the members of Siphonocryptida (Diplopoda) with the description of a new species from Nepal. *Journal of Natural History*, 43(7-8): 435-445. https://doi.org/10.1080/00222930802610428

Kudo, S.I., Akagi, Y., Hiraoka, S., Tanabe, T. & Morimoto, G., 2011. Exclusive male egg care and determinants of brooding success in a millipede. *Ethology*, 117(1): 19-27. https://doi.org/10.1111/j.1439-0310.2010.01851.x

Kudo, S.I., Koshio, C. & Tanabe, T., 2009. Male egg-brooding in the millipede *Yamasinaium noduligerum* (Diplopoda: Andrognathidae). *Entomological Science*, 12(3). 346-347. https://doi.org/10.1111/j.1479-8298.2009.00331.x

Lewis, S.G., 1984. Notes on the biology of some common millipedes of the Gunung Mulu National Park, Sarawak, Borneo. *The Sarawak Museum Journal*, 33(54): 179-185.

Liu, W., Rühr P.T. & Wesener, T., 2017. A look with µCT technology into a treasure trove of fossils: The first two fossils of the millipede order Siphoniulida discovered in Cretaceous Burmese amber (Myriapoda, Diplopoda). *Cretaceous Research*, 74: 100-108. https://doi.org/10.1016/j.cretres.2017.01.009

Loksa, I., 1967. Diplopoden aus den Sammlungen von Prof. Dr. H. Franz auf den Kanarischen Inseln. *Opuscula Zoologica*, 7(1): 133-145.

Machado, A., 1976. Introduction to a faunal study of the Canary Islands' laurisilva, with special reference to the ground-beetles. In: Kungel G (ed.). *Biogeography and ecology in the Canary Islands*. Springer. Heidelberg: 367-411. https://doi.org/10.1007/978-94-010-1566-0_13

Macias, A.M., Marek, P.E., Morrissey, E., Brewer, M., Short, D.G., Stauder, C., Wickert, K., Berger, M., Metheny, A., Stajich, J., Boyce, G., Rio, R.M., Panaccione, D., Wong, V., Jones, T. & Kasson, M., 2019. Diversity and function of fungi associated with the fungivorous millipede, *Brachycybe lecontii*. *Fungal Ecology*, 41: 187-197. https://doi.org/10.1016/j.funeco.2019.06.006

Manton, S.M., 1961. The evolution of arthropodan locomotory mechanisms. Part 7. Functional requirements and body design in Colobognatha (Diplopoda), together with a comparative account of diplopod burrowing techniques, trunk musculature and segmentation. *Zoological Journal of the Linnean Society*, 44: 383-462. https://doi.org/10.1111/j.1096-3642.1961.tb01622.x

Marek, P.E., Buzatto, B.A., Shear, W.A., Means, J.C., Black, D.G., Harvey, M.S. & Rodriguez, J., 2021. The first true millipede—1306 legs long. *Scientific reports*, 11(1), 1-8.

McClintock, D.C., 1989. The *Erica scoparia* in Madeira. *Heather Society Yearbook*: 32-36. https://doi.org/10.1038/s41598-021-02447-0

Minelli, A., 1981. Le strategie riproduttive di alcuni artropodi di fagetta. *Natura e Montagna*, 28(4): 74-76.

Minelli, A., 2015. Diplopoda – development. In: A. Minelli (ed.). *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, 2*. Brill. Leiden: 267-302. https://doi.org/10.1163/9789004188273_012

Morales, D., Jiménez, M.S., González-Rodríguez, A.M. & Čermák, J., 1996. Laurel forests in Tenerife, Canary Islands. *Trees*, 11(1): 34-40. https://doi.org/10.1007/s004680050055

Moritz, L., Blanke, A., Hammel, J.U. & Thomas, W., 2021. First steps toward suctorial feeding in millipedes: Comparative morphology of the head of the Platydesmida (Diplopoda: Colobognatha). *Invertebrate Biology*, 140(2): e12312. https://doi.org/10.1111/ivb.12312

Moritz, L., Borisova, E., Hammel, J.U., Blanke, A. & Wesener, T., 2022. A previously unknown feeding mode in millipedes and the convergence of fluid feeding across arthropods. *Science Advances*, 8(7): eabm0577. https://doi.org/10.1126/sciadv.abm0577

Murakami, Y., 1962a. Postembryonic development of the common Myriapoda of Japan XI. Life history of *Bazillozonium nodulosum* Verhoeff (Corobognatha, Platydesmidae) 1. *Zoological Magazine (Dobutsugaku Zasshi)*, 71: 250-255. [in Japanese].

Murakami, Y., 1962b. Postembryonic development of the common Myriapoda of Japan XII. Life history of *Bazillozonium nodulosum* Verhoeff (Colobognath, Platydesmidae) 2. *Zoological Magazine (Dobutsugaku Zasshi)*, 71: 291-294. [in Japanese].

Murakami, Y., 1963. Postembryonic development of the common Myriapoda of Japan XI. Life history of *Bazillozonium nodulosum* Verhoeff (Colobognatha, Platydesmidae) 3. *Zoological Magazine (Dobutsugaku Zasshi)*, 72: 40-47.

de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C. & Whittaker, R.J., 2009. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography*, 36(3): 499-514. https://doi.org/10.1111/j.1365-2699.2008.02012.x

Peacock, M.M., Beard, K.H., O'Neill, E.M., Kirchoff, V.S. & Peters, M.B., 2009. Strong founder effects and low genetic diversity in introduced populations of Coqui frogs. *Molecular Ecology*, 18(17): 3603-3615. https://doi.org/10.1111/j.1365-294X.2009.04308.x

Pocock, R.I, 1894. Chilopoda, Symphyla and Diplopoda from the Malay Archipelago. In: M. Weber (ed.). *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien, Band 3*. Brill. Leiden: 307-404. https://doi.org/10.5962/bhl.title.52289

POWO, 2022. *Plants of the World Online*. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet (http://www.plantsoftheworldonline.org/). Retrieved 14 March 2022.

QGIS Development Team, 2019. QGIS Geographic Information System. *Open Source Geospatial Foundation Project*. http://qgis.osgeo.org.

Read, H.J. & Enghoff, H., 2009. The order Siphonophorida–A taxonomist's nightmare? Lessons from a Brazilian collection. *Soil Organisms*, 81(3): 543-556.

Read, H.J. & Enghoff, H., 2018. Siphonophoridae from Brazilian Amazonia Part 1–The genus *Columbianum* Verhoeff, 1941 (Diplopoda, Siphonophorida). *European Journal of Taxonomy*, 477: 1-23. https://doi.org/10.5852/ejt.2018.477

Reip, H.S. & Wesener, T., 2018. Intraspecific variation and phylogeography of the millipede model organism, the Black Pill Millipede *Glomeris marginata* (Villers, 1789) (Diplopoda, Glomerida, Glomeridae). *ZooKeys*, 741: 93-131.

Ribaut, H., 1908. Notes Myriopodologiques IV. *Bulletin de la Société d'histoire naturelle de Toulouse*, 41: 99-108. https://doi.org/10.5962/bhl.part.5607

Rimsky-Korsakow, M., 1895. Ueber *Polyzonium germanicum* Brandt. *Trudy Sankt-Peterburgskogo Obshchestva Estestvoispytatelei, Otdelenie Zoologii i Fiziologii*, 25(2): 21-33.

Rivas-Martínez, S., Wildpret de la Torre W., del Arco Aguilar, M.J., Rodriguez Delgado, O., Pérez de Paz, P.L., García Gallo, A., Acebes Ginovés, J.R., Díaz González, T.E., & Fernández González, F., 1993. Las comunidades vegetales de la Isla de Tenerife (Islas Canarias). *Itinera Geobotanica*, 7: 169-374.

Santamaria, S., Enghoff, H. & Reboleira, A.S.P.S., 2014. Laboulbeniales on millipedes: the genera *Diplopodomyces* and *Troglomyces*. *Mycologia*, 106(5): 1027-1038. https://doi.org/10.3852/13-381

Santamaria, S., Enghoff, H. & Reboleira, A.S.P.S., 2016. Hidden biodiversity revealed by collections based research – Laboulbeniales in millipedes: genus *Rickia*. *Phytotaxa*, 243(2): 101-127. https://doi.org/10.11646/phytotaxa.243.2.1

Sierwald, P. & Bond, J.E., 2007. Current Status of the Myriapod Class Diplopoda (Millipedes): Taxonomic Diversity and Phylogeny. *Annual Review of Entomology*, 52: 401-420. https://doi.org/10.1146/annurev.ento.52.111805.090210

Silvestri, F., 1950. Segmentazione del corpo dei colobognati (Diplopodi). In: A.F. Elfströms Boktryckeri (ed.). *Proceedings of the Eighth International Congress of Entomology*, Stockholm: 571–576.

Shelley, R.M., 2003. A revised, annotated, family-level classification of the Diplopoda. *Arthropoda Selecta*, 11(3): 187-207.

Shorter, P.L., Hennen, D.A. & Marek, P.E., 2018. Cryptic diversity in *Andrognathus corticarius* Cope, 1869 and description of a new Andrognathus species from New Mexico (Diplopoda, Platydesmida, Andrognathidae). *ZooKeys*, 786: 19-41. https://doi.org/10.3897/zookeys.786.27631

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S., 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular biology and evolution*, 30(12): 2725-2729. https://doi.org/10.1093/molbev/mst197

Tsutsui, N.D., Suarez, A.V., Holway, D.A. & Case, T.J., 2000. Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences*, 97(11): 5948. https://doi.org/10.1073/pnas.100110397

Verhoeff, K.W., 1926. Über einige südalpine Chilognathen (102. Diplopoden-Aufsatz.). *Zoologischer Anzeiger*, 66(1-4): 65-81.

Verhoeff, K.W., 1928. Klasse Diplopoda, 1. Teil. In: H.G. Bronns (ed.). *Klassen und Ordnungen des Tierreichs, 5. Band, 2. Abteilung, Gliederfüssler: Arthropoda,*. Akademischer Verlag. Leipzig: 1-1071.

Verhoeff, K.W., 1935. Neue ostasiatische Colobognathen. 140. Diplopden-Aufsatz. *Zoologischer Anzeiger*, 112(3-4): 62-73.

Verhoeff, K.W., 1939. Diplopoden von der Ryukyu-Insel Okinawa. *Transactions of Biogeographical Society of Japan*, 3(2): 118-122.

Vicente, M.C. & Enghoff, H., 1999. The millipedes of the Canary Islands (Myriapoda: Diplopoda). *Vieraea*, 27: 183-204.

de Villers C.J., 1789. Caroli Linnaei Entomologia, faunae Suecicae descriptionibus aucta. Volume 4, Aptera. Lugduni. 556 pp.

Webb P.B. & Berthelot S., 1844. *Histoire Naturelle des Îsles Canaries, Tome troisième, Phytographia Canariensis, Sectio II*. Paris. 496 pp. https://doi.org/10.5962/bhl.title.60795

Wegensteiner, R., 1982. On the relationship between the ecological potence of *Polyzonium germanicum* Brandt (Diplopoda, Colobognatha) and the environmental parameters in the Vorderen Rotmoos (Lunz, NO). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, 109(3): 309-327.

Wesener, T., 2015. No millipede endemics north of the Alps? DNA-barcoding reveals *Glomeris malmivaga* Verhoeff, 1912 as a synonym of *G. ornata* Koch, 1847 (Diplopoda, Glomerida, Glomeridae). *Zootaxa*, 3999(4): 571–580. https://doi.org/10.11646/zootaxa.3999.4.7

Wong, V.L., Hennen, D.A., Macias, A.M., Brewer, M.S., Kasson, M.T. & Marek, P., 2020. Natural history of the social millipede *Brachycybe lecontii* Wood, 1864. *Biodiversity Data Journal*, 8: e50770. https://doi.org/10.3897/BDJ.8.e50770

Wood, H.C., 1864. Description of new genera and species of North American Myriapoda. *Proceedings of the Academy of natural Science of Philadelphia*, 1864: 186-187.

Yip, E.C. & Rayor, L.S., 2014. Maternal care and subsocial behaviour in spiders. *Biological Reviews*, 89(2): 427-449. https://doi.org/10.1111/brv.12060

Zuev, R.V., 2017. The relict millipede *Hirudicryptus abchasicus* Golovatch, Evsyukov et Reip, 2015, represents a species, genus, family and order new to the fauna of Russia (Diplopoda: Siphonocryptida: Siphonocryptidae). *Russian Entomological Journal*, 26(3): 283-286. https://doi.org/10.15298/rusentj.26.3.12

Supplementary material

Supplementary material containing additional images and tables with the original data are deposited on zenodo and can be accessed via the following link: https://doi.org/10.5281/zenodo.6353889