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100 years of research on the Protura: many secrets still retained

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Abstract

The Protura were discovered relatively late in the history of entomology. The first description of these minute soil arthropods was given in 1907 by the Italian entomologist Filippo Silvestri, who named them 'Protura'. Shortly thereafter his fellow countryman Antonio Berlese published two brief notes on these animals before his grand monograph of the 'Myrientomata', as he named them, appeared in 1909.

The centennial of the discovery of Protura offers the opportunity to review our knowledge about these peculiar animals. In the end, we must confess that proturans continue to retain an amazing number of secrets, including basic facts of knowledge about their biology and ecology. Up to the present, they have concealed from scientific observation their sexual life and the mode of sperm transmission. For a long time, their egg deposition and early development were completely obscure topics; only recently has it become possible to conduct first observations on their embryology. The list of open questions can be easily extended: we know only little about their nutritional biology, and next to nothing about their sensory systems, communication, physiological and ecological capacities.

The greatest progress in proturan research over the past 100 years has been made in the field of taxonomy. Nonetheless, the road of taxonomy was bumpy and the proturans proved to be awkward travel companions. Species are exceedingly difficult to determine; and the number of living scientists that are able to unambiguously identify specimens at the species level can be counted on two hands. Proturans inhabit soils in all terrestrial regions of the earth (excepting the Arctic and Antarctic regions). Presently, a total of 787 valid species has been described. Because of the high standards of Berlese's 1909 monograph, several decades would pass before morphological and anatomical research could equal or go beyond his classical landmark. In more recent times, remarkable contributions have been made to the ultrastructural investigation of internal organs and sperm morphology; hereby, the proturans proved again to be odd and unusual in many respects. The peculiarities of Protura have evoked heated debates about their phylogenetic position from the beginning, and such discussions have recently been revived by the introduction of molecular data. The review comprehends an extensive reference list on all research topics except taxonomy, which recently was compiled by Szeptycki (2007).

Keywords: Hexapoda, Apterygota, Ellipura, Nonoculata, history of research

1. Introduction

Among the numerous hexapod orders, the Protura is a latecomer to see the light of scientific inquiry. Their late discovery was, no doubt, due to their minuteness and cryptic edaphic lifestyle. Generally, they are overlooked with the naked eye, and entomologists become usually aware of these animals only after extraction from soil samples using the well-known Berlese-Tullgren apparatus.

This review is written to mark the occasion of the first centennial of the discovery of the Protura. It summarises the history of research on proturans in the various biological disciplines. A special focus will be given to the discovery and early history of research, as well as various trajectories of scientific progress up to the present. The different fields of research were previously reviewed in the excellent treatises of Denis (1949) in the Traité de Zoologie and Janetschek (1970) in the Handbuch der Zoologie. Short sections on various aspects of morphology, ecology and evolution are given in the taxonomic monographs of Tuxen (1964), Nosek (1973), and Yin (1999; in Chinese). The taxonomic literature, which amounts to the vast majority of all publications, was critically and comprehensively reviewed in the recent 'Catalogue of World Protura' by Szeptycki (2007). Therefore, taxonomic aspects are only briefly touched upon here. However, the present review contains a comprehensive compilation of the references on all remaining aspects of the Protura, in particular life history, anatomy and morphology.

2. Discovery and first descriptions occurred in Italy

Proturans were probably first noticed in Italy and the initial study of them began in Italy and was conducted by eminent Italian entomologists. According to published records, it was the amateur entomologist, Agostino Dodero (Fig. 1), who first discovered specimens of Protura on June 5, 1907, while he was searching for micro-coleopterans in the Botanical Garden of the University in Genoa (for details on Dodero´s biography, see Poggi 2009). In the next weeks he collected more individuals from natural habitats in the Ligurian mountains nearby[1]. He passed the unusual arthropods, which were not placeable into any of the known groups to Professor Filippo Silvestri (Fig. 2A), a renowned entomologist, who at that time was director of the Laboratorio di zoologia generale e agraria della R. Scuola superiore d'agricoltura in Portici near Naples (now Department of Agricultural Entomology and Zoology, University of Naples). Silvestri performed the first investigation of these creatures and published his results in December, 1907, in the first volume of the in this year founded

Fig. 1 The micro-coleopterist Agostino Dodero (1864–1937) discovered proturans in the Botanical garden Viletta Dinegro in the centre of the city of Genoa, Italy, at 1907 June 5.

Fig. 2 (p. 311) Portraits of famous proturologists: **A**: Filippo Silvestri (1873–1949); **B**: Antonio Berlese (1863–1927), photo 1915; **C**: Søren Ludvig Tuxen (1908–1983); **D**: Josef Nosek (1924–1984); **E**: Yin Wen-Ying (*1922), photo 2004; **F**: Andrzej Szeptycki (1939–2008); **G**: Romano Dallai (*1938), photo 2005; **H**: Jean François (*1933); **I**: Ryuichiro Machida (*1953), photo 2005.

[1] June 16, 1907 Montallegro presso Rapallo, July 28, 1907 Castellnuovo Garfagnana (Poggi, pers. comm.).


A
B
Antonio Berlese
1916
C
D
E
F
G
H
I

entomological journal of the laboratory in Portici of which he was the head. His description comprises 15 pages with 18 figures and gives a fairly good picture of the exoskeleton of the three tagmata (Fig. 3). Silvestri classified these unusual arthropods as a new and separate order of 'Insecta Apterygota' and attributed to them a number of traits unusual for insects. The most prominent differences to all other insects were the presence of certain abdominal characters, such as the location of the genital openings behind the 11th abdominal segment, as well as a lamina supraanale and a lamina subanale. These characters were considered by Silvestri to be ancestral for insects, and therefore he chose the name Protura for the taxon (ancient Greek *protos* = ancestral, *oura* = tail). The designation of the first described species, *Acerentomon doderoi*, was chosen in honor of its collector[2].

There is a second Italian entomologist who dealt with these arthropods from the beginning: Antonio Berlese (Fig. 2B). His first publication on the proturans appeared in August, 1908. He noted that he had discovered these minute arthropods long ago ('da molto tempo') in soil probes from the surroundings of Florence and presented a description of four additional species, as well as a new genus, *Eosentomon*, together with information on the stages of development (Berlese 1908a). In December of the same year, he published a 'Nota Preventiva' which contained a short but succinct description of the various internal organ systems of these 'bestioli' (Berlese 1908b). The latter paper contains no figures; however, Berlese announced a comprehensive work on these animals, which appeared finally in 1909. This magnificent monograph comprises 182 text pages and 17 full sized lithographic plates with 176 brilliant

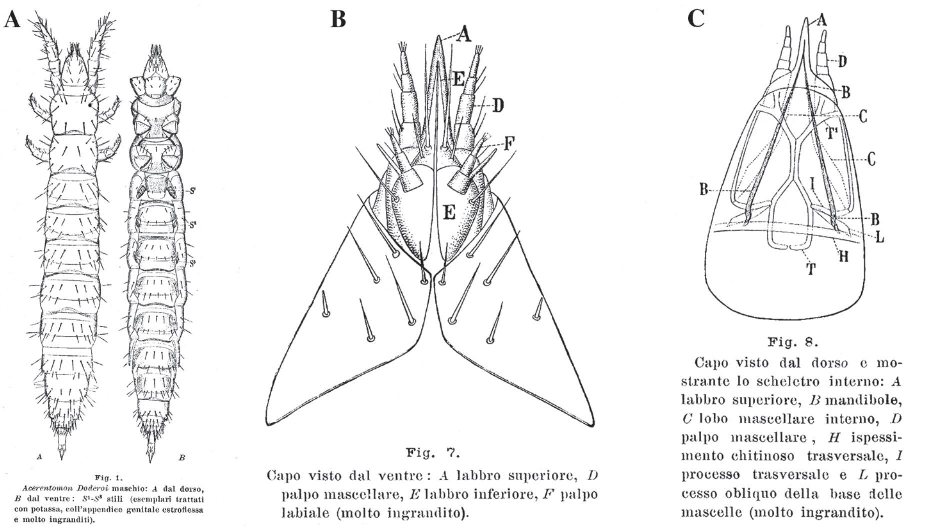
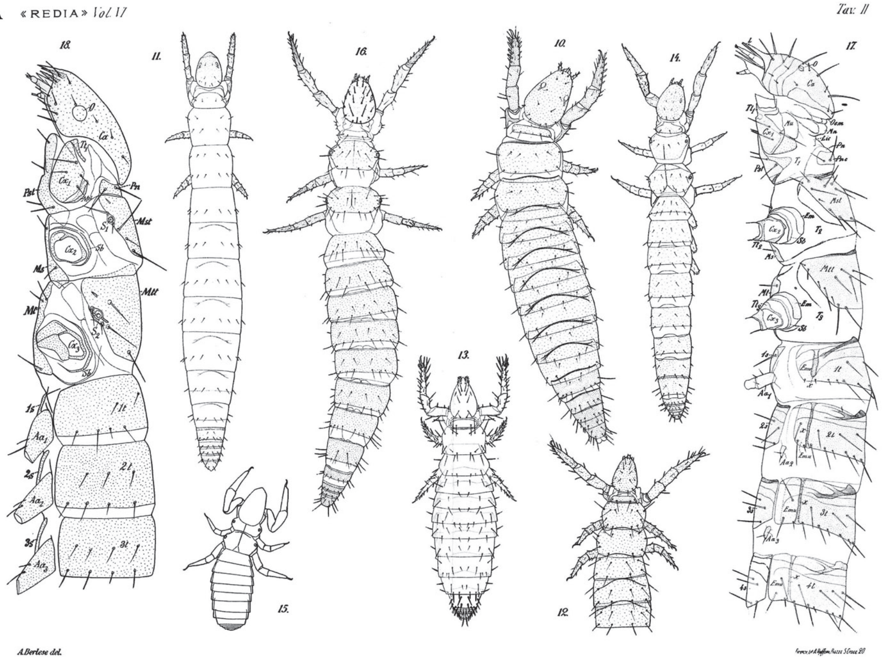


Fig. 3 The first published drawings of proturans were provided by Filippo Silvestri (1907). **A**: representation of the whole body; **B**: ventral side of the head; **C**: tentorium.

Fig. 4 (p. 313) Example of tables from the grandiose monograph of Berlese (1909). **A**: Table 2: general habitus of different species of *Acerentomon*, *Eosentomon* and *Acerentulus* **B**: Table 11 musculature of *Eosentomon transitorium* (Fig. 118) and *Acerentomon doderoi* (remaining figures).

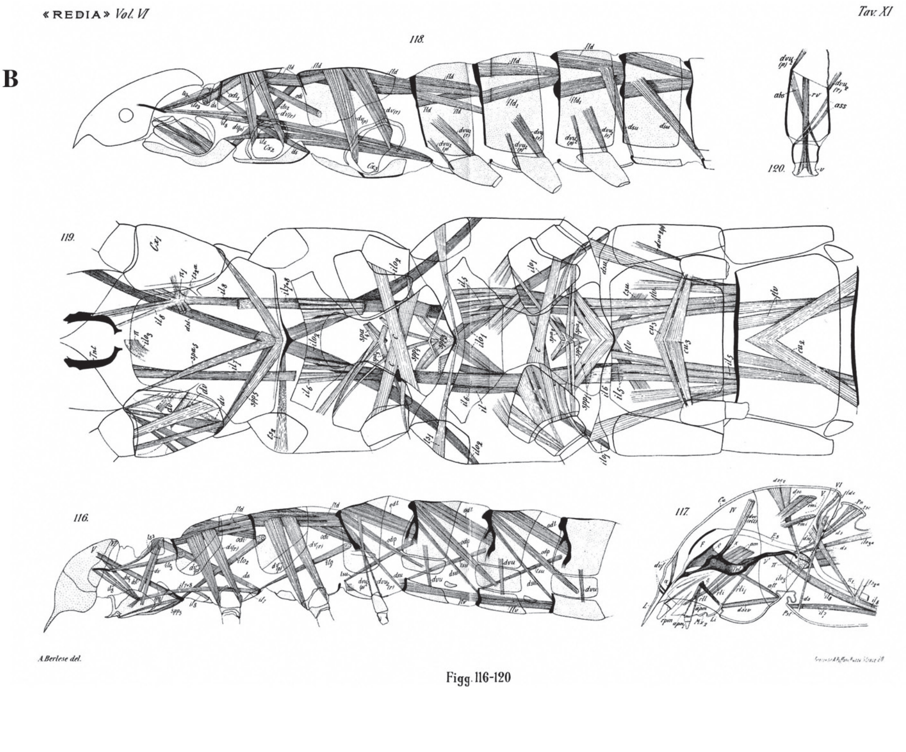
[2] In 1983, Carlo Torti examined four specimens labeled as 'cotypus *doderoi*' in the Museum of Natural History in Genoa as *A. italicum* NOSEK, 1969; regrettably, he was unable so far to analyse the lectotype (Tuxen 1960, p. 295) deposited in the Instituto di Entomologia agraria dell'Universitá di Napoli-Portici; see also Capurro et al 2009

A



Figg. 10-18.

B



Figg. 116-120

figures not only of the exoskeleton, but also the internal organization of these animals (Fig. 4). This book is an outstanding achievement and anyone who has worked on the anatomy of these animals knows how difficult it is to analyze their compact internal organization from histological serial sections. As one of the leading entomologists of his time, Berlese was director of the famous R. Stazione di Entomologia agraria in Firenze (for details of his biography, see Paoli 1928). He was the predecessor of Silvestri at the agricultural college in Portici and was appointed to Florence in 1903. Aside the above cited statement of Berlese and the time required to complete the comprehensive 1909 monograph it stands to reason that he dealt with these animals before the publication of Silvestri's first description. The professional and private relationships of Berlese and Silvestri furthermore strongly suggest that the two scientists were aware on each other´s work with the proturans and one may wonder, nay even suspect, that there was a competitive race between these two scientists. However, no clear hint to such tensions can be discerned in their publications or correspondence.

As if this were not enough, the Russian entomologist Rimsky-Korsakow (1911a) also reported that he found specimens of Protura in 1906 under the bark of decaying old fir trees. The multiple discoveries of these animals could have been triggered by the introduction of the ingenious apparatus invented by Berlese (1905, Fig. 5), by which small arthropods can be easily extracted from soil probes; however, the cited papers give no specific information on the method of collection. Altogether, we are probably justified to assume that the Protura were independently collected by several contemporaneous entomologists. In any case, the discovery of these unusual arthropods caused a sensation in the scientific community which stimulated further examination by a number of entomologists.

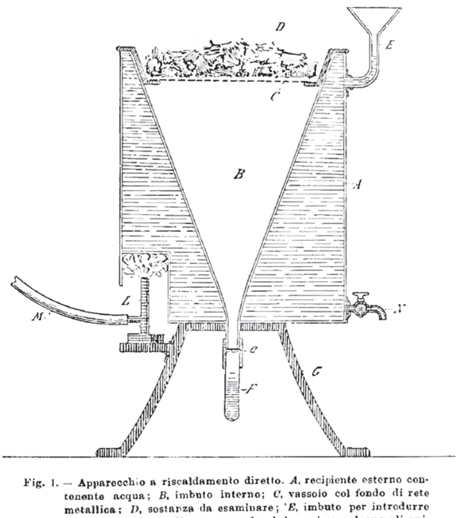


Fig. 1. — Apparecchio a riscaldamento diretto. *A*, recipiente esterno contenente acqua; *B*, imbuto interno; *C*, vassoio col fondo di rete metallica; *D*, sostanza da esaminare; *E*, imbuto per introdurre l'acqua; *F*, tubetto di vetro con alcool dove si raccolgono gli animaletti, riunito per tubo (*a*) di gomma, corto, all'apice dell'imbuto; *G*, piedi di sostegno dell'apparecchio; *L*, lampada per riscaldare; *M*, tubo di gomma che porta il gaz; *N*, rubinetto di scarico.

Fig. 5 First drawing of the famous 'apparecchio' of Berlese (1905) for the extraction of soil mesofauna. Notice the method of producing a heat gradient by a water bath encasing the funnel, which is heated by a Bunsen burner.

3. Unusual morphology and anatomy

Silvestri's description of 1907 contains an adequate overview of the external morphology of *Acerentomon doderoi*. His description of the exoskeleton was significantly deepened and complemented by the description of the internal anatomy in Berlese´s monograph of 1909. Thanks to the magnificent detail and accuracy of its figures this work set a standard, which was not surpassed by other studies for several decades. Some of his brilliant figures are still reproduced in textbooks. Berlese's monograph focused largely on the genus *Acerentomon,* while comparatively few sections were devoted to *Eosentomon.* This information bias still holds true for all published morphological works up to the present day.

Yet another study on proturans was published in 1909 by Alexander Schepotieff of St. Petersburg. Although the publication contributed nearly nothing to our understanding of these animals, it must be cited here in detail because it had a remarkable negative impact on the research on Protura for decades. Schepotieff described a proturan species from India, which despite its correspondence in many aspects with the *Acerentomon doderoi* of Silvestri, differed significantly from the latter in some points. Most importantly he explicitly stated they have antennae (Fig. 6), and the position of the genital pore is located between abdominal segments 8 and 9. The lack of antenna mentioned for *Acerentomon* in the original description seemed generally dubious to Schepotieff and he argued that the ocelli referred to by Silvestri are nothing else but the insertion sites of the antennae which must have broken off. He classified the Indian animals as a new genus of Protura and named the species *Protapteron indicum*. Börner (1910) thus differentiated two suborders within Protura: the Rhammatocera (Protapteridae)

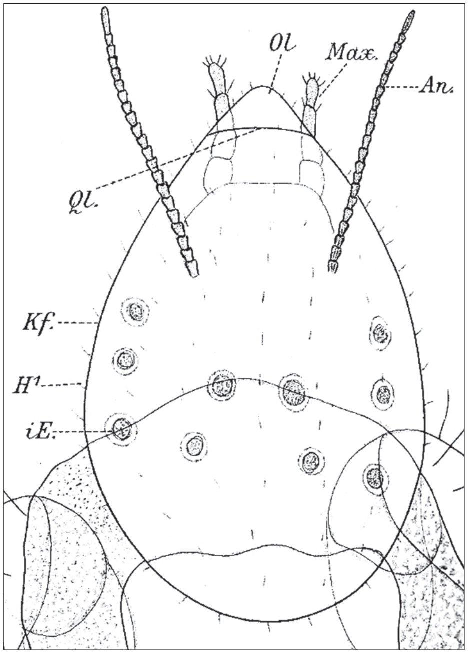


Fig. 6 *Protapteron indicum* the sole proturan described to possess antennae by Schepotieff (1909). The antennae turned out to be a product of mere imagination.

with antennae, and the Myrientomata which lack antennae. Criticisms of the description by Schepotieff arose early after its publication. Rimsky-Korsakow (1911b) examined specimens which Schepotieff had investigated, but found no traces of antennae. Furthermore, the antennae shown in Schepotieff's figures appear highly unrealistic and schematic. Considerable time passed before the scientific community conceded definitely that the antennae of *Protapteron indicum* were obviously the product of wishful thinking. Tuxen (1931) re-examined the case of antennate *Protapteron* in abundant detail as an example of scientific scandal, and he put an end to the debate saying: '*Protapteron indicum* does not exist and it is therefore not to be taken into account as part of the scientific literature on proturans proper' (p.715, translated from German).

Subsequent to Berlese, Heinrich Prell of the University of Marburg began his very precise and careful studies on the morphology and anatomy of proturans (Fig. 7). In a sense, he filled in the gaps left by Berlese, e.g. leg musculature (Prell 1912) and the tracheal system as well as the exoskeleton of *Eosentomon* (Prell 1911, 1913). Thereafter and for many years, no further work on the anatomy and morphology would appear, and the topic seemed sufficiently examined.

In 1931, another eminent proturologist entered the scene, Søren Ludvig Tuxen from Copenhagen (Fig. 2C). His doctoral thesis was a voluminous review-like publication on proturan morphology and anatomy. Tuxen was deeply impressed by the richness of the works by Berlese and Prell and found very little to add (it sufficed to merely redraw their figures making only minor changes). Tuxen's lasting achievement in his thesis was his reinterpretation of structures of the exo- and endoskeleton based on the advanced stage of insect comparative morphology. Later, he contributed to our understanding of the tentorium (Tuxen 1952) and morphology of the postembryonal stages (Tuxen 1949, 1950). The focus of his outstanding employment with proturans, however, was of taxonomical nature (see below). Apart from Tuxen only a short paper on the occurence of the heart in Protura was published in this period (Aubertot 1939).

After Berlese it lasted five decades before the morphology and anatomy was re-examined by a descendant of the great morphological school in France: Jean François from Dijon (Fig. 2H). He meticulously investigated not only *Acerentomon*, but also *Eosentomon*, in particular the head (François 1959, 1965, 1969) and thorax (François 1964, 1996), but also the male genital apparatus (François and Dallai 1989). His attention to detailed morphology was extraordinary and he offered new interpretations on several structures, such as the tentorium. Furthermore, a special value of his work is that he also comparatively analyzed the structures with those of other apterygotes, and he attempted to homologise the various structures.

An important advance in proturology was the discovery of the unusual species *Sinentomon erythranum* (Yin 1965 a, b). Morphologically this proturan stands apart from the others with respect to a number of characters, such as sutures, endoskeleton, the lack of a linea ventralis, simple-appearing mouth parts and the lack of pharyngeal gnathal and cephalo-thoracic muscles (François et al. 1992). The assessment of these characters from a phylogenetic point of view differs widely. For some proturologists, *Sinentomon* represents the ancestral ground pattern (Imadaté 1966, 1977, Nosek, 1973, Tuxen 1977, 1980, Szeptycki, 1989), while for others the numerous apparently simple characters indicate reductions of more advanced forms (Yin 1981, 1984, Dallai and Yin 1983, Xue and Yin 1989).

Beginning in the late 1960's, studies using electron microscopy enabled us to gain deeper insights into the anatomy of Protura. The pioneer and leading expert in this field is Romano Dallai from the University of Siena (Fig. 2G). He contributed a number of excellent studies,

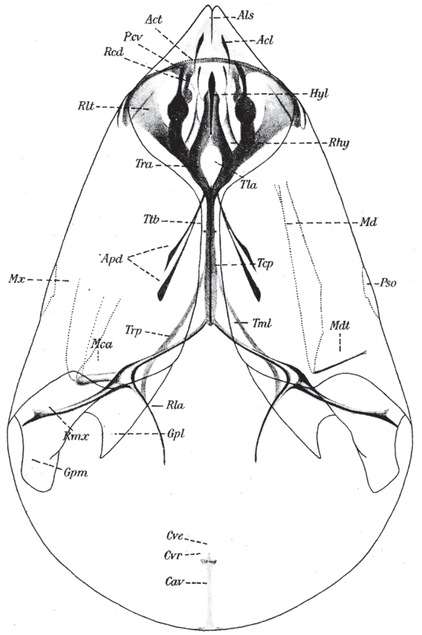


Fig. 7 Details of the head of *Eosentomon germanicum* including the cephalic endoskeleton (from Prell 1913).

partly in collaboration with other expert proturologists, such as Yin (Fig. 2E) and her research team from the Chinese Academy of Science in Shanghai, as well as François and Nosek. Several papers on the ultrastructure of proturans were also published by Jura, Klag, Bilinski and Rost-Roszkowska from the Universities of Krakow and Silesia in Poland. In the following we list the organs and organ systems which so far have been investigated at the ultrastructural level: sensory organs on the foreleg (Müller 1976, Dallai and Nosek 1980, 1981), hypopharyngeal sensilla (Dallai & François 1986), pseudoculus (Bedini and Tongiorgi 1971, Haupt 1972a, b, Xué and Yin 1989, 1991, Yin et al. 1986), cuticle (Sixl et al. 1974), tegumental glands (Condé & François 1962, Dallai & Burroni 1981, Dallai 1991), maxillary glands (François and Dallai 1986a), abdominal glands (François & Dallai 1986b), gut (Dallai 1977a, b, 1978, Dallai et al. 1987, 1989, Xué and Dallai 1992, Bilinski and Klag 1979, Rost-Roszkowska et al. 2010), Malpighian papillae (Dallai 1976), heart (François 2003b), tracheal system (Xué et al. 1993, 1994), ovaries and oogenesis (Jura 1975, Klag 1978, Bilinski 1977, Bilinski & Klag 1977, Klag and Bilinski 1984), sperm and spermatogenesis (Baccetti et al. 1973, Dallai & Yin 1983, Dallai et al. 1990, 1992, 2006, 2010a, 2010b, Xué & Yin 1990, Yin & Xué 1993, Yin et al. 1985, 1989, 1990).

4. Phylogenetic controversies from the beginning

The phylogenetic position of the Protura has been a point of controversy from the very start. Silvestri´s description evoked a number of debates in the scientific community, whether his classification of Protura among the Insecta is correct and whether they represent a new order of Apterygota. On the basis of his studies, Berlese came to a different conclusion than

Silvestri. He found that the closest affinities of Protura were to Pauropoda and Symphyla, but also to Archaeognatha and he erected a separate clade of arthropods for them closely related to myriapods and hexapods. Reflective of their 'intermediary' organization between myriapods and insects, he chose the name 'Myrientomata' (Berlese 1909). Schepotieff (1909) saw greatest similarity to Diplura and introduced the clade Prothysanura encompassing *Protapteron*, *Acerentomon* and *Campodea*. Likewise, Börner (1910) considered them as true insects. Based on a number of characters, such as the entognathous mouthparts with a labial *linea ventralis*, as well as the lack of cerci, he presumed a close relationship to Collembola. The absence of cerci was also the name which he introduced for the common higher taxon, which he named Ellipura (ancient Greek *eleipsis* = loss). Rimsky Korsakow (1911b), although recognizing similarities with Diplura, followed the view of Berlese and concluded that Protura were a separate branch of Atelocerata sharing a common ancestor with both myriapods and insects. Finally, Prell (1913) emphasised the lack of arguments which justify separation of Protura from Insecta; thus he was in agreement with Börner yet classified Protura as a separate subclass within the Hexapoda.

At this point, the discussion on the phylogenetic position of proturans seemed complete, at least it had subsided, and the view that Protura are basal hexapods and the sister group of Collembola became widely accepted until recently. The Ellipura hypothesis is generally accepted in nearly all reviews dealing with the morphology of apterygotes and the phylogeny of hexapods (Hennig 1953, 1969, Manton 1979, Boudreaux 1987, Kristensen 1975, 1981, 1991, 1997, Bitsch & Bitsch 1998, 2000, 2004), and zoological textbooks (Brusca & Brusca 1990, Ax 1999, Willmann 2003, Hickman et al. 2011).

Nevertheless, some renowned morphologists have recently raised doubts on this hypothesis. On the one hand, data exists on the unusual and unique sperm morphology of proturans which associates them neither with collembolans nor with any other group of hexapods (Yin et al. 1985, Dallai 1991, Dallai et al. 2010a, 2010b). On the other hand, new insights came from recently found features in the embryology of the proturan *Baculentulus densus* (Fukui and Machida 2006, Machida 2006). In particular, the authors refer to the ability of the serosa to differentiate into the tergum or to participate in the definite dorsal closure, a feature which is unknown for any other hexapod but which is common in myriapod and crustacean embryos.

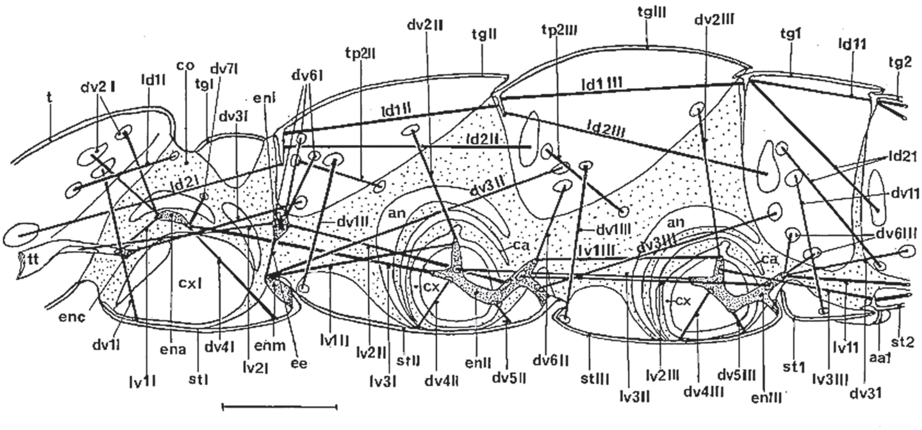


Fig. 8 Thoracic musculature of *Acerentomon* in the characteristic style of the French school of insect morphology (from François 1996).

In consideration of the conflicting arguments based on morphological evidence, the advent of molecular phylogenetics is promising for the enlightenment of the phylogenetic position of the Protura. Nevertheless, Protura are latecomers in molecular phylogenetics. The first data appeared about a decade ago (Shao et al. 1999, Carapelli et al. 2000) and data collection has proceeded very sparsely. Relevant for discussion here is that none of the published studies significantly corroborate the Protura outside the Hexapoda. With respect to the potential sister group within hexapods remarkably few molecular studies support the Ellipura hypothesis. Almost all studies support a close relationship to Diplura (Luan et al. 2003, Giribet et al. 2004, Kjer 2004, Luan et al. 2004, Giribet et al. 2005, Luan et al. 2005, Kjer et al. 2006, Mallatt & Giribet 2006, Gao et al. 2008, Dell'Ampio et al. 2009, von Reumont et al. 2009, Xie et al. 2009, Koenemann et al. 2010, Mallatt et al. 2010, Meusemann et al. 2010). The Diplura + Protura clade was named 'Nonoculata' by Luan et al. (2005) due to the lack of eyes. Aside from this feature, no other substantial synapomorphies have been published, so far. As a potential synapomorphy, Luan et al. (2005) mentioned the short papillae or absent Malpighian tubules. Szucsich and Pass (2008) additionally noted that a ventral coxa-sternite joint is exclusively shared between proturan and dipluran species and can thus serve as a potential synapomorphy of these taxa. Ellipura was only supported by a few single gene analyses based on mitochondrial genes (Shao et al. 1999, Carapelli et al. 2000, Zhang et al. 2001). Only recently the first complete mitochondrial genome was published for *Sinentomon erythranum* (Chen et al. 2011) (for a detailed review of the molecular phylogenetics of Protura, see the review of Dell´Ampio et al. in this issue).

5. History and status of taxonomic research

In a historical review, Szeptycki (2002) highlighted the major phases and milestones of taxonomic research in Protura. At the beginning, basic characters were used, such as the presence or absence of the tracheal system, as well as simple and general characters, such as body colour and dimensions (mainly body length). Later morphometric data and indices were included, such as the proportion of head and body segments and number of setae on individual segments.

In the following decades substantial progress was achieved by the discovery of new features, especially in the studies by Condé, Tuxen and Nosek. Particularly noteworthy is the inclusion of foretarsal sensilla characters by Condé (1945). A milestone in taxonomy was the excellent monograph on the 'Protura of the World' by Tuxen (1964). For the first time, a practical work for species determination was available. Tuxen´s book formed the foundation for all further taxonomic studies. In the following years, a great number of new species was described from all over the world and especially from East Asia (species of Japan were summarised in Imadaté 1974, those of China in Yin 1999). The European species were critically compiled in the book of Nosek (1973, Fig. 2D). Further development in taxonomy was marked by the introduction of numerous additional important characters, such as the chaetotaxy of nota (Rusek 1974) and head (Szeptycki 1980, 1984), the structure of certain mouthpart elements (Bernard 1990), the distribution of tegumental gland openings ('porotaxy'; Szeptycki 1988), and the structure of certain elements of the squama genitalis (Szeptycki 1991). With respect to chaetotaxy, the length, shape and proportions of individual setae and the relative position of certain setae appeared to be important (see Bernard 1990). Despite these improvements in the determination of Protura at the species level, it remains an enormous challenge for taxonomists since few experts can reliably identify these animals.

An invaluable aid for practical work is the 'Catalogue of the World Protura' published in 2007 and complied by Andrzej Szeptycki, one of the most outstanding authorities on the taxonomy of these animals (Fig. 2F). The catalogue is based on a painstaking evaluation of the relevant literature (total of 598 papers). It contains a critical list of all available names for about 72 genera and 734 valid species of Protura occurring in the world, the correct publication dates, verified references to primary descriptions, exact bibliography of all published figures and location of type material. Furthermore, information is given on geographical distribution. In the meantime, 54 additional species have been described; thus currently there is a total of 788 species. The frequency of species description throughout the years (Fig. 9) shows a slow but continuous increase with a peak in the eighties, afterwards the rate decreased (the average of new descriptions for the last decade was 7.3 species per year). A more detailed analysis shows that the description frequency is significantly dependent on the activity of single proturologists, especially when they investigate largely unexplored areas (e.g. the peak in the eighties goes back to the intensive work of Yin and Imadaté in East Asia).

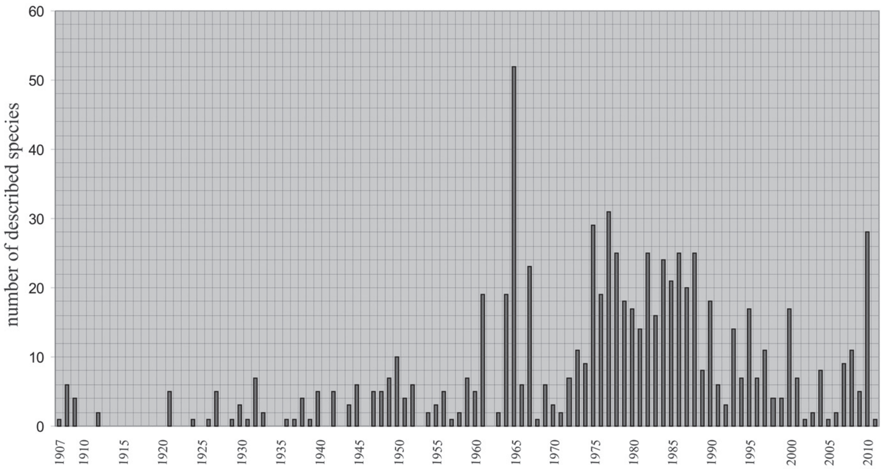


Fig. 9 Number of described proturan species per year (based on Szeptycki 2007 with updates for more recent years).

6. Classification at the family level and intraordinal phylogeny

Berlese (1909) distinguished two families: Eosentomidae and Acerentomidae. Ewing (1936) added the family Protentomidae and Price (1960) the Hesperentomidae. Tuxen (1964) in his comprehensive monograph divided the Protura into two suborders: Acerentomoidea (with the families Protentomidae and Acerentomidae) and Eosentomoidea (with the single family Eosentomidae). This system was adopted by most proturan taxonomists; however, Nosek (1973) after the discovery of the unusual *Sinentomon* (Yin 1965a, b) introduced an additional suborder: Sinentomoidea (with the single family Sinentomidae). Yin (1999), in her monograph of Chinese Protura considered Protura to represent a class of their own. Within this class, she distinguished three orders: Acerentomata with six families, Sinenomata with two families and Eosentomata with two families. Szeptycki (2007) followed the classification of Yin (1999) with some exceptions concerning the order Acerentomata. His classification comprises three orders with a total of seven families: Acerentomata (Hesperentomidae, Protentomidae, Acerentomidae), Sinentomata (Fujientomidae, Sinentomidae), and Eosentomata (Eosentomidae, Antelientomidae).

Initial attempts at a phylogenetic analysis of Protura were made by Tuxen (1963, 1980), who considered especially the mouthparts, the tarsus of the foreleg, the most posterior abdominal leglet and certain structures of the 8th abdominal segment. He clearly pointed out that the Acerentomoidea are more derived than the Eosentomoidea and discussed certain evolutionary trends among proturan families and genera. Another contribution to the elucidation of the intraordinal phylogeny came with the discovery of proturan sperm diversity (Yin 1999, Fig. 10). The most recent and detailed cladistic analysis was undertaken by François (2003a, 2006), who concluded that a well-established reconstruction of the phylogeny of proturans is not possible using the present data. Regrettably, Protura are not known in the fossil record.

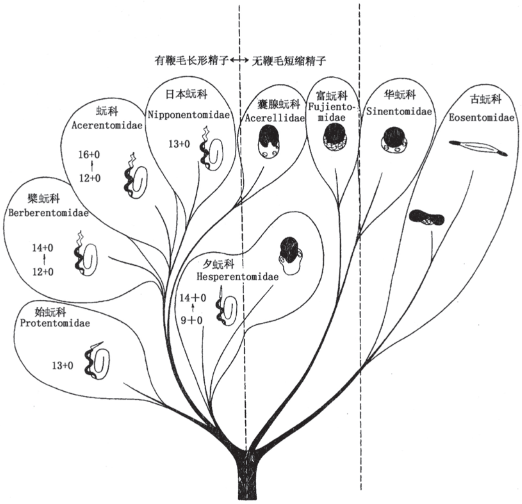


图 68 原尾虫精子演化趋势图解

Fig. 10 Intraordinal cladogram of Protura based on characters of sperm morphology (from Yin 1999).

7. Geographical distribution and ecology

Proturans are distributed in all terrestrial regions and climate zones, except the Arctic and Antarctica; their vertical distribution goes beyond the tree-line. Notes on the occurrence of proturans in distinct habitats are numerous but widely scattered among the ecological literature. However, in these works the proturans are almost never determined to the species level; thus, we know little about the ecological demands and life histories of many individual species. Janetschek (1970) very minutely compiled the older literature with respect to phenology, population densities and zoocoenotics; more recent data has been assembled by Nosek (1975, 1977), Imadaté (1973, 1981), Gunnarsson (1980), Stumpp (1990), and Krauß & Funke (1999). Proturans are found almost universally in localities where decaying organic matter and sufficient moisture are present. They occur abundantly in moist woodland humus, but are also found among dead leaves, in mouldering timber and in direct soil annexes, such as moss and lichens. Regarding their vertical distribution in the soil, they reach their highest abundance in the top soil, especially the moist humus layer (Imadaté 1974, Nosek 1977). The deepest finding thus far is 50 cm under pasture soil (Haarløv 1960). Proturans occur frequently in nests of soil-dwelling small mammals, such as voles and the European Mole (Nosek & Lichard 1962, Nosek 1973, Nosek & Vysotskaya 1976). Several species are known to occur in caves (Neuherz 1974, 1975), but no true troglobiont species has been described.

Numerous literature references concern population densities of proturans in different habitats. Janetschek (1970) compiled data for various European forests and calculated a range of 2,200 to 18,000 individuals/m^2 (most of more recent data fit into this range: see Nosek 1975, Gunnarsson 1980). Stumpp (1990) in 28 spruce stands in Germany e.g. obtained mean abundances ranging from 235 to 15,633 individuals/m^2. An extraordinarily high abundance of 91,400 individuals/m^2 is reported from a windfall area of a spruce forest in southern Germany; this high value was presumed to be related to the amount or vitality of ectotrophic mycorrhiza associated with the fine roots of young spruce trees (Krauß and Funke 1999). Such figures are generally estimations based on small individual soil probes, and one should take into consideration aggregations, patchiness, as well as seasonal fluctuations (see Tuxen 1949, Stumpp 1990). Furthermore, the collection methods used greatly influence the values, and we can assume that actual abundances are considerably higher since proturans are never entirely extracted (compare e.g. Raw 1956, who extracted with a floating method 120,000 individuals/m^2 from a grassland soil, as extrapolated by Janetschek 1970). It should be noted also that the larval stages are weakly sclerotised and probably more sensitive than the adults. Experimental autecological investigations of proturans have yet to be undertaken, except for a study on temperature tolerance (Malmström 2008) in connection with field studies on forest fire ecology (Malmström et al. 2009, Malmström 2010).

Several studies give reports on regional biodiversities, habitat segregation and species co-existence (Nosek 1975, 1977; Imadaté 1973; Stumpp 1990; Nakamura and Hagiwara 2006: Minor 2008). Especially remarkable is the study by Christian and Szeptycki (2004) who investigated the Proturan fauna of the municipal area of Vienna, Austria (encompassing 415 km^2). Samples taken from 6 representative habitat types along an urban gradient contained a total of 42 species. Seven of these were recorded exclusively in parks or artificial habitats, suggesting an unintentional introduction by anthropogenic transport. The highest abundances, species numbers and diversities were found in colline deciduous forests, with a maximum of 23 (!) syntopic species at a single sampling site in a *Quercus pubescens* forest stand. The deeper reason for this extraordinarily high local proturan diversity probably lies in the great habitat diversity of the area and the location of the city of Vienna at a biogeographic intersection.

Proturans may potentially serve as indicators for certain ecological conditions in the soil. Some reports show that the abundance of proturans may reflect an association with fungal

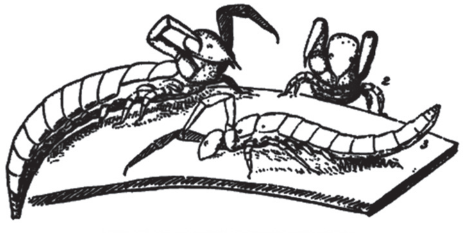


Fig. XIV. — 1, 2, *Acerentomon*; 3, *Eosentomon*.

Fig. 11 Early woodcut of Protura in living attitude (from Berlese 1909).

communities and the presence of mycorrhiza development in the soil (Stumpp 1990, Minor 2008). Furthermore, the literature contains scattered information about the impact of soil liming and pesticides on proturan populations (Hågvar 1984, Alberti et al. 1989, Stumpp 1990).

8. Life History and Development

The life history of proturans continues to hold many secrets despite long and intensive studies by numerous scientists. Till now, no one has succeeded in breeding these animals over generations. The best results stem from the research team of Ryuichiro Machida from the Tsukuba University in Japan (Fig. 2I), who recounted his methods and experiences in rearing of Protura in a separate publication (Machida and Takahashi 2004).

Feeding biology: In the past, some authors assumed that Protura have a predatory diet (e.g. Handschin 1929). This view was probably instigated by the famous figures of Berlese in which these 'bestioli' are given a threatening appearance (Fig. 11). Other authors assumed that proturans feed on decaying plant material (Ewing 1940, Paclt 1956). The first detailed observations on the feeding behaviour of proturans were made by Sturm (1959). He observed *Acerentomon gallicum* (misidentified as *Acerentomon doderoi* according to Tuxen 1961) feeding exclusively by sucking on the outer coat of ectotrophic mycorrhiza on oak and hornbeam roots. He noted further that *Eosentomon transitorium* sucked on both mycorrhizoid and free soil hyphae. His accurate description gives an outline of the sucking behaviour, which can last for an hour. Astonishingly, the animals can survive up to seven weeks without food. More recently, mycorrhiza feeding was also observed in cultures of *Baculentulus densus* (Machida and Takahashi 2003, see Fig. 3) and in a study on feeding preferences of *Nipponentomon nippon* (Mizushima 2004). Indirect support for ectomycorrhizal feeding of proturans comes from tree girdling experiments in conifer forests in northern Sweden (Malmstöm & Persson 2011). The authors assumed that a decrease in the population density of these soil arthropods after a year, was due to the fact that girdling of the trees stopped the flux of carbohydrates to the roots, thereby inhibiting the growth and long-term survival of associated fungi. Whether all proturan species feed exclusively on mycorrhiza remains to be seen. Remarkably, some collecting sites are clearly described as humid with decaying plant debris in the absence of fungi which build mycelia (e.g. Prell 1911). Likewise, new data show no significant differences in population densities between mycorrhiza habitats and adjacent soil habitats (Sawahata and Narimatsu 2005).

Behaviour and Physiology: Generally, very little is known about proturan behaviour. Using high-speed cinematography, Tichy (1988) studied the various walking patterns in Protura. Special reference is given to the front leg pair which moves largely independent of the middle and rear legs. Generally, the front legs are held upward like antennae. If they are put to the ground they seemingly have no great efficiency in locomotion but are used rather to palpate the surface. Information thus can probably be gathered via the numerous mechano- and chemoreceptors located at the tip of the front legs. The sensory physiology of proturans is still unstudied, only ultrastructural data has provided hints to the function of the sensory organs. Balkenhol (1996) studied the activity range of *Acerentomon nemorale* and recorded their locomotory activity in laboratory experiments.

Likewise, little is known about their interactions with other soil animals and potential predators. Recently, the defensive behaviour of *Acerentulus* was described, which used a sticky glandular secretion discharged from the 8th abdominal segment against a collembolan

(Hansen et al. 2010, videos: Bernard 1996, Hansen 2006). Additionally, a new species of parasitic fungi, *Hirsutella proturicola*, was recently described after it was isolated from *Baculentulus densus* (Kurihara et al. 2009).

Reproduction: No observations of sperm transfer in Protura have been published so far. It is still unknown whether Protura transfer the sperm by copulation, or indirectly, as in all other groups of apterygotan insects (review: Schaller 1971). Ewing (1940) believed to have witnessed copulation in *Yamatentomon barberi*. He described a male sitting on a female with its abdominal tip bent downward. The individuals were unintentionally disturbed but showed maximally everted genital armatures; therefore, copulation seemed conceivable to him. However, most scientists assume that Protura perform indirect sperm transfer. Ultrastructural analyses of sperm yielded a high diversity of sperm types (Baccetti et al. 1973, Dallai et al. 1989, 1990, 1992, 2010a, 2010b, Yin & Xué 1993). Especially the presence of a flagellate sperm in many species points toward indirect sperm transfer via spermatophores.

Development*:* The chorion of the minute proturan eggs may be smooth or with numerous protuberances functioning as a plastron (Bernard 1976, 1979, Larink & Bilinski 1989, Fukui and Machida 2006). Recently, proturan embryonic development was described for the first time in *Baculentulus densus* (Machida & Takahashi 2003, Fukui and Machida 2006, Machida 2006). On the one hand, it shares many features with entognathous hexapods, such as the development of a long-germ embryo, a simple blastokinesis involving only minor changes in posture, formation of a dorsal organ, and the fact that both embryo and serosa are involved in the secretion of the cuticular egg envelope. On the other hand, the serosa is able to differentiate into body wall – a feature utterly different from other hexapods, but common to myriapod and crustacean embryos. The authors succeeded in providing initial data on the development of the mouth folds in Protura, which seem to be derived from the mandibular, maxillary and labial terga. The postembryonic development likewise differs from other hexapods. Anamorphosis was already described by Berlese (1908a, 1909). Our knowledge of the postembryonic development in proturans is based mainly on Tuxen (1949, 1950, 1960, 1964), François (1960) and Szepticky (1986) (Fig. 12). The prelarva hatches with nine abdominal segments (Bernard 1976, 1979). It is a resting instar which apparently never feeds since its mouthparts are underdeveloped (Imadaté 1980). Not every moult can be linked with a gain of additional abdominal segments, but at the stage of the *Maturus junior* all abdominal segments are present, while the genitalia have yet to develop. Males of Acerentomidae undergo a preimaginal stage, in which the genitalia are not fully developed and an additional moult is required to reach the adult stage (Shrubovych & Rusek 2010). Whether adult animals continue to moult as described for other primarily wingless hexapods is a point of discussion; however no moulting of adults has been observed so far.

9. Open problems and future directions of research

The vast majority of literature dealing with Protura has a taxonomic focus. Despite much progress, Szeptycki (2002) assumed that only 10% of all extant species have been described. The detection of a number of additional characters for taxonomy during the last decades promoted the taxonomic work significantly. Nevertheless, species determination by morphological characters remains an extraordinary challenge. Therefore, the development of molecular methods for taxonomic research should be an important task in the near future (e.g. no successful DNA barcoding has yet been achieved). One tricky problem remains: positively identifying these tiny arthropods at the species level requires clearing and slide

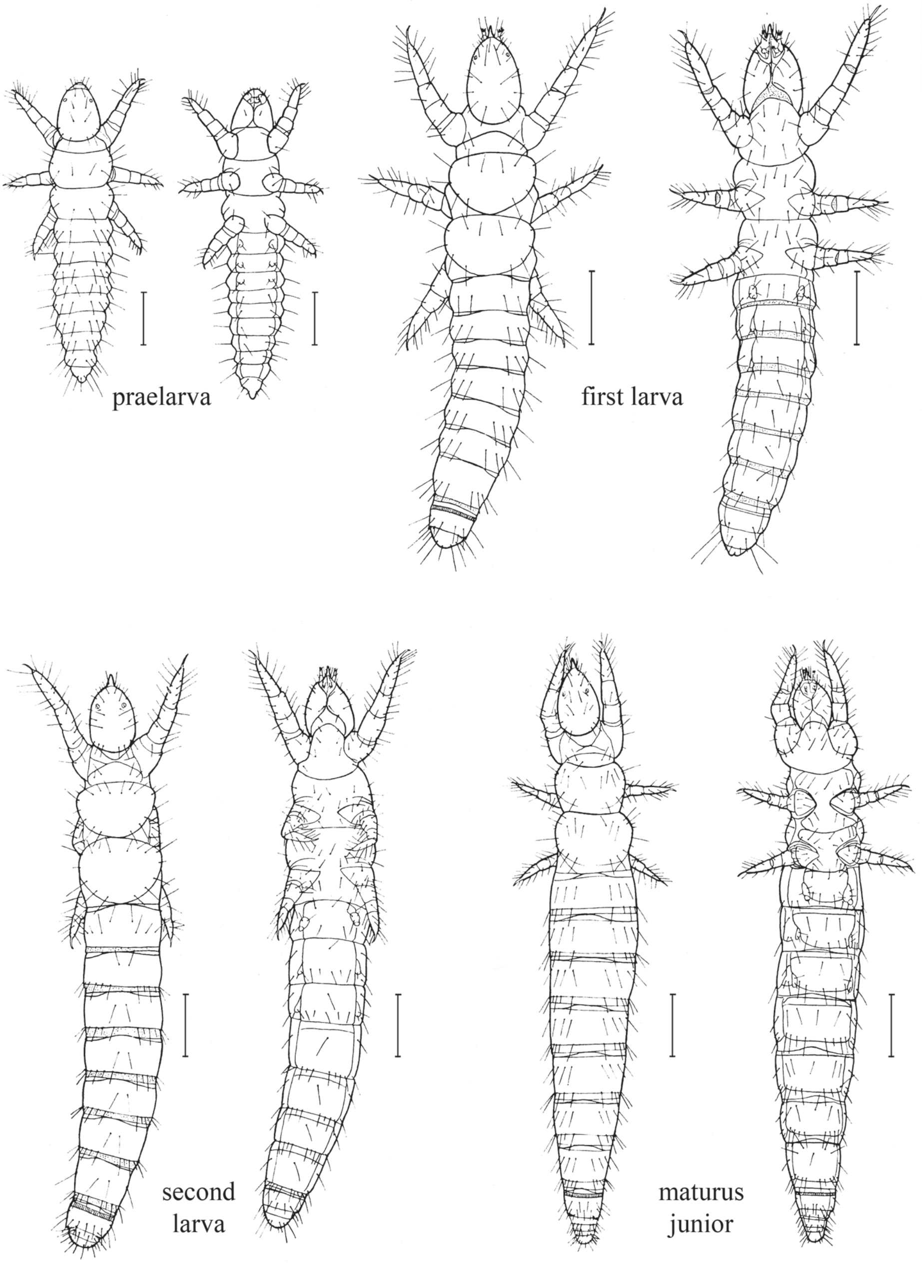


Fig. 12 Postembryonic development of *Acerentomon affine* – the prelarva hatches with 9 abdominal segments, the remaining abdominal segments are added bit by bit after different moulting phases (from Nosek 1973, after François 1960)

mounting the specimens which renders them useless for molecular analyses. Conventional DNA extraction entails complete destruction of the whole specimen. The resulting dilemma for molecular research in proturans was recently overcome by applying of a non-destructive extraction method allowing both molecular analyses and species determination on the empty exoskeletons (see the contribution of Böhm et al. in this issue). The problem with species determination concerns many other topics, especially in the area of ecology. In this context, the extraordinary high species diversity of 23 proturan species recorded from a single sampling site (Christian and Szeptycki 2004) makes us terribly aware of how difficult and time-consuming ecological studies of Protura at the species level actually are. The morphology of Protura has been generally well studied but re-examination of details would be rewarding, especially using new methods such as 3D reconstruction from serial sections and microCT. Moreover, the development of various organ systems and structures remains largely unresolved. Although, comparative morphological studies within the Protura are rare, they provide the necessary basis for development of a phylogenetic system. Regarding life history, undoubtedly the most exciting task would be the discovery of the mode of sperm transfer. In addition, much work remains to be done on the feeding ecology, since the mouthparts of individual species show distinct differences. Little is known about another wide area of research: the autecology of single species.

The present report on the status quo of our knowledge of Protura admits that, despite considerable progress in research and persistent effort over the past hundred years, these fascinating and unusual microarthropods have kept an amazing number of secrets to themselves.

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