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A synopsis of the ecology of Protura (Arthropoda: Hexapoda)

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Abstract: This publication reviews the literature on the ecology of Protura. Current knowledge is scarce, fragmentary and scattered among papers which do not all strictly deal with ecology or soil arthropods communities. Therefore all available information is summarized in order to better understand the ecology of these arthropods. The density of Protura ranges from hundreds to thousands of individuals per m². Their aggregate distribution is probably related to food (fungal hyphae) availability and quality, and to the production of aggregation pheromones. Protura tend to form species assemblages characterizing different habitats. Their populations often show an unbalanced sex ratio in favour of females, suggesting that a single male can fertilize several females, perhaps via spermatophores. For some species only females have been collected, which suggests the possibility of parthenogenesis. Our analysis of the available information on phenology and population dynamics of Protura points toward annual cycles with one, two or more peaks of reproductive activity.

Keywords: Soil - density - habitat - species assemblages - phenology.

MORPHOLOGY AND TAXONOMY

Protura are entognathous Hexapoda living in the soil. They have a tiny body size (range about 0.7-2.5 mm). Due to their unpigmented cuticle proturans are normally whitish or pale yellow; only Sinentomidae are reddish-brown. Protura have no eyes and antennae, but instead they possess a pair of pseudoculi on the head, and a pair of well-developed sensilla-bearing forelegs, which are directed forward and serve as main sensory organs (see Nosek, 1973; Hädicke *et al.*, 2015) (Fig. 1). Meso- and metanotum are equipped with a rudimentary tracheal system in Eosentomata and Sinentomidae. The abdomen has 12 segments; the first three each carry a pair of latero-ventral appendages, which can be one- or two-segmented, furnished with one to five setae. In Acerentomata and Sinentomata the abdomen has pectinate structures. On the abdominal segment VIII of the Acerentomata a so-called "striate band" is present and more or less distinctly developed.

Since their description by Silvestri (1907) many taxonomic papers have been published on Protura [for a detailed historical review on this subject see Pass & Szucsich (2011) and Galli *et al.* (2018)], among them some relevant monographs which deserve specific mention. In 1964 Tuxen published his seminal work about Protura of the World; in 1973 Nosek's monograph on European Protura appeared; Imadaté's book about Japanese species was printed in 1974; and Yin published her monograph about Chinese Protura in 1999. Nevertheless, Protura still remain one of the less known hexapods, especially from a biogeographical, ecological and systematic viewpoint.

Protura was for a long time known as an order belonging to the class Insecta, but since Yin (1984; see also Szeptycki, 2007) they are considered a separate class belonging to the superclass Hexapoda. They are widely distributed, globally with more than 800 species (748 were listed by Szeptycki, 2007) arranged in three orders, seven families and 76 genera (for more information see Galli *et al.*, 2018; Carapelli *et al.*, 2019). The order Acerentomata includes the families Hesperentomidae, Protentomidae and Acerentomidae; the order Sinentomata includes the Fujientomidae and Sinentomidae; the remaining two families, Eosentomidae and Antelientomidae, belong to the order Eosentomata. A key to the orders and keys to the families are provided below.

Note: the authorities of species and other taxon names and their references are not given in this work, but can be found in Szeptycki (2007).

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Key to orders

1A All three pairs of abdominal appendages two-segmented, with a terminal vesicle and five setae ...... **Eosentomata**
1B Abdominal appendages I two-segmented with a terminal vesicle and three to four setae; those on abdominal segment II and III two-segmented, with a terminal vesicle and three to four setae, or uni-segmented, without vesicle and with one to three setae **2**
2A Median setae present on meso- and metanotum .... **Acerentomata**
2B Median setae absent on meso- and metanotum .... **Sinentomata**

Key to Acerentomata families

1A Only abdominal appendages I two segmented 2
1B Abdominal appendages I and II two-segmented 3
2A Sternite VIII with two anterior and four posterior setae: formula 2/4 .... **Hesperentomidae** (part)
2B Sternite VIII never with 2/4 setae, normally with four anterior and none or two posterior setae: formula 4/0 or 4/2 .... **Acerentomidae**
3A All three pairs of abdominal appendages two-segmented with a terminal vesicle and four setae 4
3B Abdominal appendages I and II two-segmented with a terminal vesicle and three to four setae, appendages III uni-segmented without terminal vesicle and with two to three setae 5
4A Labial palps with tuft of setae, three distinct setae and basal sensillum; pseudoculi with a large triangular prolongation in the proximal part .... **Protentomidae** (part)
4B Labial palps with tuft of setae and three distinct setae, but without basal sensillum; pseudoculi pear-like, strongly elevated and with a median S-shaped cleft .... **Hesperentomidae** (part)
5A Abdominal sternites II-VI all with an even number of posterior setae (seta Pc always absent) .... **Hesperentomidae** (part)
5B An odd number of setae in the posterior row (seta Pc present) of at least one of the abdominal sternites II-VI .... **Protentomidae** (part)

Key to Sinentomata families

1A Spiracles on meso- and metanotum absent .... **Fujientomidae**
1B Spiracles on meso- and metanotum present .... **Sinentomidae**

Key to Eosentomata families

1A Spiracles on meso- and metanotum absent .... **Antelientomidae**
1B Spiracles on meso- and metanotum present .... **Eosentomidae**

Protentomidae, Acerentomidae and Eosentomidae are the most species-rich families and their distribution is cosmopolitan. Hesperentomidae, Fujientomidae, Sinentomidae and Antelientomidae are distributed throughout the Oriental and the Holarctic regions. The first of these four families has a wide range and is represented by the genus *Hesperentomon* in East and Central Asia, and in North America, and by the genus *Ionescuellum*, which is endemic to Europe. The other three families with only one genus each occupy smaller areas in Eastern Asia.

FOREWORD ON ECOLOGY

Protura are part of the soil mesofauna. Based on their adaptation to life in the soil and in soil-like substrates, and on their morphological features (e.g. absence of eyes and of pigmentation), Rusek (2007) classified them as Euedaphobionts. Their distribution seems to be limited only by the presence of a sufficient moisture level in the soil to allow the growth of any kind of vegetation, or by the availability of deposits of decaying organic matter (Nosek, 1975).

Protura are generally poorly known and few studies have specifically focused on their ecology. Most field work has involved studying individual habitats and/or small areas (Raw, 1956; Szeptycki, 1969; Von Neuherz & Nosek, 1975; Stumpp, 1990; Szeptycki & Sterzyńska, 1995; Christian & Szeptycki, 2004; Mitrovski Bogdanović & Blesic, 2011). Only in a few cases has ecological information about Protura been inferred on a large geographical scale based on statistical analyses of national or regional species distribution (e.g. Imadaté, 1973, 1974; Szeptycki *et al.*, 2003; Galli *et al.*, 2019). Moreover, there are few synthesis papers on this subject, and often they are not particularly detailed (e.g. Nosek, 1975, 1982).

The current knowledge about the ecology of Protura is scarce, fragmentary and scattered among papers about proturans that often are not strictly dealing with ecology or that are about soil communities in general. This paper

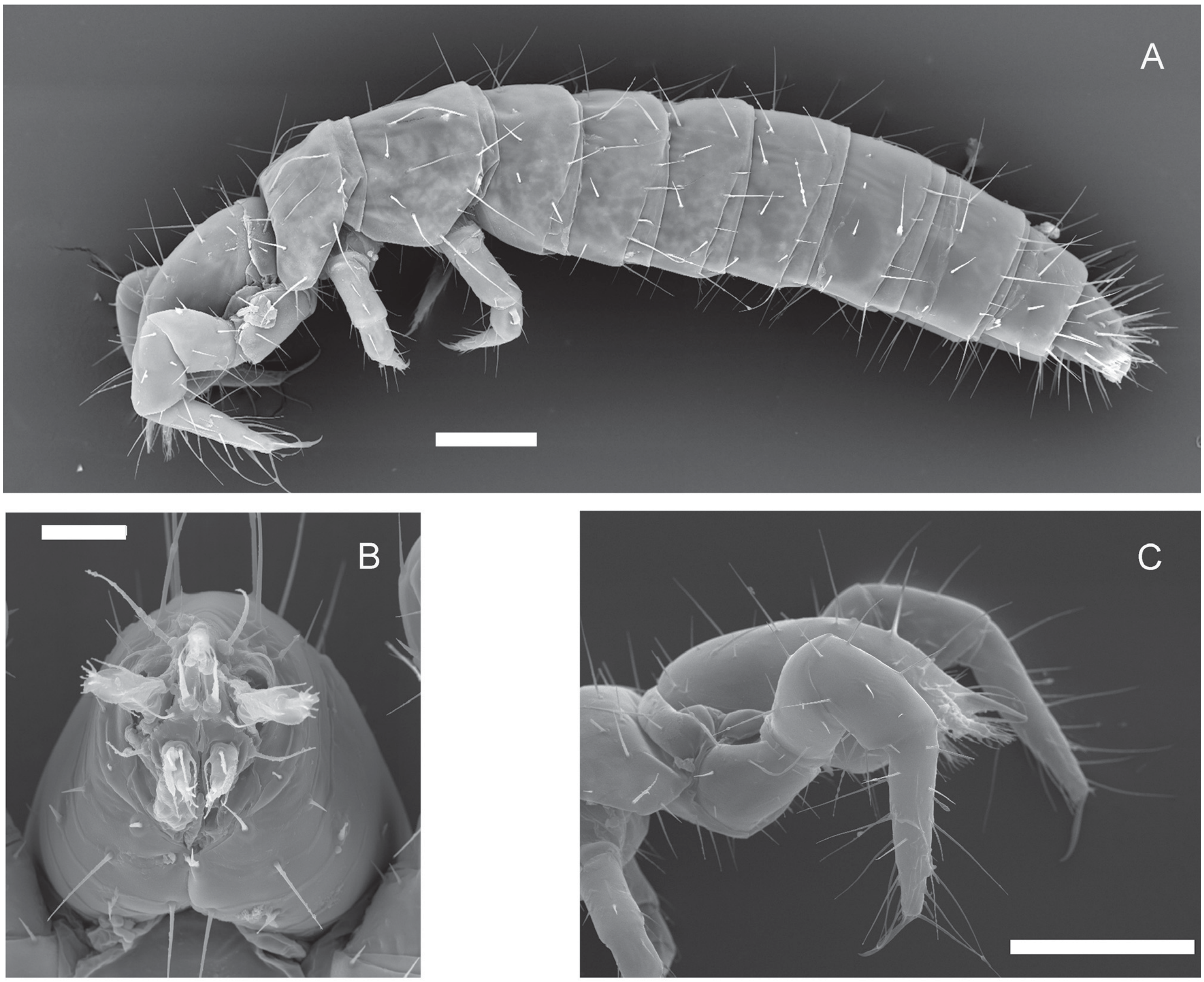

Fig. 1. *Acerentomon italicum* (SEM-micrographs). (A) Lateral view of whole specimen. (B) Detail of rostrum and entogathous mouthparts in frontal view. (C) Detail of anterior part of body with typical position of front legs directed forward as main sensory organs. Scale bars: 100 µm (A) and (C), 20 µm (B).

summarizes almost all relevant data available from the literature in order to better understand the ecology of these arthropods.

DENSITY AND DISTRIBUTION PATTERN

The density of Protura in soils ranges from some hundreds to a few thousand individuals per m². For example, during an investigation carried out in the eastern Italian Alps, in two subalpine spruce (*Picea abies*) forests growing on a calcareous bedrock, Salmon *et al.* (2008a, b) found up to 5456.3/m² (the maximum in 25 years old regeneration south-facing stands). Menta *et al.* (2015) reports a maximum spring density of 297/m² in a kiwi (*Actinidia deliciosa*) plantation and a maximum autumn value of 467/m² both in brush-wood and grassland. In differently managed vineyards Gagnarli *et al.* (2015) recorded an estimated maximum value of 4000-5000/m² during March in organic enriched soils. In soil samples collected in Liguria (NW-Italy) Galli *et al.* (2019) estimated a mean density value of 372.2 [the maximum of 2790/m² in a holm oak (*Quercus ilex*) forest].

For other areas in Europe densities ranging between 6300/m² in mixed oak-hornbeam (*Quercus* spp. - *Carpinus betulus*) forests in the Little Carpathians and 9600/m² in fir (*Abies* spp.) forests in Denmark are summarized by Nosek (1975). In temperate and boreal forests of Europe the density of Protura has been found to range from 1500 to 3900 /m² in spruce forests in Finland (Huhta & Koskenniemi, 1975). Higher density values have been recorded in forests of spruce (Gunnarsson, 1980) and Scots pine (*Pinus sylvestris*) (Axelsson *et al.*, 1973): 8400/m² and 11,400-16,000/m², respectively. More recently, Sterzyńska *et al.* (2012) detected mean densities of nearly 1200/m² in not inundated oak woods and more than 560/m² in inundated poplar (*Populus* spp.) woods in a Ukrainian river floodplain. The maximum value of Protura density estimated to date is over 90,000/m². This occurred in August in a spruce forest characterized by young plants recovering after a windfall (Krauss & Funke, 1999). However, in 28 spruce forests studied in Germany (Fig. 2A) the average density values ranged between 233 and 15,663/m² (but mostly less than 5000/m²) (Stumpp, 1989). This corresponds with the results obtained by Salmon *et al.* (2006) in regeneration stands of spruce forests in Norway. Some authors have found that proturans densities are higher in coniferous forests than in broadleaf forests (e.g. Gunnarsson, 1980), but it is important to point out that, especially under the Mediterranean climate (see paragraph "Altitudinal and vertical distribution"), population densities can be strongly influenced by seasonal climate. A good example is the gap between the July and February densities of Protura in the *Pinus halepensis* forest of Mt Carmel (Israel): 340/m² and 3910/m², respectively (Broza *et al.*, 1996).

Protura usually show an aggregate distribution. This phenomenon has been observed by some authors in different countries. For example, by Raw (1956) during his research on grasslands of Rothamsted Park Grass (UK), by Walker & Rust (1975) in three forests in Delaware, by Gunnarsson (1980) who studied the distribution and abundance of Protura in an oak wood and a spruce stand in SW Sweden, and most recently by Galli *et al*. (2019) in different habitats in Liguria (NW-Italy). This kind of distribution is quite common among soil arthropods (see Wardle, 2002) and it is thought to be due to environmental pressures and/or to the production of aggregation pheromones. For example, several species of springtails show aggregate distributions and are known to produce aggregation pheromones for sexual attraction as well to foster grouping at rich food sources. Dense aggregation may also allow Collembola to create their own ideal microclimate and prevent desiccation (see Hopkin, 1997).

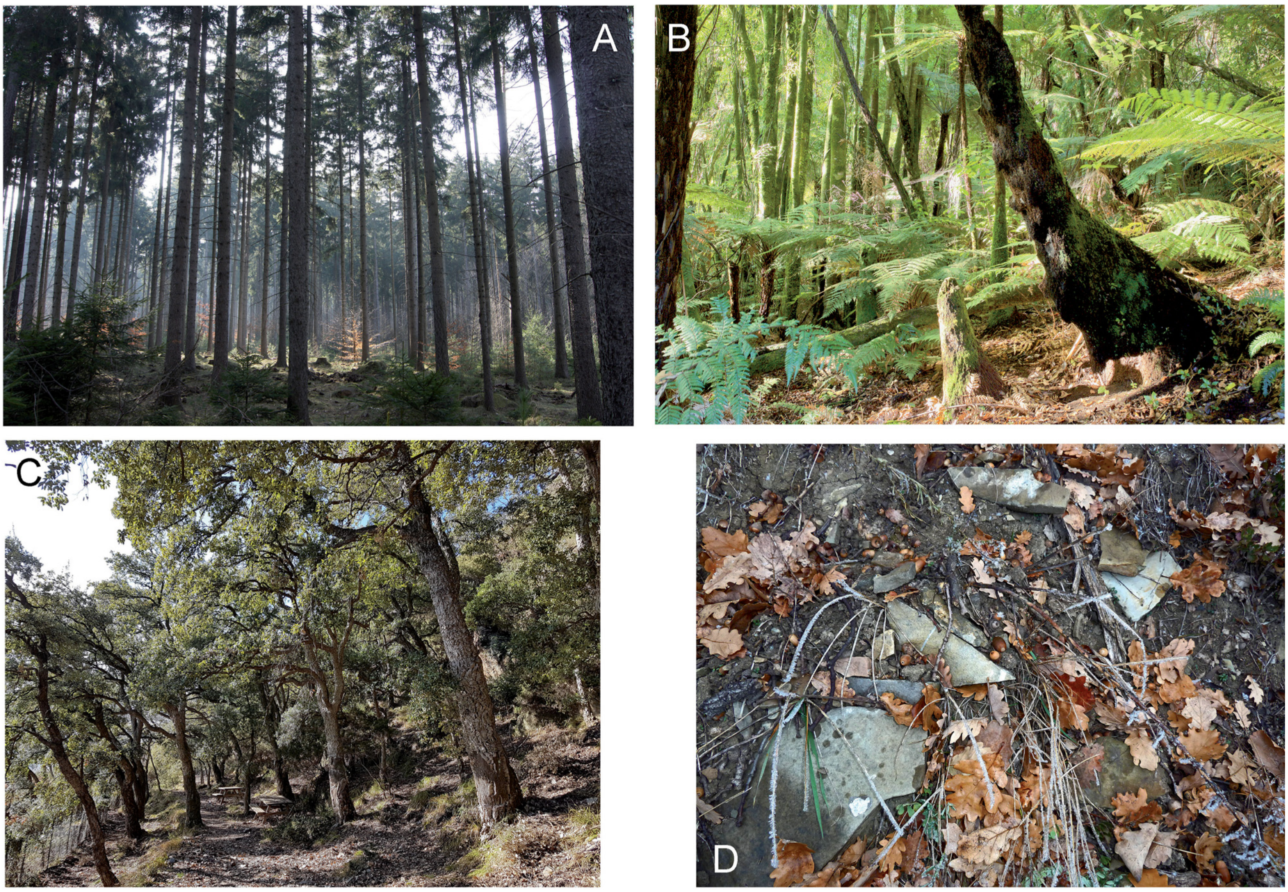

Fig. 2. Habitats of Protura. (A) An example from the Zittauer Gebirge (Germany) of the habitat with the highest recorded Protura densities, the spruce (*Picea abies*) forest (photo: B. Lang). (B) Understory of tree ferns in a regenerating podocarp (*Podocarpus* spp.) forest near the Blue Lake, Rotorua, New Zealand (photo: A. Murray). (C) Cork oak (*Quercus suber*) forest in Bergeggi (NW-Italy), one of the most studied places for soil arthropods in the Mediterranean region (photo: L. Galli). (D) Soil surface in downy oak (*Quercus pubescens*) stand over platy marl (390 m elev.) in the Wienerwald harbouring record number (23) of syntopic species (photo: E. Christian).

EDAPHIC FACTORS

Galli *et al.* (2019) analysed data collected in chestnut (*Castanea sativa*) and beech (*Fagus sylvatica*) forests on three mountains close to each other in Liguria (NW-Italy), deducing that vegetation and physico-chemical characteristics of the soils on different geological substrates (pH and granulometry) may influence Protura density. In particular, they evidenced a negative correlation between pH values and proturan densities (both log transformed) that, however, cannot be generalized. Minor (2008), analysing Protura in New Zealand forests (Fig. 2B), was unable to find any correlation between their density and soil physico-chemical properties (organic matter, nitrogen, phosphorous, pH, cation exchange capacity). The absence of a direct correlation between abundance of soil microarthropods and soil chemistry seems to be common (Laiho *et al.*, 2001). On the other hand, da Silva *et al.* (2016) found a negative correlation between pH and springtail richness, identifying soil pH as the main parameter influencing Collembola communities. Furthermore, Maraun & Scheu (2000) showed an indirect influence of pH on the density of oribatid mites. Soil acidity affects the humus form via modifying macrofauna-mediated processes (litter fragmentation and bioturbation), determining changes from a moder (preferred by oribatids) to a mull humus.

For information about the response of Protura to treatments with chemical pollutants we refer to Stumpp (1989) who evidenced a differential decrease of proturan densities following the exposure to different toxic substances.

ALTITUDINAL AND VERTICAL DISTRIBUTION

Protura can be collected in several different habitats (see for example Nosek, 1973) at elevations ranging from the sea level to the treeless zone on high mountains. At the moment the altitudinal records are held by *Delamarentulus tristani* at 3500 m elev. in the Andean pàramos (Tuxen, 1978) and by *Eosentomon validum* in the Rwenzori Mountains, Uganda, near the Bujuku Lake, at about 4000 m elev. (Condé, 1961). For an interesting study on the altitudinal succession of Protura species assemblages on the slope of a mountain, from 400 to 2000 m elev., we refer to Nakamura (1989).

Tuxen & Imadaté (1975), Shrubovych & Sterzyńska (2017) and Galli *et al.* (2019), studying Protura distribution in the Bismarck Archipelago and Solomon Islands, in the Ukraine and in Italy, respectively, observed that species occurring at higher elevations tolerate a wider range of climatic and ecological conditions and so have generally large geographical ranges. This accords with Rapoport's altitudinal rule (see Gaston *et al.*, 2008).

Information on the vertical distribution of Protura in soils is rather limited, with higher densities recorded in the first few cm (topsoil). Samples taken at different localities in Austria (Franz *et al.*, 1969) showed the highest concentration of proturans in the top 10 cm. On Hokkaido, Imadaté (1974) found that 90% of all Protura were in the top 8 cm of soil, and only *Hinomotentomon nipponicum* was collected at depths greater than 12 cm (up to 38 cm). Condé (1960) found *Proturentomon picardi* at a soil depth of 50 cm. From California (in a pine forest and in an agricultural habitat) Price (1975) and Price & Benham (1977) recorded the presence of Protura at even greater depths. Moreover, Stumpp (1989) showed the differential vertical distribution of four species of Protura, and Nosek (1975) observed the adaptive tendency that Protura living deep in the soil have smaller bodies with shorter legs. These Protura (e.g. *H. nipponicum* and some species of *Proturentomon*, *Protentomon* and *Condeellum*) also have short bacilliform or foliaceous foretarsal sensilla. Conversely, species living closer to the soil surface are generally slender and long, with longer legs, and have long and/or large foretarsal sensilla. In this context it deserves to be mentioned that Fratello & Sabatini (1979) found a positive correlation between a higher chromosome number and a smaller foretarsus.

In the Mediterranean and in other temperate areas Protura probably move up and down the soil profile in response to temperature and moisture levels. Galli *et al.* (2012) recorded that seasonal fluctuations of Protura populations in the soil of a cork oak wood (*Quercus suber*) near Bergeggi (NW-Italy; see Fig. 2C) are linked to a decrease in the number of individuals close to the soil surface during the summer drought. Similarly, in an oak forest in Serbia, Mitrovski Bogdanović & Blesic (2006, 2011) detected two periods of decline in proturan abundance (the first in winter-early spring, the second in August) due to the migration of individuals into soil layers deeper than 20 cm in order to avoid the direct influence of environmental factors such as adverse soil temperatures, moisture levels, increased number of predators and competitors, etc. A migration towards deeper soil levels during the warm season was also hypothesized by Price (1975) on the basis of results of his study in a California pine forest. In addition, Malmström (2008) demonstrated that many soil organisms (Protura included) do not survive temperatures higher than 36°C: in warmer regions this feature could induce migration to a greater depth. Nakamura (2013) evidenced a seasonal migration of *Eosentomon sakura* and *E. impar* from the soil surface (0-5 cm) down to 25-30 cm depth, probably in order to avoid severe cooling during winter. Balkenhol (1994, 1996) showed that *Acerentomon nemorale* could cover relatively large distances (maximum 80-90 cm in six days at 15°C) under laboratory conditions, but her field studies did not show any significant movement, which she assumed was due to the Protura entering into a state of torpor in response to changing and adverse soil temperature and moisture conditions. Many species of Collembola become dormant or quiescent in response to low relative humidity, and the majority of species in the Provence (France) survive the dry summer as eggs which are resistant to desiccation (see Hopkin, 1997). Furthermore, Choi *et al.* (2006) demonstrated that for *Paronychiurus kimi* major limiting factors are soil moisture levels and seasonal rainfall patterns, and that there is a significant reduction of fecundity under moisture stress.

DISTRIBUTION AND ECOLOGY

Nosek (1973, 1975, 1982) noted that European Protura form relatively stable community associations in different types of forests, presumably due to species having similar environmental requirements. Minor (2008) observed that Protura assemblage composition in New Zealand was significantly related to forest type. She also deduced that proturan abundance patterns might reflect an association with fungal communities in the soil. Similarly, Galli *et al.* (2019) outlined genera (and sometimes species) assemblages typical of some macro-habitats represented in Italy and Corsica. However, after in-depth data analyses of studies on Japanese Protura, Kaneko *et al.* (2012) concluded that vegetation was not responsible for their distribution. Assemblages characterizing different areas should be considered the result of historical waves of immigrations ("invasions") of Protura and of the current climate (temperature and rainfall). After all, Tuxen (e.g. 1977, 1978) had already highlighted the importance of biogeographical factors with respect to habitats in the distribution of Protura species.

In some studies a relationship between the ecological adaptability of species and the size of their geographical range was found. For the European Protura Nosek (1975) observed that there are species (e.g. *Eosentomon transitorium* and *Proturentomon minimum*) which have a wide range and are euryoecious, whereas other species are confined to smaller ranges and are less able to tolerate varying ecological conditions, often being restricted to natural habitats characterized by a luxuriant vegetation. Galli *et al.* (2019) found a positive linear relationship between the geographical distribution of the species in Italy and their ecological adaptability (number of habitats colonized).

The species richness of Protura for each sampled locality was studied for many sites in different countries. For example, Imadaté (1970) recorded 6-10 species/locality in natural forests of the lowlands in central Honshu, while 1-13 species/locality were collected in the whole of Japan (Kaneko *et al.*, 2012); Germany has 1-6 species at various sampling sites in spruce forests (Stumpp, 1990); 1-8 species were found in meadow soils in Serbia (Blesic, 2005) and in river floodplain forests of Ukraine (Sterzyńska *et al.*, 2012), and 1-11 species per site in Italy (Galli *et al.*, 2019). Christian & Szeptycki (2004) recorded 23 syntopic species in a *Quercus pubescens* stand over platy marl (390 m elev.) in the Wienerwald (Fig. 2D), which to date is the maximum number of species recorded from one sampling area.

Some authors (e.g. Blesic, 2002, 2004; Galli *et al.*, 2019) observed that Protura assemblages in forest soils are characterized by a greater abundance and diversity than those in meadow soils. Particularly high densities have been recorded in coniferous forests (see paragraph "Density and distribution pattern").

Some studies have focused on the faunal composition of Protura in urban areas and shown that some species are more tolerant to an urban environment than others. Szeptycki *et al.* (2003) found a very specific fauna in town parks, gardens and other anthropogenic habitats in Luxemburg. Some species such as *Acerentulus cunhai* and *Gracilentulus gracilis* are much more common in urban habitats than in natural habitats. For example, *Proturentomon discretum*, *Berberentulus polonicus* and *Eosentomon luxembourgense* were only found in towns. Conversely, some species (*Acerentomon nemorale*, *A. brevisetosum*, *Acerella remyi*, *Eosentomon silesiacum* and *E. stompi*) have not been found in anthropogenic habitats. Christian & Szeptycki (2004) described the species distribution along an urban gradient in Vienna, pointing out that some species (*E. luxemburgense* and *E. mirabile*) seem to be particularly tolerant of, and adapted to, anthropogenic habitats. Galli *et al.* (2019) observed that dominant species in urban habitats in Italy (i.e. *Acerentomon italicum*, *A. microrhinus* and *Acerentulus confinis*) were among the most common, widespread, and adaptable species in Italy. Imadaté & Ohnishi (1993) noted that the Japanese Protura comprise a southern and a northern group of species, and that members of the southern group are more tolerant to habitat degradation and urbanization. Nakamura (2014) confirmed such conclusions citing that *Eosentomon sakura*, *Paranisentomon tuxeni* and *Eosentomon tokiokai* (representatives of the southern group) were collected from soils of almost the same vegetation types in rural and urban areas, suggesting that they tolerate urbanization. *Eosentomon sakura* is particularly dominant in areas with low plant diversity and/or with lush vegetation such as young secondary forests, plantations, parks, etc., and remains largely unaffected by urbanization, thus demonstrating a high tolerance towards anthropogenic influence. *Paranisentomon tuxeni* and *E. tokiokai* prefer evergreen broadleaved forests and evergreen coniferous forests in rural and urban areas, respectively. In contrast, *Eosentomon asahi* (a species of the northern group) occurs mainly in deciduous broadleaved forests and plantations. It is less abundant in urban areas, which is probably due to its low capability to adapt to such an environment. This is not surprising given that Imadaté (1970) found this species to be extremely sensitive to environmental changes, disappearing soon after deforestation took place.

Small mammal nests are examples of another habitat where Protura have been collected. In the western

Carpathians *Acerentomon dispar* and *A. nemorale* were collected from the nests of *Apodemus flavicollis* and *Myodes glareolus*, respectively (Nosek *et al.*, 1978). Galli *et al.* (2019) identified *Acerentomon microrhinus* from a Mole (*Talpa* sp.) nest in Italy.

TROPHIC LEVEL

Protura are secondary consumers in the decomposition subsystem of terrestrial ecosystems. They are part of the detritus-based food web and depend on the energy obtained from feeding on fungal hyphae (the so called “fungal energy channel” – see Wardle, 2002) (Fig. 3). Their mouthparts are well adapted to sucking. Sturm (1959) reported *Acerentomon* sp. and *Eosentomon transitorium* feeding on beech ectomycorrhizal fungi (EMF). Likewise, Stumpp (1990), studying Protura population dynamics in spruce forests in Germany, concluded that specimen numbers correlated positively with the abundance of EMF. Malmström & Persson (2011) tested Stumpp’s hypothesis via tree-girdling experiments in *Picea abies* and *Pinus sylvestris* forests in northern Sweden. Tree girdling was assumed to stop the flux of carbohydrates to roots and associated fungi, thereby inhibiting growth and long-term survival of EMF. About one year after girdling proturan abundance decreased, indicating that they prefer feeding on EMF. Similarly, Sterzyńska *et al.* (2012) observed that differences in the distribution patterns of Protura assemblages in a Ukrainian river floodplain were highly correlated to the frequency of available ectotrophic mycorrhizae. They noted that the transition from early successional stages of riparian forests, where regular flooding promotes arbuscular mycorrhizal fungi, to older stages, where EMF are more common, was associated with an increase in Protura abundance and diversity. In a study using three *in situ* analytical methods (stable isotope labelling, neutral lipid fatty acid analysis and natural variations of stable isotope ratios) Bluhm *et al.* (2019) showed that *Acerentomon gallicum* predominantly feeds by sucking up hyphal cytoplasm of EMF.

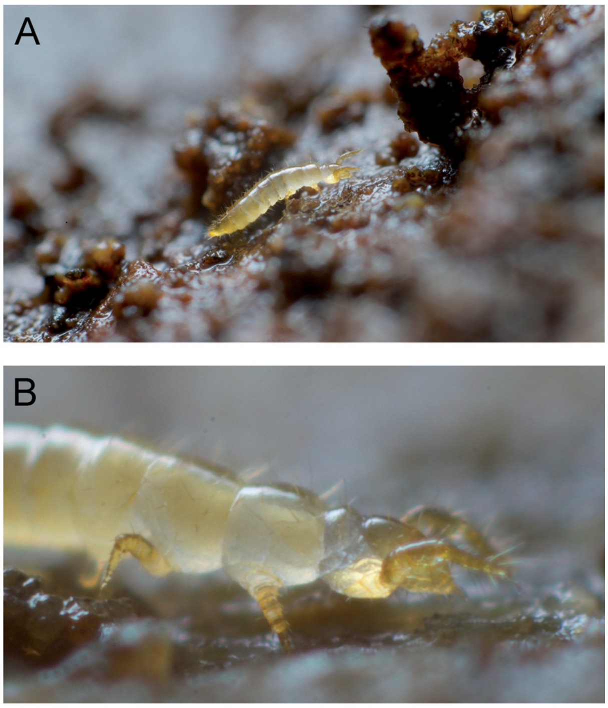

Fig. 3. *Acerentomon* specimen feeding on the ground of a beech (*Fagus sylvatica*) forest near East Pennard, UK (photos: A. Murray). (A) Whole animal. (B) Detail of anterior part of body (legs and rostrum clearly visible).

Machida & Takahashi (2004) reared proturans and observed that they often gathered around the “bush” of mycelia or mycelial strands. Individuals were sometimes observed inserting their rostrum into mycelia, presumably to feed on fungal protoplasm. These observations suggest that not all Protura species are strictly depending on EMF but can also feed on “free” hyphae. Nosek (1975) and Balkenhol (1994) came to the same conclusion by studying several species. Moreover, Kaneko *et al.* (2012) compared proturan assemblages in broadleaved forests with those in conifer forests of Japan, in which mycorrhizal species composition differed, but they did not find any clear response from Protura to different vegetation types. Therefore they rejected the hypothesis that there is a strong link between proturans and mycorrhizal fungal species.

Protura are probably the prey of other small arthropods like mites and other tiny arachnids. When analysing the behaviour of an *Acerentulus confinis* specimen, Hansen *et al.* (2010) observed a possible defence mechanism when the animal released a sticky exudate from the large gland openings on the eighth abdominal segment. When applied to the mouthparts of a small predator, such an exudate may prevent further aggression.

POPULATION DYNAMICS (PHENOLOGY AND SEX RATIO)

The phenology of Protura has not been the focus of much research. The scarcity of records of juveniles, a phenomenon already pointed out by Walker & Rust (1975), makes it difficult to identify well defined phenological patterns useful for determining the life cycles of the majority of species. The first substantial data available in the literature were those about populations of Protura in soils supporting a mixed evergreen-deciduous forest in Tokyo (Imadatè, 1974). Imadatè documented different patterns of seasonal fluctuations in the collected species: a double-peaked pattern (maxima in spring and in autumn) in *Eosentomon sakura*, a single-peaked pattern (maximum in autumn) in *E. kumei*, *Baculentulus morikawai*, *B. tosanus*, *Kenyentulus japonicus* and *Nippoentomon nippon*, and an almost constant density all year round in *E. asahi*. Similar patterns have subsequently been described by other authors (e.g. Stumpp, 1989; Balkenhol, 1994; Szeptycki & Sterzyńska, 1995), and one of the most interesting results that emerges from the comparison of different studies is that phenology of the same species can vary in different areas, probably in response to the different local climates. For example, in a study in Italy, Galli *et al.* (2016) recorded that in *Acerentomon italicum* populations juveniles were present every month in Liguria and Tuscany, but only during spring and summer in the remaining regions of northern Italy. Interestingly, Galli *et al.*, 2019 described a double-peaked phenology for *Acerentomon gallicum* in Italy, which differs significantly from the three-peaked phenology described for *A. gallicum* in Germany by Balkenhol (1994). Similarly, Mitrovski Bogdanović & Blesic (2011) described a double-peaked phenology (September and June-July) for *Eosentomon transitorium* in an oak forest dominated by *Quercus conferta* and *Q. cerris* in Serbia, which is quite different from the trend observed for this species in Italy by Galli *et al.* (2019). There two maxima of juveniles were recorded in March and from June to August (adults showing a third peak in October, when no juveniles were collected).

Another interesting feature of Protura populations is that they commonly have an unbalanced sex ratio in favour of females. This can be deduced by analysing various faunal studies (e.g. Nosek, 1973) and has been explicitly pointed out for different species by several authors. Amongst others, Gunnarsson (1980) recorded that females of *Eosentomon germanicum* in an oak wood in Sweden were more than twice as numerous as males, and Galli *et al.* (2019) observed a similar bias in 12 Acerentomata species in Italy. On the basis of the sperm structure of Protura (see Dallai *et al.*, 2010a, b), Galli *et al.* (2019) hypothesized that this imbalanced sex ratio could be related to indirect sperm transfer through spermatophores as one of the possible mechanisms which enables a single male to fertilize more females.

Some authors recorded the absence of males in populations of Protura: for example Tuxen (1967, 1985) found only females in some Australian and New Zealand species. More recently, Minor (2008) detected four species in New Zealand in which the populations were devoid of males. Shrubovych *et al.* (2014) and Galli (in Galli *et al.*, 2019) examined many specimens of *Andinentulus rapoporti* from Chile and found only females. The latter authors recorded only females in Italian populations of *Proturentomon minimum*. Though parthenogenesis in Protura has never been confirmed experimentally, the information mentioned above suggests that at least in some populations of certain species, parthenogenesis may occur.

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