

The geographic distribution of Protura (Arthropoda: Hexapoda): a review

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SUMMARY

Protura is a poorly known class of Hexapoda represented by more than 800 species belonging to 77 genera worldwide. They are tiny soil organisms with low dispersal ability, mainly attributable to water and human-mediated transfer. The analysis of biogeography of Protura is hindered by the lack of knowledge on their natural history, systematics and distribution. In order to provide a starting point for future more detailed investigations, we reviewed the available literature on their geographic distribution, making a distinction between continental and insular areas. A general overview based on Wallace's biogeographic regionalization is outlined, highlighting a maximum of known richness and endemism at the genus level in the Palearctic region, and particularly within its eastern part. Some detailed examples of disjunct distribution and their interpretation based on vicariance or dispersal events are given.

INTRODUCTION

Protura is a small class of tiny hexapods strictly adapted to life in soil and in soil-like substrates (see Galli et al., 2019). To date, nearly 800 species are known worldwide. The class comprises three orders, seven families and 77 genera (see Galli et al., 2018; Shrubovych et al., 2020). Very little is known about their autoecology, but it is undoubted that they have a low active dispersal capability. Protura are strictly soil-obligate (euedaphic) organisms whose dispersal can take place by means of floating in water (Yin et al., 1994; Resh et al., 2014). They can survive and move submerged in freshwater for up to five days (Rimsky-

Korsakow, 1911), and they also occur in soils subjected to frequent inundation (Sterzyńska et al., 2012). Hydrochory is confirmed by a live specimen of *Protentomon thienemanni* Strenzke, 1942 found in a tuft of grass washed ashore on Surtsey island, about 30 kilometers south of Iceland (Ólafsson, 1978). This species is otherwise known only from Germany, more than 1000 km far away (Szeptycki, 2007)! The importance of debris rafting for long-distance dispersal of tiny soil-dwelling arthropods has been highlighted about mites by Lindo (2020). Dispersal mediated by humans (anthropochory) has also been hypothesized for some species found in anthropogenic habitats in Central Europe (Szeptycki et al., 2003; Christian &

Szeptycki, 2004). Protura may also be transported in soil adhering to the rhizosphere of nursery plants or in the potting soil used for bed enrichment and fertilization (see Nosek, 1977). This could explain the introduction of the Palearctic *Proturentomon minimum* (Berlese, 1908) and *Gracilentulus gracilis* (Berlese, 1908) into New Zealand (Tuxen, 1985).

Many problems limit the analysis of Protura biogeography. First of all, systematics of this group is still unclear and the contribution to it of genetics is currently very limited. A fact on which there is a consensus is that the orders Sinentomata and Eosentomata (François, 2003; Dell’Ampio et al., 2011; Resh et al., 2014; Carapelli et al., 2019) form the sister group of Acerentomata. Among Eosentomata, moreover, Carapelli et al. (2019) pointed out that the Oriental genus *Zhongguohentomon* (subfam. Isoentominae) is the sister group of *Eosentomon* (Eosentominae). We can, therefore, think to the ancestor of this order close to Isoentominae. According to their morphological characters (see Galli et al., 2018; Carapelli et al., 2019), Eastern Palearctic and Oriental Antelientomidae belong to a more recent line originating from the one that culminates in Eosentomidae. Acerentomata are probably closer to Sinentomata than to Eosentomata since they are more similar for some morphological characters (see François, 2003; Galli et al., 2018). Hesperentomidae and Protentomidae form the sister group of the other Acerentomata (François, 2003; Dell’Ampio et al., 2011; Carapelli et al., 2019). On the relationships among the Acerentomidae subfamilies, Carapelli et al. (2019) highlighted that Berberentulinae and Acerentominae are sister groups. The latter are probably paraphyletic: Acerellinae and Nipponentominae should be included in them. Shrubovych (2014) made a phylogenetic analysis based on morphological characters of the northeastern Palearctic Acerentomidae and she verified the monophyly of this family.

Another problem is the lack of sufficient information about many areas, mainly due to the absence of local specialists. This disparity, as already highlighted for other taxa, can be a significant source of bias in studies on distribution of biodiversity (e.g. Fontaneto et al., 2012; Barbosa et al., 2013).

Finally, no fossils of Protura are known to date. Nevertheless, fossils were recorded for their entognathous sister groups (Carapelli et al., 2019; Giribet & Edgecombe, 2019). Collembola are known from the Devonian Rhynie Chert (400 Ma) and Diplura at least from the Cretaceous Crato Formation (113 Ma) (Penney & Jepson, 2014). Therefore, Tuxen (1978a) assumed that Protura origin dates back to Early Devonian. Furthermore, warm and stable climates and the corresponding establishment of terrestrial plants during Devonian (Scotese, 2002; House, 2020), provided the ideal conditions for the spread of terrestrial arthropods (Garwood & Edgecombe, 2011). However, due to the absolute lack of fossil records and to the shortage of phylogenetic information, we cannot discern whether Protura diversified in the Devonian before the breakup of Pangaea or originated more recently and dispersed across large geographic ranges. Giribet et al. (2014) came to the same conclusions in their phylogenetic analysis about Palpigradi, a group of tiny endogean (soil) and hypogean (caves) arachnids that suffer of the same knowledge gaps of Protura.

To the present time, few papers on Protura biogeography mainly concern individual countries or regions within. Therefore, the aim of this paper is to outline a general overview and review the available literature on this topic in order to provide a starting point for future more detailed investigations.

MATERIALS AND METHODS

The geographic distribution of genera of Protura was outlined based on the

biogeographic regions according to Wallace (1876). The Palearctic region was split into a Western and an Eastern part following Vigna Taglianti et al. (1992, 1999) for identifying the limit between them. Older data were taken from the authoritative catalogue of Szeptycki (2007). For additional information and updates, however, we made reference to Bu & Yin (2007), Nakamura (2010), Wu & Yin (2011), Bu & Palacios Vargas (2012), Shrubovych et al. (2014a,b, 2020). The current level of knowledge is too low and fragmented to adopt a finer subdivision even at the biogeographic provinces level as in the synopsis on Collembola by Christiansen & Bellinger (1995). Genus level of analysis was chosen in order to override the shortage of knowledge mentioned above and to have the possibility to use anyway older data no more verified about specimens probably misidentified at the species level.

In order to assess similarities/differences among the Protura faunas of the biogeographic regions at genus and subfamily level a UPGMA clustering was performed using software PAST version 4.02 (Hammer et al., 2001). Jaccard similarity index on data of regional presence/absence of the genera and subfamilies was used; one hundred bootstrap replicates were applied.

RESULTS AND DISCUSSION

General overview on the geographic distribution of Protura

Protura were collected in every continent except Antarctica. Less than a dozen of species were recorded slightly north of the Arctic Circle. *Yamatentomon yamato* (Imadaté & Yosii, 1956) in the Siberian tundra (Lena Delta Nature Reserve) at more than 72°19' N; *Verrucoentomon imadatei* Nosek, 1977 at

70°29'N in Alaska; *Nienna chukotka* Shrubovych, 2019 at 69°48' N in Russia; *Alaskaentomon fjellbergi* Nosek, 1977 at 69°30' N in Alaska; *Verrucoentomon canadense* (Tuxen 1955) at 68°42' and 68°24' N in Canada; *Vesiculentomon condei* (Tuxen, 1955) at 68°24' N in Canada; *Yavanna behanae* (Nosek, 1977) at 67°28' N in Alaska; undetermined specimens belonging to genera *Acerentulus* and *Eosentomon* in localities over 68° N in Alaska and Canada, respectively. For a complete review of Protura from the Arctic regions see Shrubovych et al. (2020). Conversely, the southernmost records of Protura barely reach the 46° latitude South: many specimens of *Andinentulus rapoportii* (Condé, 1963) were sampled in the Reserva Forestal Coyhaique in Chilean Patagonia (E. Lanza & L. Galli unpub.) at nearly 45°30' S, and *Tasmanentulus intermedius* Tuxen, 1985 was recorded up to nearly 46° S in New Zealand.

The distribution of genera of Protura in the biogeographic regions is shown in Table 1. The highest richness is recorded in the Palearctic where 57 out of the 77 described genera were found (45 of which in the Eastern part). The Palearctic fauna records also the highest level of endemism (23 genera, 12 of which limited to the Eastern part) (Fig. 1). This disparity can be attributed at least in part to the greater concentration of specialists in Eurasia (see the “Introduction”) since the first description of Protura (see Pass & Szucsich, 2011). The distances among Protura faunas of the regions examined is shown in Fig. 2. A first dichotomy separates the strongly supported cluster Eastern Palearctic-Oriental from one gathering the other regions. This latter group is in turn divided into a cluster formed by the other Gondwanan regions (Neotropical-Afrotropical-Australian) and one formed by Western Palearctic and Nearctic.

Table 1. Distribution of subfamilies and genera of Protura in the biogeographic regions. Distribution of genera belonging to monotypic families or subfamilies is shown at the highest taxonomic level. Question marks indicate records considered doubtful according to Szeptycki (2007). In brackets are given detailed geographical indications when the records from a biogeographic region refer to individual countries. Families/subfamilies are highlighted in bold. The number of genera known for each region is shown in the last row.

Genus	Nearctic	W-Palearctic	E-Palearctic	Neotropical	Afrotropical	Oriental	Australian
Hesperentomidae Hesperentominae Price, 1960	x	x	x			x	
<i>Hesperentomon</i> Price, 1960	x		x			x	
<i>Ionescuellum</i> Tuxen, 1960		x					
Hesperentomidae Huhentominae Yin, 1983 - <i>Huhentomon</i> Yin, 1977			x			x	
Protentomidae Hinomotentominae Yin, 1999 - <i>Hinomotentomon</i> Imadaté, 1973			x (Japan)				
Protentomidae Condeellinae Tuxen & Yin, 1982	x		x		x	x	x
<i>Condeellum</i> Tuxen, 1963			x (China)		x (Reunion)	x	x (Solomon Islands)
<i>Neocondeellum</i> Tuxen & Yin, 1982	x		x			x	
<i>Paracondeellum</i> Yin, Xie & Zhang, 1994						x	
Protentomidae Protentominae Ewing, 1936	x	x	x	x	x	x	x
<i>Protentomon</i> Ewing, 1921	x	x		x	x	x	x?
<i>Proturentomon</i> Silvestri, 1909	x	x	x				x? New Zealand
Acerentomidae Berberentulinae Yin, 1983	x	x	x	x	x	x	x
<i>Acerentuloides</i> Ewing, 1921	x						
<i>Acerentulus</i> Berlese, 1908	x	x	x	x			x
<i>Amazonentulus</i> Yin, 1989				x			
<i>Amphientulus</i> Tuxen, 1981			x (Korea?)	x?	x (Madagascar?)	x	x
<i>Andinentulus</i> Tuxen, 1984				x			
<i>Australentulus</i> Tuxen, 1967					x (Madagascar)	x	x
<i>Baculentulus</i> Tuxen, 1977	x	x	x	x	x	x	x

Genus	Nearctic	W-Palearctic	E-Palearctic	Neotropical	Afrotropical	Oriental	Australian
<i>Berberentulus</i> Tuxen, 1963	x	x		x	x	x	x
<i>Bolivaridia</i> Bonet, 1942	x (Texas)			x	x	x	
<i>Brasilentulus</i> Nosek, 1973				x	x		
<i>Brasilidia</i> Nosek, 1973				x			
<i>Chosonentulus</i> Imadaté & Szeptycki, 1976			x (Korea and China)				
<i>Delamarentulus</i> Tuxen, 1963				x	x		
<i>Gracilentulus</i> Tuxen, 1963	x	x	x	x	x	x	x
<i>Kenyentulus</i> Tuxen, 1981			x	x	x	x	x
<i>Madagascaridia</i> Nosek, 1978					x (Madagascar)	x (China)	
<i>Maderentulus</i> Tuxen, 1963		x					
<i>Najtentulus</i> Szeptycki & Weiner, 1997		x					
<i>Neobaculentulus</i> Yin, 1984			x			x	
<i>Notentulus</i> Yin, 1989				x		x	
<i>Podolinella</i> Szeptycki, 1995		x					
<i>Polyadenum</i> Yin, 1980						x (China)	
<i>Proacerella</i> Bernard, 1975	x	x					
<i>Silvestridia</i> Bonet, 1942		x	x	x	x	x	x
<i>Tasmanentulus</i> Tuxen, 1985							x
<i>Tuxenidia</i> Nosek & Cvijović, 1969		x					
<i>Vindobonella</i> Szeptycki & Christian, 2001		x					
<i>Yinentulus</i> Tuxen, 1985							x
<i>Zangentulus</i> Yin, 1983			x (China)				
Acerentomidae Acerentominae Silvestri, 1907	x	x	x			x	
<i>Acerentomon</i> Silvestri, 1907		x					
<i>Filientomon</i> Rusek, 1974	x		x			x	
<i>Fjellbergella</i> Nosek, 1978	x		x (Russian Far East)				
<i>Huashanentulus</i> Yin, 1980			x			x	
<i>Orinentomon</i> Yin & Xie, 1993	x (Alaska)		x (China)				

Genus	Nearctic	W-Palearctic	E-Palearctic	Neotropical	Afrotropical	Oriental	Australian
<i>Sugaentulus</i> Imadaté, 1978			x				
<i>Tuxenentulus</i> Imadaté, 1973	x		x			x	
<i>Wenyingia</i> Imadaté, 1986			x (Japan)				
<i>Yamatentomon</i> Imadaté, 1964			x				
<i>Yichunentulus</i> Yin, 1980			x (China)				
<i>Liaoxientulus</i> Wu & Yin, 2011			x (China)				
Acerentomidae							
Nipponentominae	x	x	x				
Yin, 1983							
<i>Alaskaentomon</i> Nosek, 1977	x (Alaska)						
<i>Callientomon</i> Yin, 1980			x (China)				
<i>Imadateiella</i> Rusek, 1974			x				
<i>Nienna</i> Szeptycki, 1988			x				
<i>Nipponentomon</i> Imadaté & Yosii, 1959	x		x				
<i>Mastodonentomon</i> Sshrubovych et al., 2020	x						
<i>Noldo</i> Szeptycki, 1988		x	x				
<i>Nosekiella</i> Rusek, 1974		x	x				
<i>Paracerella</i> Imadaté, 1980	x		x				
<i>Verrucoentomon</i> Rusek, 1974	x	x	x				
<i>Nanshanentulus</i> Bu & Yin, 2007			x (China)				
<i>Vesiculentomon</i> Rusek, 1974	x						
<i>Nosekientomon</i> Shrubovych, Rusek & Bernard, 2014	x						
<i>Yavanna</i> Szeptycki, 1988			x				
Acerentomidae							
Acerellinae Yin, 1983		x					
- <i>Acerella</i> Berlese, 1909							
Fujientomidae Tuxen & Yin, 1982 - <i>Fujientomon</i> Imadaté, 1964			x			x	
Sinentomidae Yin, 1965 - <i>Sinentomon</i> Yin, 1965			x			x	

Genus	Nearctic	W-Palearctic	E-Palearctic	Neotropical	Afrotropical	Oriental	Australian
Eosentomidae Isoentominae Yin, 1983	x	x	x	x	x	x	x
<i>Isoentomon</i> Tuxen, 1975	x (Mexico)	x (France, Corsica, Canary Islands)		x	x		x
<i>Osientomon</i> Nakamura, 2010			x			x	
<i>Madagascarentomon</i> Nosek, 1978					x (Madagascar)		
<i>Zhongguohentomon</i> Yin, 1979						x (China)	
Eosentomidae Eosentominae Berlese, 1909	x	x	x	x	x	x	x
<i>Eosentomon</i> Berlese, 1908	x	x	x	x	x	x	x
<i>Styloentomon</i> Copeland, 1978	x						
Eosentomidae Anisentominae Yin, 1983			x			x	
<i>Anisentomon</i> Yin, 1977			x			x	
<i>Neanisentomon</i> Zhang & Yin, 1984						x (China)	
<i>Paranisentomon</i> Zhang & Yin, 1984			x			x	
<i>Pseudanisentomon</i> Zhang & Yin, 1984			x			x	
Antelientomidae Yin, 1983 - <i>Antelientomon</i> Yin, 1974			x			x	
Total number of genera	26	23	45	18	17	33	15

Focusing on the island faunas, the vast majority of Protura on oceanic islands belong to genera with wide distributions, often cosmopolitan and sub-cosmopolitan. This can be related to the adaptability of these genera that allow them to disperse across the oceans and colonize new lands in agreement with a relationship between the ecological adaptability of taxa and the size of their geographical range already outlined by some authors (see Galli et al., 2019).

Review of literature on regional/local fauna biogeography

Many works on regional or local fauna with some remarks on Protura zoogeography were published since the second half of the 20th century. What generally emerges is the difficulty of drawing general conclusions due to the limited information available for many areas. Another critical aspect is that sometimes interpretations of Protura distribution from literature are not strongly supported by empirical evidence.



Figure 1. Genera endemic to individual biogeographic regions. Palearctic is split into western and eastern parts (see text); * indicates genera shared between them.

In chronological order, Tuxen (1967) noted that the Australian Protura fauna is sharply different from that of other continents; the known species belong to few well defined groups and into each group they are closely related. Szeptycki (1969), analyzing the fauna of Ojcow National Park in Poland, explicitly stated the scarcity of information on the distribution of most species. Nevertheless, based on more detailed data available for Collembola of the same area, he was able to hypothesize that species more adapted to cool habitats could have immigrated from the Carpathians during the “postglacial optimum of beech” forests, while those of warm environments would be relicts from the postglacial optimum for xerothermic associations. The short paragraph about phylogeny and zoogeography in Nosek’s (1973) monograph on European Protura is substantially uninformative, just pointing out which genera are dominant or endemic on each continent. Tuxen’s papers (1977a, 1978a) about Brazilian Protura can be considered the first attempt to analyze the worldwide distribution of this taxon. Based on the plate tectonics knowledge and on the study of the species

collected in Brazil and their alleged relationships with those present in other continents, he hypothesized an history of the geographic distribution of some taxa mainly based on vicariance events. However, 40% of genera were still unknown at the time and phyletic relationships he hypothesized do not fully coincide with what is currently understood on the Protura phylogeny. Prabhoo (1986) analyzed the South Indian fauna. He referred to Tuxen’s (1978a) biogeographical analysis and simply distinguished between those he defined “Pangean” genera (such as *Protentomon*, *Gracilentulus* and *Eosentomon*) and “Gondwanan” ones (e.g. *Silvestridia* and *Bolivaridia*). Yin (1989) studied the similarities among species assemblages of four Chinese subtropical mountains and her biogeographical analysis was limited to the identification of groups of species typical of different part of China. Moreover, Yin et al. (1994) examined the phylogeny and biogeography of Protentomidae subfamily Condellinae (Fig. 3) and hypothesized an Indo-China center of origin for the Indo-Pacific genus *Condeellum* and the Indo-China, Eastern Palearctic and Nearctic *Paracondeellum* and *Neocondeellum*.

Bu et al. (2014) in their in-depth study of the Protura in Russian Far East pointed out that there were no Holarctic and trans-Palearctic species (unlike what was recorded about other arthropods) while there were many endemic species. They concluded that Protura is a group with high endemism and a low level of biogeographical “noise” making them a potentially good candidate for detailed biogeographical analyses when more information will become available for other areas. In a contemporary paper on a similar fauna, the northeastern Palearctic Protura, Shrubovych (2014) hypothesized northeastern Asia as the main center of origin of Holarctic species with Beringia acting as a land-bridge for faunal interchanges between North America and Eurasia. Shrubovych & Sterzyńska (2017) studied proturans of the Transcarpathian region and documented its high species richness and percentage of endemics. They stressed the importance of this area as biogeographical transition zone for soil microarthropods across Mediterranean, Pannonian, Alpine and Continental ecoregions. Finally, Shrubovych et al. (2020) reviewed the proturans of the Arctic and found that species occurred outside the largest extent of ice-sheets during the last Pleistocene glaciation. Moreover, they highlighted that *Verrucoentomon montanum* (Martynova, 1970) and *V. rafalskii* Szeptycki, 1997, known from cool or mountainous areas of Central Asia, can be regarded as Pleistocene glacial relicts that were able to survive on refuges represented by non-glaciated mountaintops. A similar pattern of current distributions in areas corresponding to Pleistocene ice-free refuges was recorded in the Alps for some cave arachnids (Mammola et al., 2018a,b) and in Alaska for Diplura (Sikes & Allen, 2016). Post-glacial recolonization has been inferred for Protura and Diplura in southern Canada and southern Fennoscandia (Szeptycki, 2007; Sikes, 2019). Arctic species of Protura have mainly regionally restricted distributions or are known only from their type localities even though it must be kept in mind that sampling in these areas is limited to few

sites. These small distributions and the morphological differences among some taxa, when compared to southern species, suggest a relict origin and a high level of endemism in arctic proturans (Shrubovych et al., 2020).

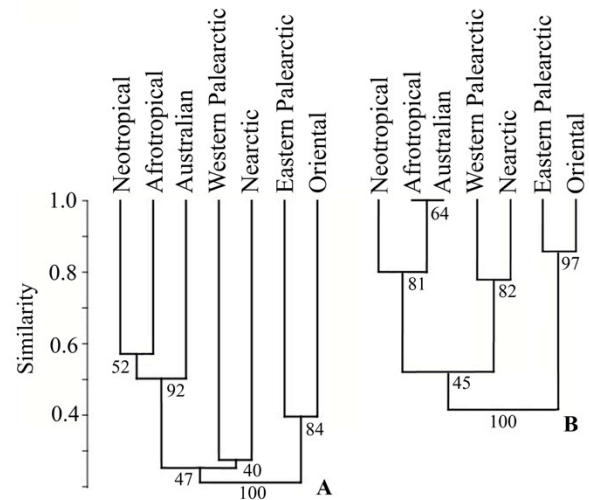


Figure 2. A) UPGMA clustering using Jaccard similarity index on data of regional presence/absence of Protura genera in the biogeographic regions. B) Same as A based on data about subfamilies.

Review of literature on island Protura biogeography

The Japanese fauna was the subject of many in-depth studies also from a biogeographical point of view (e.g. Imadaté, 1974). Kaneko et al. (2012) analyzed biogeographical patterns in Japan Protura trying to reconstruct the history of their invasions. They analyzed data about 71 taxa recorded in 3,110 sites for which habitat and climate were known. The starting point was the hypothesis of Imadaté & Ohnishi (1993) that in Japan there were two groups of proturans of different origins, based on their alleged affinities, ecology and distribution. One group of species is supposed to be from Eastern Siberia via Sakhalin to Hokkaido, or through the Korean Peninsula to Northern Kyushu. The other group is thought to have a southern origin in tropical Asia and to have invaded Kyushu from south and east China. Kaneko et al. (2012) confirmed that there are a northern (Hokkaido, Tohoku) and an “other origin” groups that have

become separated. Such results would match the geological knowledge about the origin of the Japanese Archipelago. These islands were part of the continent until 22 Ma and became an archipelago about 14 Ma (Saito et al., 2006). Ryukyu and Kyushu became separated by the Tokara Strait around one Ma, and Hokkaido and Tohoku were separated by the Tsugaru Strait about 150,000 years ago (Ohshima, 1990). During the Pleistocene, until about 10,000 years ago, Kyushu and Hokkaido were

connected several times to China, the Korean Peninsula, and Sakhalin. Therefore, both northern and southern ways to Japan were available one Ma, and dispersal of Protura from Hokkaido to Kyushu would have been possible for almost one million years. In conclusion, these authors highlighted that present distribution of species assemblages is mainly shaped by climate (temperature and precipitation).

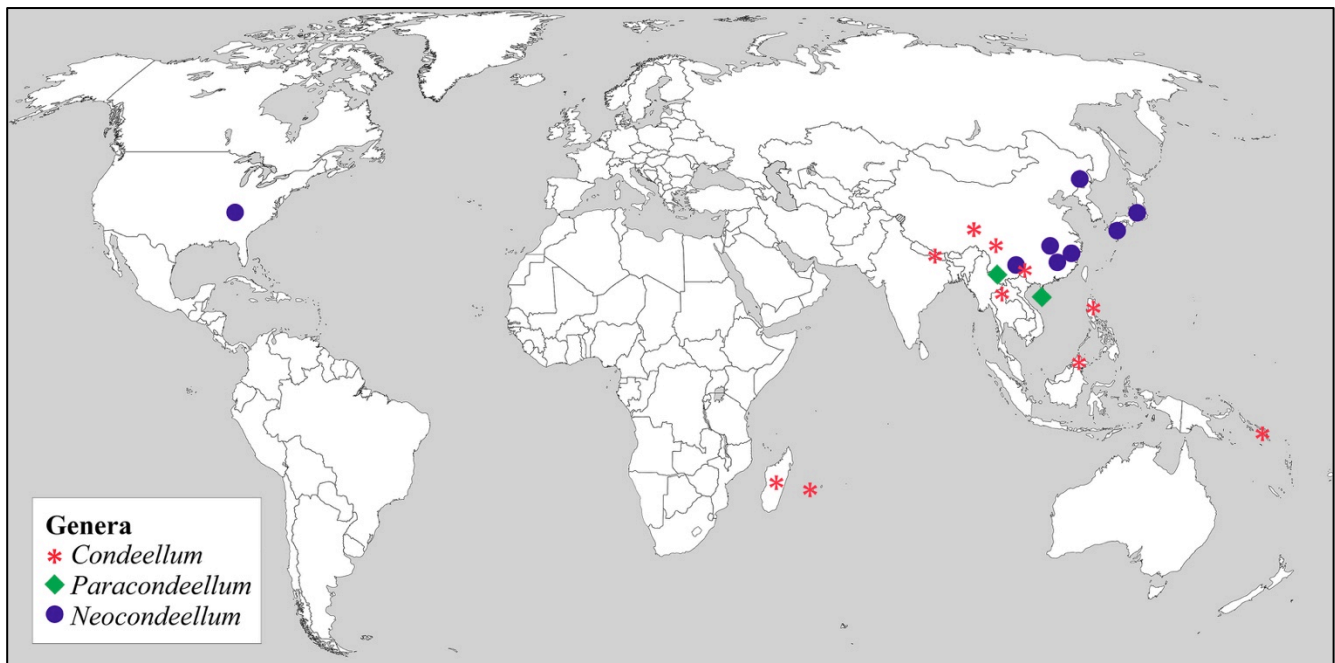


Figure 3. Distribution of Protentomidae Condeellinae (based on data from Szeptycki, 2007; Bu et al., 2019).

Several other islands faunas have been studied in some detail and related zoogeographic remarks were outlined. In their analysis of the Protura of the Caribbean islands the authors (Nosek, 1978; Nosek & Mari Mutt, 1978, 1980) highlighted the presence of two endemic species - *Eosentomon mutti* Nosek, 1978 and *E. puertoricensis* Nosek, 1978 - with Central and South American affinities, and of three taxa with a Gondwanan distribution: *Bolivaridia perissochaeta* Bonet, 1942, *Kenyentulus kenyanus* (Condé, 1948) and *Delamarentulus tristani* (Silvestri, 1938). This fits what Crews & Esposito (2020) evidenced in their synthesis about the origin and chorology of Caribbean terrestrial arthropods. Lindroth et al. (1973)

published a comprehensive work about the colonization of Surtsey island that emerged from the sea by volcanic eruption in 1963 about 30 kilometers south of Iceland. No proturan was sampled, but the nearby (10 km from Iceland) and larger Heimaey island (of Late Pleistocene origin) was inhabited by *Eosentomon delicatum* Gisin 1945 that was already known for Iceland. A live specimen of *Protentomon thienemanni* was found in a tussock washed ashore Surtsey island in August of 1974 (Ólafsson, 1978). This species is otherwise known only from Germany. Protura were no more listed in the following report on Surtsey land-arthropod fauna (Ólafsson, 1982). In his study on the Madeiran fauna Tuxen

(1982) hypothesized a recent proturan colonization from Europe (probably Portugal) that “may be brought with soil by man”. Similarly, Szeptycki (2004) pointed out the lack of endemic species in the Canary Islands and he interpreted the known ones as species introduced by humans. Betsch & Nosek (1978) and Betsch & Cassagnau (1996) pointed out that the proturans of Madagascar, with a high percentage of endemics, include species close to those belonging to African fauna or the Indo-Australian fauna. Tuxen (1978b) studied also the Protura of Seychelles and he observed that fauna of Madagascar-Mascarene area includes Gondwanan species whose origin he supposed could be traced back to more than 100 my before the splitting up of the Gondwana supercontinent. Bu et al. (2019) recorded 11 genera and 34 species from the island of Hainan (China), most of which belonged to Eosentomidae and Acerentomidae Berberentulinae that are widely distributed and with a high species richness in China. The fauna of this island is similar to those of neighboring mainland regions (Guangdong, Guangxi, and Yunnan provinces). This result fits the geological history of Hainan Island (Wang, 1991; Zhang & Fang, 2012) that, until the Quaternary Period (2.5 Ma), was connected to Leizhou Peninsula of Guangdong Province and became permanently separated from the mainland at the end of the Quaternary Period. Imadaté (1989) briefly noted that the species from Java are mostly Asian elements typical of tropical and/or temperate areas and only *Australentulus phrachedee* (Imadaté, 1965) belongs to a genus known also from Australia and Madagascar. For the Bismarck archipelago and Solomon Islands, Tuxen & Imadaté (1975) concluded that the faunas of these islands are related to each other and would be mainly originated in East Asia, even though there are also species with Australian affinities. The same was said also for the comparable fauna of New Hebrides studied two years later by Tuxen (1977b). In his monograph on New Zealand Protura, Tuxen (1985) proposed a Gondwanan origin and hypothesized that they reached these

islands in the Late Jurassic between the Rangitata Orogeny (142–99 Ma) and the opening of the Tasman Sea (about 80 Ma). The exceptions are two introduced species: *Proturentomon minimum* and *Gracilentulus gracilis* (Tuxen, 1985). About the former, only female specimens are known in all its range and it is supposed to be obligate parthenogenetic (see Galli et al., 2019); on the latter Tuxen (1985) put in evidence that in the southern continents populations only females are known. Minor (2008) updated such information adding the widespread *Berberentulus capensis* (Womersley, 1931) to New Zealand Protura species list: even in this case only female specimens were collected there. It is likely that, as already known for other taxa (see e.g. Nelson et al., 2010), some proturans adopt thelytoky as a strategy for colonization of new territories (see also Minor, 2008).

Emblematic examples of distribution

One of the most interesting cases of distribution is that of *Delamarentulus tristani*, known from Central and South America (Costa Rica, Brazil, Colombia, Jamaica) and Tropical Africa (Angola, Cameroon, Ivory Coast). This species can be defined amphi-Atlantic in the broad sense and its disjunct distribution was considered due to vicariance by Tuxen (1977, 1978a). This author also inferred from the conspecific status of the New and Old World populations that “the evolution in time of Protura is a very slow process”, since after at least 100 my of isolation the species did not show morphological differentiation (at least for the features examined). Moreover, the vicariance due to the drift of South America away from Africa is the event that probably led to speciation the genus *Brasilentulus*, which is present with one species (*B. huetheri* Nosek, 1973) in Brazil and another (*B. africanus* Tuxen 1979) in Gabon (Fig. 4). On the other hand, a dispersalist hypothesis would seem more likely for the Canary Islands species *Baculentulus macqueeni* (Bernard, 1975) and *Isoentomon serinus* Szeptycki, 2004 known also from and USA (Michigan) and Brazil, respectively. In

addition, this last species is closely related to *I. myrmecobium* Tuxen, 1975 from Brazil and *I. pseudosaharensis* (Tuxen, 1967) from Australia. The recent volcanic origin of Canary Islands would seem incompatible with vicariance (see also Szeptycki, 2004). Nevertheless, this process cannot be excluded according to the model outlined by Grehan (2016). This author, for some Macaronesian species with American relatives, proposed a sequential colonization of newly formed islands within the Atlantic from the Mesozoic.

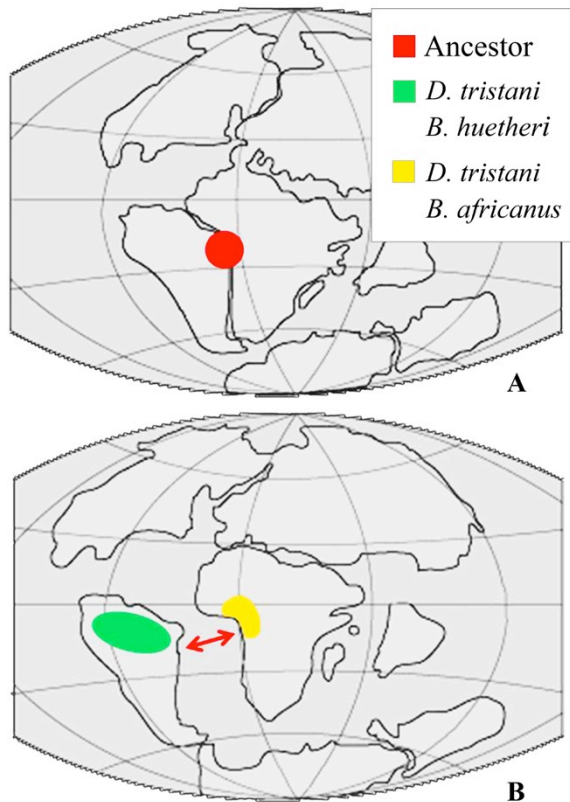


Figure 4. History of distribution of three Gondwanan taxa: *Delamarentulus tristani* (Silvestri, 1938), *Brasilentulus huetheri* Nosek, 1973 and *B. africanus* Tuxen 1979. A) Triassic hypothetical distribution of the ancestor of each taxon. B) Cretaceous distribution after the separation between South America and Africa (maps from Lindeberg, 2001, modified).

A case of undoubted interest is represented by *Amphientulus zelandicus* Tuxen, 1985. This species, belonging to a Gondwanan genus mainly represented in Australia (six species out of a total of nine), shows a distribution (Fig. 5) that fully lies west of the

New Zealand Alpine Fault (see Heads, 2017). This fault, active about 23 Ma, was located at a new boundary between the Indo-Australian Plate and the Pacific Plate and acted as a physical barrier that shaped the boundaries of some species distribution. Therefore, *A. zelandicus* can be considered a fine example of the correlation between current species distribution in New Zealand and its tectonic features already highlighted for ghost moths by Grehan & Mielke (2019). The same kind of distribution is true for all the species of genus *Eosentomon* recorded in New Zealand: just one locality within the range of *E. maximum* Tuxen, 1985 is east of the Alpine fault.

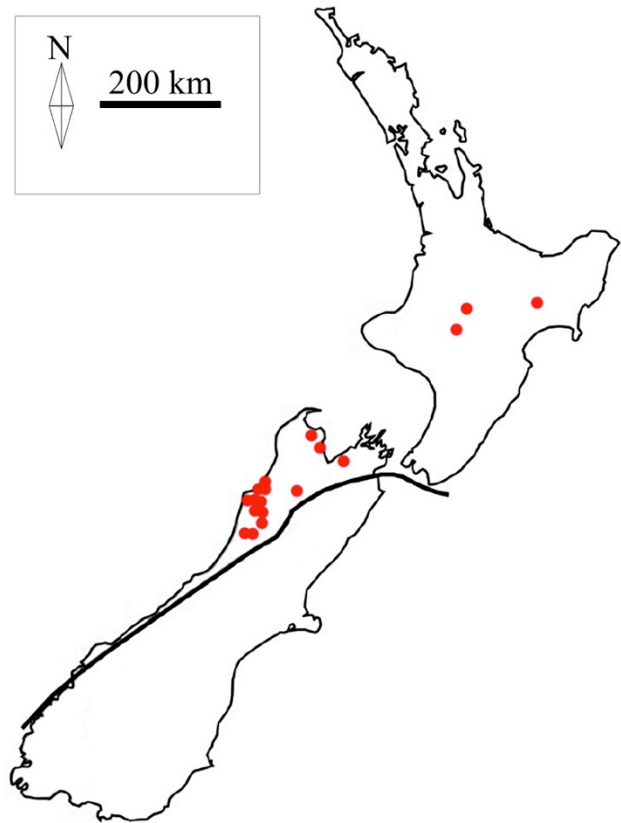


Figure 5. Distribution of *Amphientulus zelandicus* Tuxen, 1985 in New Zealand. All the localities where this species is known lie west of the Alpine Fault (the thick line - based on maps available in Grehan & Mielke, 2019).

It deserves more insight the pattern that can be outlined analyzing the composite faunas of the archipelagos of volcanic islands east of New Guinea and Australia: Bismarck, Solomon

and New Hebrides (Fig. 6). Unfortunately, nothing is known about New Guinea and New Caledonia Protura. On the other hand, on these islands, proturans have been studied and brief biogeographic remarks from literature were already mentioned (Tuxen & Imadatè, 1975; Tuxen, 1977b). Some of these islands' species are known also from areas far away from Melanesia; moreover, the authors identified closer relatives to the endemic species from Borneo, Australia and New Zealand. More in detail, species belonging to three genera were found. Genus *Berberentulus* with two endemic species of uncertain affinities - *B. buchi* Tuxen & Imadatè, 1975 (Bismarck Archipelago) and *B. rennellensis* Tuxen & Imadatè, 1975 (Solomon Islands) – and *B. capensis*, known from Maryland, Massachusetts (USA), Portugal, France, Canary Islands, South Africa, Kerala (India), New South Wales (Australia) and New Hebrides. Genus *Silvestridia* with two species. *S. keijiana* (Imadatè, 1965), known from Kerala (India), Thailand, Borneo and Solomon Islands; *S. solomonis* (Imadatè, 1960) from Kerala (India) and Solomon Islands. Genus *Eosentomon* with three species known also outside Melanesia: *E. oecaniae* Tuxen & Imadatè, 1975 (Australia, Bismarck Archipelago, Solomon Islands, New Hebrides), *E. sakura* Imadatè & Yosii, 1959 (Korea, Japan, China, Taiwan, Bismarck Archipelago, Solomon Islands, New Hebrides) and *E. wygodzinskyi* Bonet, 1950 (Brazil, Seychelles, Philippines, Solomon Islands, New Hebrides, New Zealand). Other species are endemic. *E. melanesiense* Tuxen & Imadatè, 1975 (Bismarck Archipelago, Solomon Islands) is related to *E. dawsoni* Condé, 1952 from New Zealand (North Island); *E. notiale* Tuxen & Imadatè, 1975 (Solomon Islands) and *E. guadalcanalense* Tuxen & Imadatè, 1975 (Solomon Islands) are close to each other and to *E. imadatei* Tuxen, 1967 from Australia; *E.*

penelope Tuxen, 1977 (New Hebrides) and *E. solomonense* Tuxen & Imadatè, 1975 (Solomon Islands) are related to each other and to *E. gimangi* Imadatè, 1965 from Borneo (Brunei); *E. noonadanae* Tuxen & Imadatè, 1975 (Bismarck Archipelago, New Hebrides) affinities are uncertain. Hydrochory events following different directions from “source areas” to these islands are favored by seasonal changes of the main ocean currents (Steinberg et al., 2006) and even by those changes of currents that have accompanied major climatic changes during last geological periods (e.g. Filippelli & Flores, 2009).

In conclusion, in order to offer a food for thought for future research, we want to introduce a couple of examples of disjunct distributions for which we hypothesize an interpretation. We can assume that passive dispersal mediated by man caused the distribution of *Isoentomon atlanticum* (Condé, 1947) both in Southwest Europe (Northern Pyrenees - France, Corsica) and Brazil (Minas Gerais). On the other hand, we suggest a vicariance event in the case of *Baculentulus breviunguis* (Condé, 1961), which is known from Madagascar, Reunion, India, Thailand, China (Yunnan) and Australia (Szeptycki, 2007). The closest species (Condé, 1961) is *Baculentulus evansi* (Condé, 1961) from Uganda and Congo Democratic Republic. We suggest that the common ancestor of these species was distributed in the central and eastern part of Gondwana and they originated in allopatric isolation after the major breakup phase that separated its western (South America and Africa) and eastern (Madagascar, India, Australia) parts (about 170 Ma; Geiger et al., 2004). In such cases, in order to examine the hypotheses proposed, the support of more solid information than current one would be needed, especially from the molecular phylogenetics.

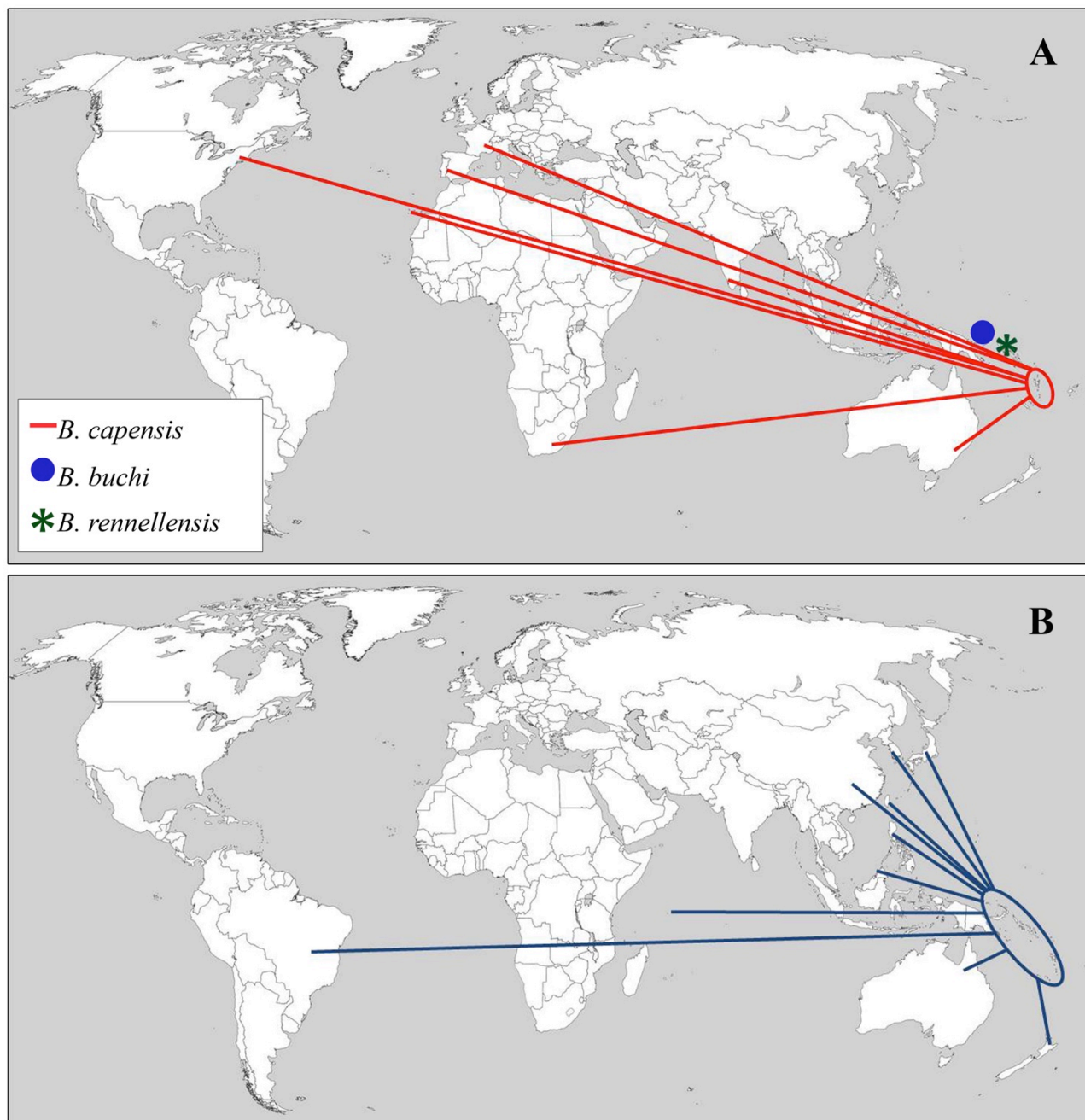


Figure 6. Melanesian Protura and their relatives all over the world. The ellipses circumscribe the Melanesian area of taxa; the lines intercept the extra Melanesia areas of species and those related to them. A) Genus *Berberentulus*. B) Genus *Eosentomon*.

CONCLUSIONS

Protura still remains a poorly known taxon for many aspects of their biology, natural history and distribution. Due to the absolute lack of fossil records and to the shortage of phylogenetic information (especially those coming from genetic analyses), we cannot discern whether Protura diversified in the

Devonian (as already suggested by Tuxen, 1978a) before the breakup of Pangaea or originated more recently and dispersed across large geographic ranges. Giribet et al (2014) came to the same conclusions about Palpigradi, a group of tiny arachnids that suffers of the same knowledge gaps of Protura.

We reviewed the available literature on Protura biogeography, outlining some general information about the distribution of the 77 genera known worldwide (Szeptycki, 2007; Galli et al., 2018; Shrubovych et al., 2020) within the Wallace's biogeographic regions. Moreover, based on cases from continental and insular fauna, we highlighted examples of species disjunct distributions for which both vicariance and dispersal events have been evoked. Dispersal of these tiny euedaphic arthropods can be mediated by man (Nosek, 1977; Tuxen, 1985; Szeptycki et al., 2003; Christian & Szeptycki, 2004) or water (Olafsson, 1978; Yin et al., 1994; Resh et al., 2014). In fact, long-distance dispersal of tiny soil-dwelling arthropods through debris rafting is known (Lindo, 2020).

Our review aims to provide a starting point for future more detailed investigations. Molecular studies about Protura are to date in an incipient phase; future research is needed for a better insight of their phylogeny as a prerequisite to deepen the study of their biogeography.

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