



MINOR REVIEW

Diversity, ecology, distribution and biogeography of Diplura

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Abstract. 1. Diplura is the sister group to insects and one of the three basal hexapod groups with unique entognathan mouthparts. The order is divided into 10 families, which include 1008 species in 141 genera, with a high proportion of monotypic genera. They are ubiquitous in soils and subsurface terrestrial habitats, as well as have an important role in overall biogeochemical cycles.

2. We present the first comprehensive review of the global biodiversity and ecology of Diplura. We highlight four aspects of this basal hexapod group: diversity in morphological body plans and sizes; ecology in terrestrial environments from soil to caves; food preference and trophic levels, and their biogeographical and paleobiogeographical significance.

3. Diplura depends on high humidity and moderate temperatures. They are presumably very sensitive to anthropogenic pressures and climate change, and therefore are a suitable model for ecophysiological studies and evident priority targets for conservation.

4. We conclude that the future efforts should focus on establishing a molecular phylogeny to clarify the relationships between and within families, as well as to reveal global biogeographical patterns. This will require an increase in sampling effort in several regions of the globe, especially in tropical regions.

Key words. Apterygota, basal Hexapoda, cave ecosystems, Entognatha, soil organisms, subterranean biodiversity.

Introduction

Diplurans are one of three entognathous hexapod groups present in almost every soil, cave or other empty subsurface space. This order is poorly represented in the scientific literature with only about 900 publications since Linnaeus wrote the *Systema Naturae* (1761–1767). In spite of their ubiquity in subsurface terrestrial habitats, diplurans have been mostly forgotten in ecological studies and remain without a solid worldwide revision since the monograph of campodeids by Condé (1956) and the Diplura checklist by Paclt (1957). A handful of zoologists have devoted

their scientific career to diplurans, beginning with Filippo Silvestri (1873–1949) from Italy; from France: Jean Robert Denis (1893–1969), Bruno Condé, and Jean Pagés (1925–2009); from Germany: Petr Wygodzinsky (1916–1987); from Czech Republic Juraj Paclt (1925–2015); from Russia: Boris Pimenovitch Chevrizov (1951–1993); from USA: Leslie M. Smith (1903–1976) and Mark Alan Muegge (1956–2015); and finally from Uruguay: Pablo R. San Martín (1933–1969).

Diplura is considered the sister group to insects and thus the closest group among the three basal hexapods that include Collembola and Protura (Beutel *et al.*, 2017). Hexapods became terrestrial most likely in early Ordovician (Misof *et al.*, 2014), acquiring breathing capacity through a tracheal system, excretory activity through Malpighian tubules (which are reduced or absent in some families), and reproduction with indirect sperm transference by spermatophores (Beutel *et al.*, 2017). The oldest

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record of a truly dipluran fossil dates back to the Lower Cretaceous from Brazil (Wilson & Martill, 2001). However, a japygid-like doubtful dipluran fossil was described from the Upper Carboniferous (Kukulová-Peck, 1987). Another four fossil species of campodeids and japygids have been described hitherto (Paclt, 1957).

As hexapods, diplurans have an insect-like body plan with three tagmata: head, thorax, and abdomen. The head has two frontal antennae with all antennomeres equipped with their own set of muscles and unique entognathous mouthparts, partially hidden into two oral folds. The three thoracic segments lack wings (apterygote hexapods) and have a pair of similar legs ending in a simple tarsus with two claws (pretarsus). The abdomen is divided into 10 complete segments, some with vestiges of legs represented by a pair of articulated styli and eversible, water absorbing vesicles (Weyda, 1976). The last abdominal segment bears the typical paired cerci, responsible for the common name two-pronged bristletails or ‘double tails’, that evolved into a great variety of shapes and function differing among families (Fig. 1).

Diplurans have successfully colonised hypogean habitats in soils and in the vast network of caves. They have thrived in all kind of dark cryptic terrestrial habitats (Racovitza, 1907; Condé, 1956; Sendra *et al.*, 2020b). Diplurans have a fragile depigmented cuticle with punctually sclerotized areas at the tip of the buccal pieces, in the pretarsus and, in some families, in some distal abdominal segments – including the cerci. Colour in some diplurans is due to sub-epidermal soluble fats, which give a few species a yellowish to pinkish colour, or a mix of different patterns as in heterojapygids and some campodeids species (Condé, 1956; Paclt, 1956). Diplurans have a vermiform and flattened body, which gives the group a great mobility and capability to move along the subterranean network of sometimes extremely narrow and tiny spaces. To move in these completely dark environments, the eyeless diplurans possess numerous kinds of mechanoreceptors and other types of sensorial sensilla,

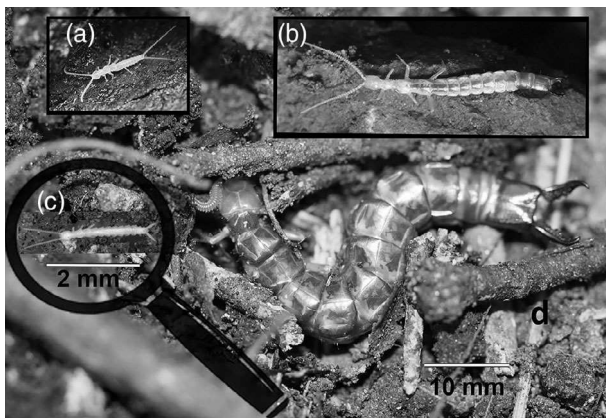


Fig. 1. Overview of Diplura habitus. (a) Campodeidae; (b) Japygidae; (c) Projapygidae and (d) Heterojapygidae. Scale bars: (a), (b) and (d) = 10 mm; (c) = 2 mm. [Color figure can be viewed at wileyonlinelibrary.com]

presumably to detect gradients in humidity, temperature and/or CO₂ variations. In hypogean environments, diplurans play an important role in plant litter decomposition and in the generation of soil microstructure, occupying different trophic levels in the soil as well as in cave-ecosystems (Condé, 1956). They host bacteria, protozoa, fungi, nematodes or other arthropods, and they feed on a wide range of food sources ranging from fresh or decomposing plants to dead or alive animals, including microorganisms and fungi (Condé, 1956; Sendra *et al.*, 2020b).

Here we provide a critical review of the order Diplura based on the current bibliography to highlight four aspects of this basal hexapod group: diversity in morphological body plans and sizes; ecology in subsurface environments from soil to caves; food preference and trophic levels and their biogeographical and paleobiogeographical relevance.

Diversity

The order Diplura comprises hitherto 1008 species and 88 subspecies in 141 genera, with a high proportion of monotypic genera (60 genera, 43%) (Figs 1 and 2) (Supporting Information Table S1). This biodiversity is unequally distributed into 10 families, which exhibit a large variety in body size and shape, behaviour, reproduction, and habitat preferences (Denis, 1949; Koch, 2001; Sendra, 2015). Campodeidae, with 491 species (49% of dipluran biodiversity), and Japygidae, with 343 species (34%), account for 83% of all dipluran species. Anajapygidae, Dinjapygidae, Heterojapygidae, Octostigmatidae, and Procampodeidae represent only 2% of the order's total biodiversity, while the remaining three families – Evalljapygidae, Parajapygidae and Projapygidae – contribute up to 15%. Dipluran biodiversity is similar to the other basal hexapod orders, being slightly higher than in Protura (800 spp.), but lower than in Collembola (nearly 9000 spp.) (Rusek, 1998; Galli *et al.*, 2019; Potapov *et al.*, 2020).

Currently, diplurans are divided into three superfamilies, Campodeoidea, Projapygoidea and Japygoidea, and each has a well-distinguished body plan (Denis, 1949; Pagés, 1959, 1989; Koch, 2001; Sendra, 2015). These three taxa show substantial differences in terminal abdominal cerci, mouthparts, first urosternite, tracheal system, and ovary structure (Denis, 1949; Pagés, 1959, 1989).

Campodeoidea comprises two families: Procampodeidae and Campodeidae, both characterised by bearing two long and pluriarticulated cerci. The mouthparts include mandibles with a protheca, maxillae without palps, and a labium with a pair of palpiform processes and an additional pair of spheroidal palps. The first urosternite bears two subcoxal appendages in lateral position. In the open tracheal system, spiracles are restricted to the thorax. Finally, the ovary is simply formed by two sacs similar in shape to the testis (Denis, 1949; Pagés, 1959, 1989).

Projapygoidea includes three families: Anajapygidae, Octostigmatidae, and Projapygidae, all of them characterised by bearing two short but pluriarticulated cerci. Each cercus has an apical orifice, which is the exit of abdominal spinning glands. As to the mouthparts, like in Campodeoidea the mandibles have a protheca. The maxillae however have palps and internal pectinate

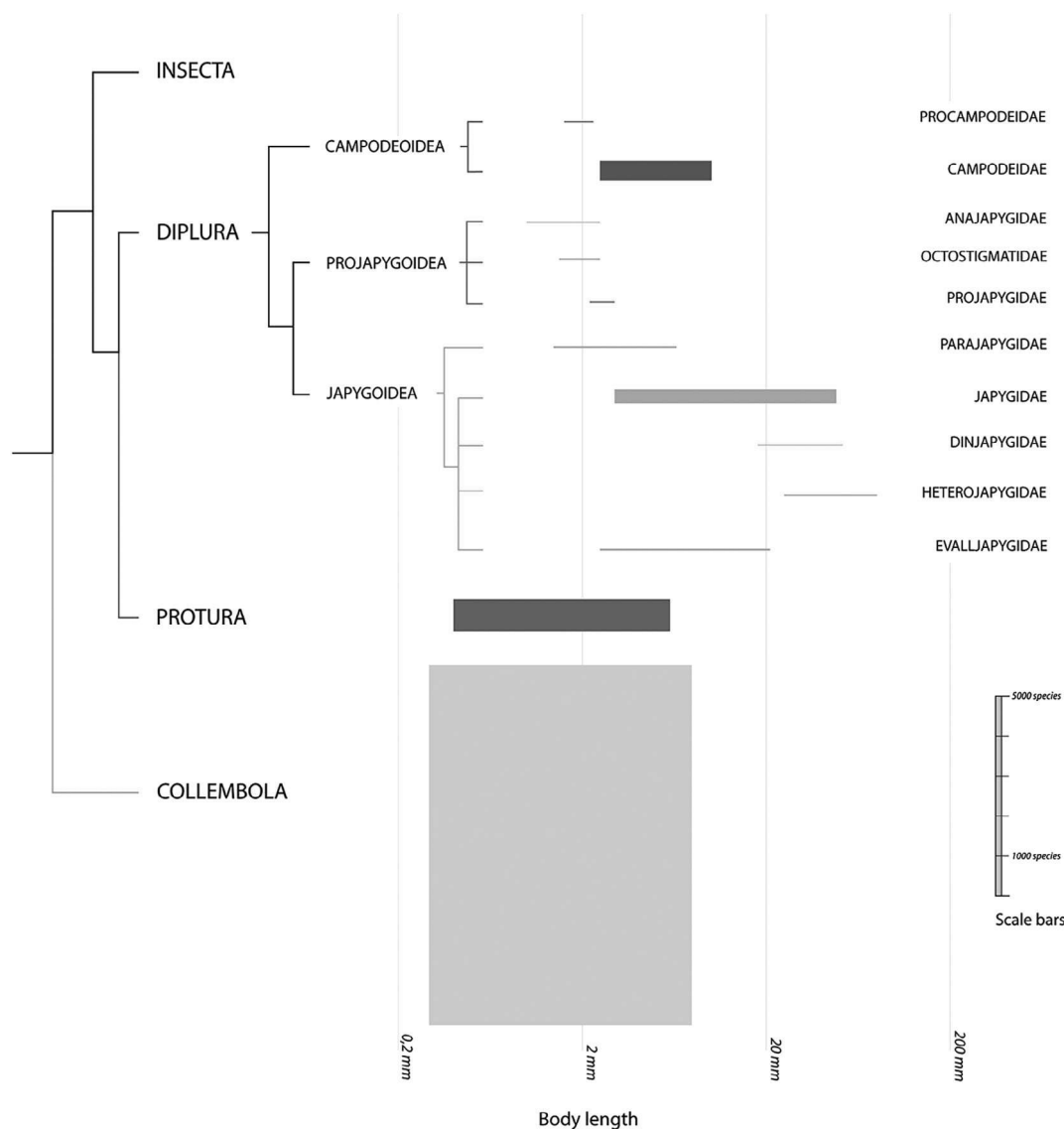


Fig. 2. Phylogeny, taxonomical diversity and body length in Diplura compared with Protura and Collembola. Diplura phylogeny adapted from Koch (2001). [Color figure can be viewed at wileyonlinelibrary.com]

laciniae. The labium has one pair of palpiform processes in addition to a pair of more or less developed palps. The first urosternite bears lateral styli in addition to two internal subcoxal appendages. The tracheal system opens with thoracic and abdominal spiracles. Finally, the ovary is divided into two oviducts with two ovarioles each (Denis, 1949; Pagés, 1959, 1989).

Japygoidea comprises five families: Japygidae, Evalljapygidae, Parajapygidae, Heterojapygidae, and Dinjapygidae, all of which bear unarticulated pincer-shaped cerci. At the hind end, the 8–10 abdominal segments are well sclerotized, bearing the musculature of the cerci. The mandibles lack a prosthema, and the maxillae have palps and an internal pectinate lacinia. The tracheal system opens with thoracic and abdominal spiracles.

Finally, the ovary is divided into two oviducts with seven ovarioles each (Denis, 1949, Pagés, 1959, 1989).

Below the family level, diplurans display minimal morphological diversity. Delimitation between species, subgenera, genera, and subfamilies depends mostly on chaetotaxic characters of large setae (macrosetae), sensilla patterns, modifications in the glandular and sensorial structures of the first urosternite, and in some families on the shape and number of teeth in the pincer-like structure of the cerci (Silvestri, 1912; Denis, 1930; Pagés, 1953, 1984; Condé, 1956; Smith, 1962). Bareth (1968) suggested the use of the variability in the shape of spermatozoids fascicles and spermatozophors in Campodeoidea as a taxonomic character. Recently, scanning electron microscopy studies have provided

additional details about cuticular structures, setae, and sensilla (Sendra *et al.*, 2019, 2020a). Morphological characters fail to provide a clear phylogeny below family level and hitherto molecular data for dipluran species is still very scarce. Consequently, only first advances in molecular analysis, with poor taxonomic clarifications, have been produced (Luan *et al.*, 2004; Bu *et al.*, 2012; Chen *et al.*, 2014).

The body size in diplurans ranges from nearly 1 mm up to 80 mm, a wide variation among soil and cave fauna. Diplurans are considered from mesofauna to megafauna following the classification of soil arthropods according to size (Eisenbeis & Wichard, 1987). Body length in diplurans has a wider range than in the other basal hexapods whose body length is up to 5 mm in proturans and 9 mm in springtails (Fig. 2). Procampodeids, anajapygids, octostigmatids, and a few parajapygids species are less than 2 mm long. The body length of most diplurans ranges from 2 mm to 2 cm, and it includes all campodeids, evalljapygids, projapygids, and the majority of japygids and parajapygids. Only a few japygids (including most cave-adapted species), dinjapygids, and heterojapygid families exceed a body length of 20 mm (Figs 1 and 2).

Ecology

All diplurans inhabit soil and subsurface terrestrial habitats, extending from non-consolidated debris in soils to network of voids in the bedrock, including caves (Condé, 1956; Sendra *et al.*, 2020b) (Fig. 3).

Diplura, due to their soft body and thin cuticle, depend on high humidity and moderate temperatures (Condé 1956). Campodeids are extremely hydric and have a high transpiration rate, for example, in *Campodea* the average loss of water mass is $77.4\% \text{ h}^{-1}$ at 100% relative humidity and 22°C (Eisenbeis & Wichard, 1987). Japygids are considered more thermophilic and mesic than other diplurans (Eisenbeis & Wichard, 1987) and have their optimal humidity around 85%, while campodeids and parajapygids are known to have an optimal fitness under 100% relative humidity (Pagés, 1967b).

Diplurans are well known and mostly diversified in temperate forests with rich soils, but they are also found under the bark of tree logs and in mosses (Condé 1956). Coexistence or syntopy of dipluran species is reported in forest soil habitats, with up to four different campodeid species found in oak woods in Europe (Blesić, 1987). Dipluran diversity is reduced in boreal forests, while in tropical forests campodeids are represented mostly by the *Lepidocampinae* subfamily in the litter layers, rotten wood or soil, and in tree epiphytes, while japygids are abundant in deep soil layers (Delamare Deboutteville, 1950; Condé, 1956). Soils of scrublands and meadows are occupied by the smallest diplurans such as parajapygids, campodeids or projapygids. Under stones, it is possible to find the largest diplurans, such as big japygids, heterojapygids, and dinjapygids. In dry regions, diplurans survive in sites that retain humidity such as temporal water courses, oasis, or caves (Condé, 1956). Diplurans have also been collected by chance in ant or termite nests (Silvestri, 1916; Condé, 1956), as well as in mammal nests (Condé, 1956).

In caves, diplurans from the families Campodeidae and Japygidae are found in karst and in volcanic formations all around the world, except in extreme cold or dry regions or areas that experienced these extreme conditions in the past (Sendra *et al.*, 2020b).

Diplurans can be found along a wide altitudinal range from the sea level to high mountain areas (Condé, 1956; González, 1964; Pagés, 1975). Some parajapygids species inhabit the sand or gravel substratum in intertidal areas (Pagés, 1975; Bu *et al.*, 2012). To survive in floodable soils, *Parajapyx adisi*, which lives in the Central Amazonia forests, builds a cocoon using the urosternal glands to survive for months (Adis & Pagés, 2001). Some campodeids have also been found at river floodplains (Condé, 1960), including temporal water courses (Sendra *et al.*, 2017) and in the so-called alluvial mesovoid shallow substratum (MSS) (Ortuño *et al.*, 2013). At high altitudes, diplurans can be found in alpine meadows and scree slopes (Sendra *et al.*, 2017), even when those are seasonally covered by snow. Almost 50 species have been collected above 2000 m a.s.l., and only a few above 3000 m a.s.l.; these high-altitude species include five campodeids, two japygids, and two species of the gigantic species of the dinjapygid family: *Dinjapyx barbatus* and *Dinjapyx michelbacheri* in the Andes' Altiplano (González, 1964). The campodeid *Lepidocampa weberi nepalensis* keeps the highest altitude record for the order; it was collected in Nepal at 4800 m a.s.l. (Condé & Jacquemin-Nguyen, 1968).

In well-stratified soils, diplurans occupy all soil horizons. Larger species occupy the upper layers represented by O and A-horizons and are comprised by the larger campodeids and japygids, including the giant species of dinjapygids and heterojapygids. Smaller species live in the narrower pores of the B-horizon, where only diplurans with a tiny body (usually under 2 mm body length and short appendages) can move. Most diplurans are not actively tunnelling and burrowing soil animals, however, japygids can build microtunnels in the soil matrix (Pagés, 1967b), a behaviour that is more evident in heterojapygids (Tillard, 1924). The lower soil layer, the C-horizon (or MSS) is occupied by soil diplurans. In case of a physical connection of caves with the C horizon, this MSS can be inhabited by cave-adapted diplurans (Bareth, 1983; Sendra *et al.*, 2017). The vast cave-ecosystems are found below the soil or under the rock surface and consist of a network of cracks and voids from 5 mm to hundreds of meters in consolidated rocks (Moldovan *et al.*, 2018; Culver & Pipan, 2019). These large subterranean areas are inhabited by a cave-adapted fauna, mostly campodeids and japygids with larger and slender bodies and appendages than their soil-adapted relatives (Sendra *et al.*, 2020b).

Very few studies have focused on the abundance of diplurans in their habitats (e.g. Christian, 1992). The abundance of *Diplura* per habitat is far from being known. Drift (1951) found 100 individuals m^{-2} of campodeids at the base of old litter in the humus/mineral soil layer in a beech forest in temperate Europe, whereas Blesić (1987) reported 440–1804 individuals m^{-2} in an oak forest. High specimen density values are also recorded for small parajapygids living in crops, from 118 individuals m^{-2} collected at 5 cm depth in a wheat field in Australia (Greenlade & Luan, 2018) to 1810–5500 individuals m^{-2} at 30 cm depth in a

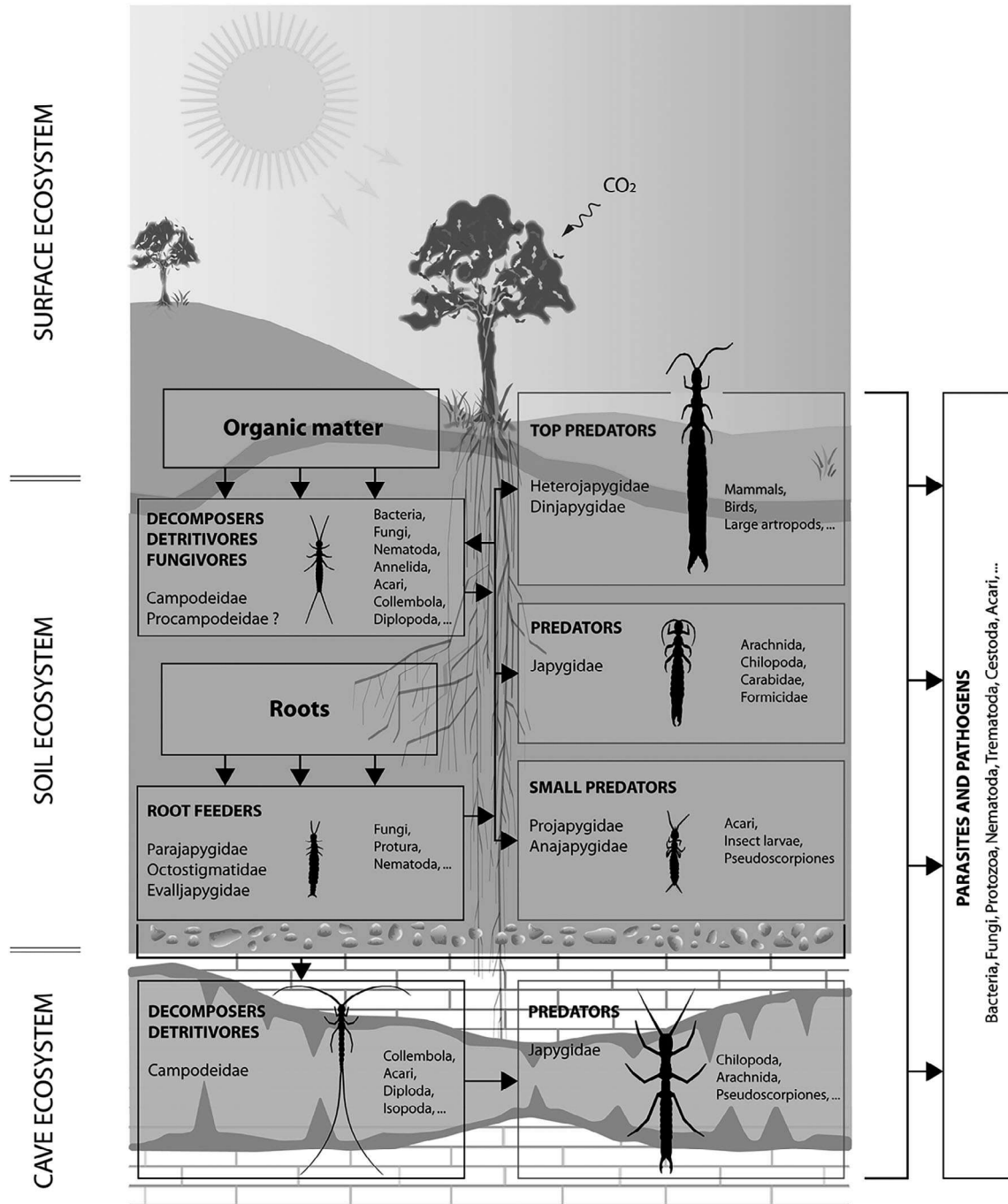


Fig. 3. Conceptual model of Diplura habitats, habitus and trophic relationships. [Color figure can be viewed at wileyonlinelibrary.com]

clover field in USA (Macklin, 1956). A behavioural study with japygids estimated 30 specimens of *Dipljapyx humberti* to be an average number in a volume of garden soil of 60 × 40 × 50 cm (Pagés, 1967a). For the other families of Diplura there is no density data available, but sampling revealed great abundance for evalljapygids, for example, *Evalljapyx helferi* was described from a single locality from a redwood humus with 1500 specimens in California,

USA (Smith, 1959); for projapygids, San Martín (1963) quoted 32 specimens under a single stone in Uruguay; and for octostigmatids, Rusek (1982) mentioned 51 specimens of *Octostigma herbivora* in a soil sample from a peanuts plantation in Tonga Islands.

Aggregation behaviour has not been observed in any dipluran family, while some conspecific avoidance and cannibalism seem to be common among campodeids (Gunn, 1992). Territorial

behaviour has been suggested for the predatory japygids (Pagés, 1967a).

Cave-adapted dipluran populations seem to maintain constant numbers along the year (Sendra & Reboleira, pers. obs.). Diplura in the MSS show variable seasonal patterns of abundance, that is, peaking at different seasons in different localities (Eusébio *et al.*, ; Sendra *et al.*, 2017), while soil diplurans show strong annual variations (Mitrovski-Bogdanović & Blesić, 2006; Sendra *et al.*, 2017). This seasonal variation correlates with the degree of development of the reproductive glands in some campodeid species (Bareth, 1968). Adult females of soil campodeids lay eggs all year round, except from November to February, during a 2-year lifespan (Orelli, 1956). Observational studies of *Campodea lankasteri* in a rhizotron showed a higher abundance from May to mid-September, accounting for approximately 9% of total soil fauna abundance (Gunn, 1992). Blesić (1987) reported minimal population size of campodeids during the winter in oak forest, similar results were obtained in other sampling studies (Sendra *et al.*, 2017). In the case of japygids, which have a lifespan longer than 6 years, Pagés (1963) showed less seasonal variation, perhaps because they survive the annual climatic variation by reaching deeper layers during periods with extremes temperatures (Hairston & Byers, 1954; Gyger, 1960). Pearse (1946) remarked that parajapygids keep regular activity throughout the year.

While other entognaths, as springtails, have long been used as model and indicator taxa in soil and ecotoxicology studies (Smit & Van Gestel, 1998), our knowledge on the effects of contaminants in Diplura remains extremely scarce. The effect of seasonal variation in cadmium (Cd) bioaccumulation for *Campodea staphylinus* living within litter and with high metal concentration was studied by Janssen *et al.* (1990). The study showed a significant higher Cd concentration in spring and summer compared to fall and winter seasons, matching the increment in body mass. The same study pointed out that *C. staphylinus* showed a higher Cd bioaccumulation compared to other soil faunal groups, such as carabid beetles and Mesostigmata mites. The midgut epithelial cells of *C. (Monocampa) devoniensis* were microanalysed and their electron-dense granules were found to be strongly influenced by the environmental bioavailability of metals with the capacity to bioaccumulate Fe, Mn, Zn, Pb, and Cu (Pigino *et al.*, 2005). Another study on the effects of increasing soil metal contamination on arthropod communities suggests that Diplura (together with the other entognaths orders) may tolerate high concentrations of Pb and Sb in soils (Migliorini *et al.*, 2004). Diplurans have also been reported to be influenced by soil acidity (Paoletti *et al.*, 1996). The potential of Diplura as relevant taxa for evaluating anthropogenic disturbance in soils has been highlighted because they are well represented in all kinds of soil and subsurface habitats and are impacted by environmental changes (Blasi *et al.*, 2013).

Food preference and trophic levels

Overall, diplurans play multiple roles in soil food webs – from primary consumers of root plants and detritivores, to secondary and tertiary consumers, and they can even be top invertebrate

predators. Their feeding preferences vary across families and are related to size, shape of mandibular and maxillar structures, and to the type of terminal cerci (Christian & Bauer, 2005). Campodeids (up to 10 mm body length) have long, fragile, multiarticular cerci and mouthparts with grasping and crushing function. They are omnivores with a generalist diet, eating from fresh roots, fungal hyphae and spores to decay organic matter or even tiny invertebrates, so they can be considered either decomposers or primary and secondary consumers (Bareth, 1986; Gunn, 1992; Blesić, 1999; Christian & Bauer, 2005). Japygoidea (up to 6 cm body length) have unsegmented pincer-shaped cerci, heavily sclerotized and muscled, with offensive and defensive roles, and mouthparts optimised for perforating and tearing. Thus, they are mostly predators feeding on small arthropods such as mites, springtails, symphylans, insect larvae and others diplurans, and very rarely feed on terrestrial isopods, but they are also known to feed on organic debris and fungal mycelia and spores (Christian & Bauer, 2005). Within Japygoidea, japygids are predators while heterojapygids and dinjapygids are top invertebrate predators, thus representing the highest level of the trophic pyramid for all invertebrates. For instance, in the Andes, dinjapygids have been reported to apparently exclude scorpions and occupy their ecological 'niche' (González, 1964). Parajapygid species feed on plant roots including crops (Reddell, 1985); evalljapygids probably also mostly feed on plants since no animal remains have been found in the guts of many species (Smith, 1959), with the exception of one *Evalljapyx macswaini* specimen that had insect parts in its gut, probably thrips (Smith, 1960). Finally, Projapygoidea (~2 mm) have short multi-articulated glandular cerci with a defensive and offensive function, showing a mixed feeding behaviour by preying on microarthropods such as mites and tiny pseudoscorpions (San Martín, 1963) but also consuming plant roots (Rusek, 1982).

Diplurans are predated by several arthropod groups. Larger diplurans feed on smaller diplurans and at the same time are known to be predated by centipedes and ground beetles (Kasaroff, 1935; Gunn, 1992).

Symbiotic interactions surrounding diplurans, most of the time with unclear dependence degrees, comprise a wide range of organisms including bacteria, hyphae and spores of fungi, 'Amphoromorph' fungi, Gregarina cysts, larvae of Gordiidae nematomorphs, and nematode larvae or Acari (Paclt, 1957; Bareth, 1974).

Distribution and biogeography

The order Diplura is an ideal model for biogeographical studies; diplurans are wingless hexapods with limited dispersal capacities and with little tolerance to temperature variations and dryness. Besides, many species live confined in underground habitats, and the taxon has its ancient origin in the Early Ordovician, reflected in a Pangean distribution for the most species-rich families (i.e., Campodeidae and Japygidae) and more limited distribution ranges for the rest of the families (Tables 1 and 2).

Nevertheless, some ecological traits can complicate the understanding of their biogeographical patterns. For example, some campodeids and parajapygids can survive in temporal interstitial

flooded habitats for long periods (Condé, 1960), and parajapygids can produce resistant cocoons (Adis & Pagés, 2001) that can be easily dispersed. Some species are considered invasive, such as *Campodea (Monocampa) devoniensis*, native to Western Europe but found in urban gardens and city surroundings around the world, as well as in certain Darwinian islands (those never connected to mainland) such as Saint-Helena or the Canaries (Paclt, 1966; Condé & Bareth, 1970). The lack of an internal phylogeny (Sendra *et al.*, 2020b), and the large geographical sampling bias (54% of all known Diplura records are located in France, Italy, Spain and USA), are currently the two major limitations to understand the biogeographical history of the taxon.

Diplurans have been found in all continents, except in Antarctica, since they never managed to overpass the Polar circles. This vast distribution is somewhat smaller compared to the two other basal hexapod groups, where Protura slightly overpass the Arctic Circle (Galli & Rellini, 2020) and Collembola even managed to colonise Antarctica (Ávila-Jiménez & Coulson, 2011). Among diplurans, only campodeids have been found living in northern latitudes. For instance, *Campodea (C.) fragilis* was recorded from Vega Island, Norway (Lie-Pettersen, 1907), located at 65°N, slightly South of the Arctic Circle, and two other campodeids, *Metriocampa allocerca* and *Metriocampa rileyi*, were found at 64°N and 56°N in Alaska, respectively (Sikes & Allen, 2016). At the lowest southern latitudes there is again another a campodeid, *Campodea (Campodea) lahillei*, which was found at 49°S in the Santa Cruz province, Argentina (Silvestri, 1931). Japygids and Evalljapygids species are restricted to warmer areas although two species, *Dipljapyx humberti* and *Metajapyx leruthi*, have been found at 50°N in Belgium (Silvestri, 1948), and *Evalljapyx saundersi* was located at 49°N in Vancouver Island, Canada (Saunders, 1946; Pagés, 1996).

Regardless of the aforementioned limitations, the existing data (1008 described species sampled, Supporting Information Table S1, from more than 7000 localities around the world) permit to delimit distribution patterns, as well as to arrive at some paleobiogeographical conclusions. For instance, the biogeographical distribution of diplurans follows the general patterns described by Darlington (1957) and Vigna Taglianti *et al.* (1992, 1999). According to that criteria, Diplura fall into the W-Palearctic, containing the distribution areas of 35% of all diplurans and 43% of all dipluran genera. In the whole

Holarctic, the percentages rise to 56% of the species and 90% of the genera. Surely, such high numbers may be influenced by the biased sampling and lack of taxonomical studies in other regions.

At the family level (Table 1), the Holarctic region is characterised by the high diversity of campodeids (336 out of the 491 species) and by two highly diverse genera, the cosmopolitan *Campodea* (143 out of the 180 species) and the endemic *Plusiocampa* (70 species), as well as a good representation of japygids (139 out of the 340 species). In addition, the Palearctic region is characterised by its endemic and small procampodeid family (2 species). In the Ethiopian and Neotropical regions, three families are noteworthy because of their diversity: japygids (126 out of the 340 species), parajapygids (37 out of the 62 species), and projapygids (36 out of the 42 species). The Oriental region shows a high diversity of japygids (58 out of the 340 species) (Table 1). The five species of the anajapygid family are distributed in the Holarctic (3 species.), Oriental (1 sp.), and Neotropical (1 species) regions (Table 1). The rest of the families, all with a very low number of species, have more restrictive distribution ranges. Two of the three octostigmatid species live in the Oriental region and one in the western Australian island. The 10 heterojapygids occupy the Eastern Palearctic (five species) and Australian (five species) regions. And finally, the five species of dinjapygids live exclusively in east territories of the Neotropical region (Table 1).

The current distribution of Diplura is linked to the fragmentation of Pangea and drift during the Mesozoic and Cenozoic era (Table 2). As mentioned above, not only campodeids and japygids but also parajapygids show a Pangean distribution, which is a distribution that can also be inferred in some monophyletic lines such as the tachycampoids (Bareth & Condé, 1981; Sendra *et al.*, 2020a, 2020b). For the Campodeidae family, Laurasia was probably their centre of diversity judging from the high number of species and genera (381 out of the 491 species and 41 out of the 58 genera) found in Eurasia and North America, which include some shared taxa such as *Campodea* s. str., *Litocampa*, *Podocampa* and *Metriocampa*. Some campodeids genera and subgenera have a Gondwana distribution, and they are found in most of its remains landmasses, for example, *Notocampa* (New Zealand, Australia, Madagascar, Africa and South-America), *Lepidocampa* (Australia, India, Madagascar, Africa and

Table 1. Number of Diplura species and genera (between brackets) per family by biogeographical regions.

	E-Palearctic	W-Palearctic	Nearctic	Australian	Oriental	Ethiopian	Neotropical	Holarctic	World
Campodeidae	30 (12)	246 (19)	92 (16)	20 (8)	20 (8)	47 (14)	45 (13)	366 (38)	491 (58)
Procampodeidae		1 (1)	1 (1)					2 (1)	2 (1)
Projapygidae		4 (2)		1 (1)	2 (1)	8 (2)	28 (4)	4 (2)	42 (4)
Anajapygidae		1 (1)	2 (2)		1 (1)	1 (1)		3 (2)	5 (2)
Octostigmatidae				1 (1)	2 (1)				3 (1)
Japygidae	18 (7)	89 (17)	32 (7)	20 (5)	58 (13)	63 (17)	63 (13)	139 (27)	340 (61)
Parajapygidae	3 (1)	9 (1)	5 (2)	4 (1)	8 (1)	20 (2)	17 (2)	15 (2)	62 (4)
Evalljapygidae			26 (3)				22 (3)	26 (3)	47 (5)
Dinjapygidae							6 (1)		6 (1)
Heterojapygidae	5 (4)			5 (1)				5 (4)	10 (4)
Total taxa by region	56 (24)	350 (41)	158 (31)	51 (17)	91 (25)	139 (36)	181 (36)	560 (79)	1008 (141)

Table 2. Number of Diplura species and genera (between brackets) per family in the different Pangea tectonic plates.

	North-		South-							W-Gondwana		
	Eurasia	America	Laurasian	New Zealand	Australia	India	Madagascar	Africa	America		Gondwana	E-Gondwana
Campodeidae	280(31)	104(18)	381(40)	1(1)	19(8)	4(2)	13(4)	49(18)	35(13)	113(27)	31(8)	83(24)
Procampodeidae	1(1)	1(1)	2(1)					1(1)		1(1)		1(1)
Projapygidae	1(1)		1(1)		1(1)	1(1)		11(2)	29(4)	41(4)	2(1)	39(4)
Anajapygidae		2(2)	2(2)			1(1)		2(1)		3(1)	1(1)	2(1)
Octostigmatidae	2(1)		2(1)		1(1)					1(1)	1(1)	
Japygidae	136(31)	35(7)	171(35)	2(1)	17(4)	23(4)	1(1)	66(20)	60(14)	168(35)	42(8)	126(30)
Parajapygidae	13(1)	8(3)	20(3)		4(1)	1(1)		27(2)	12(1)	42(2)	4(1)	38(2)
Evalljapygidae		34(4)	34(4)						12(2)	12(2)		12(2)
Dinjapygidae									6(1)	6(1)		6(1)
Heterojapygidae	5(4)		5(4)	1(1)	4(1)					5(1)	5(1)	
Total taxa by plate	438(70)	184(35)	618(91)	4(3)	46(16)	30(9)	14(5)	156(44)	154(35)	402(75)	86(21)	307(65)

South-America), and *Campodella* (Australia, Madagascar and Africa). In addition to these genera, *Campodea* (*Indocampa*) is restricted to landmasses from East-Gondwana (Australia, India, and Madagascar), whereas *Natalocampa* is restricted to South-America and South-Africa (West-Gondwana). The diversity centre for japygids is uncertain; today's Laurasia territory has 173 species and 35 genera, meanwhile today's Gondwana holds 168 species and the same number of genera. Some japygid genera, such as *Metajapyx* and *Occasjapyx*, are good examples of the connection between the Laurasian plates and their split in the Early Cenozoic. Several japygid genera are shared between Gondwana plates, such as *Mesjapyx* (Australia, India, Madagascar, and Africa), *Indjapyx* (Australia and India), and *Austrjapyx*, *Hapljapyx* and *Teljapyx* (Africa and South-America). In the case of the projapygids, the massive diversity in the Gondwana territory, with 41 out of the 42 species (39 species mostly in Western Gondwana, today's Africa and South-America) indicates its probable centre of origin in the Early Cretaceous before the opening of the South Atlantic. In parajapygids, the existence of a hot diverse centre is Africa with 27 out of the 62 species, followed by Eurasia with 13 species and South-America with 12, makes it difficult to decide on its probable centre of origin. Furthermore, parajapygids can live in the marine coast and fluvial sediments, giving them a certain capacity for long distance dispersal and to colonise new regions. This can explain the presence of *Parajapyx isabellae* in all continents (Greenlade & Luan, 2018). The distribution range of evalljapygids reaches from the western regions of North America (34 out of the 47 species) throughout South America (12 species). The dinjapygids, with six species, are distributed in the western South America, and their proposed close phylogenetic relationship with the Heterojapygidae (with 10 species in Australia, New Zealand, and Eurasia) probably implies a wider Pangean distribution of the common ancestor (Markus Koch, pers. comm.). The remaining dipluran families: procampodeid, anajapygid, and octostigmatid, have a handful of species, making it impossible to suggest any centre of origin, but their relationship with the other families suggests, at least, a Laurasian and Gondwanan origin for procampodeids and anajapygids, respectively (Table 2).

Final remarks and future perspectives

In summary, as this review has shown, Diplura is an important and abundant group, both in soils and cave ecosystems, occupying a variety of trophic levels. With their ancient origin, Diplura is a crucial taxon to understand the early phase of insect evolution, the most diverse group of animals on Earth. Diplura is also an impressively diverse group with an astonishing variety of shapes and morphologic body plans, including unique sensorial and glandular structures. Nevertheless, diplurans have attracted scarce attention from zoologists, and as a result the knowledge is often restricted to taxonomy and geographically biased. Future efforts in the study of the order Diplura should focus on:

- Establishing a molecular phylogeny to clarify the relationships between and within families, as well as the biogeographical and paleobiogeographical patterns;

- Increasing the sampling effort in several regions of the globe, especially in the tropical regions;
- Including Diplura into soil and cave ecological studies, reflecting their importance in both ecosystems;
- Generating ecotoxicological information to understand the ecophysiological tolerance of Diplura;
- Exploring their potential to serve as indicator species in global change studies, as expected looking at their narrow hydric and thermal tolerance.

Despite of poorly known, the ubiquity of Diplura in terrestrial ecosystems, paired with their sensitivity to environmental change, makes them important target key species for conservation, which should not be neglected in environmental assessment.

Acknowledgements

We would like to thank Loris Galli, who inspired us with his studies on Protura, to Nikolaus Szucsich and L'ubomír Kováč for their careful review, to Teresa Molina Jiménez and Ricardo Giménez Mezquita for support in producing Figs 2 and 3, to Lucia Maltez for the English revision, to Louis Deharveng for the Projapygidae image in the Fig 1c, and to Yunxia Luan for the Heterojapygidae photo in Fig. 1d. AJ-V was supported by the Spanish Ramón y Cajal Program (RYC-2013-14441), which is financed by the Spanish Ministry of Science, Innovation and Universities. ASPSR is funded by a research grant (15471) from the VILLUM FONDEN.

Data availability statement

Data are available in the cited references.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Species and subspecies of the order Diplura.

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Accepted 10 February 2021

Editor: Raphael Didham; Associate Editor: Thomas Bolger