Phylogeny of the Symphyla (Myriapoda)

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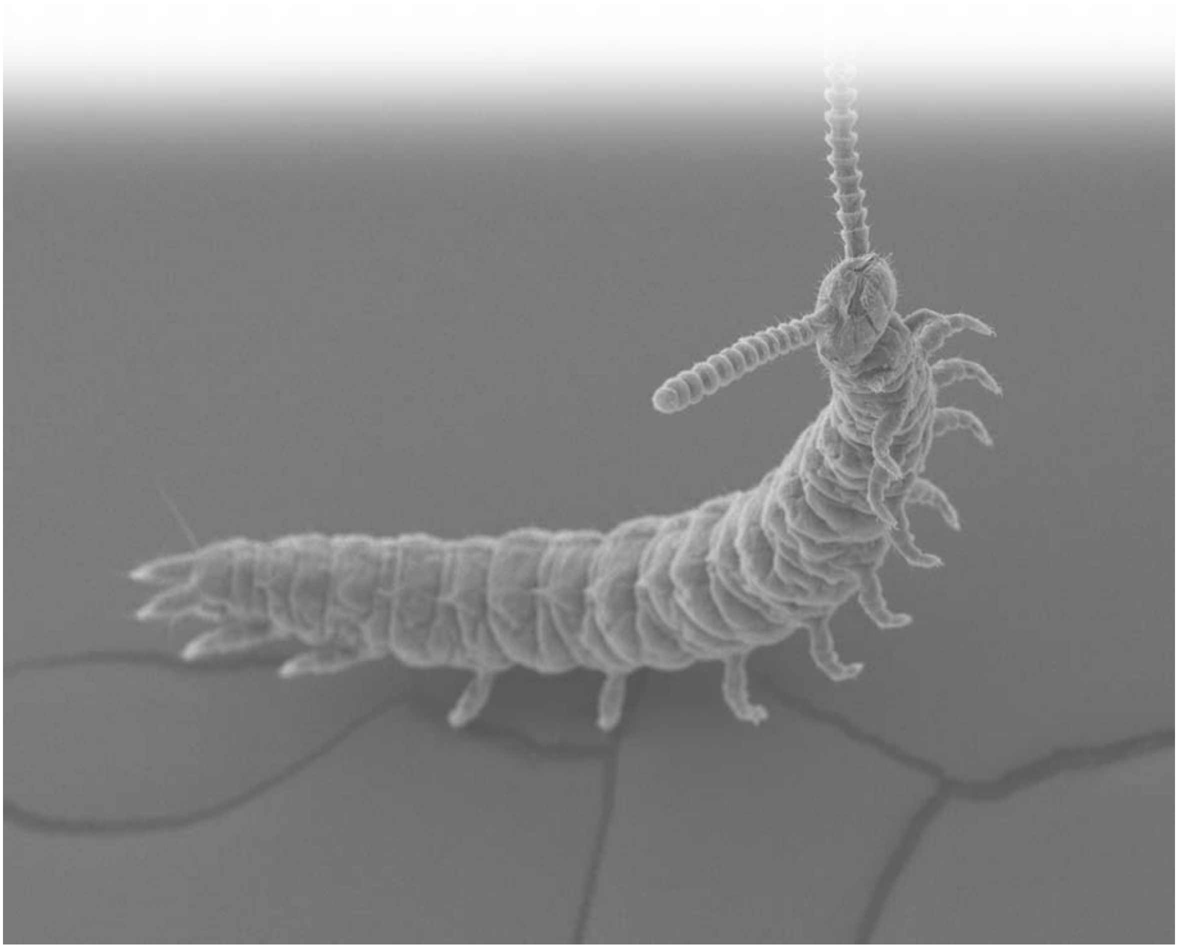

Scolopendrellopsis (Symphylellopsis) subnuda

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Contents

General Introduction

The Symphyla are the smallest subgroup of the Myriapoda. They are minute centipede-like animals (with an average length of 1-8 mm), representatives of the soil fauna. Their soft, flexible and unpigmented body is suited to subterranean life in soil (Verhoeff 1934). They also present other typical adaptations to subterranean life habits, such as the lack of eyes, the presence of long monoliform antennae and numerous mechanoreceptors, chemoreceptors and hygroreceptors. However, they can leave soils, and sometimes occur in leaf litter, under bark and moss or inclusively on trees in tropical regions (Adis & Scheller 1984). Moisture seems to be the most important factor determining their habitat (Waterhouse 1968).

They are presumably a geologically old group (Scheller & Adis 2002). Their minimal age has been dated from the mid Silurian, about 430 million years (Edgecombe 2004), although the only fossil symphylans are known from amber with an age of 25-50 million years (Poinar & Edwards 1995, Scheller & Wunderlich 2004). Their biogeography agrees with their old estimated age, since they have a worldwide distribution which varies among the different genera. Some seem to have a typical Gondwanan disjunctive distribution (table 1). Although the fact that symphylans can be found throughout the world, they have been relatively neglected in biogeographical studies, and one of the main reasons is their complex taxonomy (Scheller & Adis 2002).

Like all myriapods, their body is divided into only two regions: head and trunk. Contrary to the other subgroups (chilopods, diplopods and pauropods), the symphylans have a relatively uniform morphology among their representatives. The head is well demarcated from the trunk and carries a pair of long antennae with many segments and a pair of Tömösváry's organs – or postantennal organs – which are probably hygroreceptors (Haupt 1971). In the middle of the dorsal part, the head presents a central rod, a longitudinal thickening in the integument. There are three pairs of mouthparts: one pair of mandibles and two pairs of maxillae, the posterior pair of which is fused to a functional labium that continues backwards by a pair of proximal arms (*sensu* Snodgrass 1950). Behind them, a pair of cervical sclerites continues onto the ventral part of the first trunk segment (Snodgrass 1952). The trunk comprises 14 segments and bears 12 pairs of legs in the adult stage (Scheller 2005).

The two last segments are devoid of legs. A pair of conical cerci – or spinnerets (*sensu* Snodgrass 1952) – with spinning glands are present at the end of the last segment, as well as one pair of sense calicles – trichobothria or bothriotrichs (*sensu* Kraus & Kraus 1994). The dorsal side has 15-24 tergites – or scuta (*sensu* Hansen 1903) – while the ventral side presents sclerites reduced to small plates to which paired coxal sacs and styli are associated. The first pair of legs is shorter than the following ones, and often completely reduced.

General knowledge of this group is still incomplete and the main reason is that research on Symphyla has been restricted to questions on the affinities of this group (Scheller 2005). Since Scopoli (1763) described the first symphylan species, they have formerly been included in the chilopods. Ryder (1880) pointed out that they have as many similarities to insects as they do to myriapods, and suggested that perhaps they represent "the last survival of the form from which insects may be supposed to have descended". Accordingly, he named the new group Symphyla (which essentially means "group-linking") "in reference to the singular combination of myriapodous, insectean and thysanurous characters which it presents" (Ryder 1880). Since the erection of the "well named" new group (*sensu* Hansen 1903 and Verhoeff 1934), the Symphyla have represented a phylogenetical enigma within Arthropoda and have been proposed as sister group of varying taxa (see further details in chapter 3). Currently, some tend to confirm that the Symphyla together with Diplopoda and Pauropoda form a monophyletic group named Progoneata, which is traditionally united with Chilopoda in a monophyletic Myriapoda (e.g. Edgecombe 2004, Edgecombe & Giribet 2002). Nevertheless, the phylogenetic significance of the progoneate condition (anterior position of the genital opening) in Symphyla has been questioned (Tiegs 1945, Tiegs & Manton 1958). In addition, recent molecular studies assign them to different positions within Myriapoda (e.g. Gai *et al.* 2008, Podsialdlowski *et al.* 2007, Regier *et al.* 2005) or inclusively very basal to Arthropoda (e.g. Mallat & Giribet 2006, Reumont *et al.* 2009).

The majority of the published studies on the Symphyla focus on a few species, usually of the genera *Scutigerella* and *Hanseniella.* Both genera represent the largest and most common symphylan and are, therefore, the easiest representatives to obtain and to study. For example, some species of these genera cause pests to growing crops both in fields and hothouses (e.g. Berry & Robinson 1974, Morais & Silva 2009). Consequently, knowledge on these two genera, especially on the species *Scutigerella immaculata*, is considerably broad: general morphology (e.g. Michelbacher 1938, Packard 1881), mouth parts (e.g. Snodgrass 1950), musculature and endoskeleton (e.g. Manton 1964, Ravoux 1975), ultrastructure of sensorial organs (Haupt 1970, 1971), endocrinology (e.g. Juberthie-Jupeau 1961, 1979, 1980), morphology of spermatozoa (Dallai & Afzelius 2000), reproduction (Berry 1972, Juberthie-Jupeau 1963), embryology and postembryological development (Tiegs 1940, 1945), ecology (e.g. Berry & Robinson 1974, Edwards 1958, 1959, 1961), DNA mitochondrial and nuclear sequences (e.g. Podsialdlowski *et al.* 2007, Regier *et al.* 2005), etc.

The Symphyla comprise about 200 species, classified into two subgroups with taxonomic rank of family: Scutigerellidae, with 5 valid genera, and Scolopendrellidae, with 9 genera (table 1) (Scheller 1982, Scheller & Adis 2002). The Scutigerellidae are usually larger (about 4-8 mm long) and more robust. All of them have 15 thick dorsal scuta and are swift runners. In contrast, the Scolopendrellidae are usually smaller (about 1-4 mm long) and slender. Their scuta are thin and have either partly long, pointed, posterior prolongations or are reduced to small oval plaques, and their number varies among the different genera (Scheller 1982). The more heterogeneous morphology and their size have hampered the study of the Scolopendrellidae and only a few studies have addressed the biology of this subgroup in a non-exclusively taxonomical view. Verhoeff (1934), Ribaut (1931) and Ravoux (1962) are the only authors who have studied different aspects on the biology of Symphyla including representatives of Scolopendrellidae. These researchers considered some scolopendrellids, those which present the highest number of scuta, as the most primitive symphylans and proposed a gradual reductive trend in the evolution of the different genera. This view has not been accepted by Tiegs (1940) and Manton (1977), who claimed that the most primitive state is the lowest number of scuta in Scutigerellidae.

Genus	Species	Distribution
Family **Scutigerellidae**		
Scutigerella	about 35	Subcosmopolitan, mainly in the north temperate zones
Hanseniella	about 80	Subcosmopolitan, mainly in the tropics and warm temperate zones.
Millotellina	9	Africa, Madagascar, Reunion, Ceylon, New Guinea and Australia (East-Gondwanan distribution).
Scolopendrelloides	3	South-East Asia, Australia
Scopoliella	1	North America
Family **Scolopendrellidae**		
Scolopendrella	1	Europe
Symphylella	about 40	Subcosmopolitan
Scolopendrellopsis	15	Subcosmopolitan
Ribautiella	9	Africa and South America
Geophilella	2	South Europe and North America
Parviapiciella	1	Mediterranean region and Canary Islands
Remysymphyla	3	Minorca, Morocco, Madagascar, Reunion, Ceylon (East-Gondwanan distribution).
Neosymphyla	1	Ghana (Africa)
Symphylellina	1	New Caledonia
Total species	about 200	

Table 1. Genera of Symphyla with number of species and inferred distribution, based in citations in the literature (for summarised information, see Hansen 1903, Naumann & Scheller 1977, Rochaix 1955, Scheller 1961, 1971, 1982, 1986, 2004, 2007; Scheller & Christian 2000).

The phylogenetic interrelationships among the symphylan genera are completely unclear, since no cladistic analysis has yet been performed to unravel their natural history. It is likely that the lack of understanding of their phylogeny is the reason for the uncertain position of this group among the arthropods. It is known that topologies of higher level phylogenies can be affected by the taxon sampling (Bininda-Emonds *et al.* 1998). To date, it has never been tested whether the *Scutigerella* and *Hanseniella* species chosen for morphological and molecular comparisons thus far, represent an accurate taxon sampling for this group. Likewise, this could also be the reason why some characters of these representatives have been difficult to interpret and have been frequently categorized as "particularly refined" or "aberrant" (e.g. Snodgrass 1950, Klass & Kristensen 2001, Mallat & Giribet 2006, Reumont *et al.* 2009). In addition, some genera of both families are practically unknown, especially those which have a restricted distribution area (see Table 1).

The objective of the present study is a first approach to clarify the phylogeny of the Symphyla. For this purpose, the morphology of 15 species belonging to 7 genera is studied in detail. In order to obtain phylogenetical information of character-sets independent to the taxonomy, the internal anatomy of the head of 5 species belonging to different genera has been also investigated. This provides the first data of the skeletotmuscular system of scolopendrellid species, what contributes in having a broader view on the anatomy of the Symphyla for comparisons with other myriapod groups. Finally, the information generated in this study is compiled in a data matrix to perform cladistic analyses. The resolution of the shortest trees enables to select the most appropiate representatives of this group for comparisons with other taxa within Myriapoda and Arthropoda. Furthermore, the knowledge of the phylogeny throws light to understand the evolution of the Symphyla and to reconstruct the hypothetical symphylan ground pattern.

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Chapter 1

Contribution to the taxonomy of the European Symphyla

with new distributional data.

Introduction

The Symphyla have a worldwide distribution as inhabitants of moist soils. They are present in almost all of Europe, and the symphylan diversity increases in genera and species towards the south region of the continent (Scheller 2009). Although our knowledge of the European fauna has recently grown for most of animal groups (e.g. Bisby *et al*. 2009, Gardi *et al*. 2009; Fernández 2006), previous biogeographic studies have always neglected the symphylans for reasons of their complex taxonomy (Scheller & Adis 2002).

Taxonomy of the Symphyla is based mainly on body size, number and morphology of scuta, morphology of the first pair of legs, size of styli, morphology of cerci and sense calicles, and shape of the central rod of the head for differentiating among genera, whereas specific determination is based mainly on the chaetotaxy of the head, antennae and scuta, and on variation of small structures (Domínguez 1992; Edwards 1959a, b; Scheller 1961).

The main problem regarding determination is that many of the diagnostic characters are only partially understood and difficult to see under a light microscope. Turner and Edwards (1974) recommended the utilization of scanning electron microscopy (SEM), since it provided a clearer observation to differentiate symphylan species. They stressed the importance of SEM as a solution for the problem of recognizing all taxonomic characters unambiguously.

Another reason for the lack of knowledge on the symphylan distribution is the difficulty in collecting them. Despite their vast distribution, their abundance in soil is normally very low compared to other soil animals, frequently occurring alone or in small aggregations (Lagerlöf & Scheller 1989, Reeve & Berry 1977). An additional problem is that in order to collect symphylans, it is necessary to extract them from a large quantity of soil. This is particularly relevant for specimens of the family Scolopendrellidae, which are smaller than the Scutigerellidae and more commonly found in deeper levels of the soil (Domínguez 1992, Mas 1985, Scheller & Adis 2002).

Through the compilation of a great deal of material, the present study aims to contribute to a better understanding of the taxonomy of European symphylans using new observational techniques. In addition, the study of different species brings about new data on the distribution of the Symphyla in Europe, with special focus on Spain.

Material and methods

1. Material studied

Specimens examined in this study were extracted from soil samples taken during field trips, principally to Spain, and provided by collaborators from different places of Europe. Additional specimens stored in 70% ethanol were loaned from several collections. The search for specimens has focused in Spain, specially the north-east region, since this country present the highest diversity in both genera and species of Symphyla in Europe (Scheller 2004) and the occurrence of different species is relatively well documented, in comparison with other parts of the continent (Mas 1985, Domínguez 1992).

Loaned material:

- Specimens from Catalonia (north-east Spain) donated by Antoni Serra and Eduardo Mateos (Universitat de Barcelona). This material was collected at Font Groga (Barcelona, 13.02.1997), Taradell (28.05.2004), Fageda d´en Jordà (19.11.2004), Canyamars (Dosrius, 15.03.2005), Sant Llorenç Munt (06.1997), Castellsapera (24.02.1998) and Serra de l´Obac (13.03.2003).
- Additional specimens from Catalonia (north-east Spain) donated by Francisco Yagüe (Museo Nacional de Ciencias Naturales, Madrid). This material comprises specimens from Plana San Vicente (num 20.06/30), Montaguit (num 20.06/31), Tamariu (num 20.06/37), Mataró (num. 20.06/59), Llafranc (num 20.06/87) and L´Estartit (num 20.06/88), and was collected between 1957 and 1961.
- Specimens from Yepes (Toledo, Plateau of Castile, Spain) collected by José Carlos Simón (Universidad Autónoma de Madrid) in spring 2007.
- Specimens from Jábaga (Cuenca, Plateau of Castile, Spain) collected by María José Luciáñez (Universidad Autónoma de Madrid) in a burnt forest of *Pinus nigra* in June 2005.
- Specimens from Bértiz and Funes (Navarra, north Spain) donated by Arturo H. Ariño (Ecology Museum of Zoology, Universidad de Navarra).
- Specimens from Xistral Mountains (960m, 43º82'N 07º57'W, Galicia, north-west Spain) and Nob End (Bolton, United Kingdom) donated by María Jesús Iglesias Briones (Universidad de Vigo).
- Specimens from Ischia (Italy) collected by Markus Koch, specifically in San Montano (40º45'N 13º52'E) and Monte Epomeo.
- Specimens from Bulgaria and Georgia donated by Pavel Stoev (National Museum of Natural History of Sofia). The specimen from Bulgaria was collected 16.07.2006 in the cave Potoka (1150m, 41º34.890'N 24º48.203E, Dolno Vlahovo, Western Rhodopes Mountains), under stones in clay by B. Petrov, and the one from Georgia, on 22.07.2006 in Imereti (542m, 42º16'N 42º57'E), in a broad-leaf forest by S. Lazarov and P. Stoev.

The taxonomic studies were completed with specimens of *Scolopendrellopsis (Scolopendrellopsis) microcolpa* (Muhr, 1881) from Görlitz (Germany) donated by H. Stöhr (Museum für Naturkunde Görlitz, Germany: MfNG) (specimens num. 10548 and 9449), and *Hanseniella agilis* Tiegs, 1939 from Australia donated by Georg Mayer (University of Melbourne).

2. Field trips and soil fauna extraction

Specimens from La Rioja (north Spain) were extracted in the Environmental Sciences Centre of the CSIC (Spanish National Research Council) in 2005 during a study on bioindicators from different cropping systems (Gutiérrez *et al.* 2007) undertaken in the Oja-Tirón Valley, specifically in the localities Bañares, Leiva, San Torcuato, and Tormantos.

Field trips were undertaken to Catalonia (north-east Spain) and to Minorca (Balearic Islands, Spain) (22.-27.02.2007), due to the high diversity of Symphyla documented in these places (Domínguez 1992, Juberthie-Jupeau 1961, Mas 1985). During the first sampling in Catalonia (23-28.11.2006), soil samples were taken at the Collserola Park (Barcelona, 366-445 m, 41°25'N 02°06'E) and in Berga in a *Fagus sylvatica*-woodland near to the Queralt Sanctuary (about 1185 m, 42°06'N 01°49'E). During the second sampling in Catalonia (05-12.04.2008), samples were taken in Gironella in a *Quercus ilex*-wodland (560m, 42º01'N 01º52'E), in La Pobla de Lillet in a *Salix*-wodland on the bank of the Llobregat river (847m, 42º14'N 01º58'E) and in a *Fagus sylvatica*-woodland near to the Falgars Sanctuary (about 1240m, 42º13'N 01º56'E), in

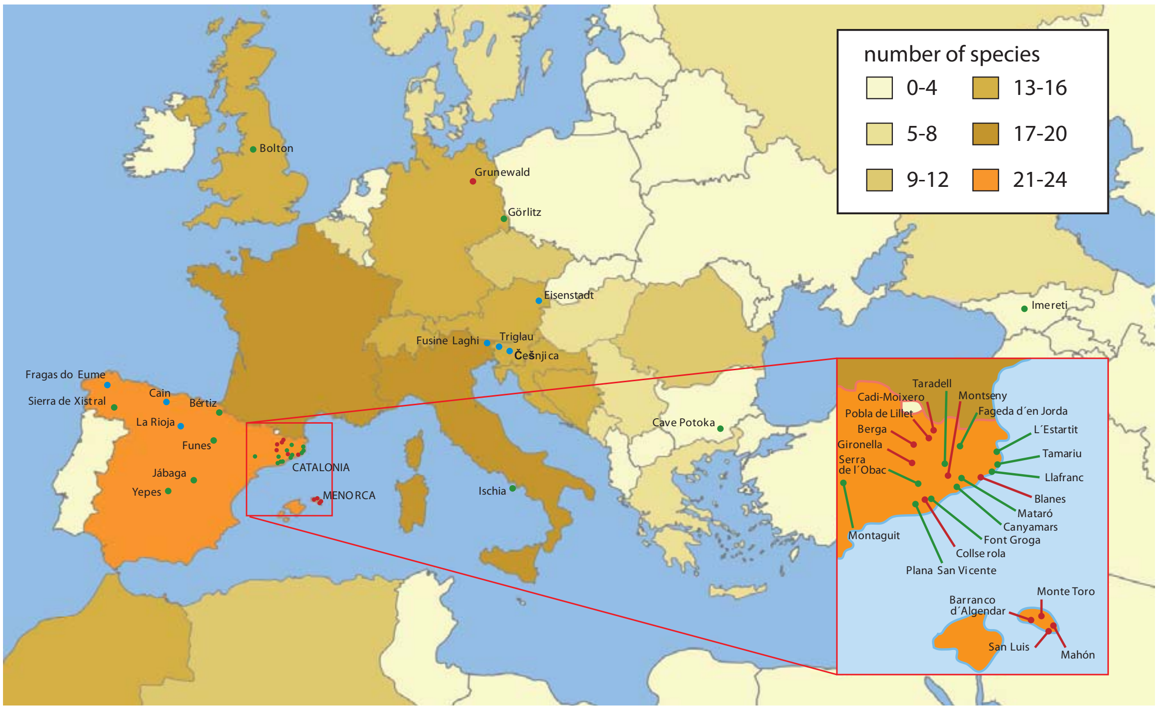


Fig. 1. Origin of the studied material shown on a cartogram of Europe and North Africa. Red points are localities of field trips; blue, origin of provided soil samples; green, localities of loaned material. Colours of countries represent the number of cited species in each (see legende). Data obtained from Fauna Europaea (Scheller 2004), and compiled for North Africa and Turkey from Aubry & Masson (1952, 1953) and Scheller (1990).

several places of the Cadí-Moixeró Natural Park (1230-1950m 42º15-16’N 01º57-58’), in the Montseny Natural Park (495m, 41º46’N 02º22’E) and in Blanes next to the CSIC-laboratory (100m, 41º40’N 2º47’E).

In Minorca, soil samples were taken in Mahón southern outskirts, under *Ligustrum vulgare* (61 m, 39°52’N 04°15’E); in San Luis, under *Quercus ilex ilex* (51 m, 39°50’N 04°15’E); in Monte del Toro, under *Pinus halepensis* (about 300 m, 39°59’N 04°06’E); and in Barranco d´Algendar, in a forest of *Quercus ilex ilex* and *Salix* sp. (32-70 m, 39°58’N 03°57’E).

In Berlin (Germany), soil samples were taken in the Grunewald (40m, 52º27’N 13º15’E), in an *Acer platanoides*-woodland during different samplings in the spring and summer of 2007 and 2008.

Soil samples of about 500g were taken at random intervals with a shovel at a depth of 10-15cm. The total soil quantity was about 6kg in the Catalonia first sampling, 33kg in the second one and about 18kg in Minorca. Soil fauna was extracted for about 2 weeks in the laboratory using a Kempson apparatus (modified according to Adis, 1987), which works on the same principle of the Berlese funnels, taking advantage of the vertical migrations of soil arthropods as a reaction against light and dryness.

Additional soil samples from Austria, Italy, Slovenia and north Spain were kindly provided by collaborators and specimens were extracted through the same procedure. Samples from Eisenstadt (255m, 47°51’N 16°31’E, Austria) were taken 24.05.2008 by Alexander Gruhl. Samples from Češnjica (Slovenia) were taken in a *Picea abies*-woodland 02.12.2007 by Eva Varl. Samples from Triglau National Park (Slovenia) and Fusine Laghi (Italy) were taken in a *Picea abies*-woodland 13-15.03.2007 by Belén Benito. Samples from Cain (490m, 43°12’N 4°54’W; Asturias, north Spain) were taken 07.06.2008 by Fernando Domínguez and Irene Camacho. Samples from As Fragas do Eume Natural Park (Galicia, north-west Spain) were taken in July 2006 by Francisco Paños.

Altogether, about 580 specimens were obtained and studied using four different microscopical techniques. For species determination, keys by Domínguez (1992), Edwards (1959a, b) and Scheller (2006) were used.

3. Microscopy

The material was studied by light microscopy, fluorescence microscopy, confocal laser-scanning microscopy (cLSM) and scanning electron microscopy (SEM).

Specimens from La Rioja (Spain) were fixed in 70% ethanol and subsequently stored in lactic acid and warmed for 5-10 min to clear them. They were then embedded in Hoyer’s fluid (Kraus 1984) and studied by Normaski interference contrast with an Olympus BX50 light microscope. Loaned specimens from Funes (Navarra, Spain) had already been mounted for light microscopy.

Specimens extracted from soil samples were fixed in Bouin´s fluid (modification according to Duboscq-Brazil) at room temperature and stored in 70% ethanol. Some specimens were observed directly under a cover slip with an Oympus BX61 fluorescence microscope using ultraviolet illumination and with a cLSM. For cLSM imaging, specimens were mounted on slides directly in 70% ethanol or using CitiXour Glycerol solution. Confocal image stacks were taken on a Zeiss LSM 410 and a Leica TCS SPE, using the green laser (543 nm) on a 70 % power setting. ImageJ with WCIF plugin bundle was used to process digital image stacks and to generate projection views. Three-dimensional inspection was done by volume rendering using AMIRA 3.0 software (Template Graphics Software).

For scanning electron microscopy, specimens in 70% ethanol were dehydrated in a graded series of ethanol up to 100%, critical-point-dried with carbon dioxide in a Balzer CPD 030 and subsequently sputter coated with gold using a Balzer Union SCD040. Taxonomic characters of the specimens were examined in a FEI Quanta 200 SEM at 20 kV.

4. Terminology

Terminology used for the traditional characters in symphylan taxonomy follows Scheller´s descriptions (e.g. Scheller 1961, 1986; Scheller & Adis 2002). For a matter of convenience the term “scuta” is used rather than “tergites” (explication in Chapter 3). Terminology of other structures follows Snodgrass (1952). In order to avoid possible confusion in recognition the sternal plates of the second trunk segment (of which the posterior ones are considered as modified coxal sacs; Snograss 1952), the terms “anterior and posterior sternal plates” are preferently used.

Results and discussion

1. Resolution of different microscopy methods.

Taxonomic characters presented a lower resolution in light microscopy than the other used techniques (Fig 2A,B). The same problems that Turner & Edwards (1974) pointed out were present in these observations. The main taxonomic characters are difficult to see because appropriate mounts are difficult to make. In addition, certain characters used in determinations were affected by factors such as the type of mounting, pressure of the cover slip and position of the specimens. The number of scuta was difficult to count in the transparented specimens and nearly impossible in specimens contracted during the fixation.

Fluorescence microscopy increased the resolution of these characters, due to the natural fluorescence of the arthropod cuticle (Fig 2C,D). However, observation of three dimensional structures, such as the head and the surface of the cerci, was difficult.

This problem was resolved using cLSM imaging (Fig 2E), since 3D models are generated (Fig 2F) based on the principle of optical sectioning (Kaus *et al*. 2003). As it has already been observed in other arthropods (Klaus & Schawaroch 2005, Lee *et al*. 2009), the resolution of the volume renderings has resulted in sufficient and inclusive observations of the chaetotaxy of the scuta were possible (Fig. 2G). Species determination through fluorescence microscopy and cLSM enabled the utilisation of the material for further studies about the internal anatomy. However, some characters such as the chaetotaxy of the legs were difficult to observe under these techniques.

SEM observation has proved the fastest and easiest way to determine the species (Fig. 3-8). As Turner and Edwards (1979) pointed out, the great depth of focus with all magnifications and three-dimensional manoeuvrability of the specimens provide a greater resolution. In addition to this, many characters can be studied with the same specimen. This last advantage was decisive in the present study, since only a few specimens were obtained per species. For all these reasons, most of the specimens were determined using this technique.

2. List of species with remarks on the taxonomy

Since there are no up-to-date extensive studies of the symphylan species by SEM, additional characters in the taxonomy were examined, and proved to be as adequate as the traditional ones for genus determination. From the publication of the first key to the genera of Symphyla by Edwards (1959b) to the most recent reviews on the systematics of this group (Domínguez 1991, Scheller 1961, 1986; Scheller & Adis 2002), the main diagnostic characters have been the number and morphology of the scuta. These characters are decisive, but sometimes problematic. Symphylans present an elongated body which is normally fixed in different positions in the mounts, sometimes not presenting all scuta for the observation. In addition, the number of the scuta is lower in immature specimens. The head and the first trunk segments or the cerci and the last segments are normally visible in all specimens, independently of the position. It has been observed that different genera present variation in several characters belonging to these parts of the body. The following remarks on the taxonomy focus especially on these character sets which are easy to observe through SEM, and illustrated in the figures 9-17. The study of this variation among different species has lead to a new identification key proposed for the European genera of Symphyla.

In total, 15 symphylan species were identified. Data on their distribution are sorted in the following by locality in the order described under Material and Methods. Juvenile stages are indicated with their corresponding number of leg pairs in parentheses.

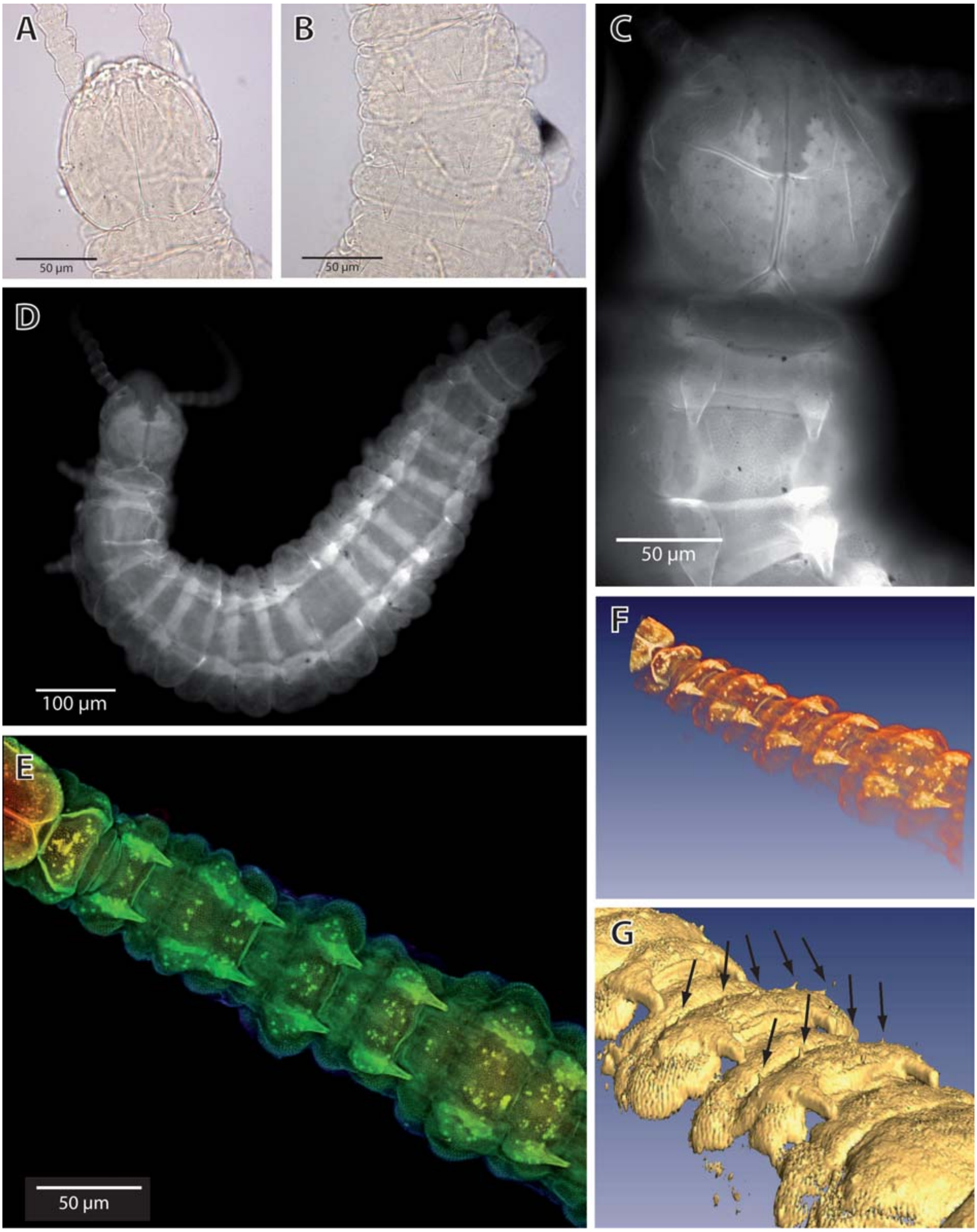


Fig. 2 Symphylan specimens belonging to *Scolopendrellopsis (Symphylellopsis)* under different microscopic techniques. A and B, transmitted light bright-field microscopy. C and D, fluorescence microscopy using ultraviolet illumination. E, F and G, cLSM: E, maximum intensity projection; F, 3D model generated in Amira; G, volume rendering showing chaetotaxy on scuta (*arrows*).

SCUTIGERELLIDAE Bagnall, 1913

Genus *Scutigerella* Ryder, 1882.

Scuta: 15. First scutum smaller and transversally spread. Rounded lateral margins of the scuta 2-14 normally evident, but in different grades depending on the species (Fig 3, 4). However, the most typical character of this genus – the presence of a deep cavity beneath middle of caudal margin of last scutum between cerci – is not visible through SEM, since it is overlapped by the last scutum and only a slight depression in the posterior margin of the last scutum is visible (fig. 15A).

Head: In all studied species is more or less rounded, somewhat heart-shaped with two lobes on the posterior margin, a bit longer than broad – but not 1.25 times longer – and broadest behind the middle (fig. 9C). Cephalic capsule uniformly sclerotized with smooth surface, as well as the mouth parts. Central rod distinct, unbroken and extends from the middle of the head to the posterior end. Posterior branches distinct, meeting with the central rod at the most posterior point of the head. Cephalic lobes with straight margins. Spiracles in the membrane above the mandibles well visible. Tömösváry's organ conspicuous, both exterior wall of the chamber and opening (fig. 15A). Second maxillae clearly divided by the longitudinal median groove. A transversal groove between the most anterior part and the rest is also present. The anterior part bears three terminal protuberances. Posterior border of second maxillae clearly delimited, and both sclerites (anterior plates of the second maxillae) terminate in an angle at the most posterior part, meeting medially each exterior margin. Proximal arms of the second maxillae distinct but not very conspicuous (fig. 11A).

First trunk segments: Cervical plates short and not very conspicuous. First pair of legs 4-jointed, more than half as long as following pairs. Sternal plates of first trunk segment separated medially, with smooth surface and bearing three setae. Coxae of first pair of legs meeting medially. Anterior sternal plates of the second segment pubescent and kidney-like (fig. 13C).

Cerci: uniform, without any variation at the apical part. Scales present but faintly visible (fig. 16A).

Sense calicles with spiny external scales and inner wall of the sense calicles smooth (fig. 17A).

- ***Scutigerella cf. immaculata*** (Newport, 1845)
  Catalonia (Spain): Fageda d´en Jordà, 1 adult; Font Groga, 1 adult.
  Navarra (Spain): Bértiz 6 adults, 3 juveniles (11), 1 juvenile (10), 3 juveniles (9), 2 juveniles (8).
  Fusine Laghi (Italy): 1 adult.
  Češnjica (Slovenia): 1 adult, 1 juvenile (11).
  Imereti (Georgia): 1 adult.

REMARKS: This species is characterized by a distinctly emarginate posterior margin of the second scutum of the trunk and by the homogeneity of the setae on the second scutum (fig. 3A, B).

- ***Scutigerella cf. causeyae*** Michelbacher, 1942

  Xistral (Galicia, Spain): 4 adults, 2 juveniles (10), 1 juvenile (9), 1 juvenile (8)
  Grunewald (Berlin, Germany): about 50 adults and juveniles.

  REMARKS: Posterior margin of second scutum only slightly emarginate (fig. 3C, D). It does not present any projection on the first pair of legs (fig. 4E).

- ***Scutigerella cf. echinostylus*** Scheller 1968

  Asturias (Spain): 1 adult.

  REMARKS: The appearance of the scuta in this species is very similar than the one in *S. causeyae*, with the posterior margin only slightly emarginate (fig. 4D). The most conspicuous difference between them is the presence of a peg-like process on the lower side of the femur of the first pair of legs in *S. echinostylus* (fig. 4F).

- ***Scutigerella cf. hauserae*** Scheller 1990

  Cave Potoca (Bulgaria): 1 adult.

  REMARKS: Posterior margin of the second scutum only slightly emarginate too (fig. 4D). The extremely long antennae, with 40-60 segments (54 in the studied specimen) are typical of this species particular to caves (fig. 4C).

Genus *Hanseniella* Bagnal, 1913

Scuta: 15. First scutum smaller and transversally spread. Scuta 2-14 convex posteriorly and last scutum straight, without any depression (fig. 16B). Large anterolateral setae at least on scuta 2 and 3 (fig. 5).

Head: In both studied species the head is rounder than in *Scutigerella*, with nearly the same breadth as length and straight posterior margin, without lobes and broadest in the middle (fig. 9A, B). Sclerotization of the head homogeneous, with smooth surface, as well as mouth parts. Central rod only present in the central part of the head, with its posterior end not at the end of the head, but in a more medial part. In this more anterior point the posterior branches – if present – meet with the central rod. Cephalic lobes with straight borders. Spiracles in the membrane above the mandibles visible. Tömösváry's organ very conspicuous, as a protuberance with an opening (fig. 15B). Second maxillae with complete median groove and transversal groove between the most anterior part and the rest. Terminal protuberances at the anterior part present. Posterior border of the anterior plates clearly delimited, broad, where the exterior margins are not in contact with each other. Proximal arms of the second maxillae weakly distinct (fig. 11B).

First trunk segments: Cervical plates short and not very conspicuous. First pair of legs 4-jointed,

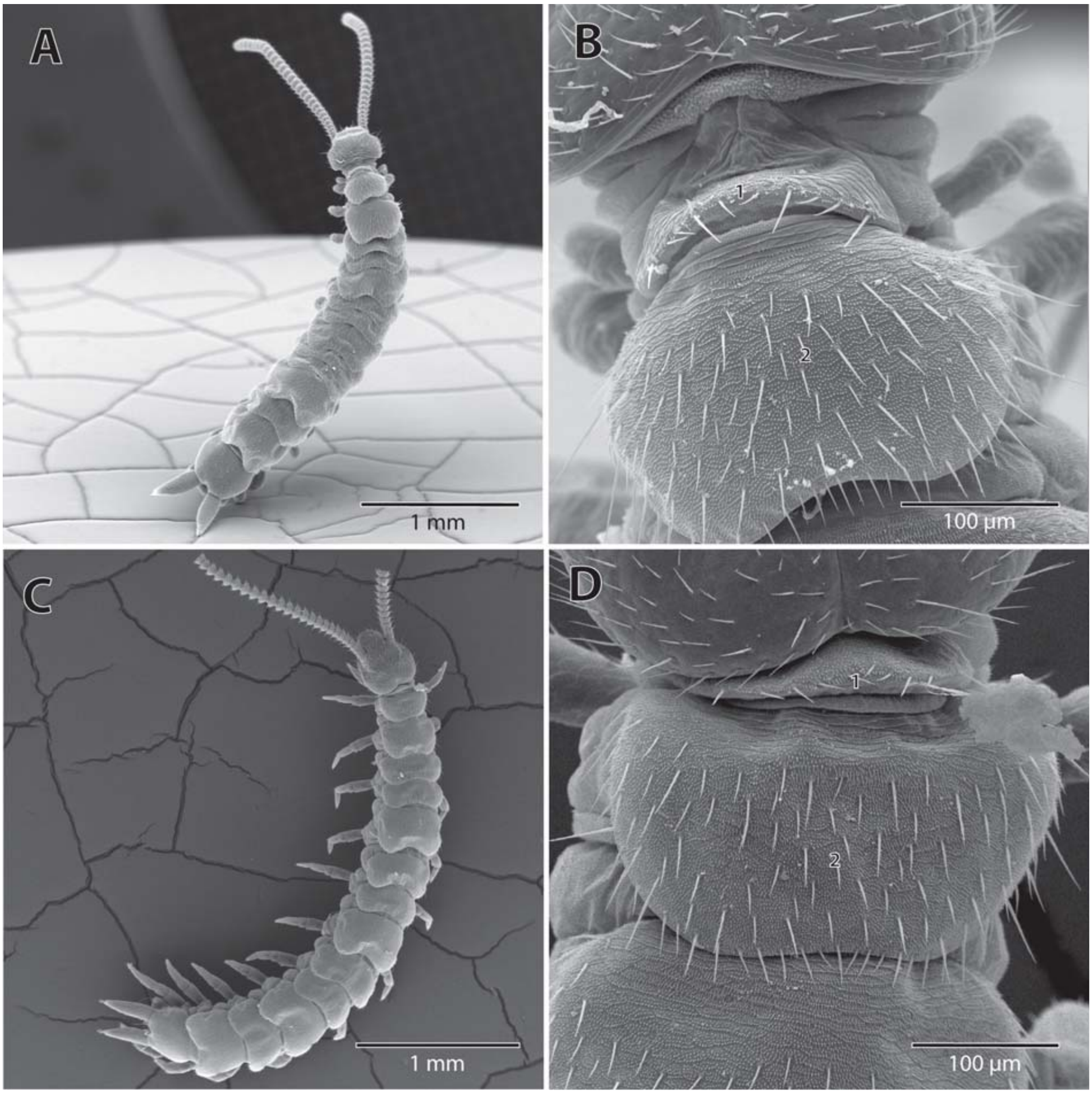
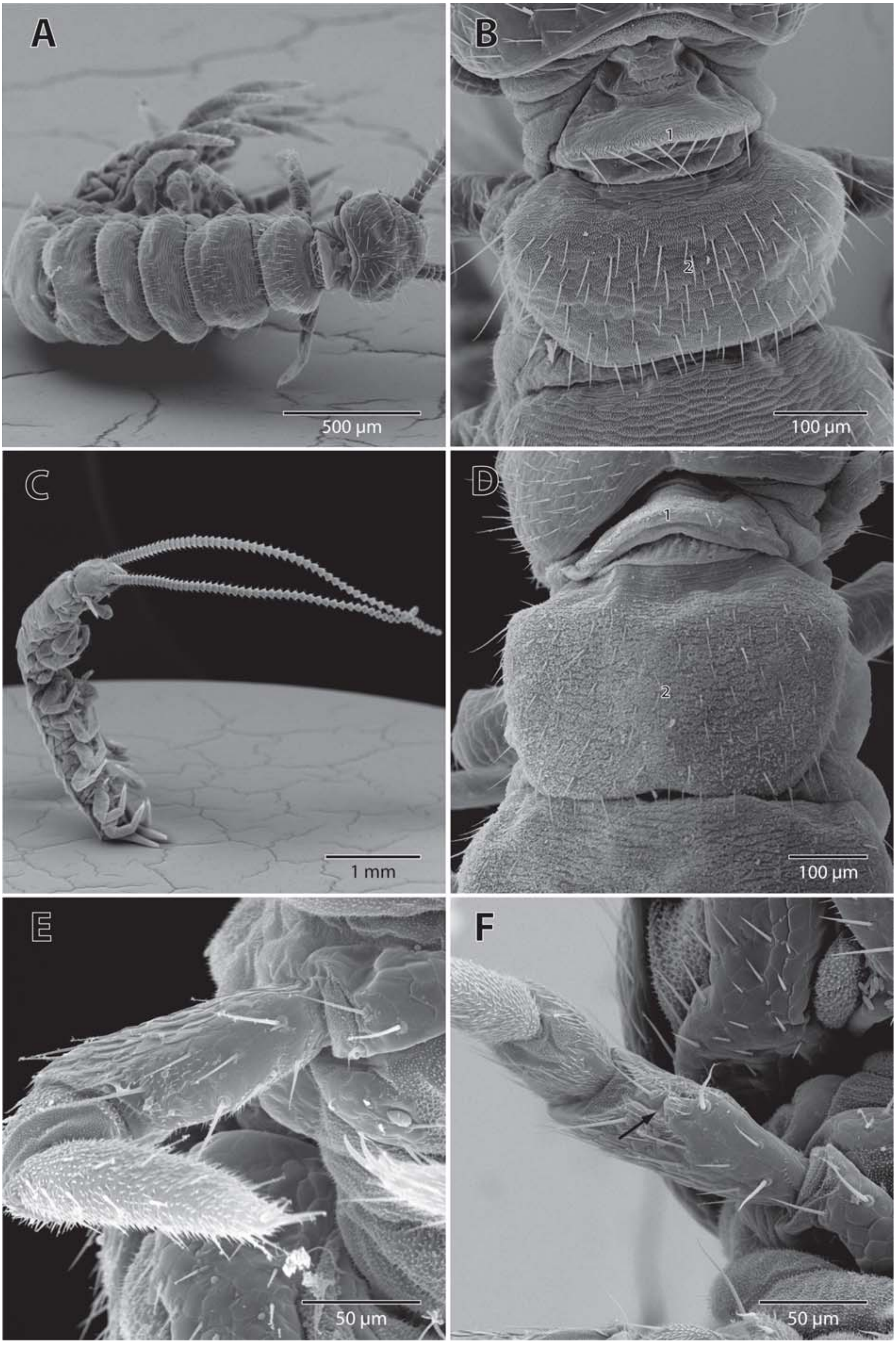


Fig. 3 SEM micrographs of *Scutigerella* species, whole specimen (left) and first (*1*) and second *(2)* scuta (right). A and B, *Scutigerella cf. immaculata*; C and D, *Scutigerella cf. causeyae.*

Fig. 4 SEM micrographs of *Scutigerella* species, whole specimen (A, C) and first (*1*) and second *(2)* scuta (B, D). A and B, *Scutigerella cf. echinostylus*; C and D, *Scutigerella cf. hauserae*. E and F, detail of the ventral side of the femur of the first leg in *S. causeyae* (E) which does not present any process, and *S. echinostylus* (F) showing the peg-like process (arrow).

more than half as long as following pairs. Sternal plates of first trunk segment not very conspicuous and lacking setae. Coxae of first pair of legs meeting medially. Anterior sternal plates of the second trunk segment pubescent and kidney-like (fig. 13A, B).

Cerci: pubescent, with an elongated and thinner terminal area. Scales present but faintly visible (fig. 16B).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Sense calicles with spiny external scales and inner wall smooth (fig. 17B).

- ***Hanseniella cf. nivea*** (Scopoli, 1763)

  Češnjica (Slovenia): 4 adults, 3 juveniles (11), 1 juvenile (10).

  REMARKS: This species is widespread in the Mediterranean region and is the only frequent representative of this genus, typical from tropical regions, in Europe. Scuta with regular rounded posterior margin (fig. 5A, B). Head with regular rounded shape, as long as broad. Posterior branches of central rod present (fig. 9A).

- ***Hanseniella cf. agilis*** Tiegs 1939

  Material studied: 7 adults from Australia.

  REMARKS: Scuta more transversally spread (fig. 5C, D). Head broader than longer with lateral angles at point of articulation of mandible (fig. 9B).

SCOLOPENDRELLIDAE Newport, 1845

Genus *Scolopendrella* Gervais 1839

Scuta: 17, well sclerotized (fig. 6A, B). First scutum reduced to a pair of sclerotized rows with a lateral exterior angle on each and bearing two or three setae. Paired posterior projections in all scuta except on 14, 16 and 17. Posterior projections triangular in the scuta 2 and 3, with a deeply curved posterior border between them, and small pointed projections in the rest of scuta, with rounded posterior border in the space between them (fig. 6B). Posterior border of last scutum straight.

Head: Elongated from dorsal view (more than 1,25 times longer than broad), but with posterior rounded border in lateral view. Head capsule completely sclerotized with smooth surface, as well as the mouth parts. Setae of the cephalic lobe and mouth parts with a conspicuous ring-shape basis. Central rod divided in the middle, with no frontal branches. Median branches present, without contact with the central rod. Posterior branches present but disappear towards the posterior end (fig. 9D). Whole structure of the Tömösváry's organ visible, both the chamber and the opening. Margins of the cephalic lobes straight. Spiracles in the membrane above the mandible present, but very small and partially covered by a fold (fig. 15C). There is a protuberance beside the first-maxillary palp. Second maxillae separated by the median groove and transversal groove present, dividing the anterior setae-bearing part from the rest. Surface of second maxillae pubescence only in the middle; exterior parts smooth. Posterior end of the anterior plates of the second maxillae gradual; there is no clear delimitation between them and the membrane behind them. Proximal arms of second maxillae visible (fig. 11C).

First trunk segments: Cervical plates long, very conspicuous, of thick and smooth cuticula. First pair of legs 3-jointed, less than half as long as following pairs. Sternal plates of first trunk segment rounded and smooth, separated medially and bearing three setae. Coxae of first pair

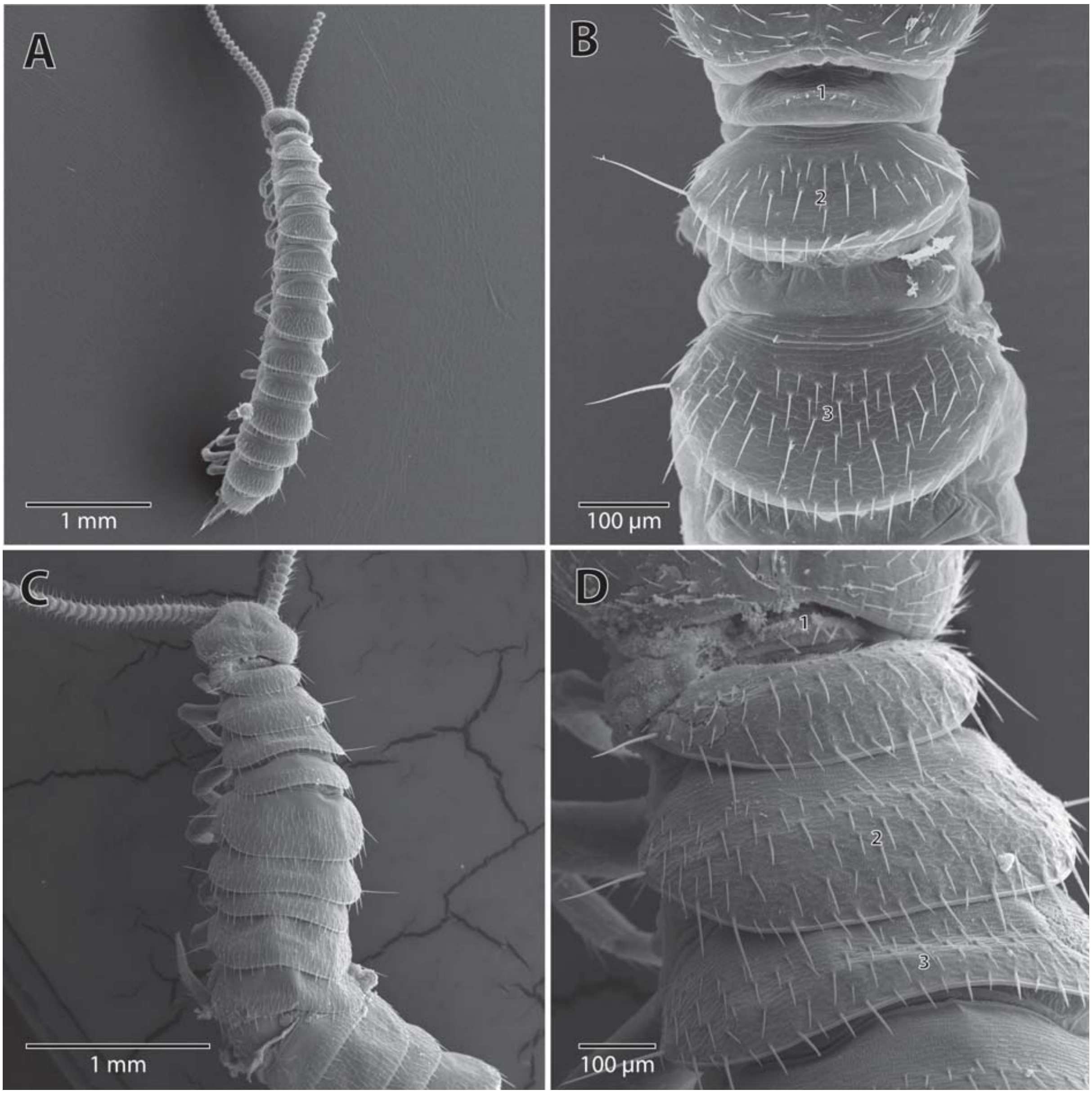


Fig. 5 SEM micrographs of *Hanseniella* species, whole specimen (left) and first (*1*), second *(2)* and third (*3*) scuta (right). A and B, *Hanseniella cf. nivea*; C and D, *Hanseniella cf. agilis*.

of legs angular, somewhat triangular and glabrous, meeting medially. Anterior sternal plates of second trunk segment pubescent, more or less rounded (fig. 13D).

Cerci: pubescent, with scales faintly visible. Apical part with longitudinal ridges (fig. 16C).

Sense calicles: external part without scales. The whole margin of the sense calicles present small digitiform appendages in two rows and additional groups at the dorsal part (fig. 17C).

- ***Scolopendrella notacantha*** Gervais, 1839

  Catalonia (Spain): Castellsapera, 1 juvenile (10); L´Estartit, 3 adults; Sant Llorenç Munt, 1 adult; Serra de l´Obac, 1 adult.

  Catalonia (Spain) second sampling: Blanes, 2 juveniles (10).

  REMARKS: This species is recognized by the semi-circular posterior margin of the clearly-demarcated first scuta as it bears belts of longitudinal striae (fig. 6B).

Genus *Geophilella* Ribaut, 1913.

Scuta: 22, reduced to paired plates without any posterior projection (fig. 6C, D). First scutum reduced to a pair of straight longitudinal rows with two or three setae each. Two last scuta well developed, with straight posterior border.

Head: elongated and flattened. Surface of the head capsule heterogeneously sclerotized. Areas less sclerotized with erect pubescence, which confers a granular aspect to the surface. Posterior sclerite that links both cephalic lobes, and frontal part more sclerotized, of smooth and thick cuticle. Central row divided, and reinforced by smooth and thick cuticle too. Only median branches present, short and also reinforced with cuticula. The meeting point of the median branches with the central rod forms a cruciform cuticular structure (fig. 10A). Only the opening of the Tömösváry's organ visible. Margins of the cephalic lobes straight. Setae of the cephalic lobe and mouth parts with a conspicuous ring-shape basis. Tracheae in the membrane above the mandibles slightly visible, almost covered by a fold of the membrane (fig. 15D). Protuberance beside the first-maxilary palp conspicuous. Second maxillae completely separated by the median groove and transversal groove present. Surface of second maxillae pubescence only in the middle; exterior parts smooth. Posterior end of second maxillae gradual. Proximal arms of second maxillae visible (fig. 11D).

First trunk segments: Cervical plates very conspicuous, of smooth and thick cuticle. First pair of legs 3-jointed, less than half as long as following pairs. Sternal plates of the first trunk segment rounded, pubescent, with two or three setae and separated medially. Coxae of the first pair of legs angular, somewhat triangular, glabrous and meeting medially. Anterior sternal plates of the second trunk segment more or less rounded and pubescent (fig. 14A).

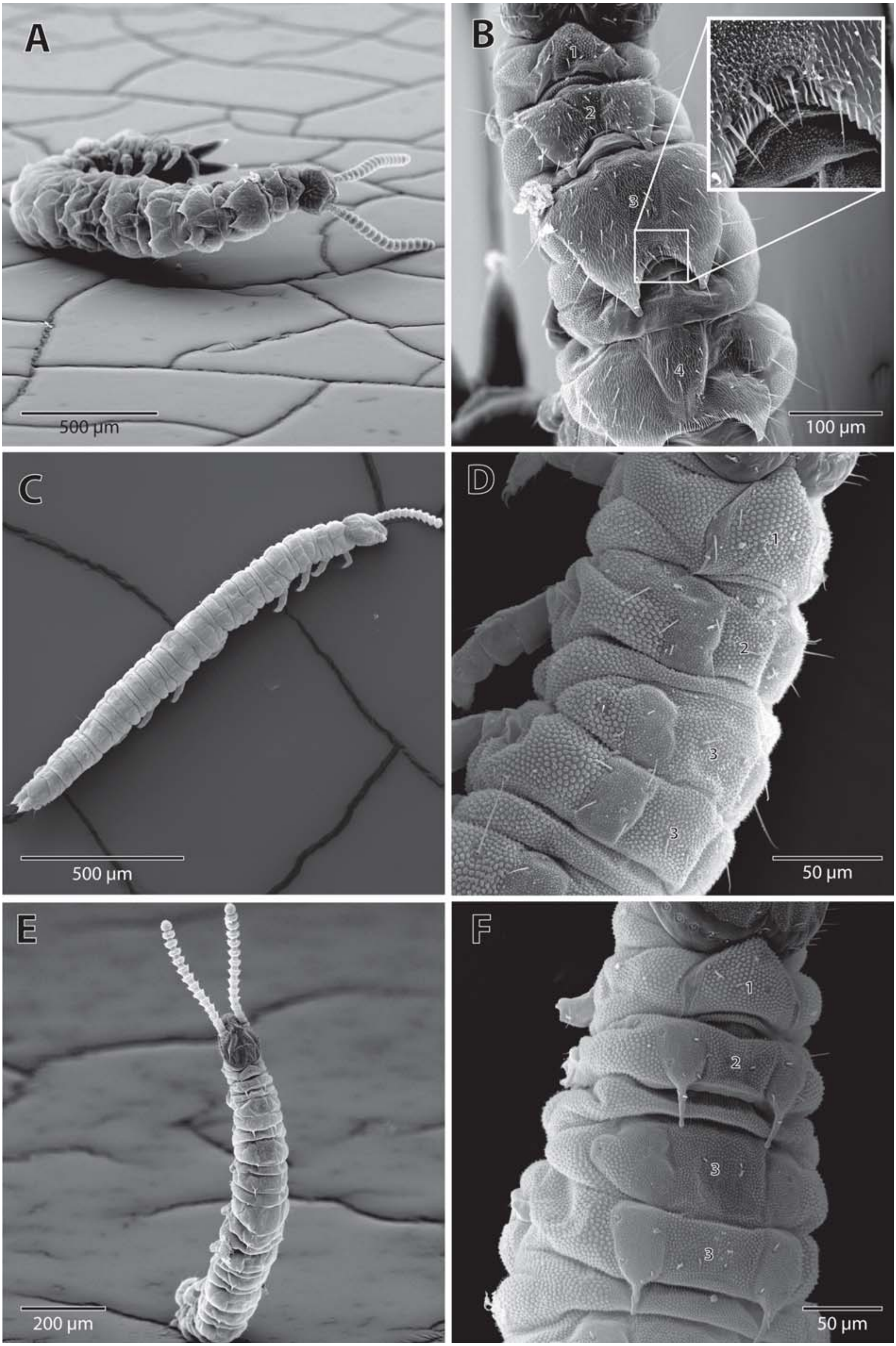
Cerci: short (only about twice longer than broad), covered by very conspicuous scaly cuticular ridges. Apical part with longitudinal ridges (fig. 16D).

Sense calicles: Without scales on the exterior part. Digitiform appendages only present as small groups in the dorsal part of the margin (fig. 17D).

- ***Geophilella pyrenaica*** Ribaut, 1913
  Navarra (Spain): Bértiz, 1 juvenile (10); Funes, 1 adult, 3 juveniles (11), 1 juvenile (10), 1 juvenile (9).
  La Rioja (Spain): Leiva, 2 adults, 2 juveniles (10), 1 juvenile (8).
  Catalonia (Spain) second sampling: Gironella, 1 adult.
  As Fragas do Eume (Galicia, Spain): 3 adults, 1 juvenile (10), 2 juveniles (9), 1 juvenile (8).

→

Fig. 6 SEM micrographs of scolopendrellid species, whole specimen (left) and first scuta (numbers indicate the tergal areas of each scuta) (right). A and B, *Scolopendrella notacantha*; C and D, *Geophilella pyrenaica*; E and F, *Parviapiciella balcanica*.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Genus *Parviapiciella* Mas & Serra, 1993.

Scuta: 22, reduced to paired plates, with digitiform posterior projections on scuta 2, 4, 5, 6, 8, 9, 10, 12, 13, 14 and 16 (fig. 6E, F). First scutum reduced to a pair of straight longitudinal rows without setae. Two last scuta well developed, with straight posterior border.

Head: The morphology and sclerotisation pattern of the head capsule is identical to the one in *Geophilella* (fig. 10B). The only differences are that there are no visible spiracles (fig. 15E). Ring-shaped basis of the setae also present, as well as the protuberance beside first-maxilary palp. The second maxillae present the same surface pattern as in *Geophilella*. The most notable difference is that the median groove between both maxillae is very weak and only visible in the middle (fig. 12A).

First trunk segments: the features of the ventral sclerites and first pair of legs are also very similar than the ones in *Geophilella* (fig. 14B).

Cerci: with the same scaly pattern than *Geophilella* and apical part with longitudinal ridges too (fig. 16E). They are not as short as in *Geophilella* (more than twice as longer as broad).

Sense calicles: Exterior part without scales. Digitiform appendages only in a row on the inner wall of the sense calicle. The exterior margin is surrounded by folds, similar than petals (fig. 17E).

- ***Parviapiciella balcanica*** (Remy, 1943)

  Catalonia (Spain): Taradell, 1 adult, 1 juvenile (9)

  REMARKS: This is the only species for the newest genus of Symphyla. When Mas & Serra (1993) created this genus to place this species from *Scolopendrellopsis*, they remarked not only on the lack of posterior projections in the last scuta, but also on the similarities of the scuta and cerci to this species and *Geophilella*. The observed features in the head and in the ventral part of the first trunk segments are additional characters that support the affinity of both genera. The present description also contributes to the incomplete knowledge of the taxonomy of this rare species (Scheller & Christian 2000).

Genus *Symphylella* Silvestri 1902

Scuta: 17. First scutum transversally spread. Rest of scuta well sclerotized, with paired triangular projections except in the scuta 14, 16 and 17 (fig. 7). Posterior margin of the space between triangular projections straight in the anterior scuta, but curved in the fourth. Posterior border of last scutum straight.

Head: elongated and flattened, homogeneously sclerotized in its entirety and pubescent. Mouthparts likewise pubescent. Central rod not interrupted, with frontal and median branches present as a soft line without pubescence. Frontal branches V-shaped and median branches in contact with the central rod. Posterior branches absent. Most frontal point of the head with a thicker cuticle, smooth, very demarcated from the rest of the head. Postantennal row present but not very conspicuous (fig. 10C). Only exterior opening of the Tömösváry's organ

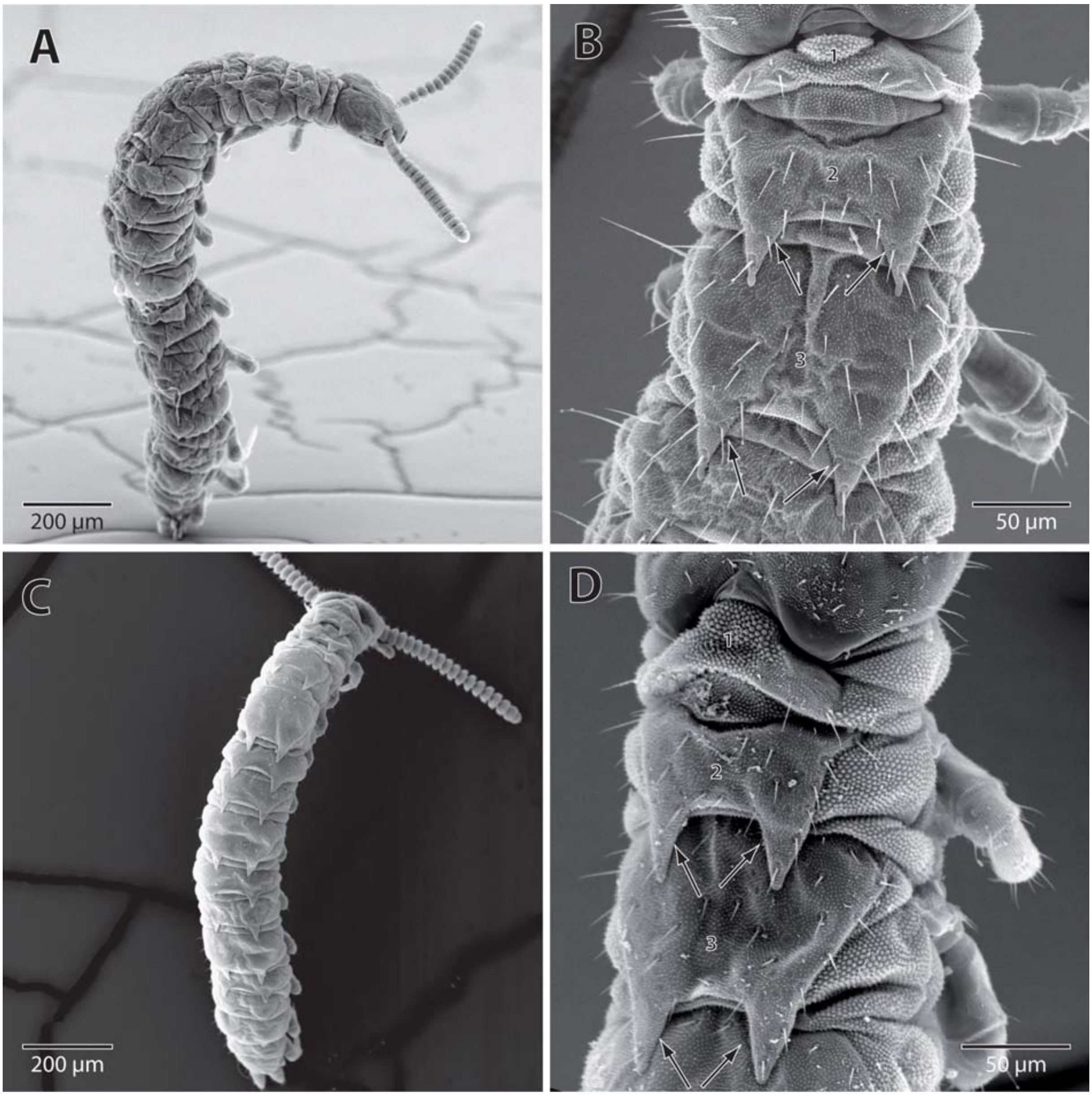


Fig. 7 SEM micrographs of *Symphylella* species, whole specimen (left) and first three scuta (*1-3*) (right). A and B, *Symphylella vulgaris*; C and D, *Symphylella elongata*. The presence or absence of setae on the inner edge between inner basal and apical setae on the triangular appendages of the anterior scuta is a specific diagnostic character to differenciate both species (*arrows*).

visible. Dorsal margin of the cephalic lobes vertical, pointed forwards in the head-mandible articulation. Tracheae in the membrane above the mandible absent (fig. 15F). Median groove between second maxillae entirely present, but transversal groove absent. Posterior end of second maxillae gradual. Proximal arms of second maxillae arising behind them, conspicuous, of thick cuticle (fig. 12B).

First trunk segments: Cervical plates long, conspicuous, of thick and smooth cuticula. Little hairy knobs instead of first pair of legs. Coxae and sternal plates not discernible, instead there is a pair of slight plates separated medially. Anterior sternal plate of the second trunk segment pubescent, slightly elongated longitudinally (fig. 14C).

Cerci: pubescent, without scales. Apical part with transversal ridges (fig. 16F).

Sense calicles: Exterior part covered by spiny scales. Margin of sense calicle smooth, without visible digitiform appendages (fig. 17F).

- ***Symphylella vulgaris*** (Hansen, 1903)

  Catalonia (Spain): Plana San Vicente, 2 adults; Taradell, 2 adults.
  Yepes (Toledo, Spain): 5 adults.
  Jábaga (Cuenca, Spain): 1 adult.
  Navarra (Spain): Bértiz, 1 juvenile (9).
  La Rioja (Spain): Bañares, 2 adults, 1 juvenile (10); Leiva, 1 juvenile (8); Tormantos, 1 adult.
  Catalonia (Spain) second sampling: La Pobla de Lillet, Llobregat river, 1 juvenilee (11), and Falgars Sanctuary, 3 adults. Montseny, 1 adult.
  Minorca (Spain) sampling: Mahón, 8 adults, 4 juveniles (11), 2 juveniles (10); Barranco d´Algendar, 1 adult.
  Grunewald (Berlin, Germany): 3 adults, 1 juvenile (11), 1 juvenile (9).
  Eisenstadt (Austria): 1 adult.
  Češnjica (Slovenia): 1 adult, 1 juvenile (10).

  REMARKS: Main taxonomical features of this species are a transverse row of six setae on the first scuta and the presence of at least one seta between inner basal seta and apical seta on the triangular projections of the anterior scuta (Fig. 7B).

- ***Symphylella elongata*** Scheller, 1952

  Catalonia (Spain): Canyamars, 1 adult.
  Catalonia (Spain) second sampling: Cadí-Moixeró, 2 juveniles (11).

  REMARKS: This species also has a transverse row of six setae on the first scutum, but it differs from *S. vulgaris* in the absence of setae on the inner edge between inner basal and apical setae on the triangular projections of the anterior scuta (Fig. 7D).

Genus *Scolopendrellopsis* Bagnal, 1913

Scuta: 21 or 22, since the third scutum is completely subdivided in *S. arvernorum* and sometimes partially in *S. subnuda* and *S. selgae*. First scutum trapezoidal, granulate, with a transversal row of setae. Paired triangular projections in all scuta except in the 6, 10, 14, 17, 18, 20 and 21 (fig. 8). Triangular projections separated by an area with straight posterior margin in all scuta. Posterior border of the last scutum straight.

Head: Elongated and flattened. Surface mainly with short erect pubescence, heterogeneously sclerotized, with posterior sclerite that links both cephalic lobes, and anterior part more sclerotized. These sclerites are not as conspicuous as in *Geophilella* and *Parviapiciella* since its surface is also pubescent, so the difference in comparison to the non-sclerotized area is not as remarkable. Central rod broken in the middle, and reinforced by smooth and thick cuticle in the posterior half. Frontal and median branches can be present or not, depending on the species. Postantennal rods also present in different grades of sclerotisation. Anterior part of the head without pubescence (fig. 10D-F). Exterior opening of the Tömösváry's organ rarely visible – if visible, very weakly – since it is covered by little prickles of the surface. Dorsal margin of cephalic lobes vertical, pointed forwards at the head-mandible articulation. Tracheae in the membrane above the mandible absent (fig. 15G, H). Median groove between second maxillae entirely present, but transversal groove absent. Posterior end of second maxillae gradual. Proximal arms of second maxillae arising behind them, conspicuous, of thick cuticle (fig. 12C, D)

First trunk segments: Cervical plates long and pubescent. First pair of legs 3-jointed, less than half as long as following pairs. Sternal plates of the first trunk segment pubescent, without setae, triangular and meeting medially at their posterior end, separating the coxae of the first pair of legs. Anterior sternal plate of the second trunk segment pubescent, bearing setae and more or less rounded (fig. 14D).

Cerci: pubescent, without scales. Apical part with transversal ridges (fig. 16G, H).

Sense calicles: With no scales on the exterior part. Margin of sense calicles smooth. Inner wall of the sense calicles with three or four rows of digitiform appendages (fig. 17G, H).

- ***Scolopendrellopsis (Scolopendrellopsis) microcolpa*** (Muhr, 1881)

  La Rioja (Spain): San Torcuato, 1 juvenile (11).

  The only specimen found was identified using light microscopy. For this reason, two additional specimens from the Museum für Naturkunde in Görlitz (Germany) have been also studied. However, both animals were unfortunately damaged and for this reason, both the identification and the diagnosis characters described below have to be taken cautiously.

  REMARKS: Frontal branches of the head's central rod present as a groove. Median branches seem to be also present. Postantennal rods not very conspicuous (fig. 10D). The presence of a seta inserted between inner basal and apical setae is a traditional diagnostic character for this species.

- ***Scolopendrellopsis (Symphylellopsis) arvernorum*** Ribaut, 1931

  Yepes (Toledo, Spain): 1 adult.
  Jábaga (Cuenca, Spain): 5 adults, 1 juvenile (10).
  Fragas do Eume (Galicia, Spain): 3 adults, 1 juvenile (9), 4 juveniles (8).

  REMARKS: This species differs from all other *Scolopendrellopsis* species known so far in the transverse subdivision of the third scutum into two scuta (fig. 8C). This feature is difficult to discern with a light microscope, since the border of the scuta is often diffuse (personal observation). The frontal and median branches of the head's central rod are absent (fig. 10E).

- ***Scolopendrellopsis (Symphylellopsis) subnuda*** (Hansen, 1903)

Catalonia (Spain): Montaguit, 1 adult, 1 juvenile (11); Tamariu, 1 adult; Mataró, 2 adults.

Yepes (Toledo, Spain): 2 adults.

La Rioja (Spain): Bañares, 3 adults, 1 juvenile (11), 8 juveniles (10), 2 juveniles (9), 2 juveniles (8); Leiva, 1 adult, 1 juvenile (11), 4 juveniles (10), 2 juveniles (9) , 1 juvenile (8); San Torcuato, 1 juvenile (11), 1 juvenile (9), 1 juvenile (8); Tormantos, 1 juvenile (10).

Catalonia (Spain) first sampling: Collserola, 4 adults; Berga, 1 adult, 1 juvenile (10).

Catalonia (Spain) second sampling: Cadí-Moixeró, 8 adults, 2 juveniles (11), 3 juveniles (10)

Minorca (Spain) sampling: Mahón, 25 adults, 6 juveniles (11), 2 juveniles (10), 1 juvenile (9), 1 juvenile (8); San Luis, 1 juvenile (11); Barranco d´Algendar, 8 adults, 2 juveniles (11), 1 juvenile (10), 1 juvenile (8); Monte del Toro, 2 adults, 1 juvenile (8).

Grunewald (Berlin, Germany): about 30 adults and juveniles.

Nob End (Bolton, United Kingdom): 8 adults, 1 juvenile (11), 3 juveniles (10).

Italy: San Montano (Ischia), 1 juvenile (8); Monte Epomeo (Ischia), 1 juvenile (8); Fusine Laghi, 2 adults.

Slovenia: Triglau, 1 juvenile (11), 2 juveniles (10); Češnjica, about 140 adults and juveniles.

REMARKS: *S. subnuda* is the most common species obtained in the soil samples' extractions. The median branches are present as a groove, meeting medially with the central rod of the head. The frontal branches are also present, as a well sclerotised rod that connects both postantennal rods, which are also very conspicuous. In the frontal part of the head it presents a reticulate surface (fig. 8E).

- ***Scolopendrellopsis (Symphylellopsis) selgae*** Domínguez 1984

Catalonia (Spain): Llafranc, 1 juvenile (10), 1 juvenile (9); Tamariu, 1 juvenile (8); Taradell, 2 adults, 1 juvenile (10).

Navarra (Spain): Bértiz, 15 adults, 7 juveniles (11), 8 juveniles (10); Funes, 4 adults, 1 juvenile (11), 1 juvenile (10), 1 juvenile (9).

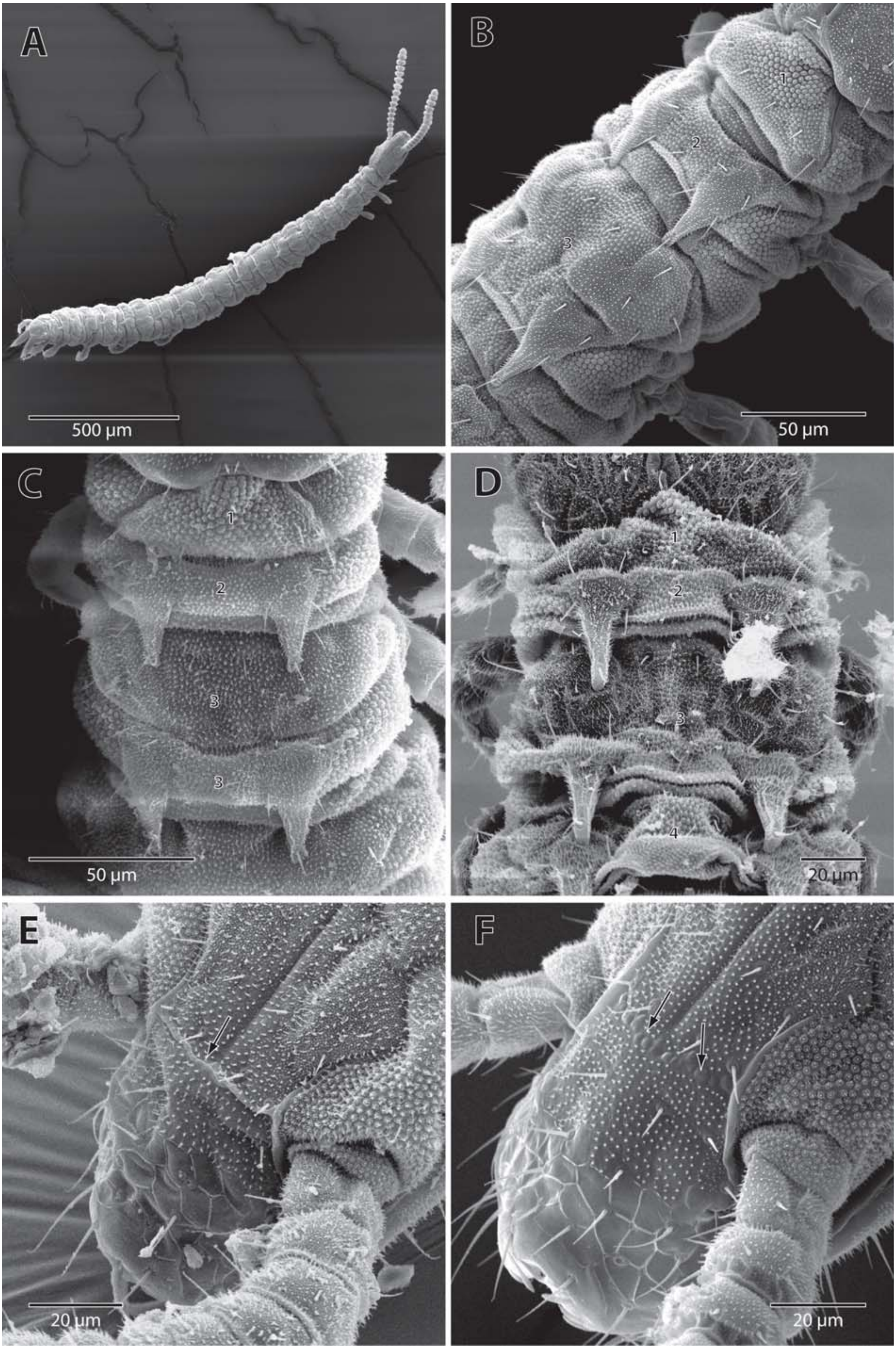
Catalonia (Spain) second sampling: Blanes, 2 juveniles (11); Gironella, 3 adults, 1 juvenile (10), 1 juvenile (9); La Pobla de Lillet, Falgars Sanctuary, 2 adults, 1 juvenile (11), 1 juvenile (10); Montseny, 42 adults and juveniles.

REMARKS: This species is very similar to *S. subnuda*. The main diagnostic character is the shape of the frontal branches of the central rod of the head, which is a row of small protuberances (fig. 8F). In addition, the first scutum is smaller than in *S. subnuda* and presents one more pair of setae on the third scutum.

All generic characters belonging to the head, first trunk segments, cerci and sense calicles above described are proposed as diagnostic characters and illustrated in the figures 9-17. Genera which do not present intrageneric variation are illustrated only with one species.

→

Fig. 8 SEM micrographs of *Scolopendrellopsis* species. A, whole specimen of *Scolopendrellopsis (Symphylellopsis) subnuda.* B, C and D, first scuta (numbers *1-3* indicate the tergal areas) of *Scolopendrellopsis (Symphylellopsis) subnuda* (B), *Scolopendrellopsis (Symphylellopsis) arvernorum* (C) and *Scolopendrellopsis (Scolopendrellopsis) microcolpa* (museum specimen num. 9449, MfNG) (D). E and F, detail of the frontal branches (*arrow*) head´s central rod in *Scolopendrellopsis (Sym.) subnuda* (E) and *Scolopendrellopsis (Sym.) selgae* (F).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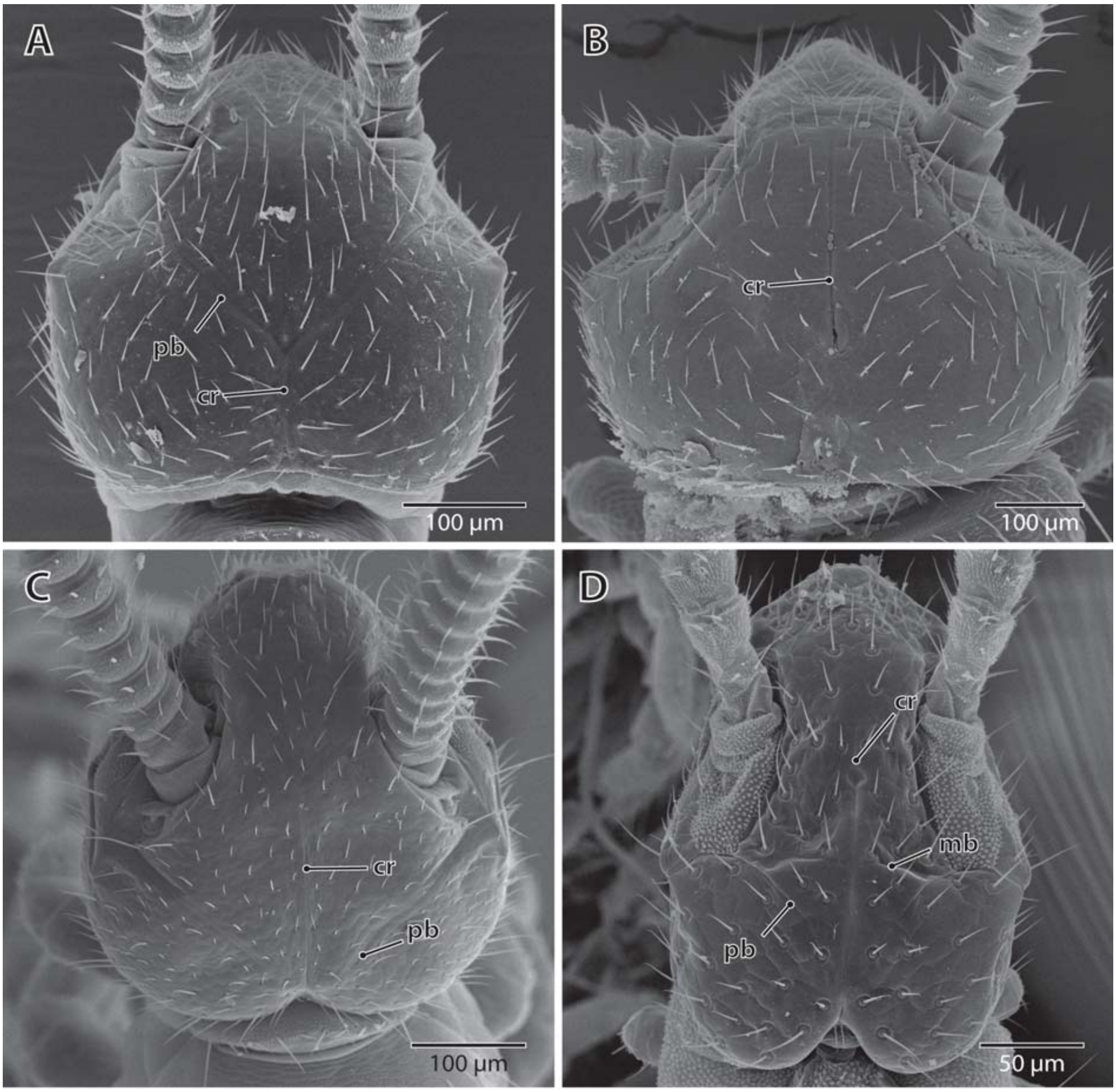
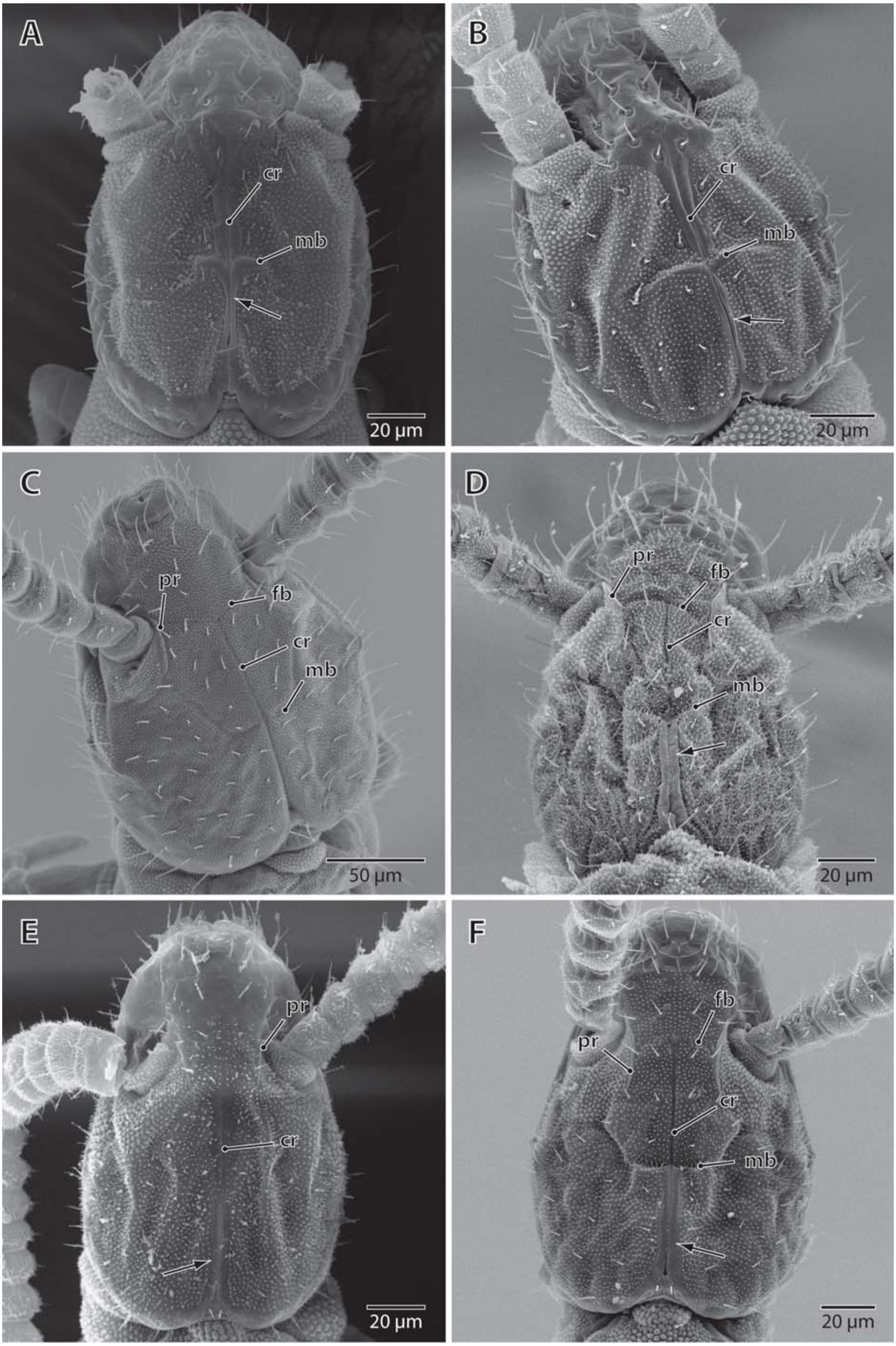


Fig. 9 SEM micrographs showing features of the dorsal side of the head in different symphylan genera. Genera which do not show intrageneric variations are represented only by one species. (A) *Hanseniella cf. nivea,* (B) *Hanseniella cf. agilis,* (C) *Scutigerella cf. causeyae,* (D) *Scolopendrella notacantha*. Abbreviations: *cr*, central rod; *mb*, median branches of the central rod; *pb*, posterior branches of the central rod.

Fig. 10 SEM micrographs showing features of the dorsal side of the head in different symphylan genera. (A) *Geophilella pyrenaica*, (B) *Parviapiciella balcanica,* (C) *Symphylella vulgaris,* (D) *Scolopendrellopsis (Scolopendrellopsis) microcolpa* (museum specimen num. 9449, MfNG)*,* (E) *Scolopendrellpsis (Symphylellopsis) arvernorum,* (F) *Scolopendrellopsis (Symphylellopsis) selgae*. Abbreviations: *fb*, frontal branches; *cr*, central rod; *mb*, median branches of the central rod; *pr*, postantennal rod. *Arrow*: cuticular reinforcement of the central rod.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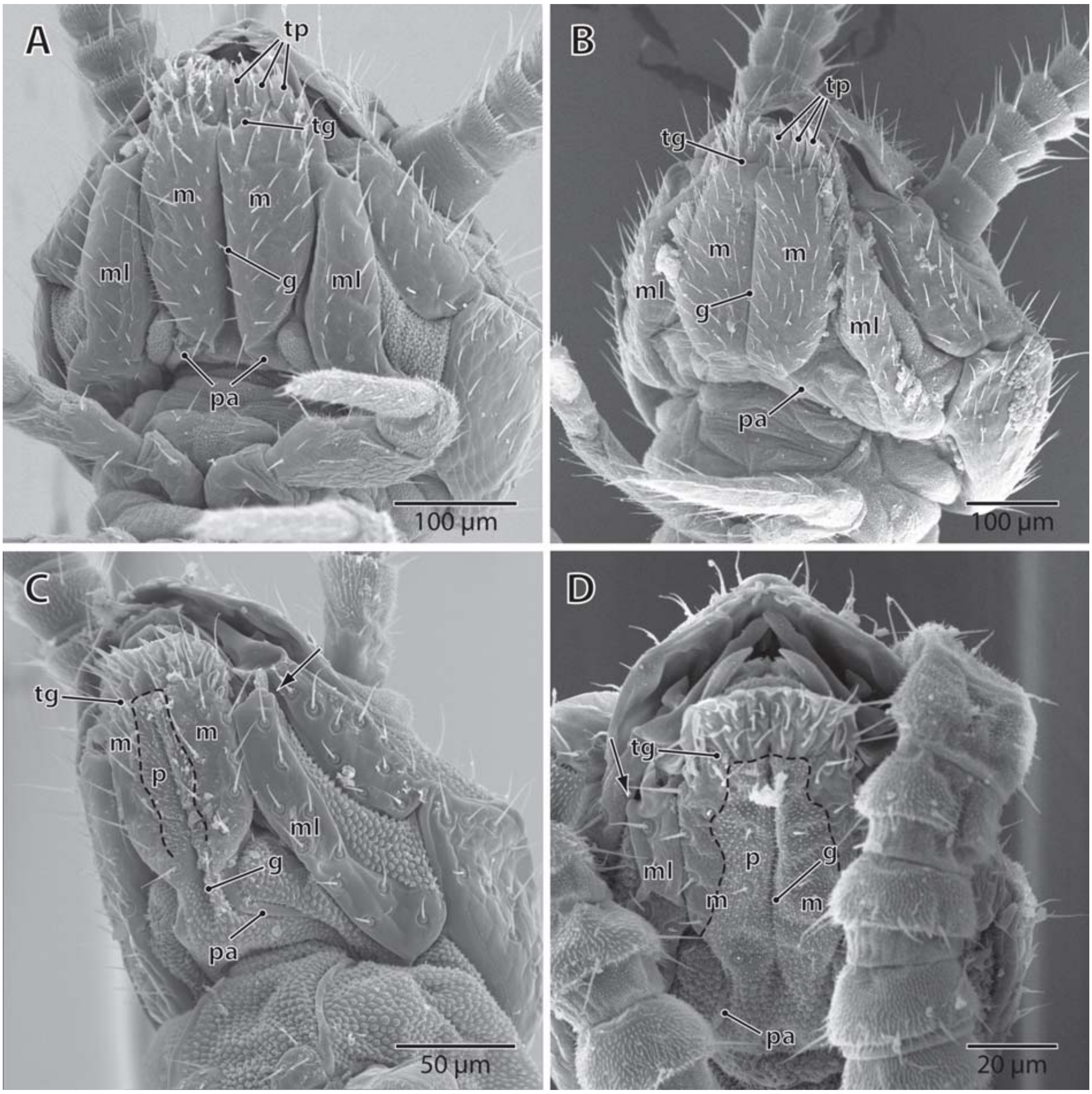

Fig. 11 – SEM micrographs showing features of the ventral side of the head in different symphylan genera. Genera which do not show intrageneric variations are represented only by one species. (A) *Scutigerella cf. echinostylus*, (B) *Hanseniella cf. agilis,* (C) *Scolopendrella notacantha,* (D) *Geophilella pyrenaica*. Both anterior plates (*m*) of the second maxillae are separated by the median groove (*g*), and continue backwards as the second-maxillary proximal arms (*pa*). The transversal groove (*tg*) divides the most anterior part of the second maxillae of the rest. Both first species present three terminal protuberances (*tp*) at this anterior part, while both last do not present it so clearly, but several rows of setae pointing forwards. In these last two, the second maxillae show a central area of pilose surface (*p*, delimited by a broken line). The first maxillae (*mI*) show a lateral protuberance (*arrow*) beside the palp in these species.

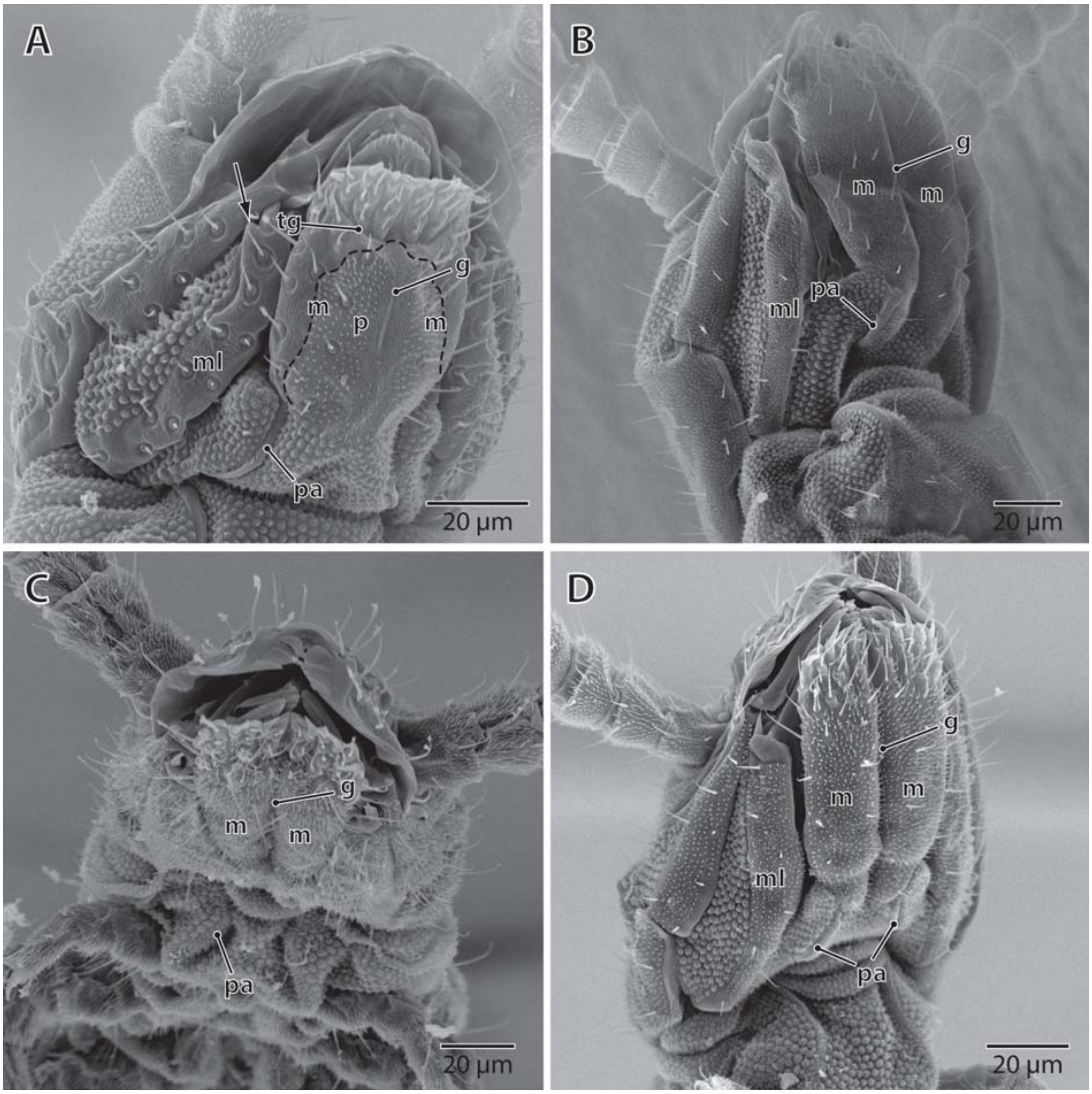

Fig. 12 SEM micrographs showing features of the ventral side of the head in different symphylan genera. (A) *Parviapiciella balcanica*, (B) *Symphylella vulgaris,* (C) *Scolopendrellopsis (Scolopendrellopsis) microcolpa* (museum specimen num. 9449, MfNG)*,* (D) *Scolopendrellopsis (Symphylellopsis) subnuda*. The first species shows the transversal groove (*tg*), the pilose area in the second maxillae (*p*, delimited by a broken line) and the protuberance beside the first-maxillary palp (*arrow*). Due to the position of the museum´s specimen of (C) *Scolopendrellopsis (Scolopendrellopsis) microcolpa* on the stub*,* some structures such as the proximal arms of the second maxillae are not visible. Abbreviations: *g*, median groove; *m*, anterior plate of the second maxillae; *mI*, first maxillae; *pa*, proximal arms of the second maxillae.

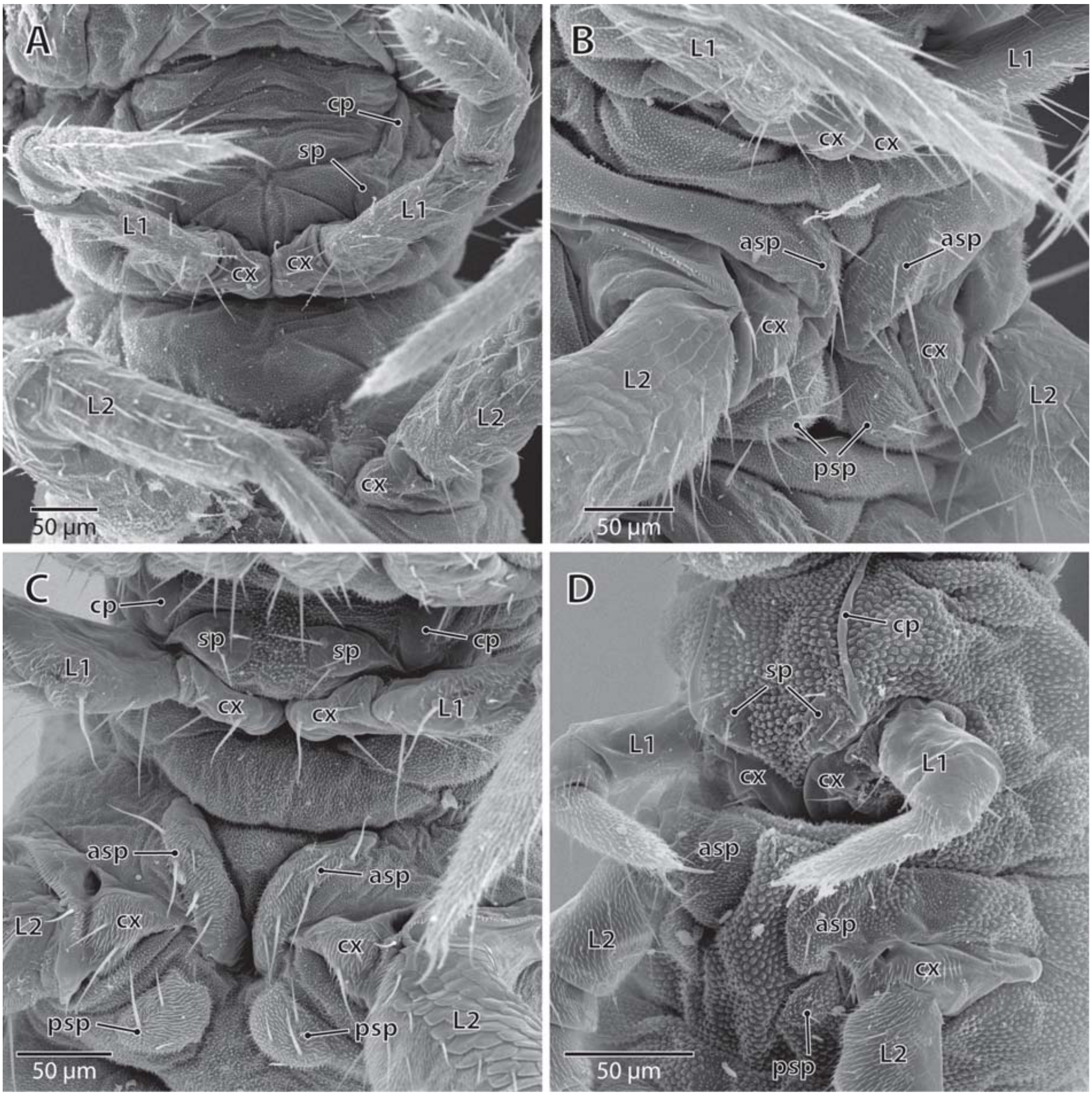

Fig. 13 SEM micrographs showing features of the first and second trunk segments in ventral view in different symphylan genera. Genera which do not show intrageneric variations are represented only by one species. (A and B) *Hanseniella cf. nivea*, (C) *Scutigerella cf. echinostylus,* (D) *Scolopendrella notacantha*. Abbreviations: *asp*, anterior sternal plate of the second segment; *cp*, cervical plate; *cx*, coxae; *L1*, leg of the first pair; *L2*, leg of the second pair; *psp*, posterior sternal plate of the second segment; *sp*, sternal plate of the first segment.

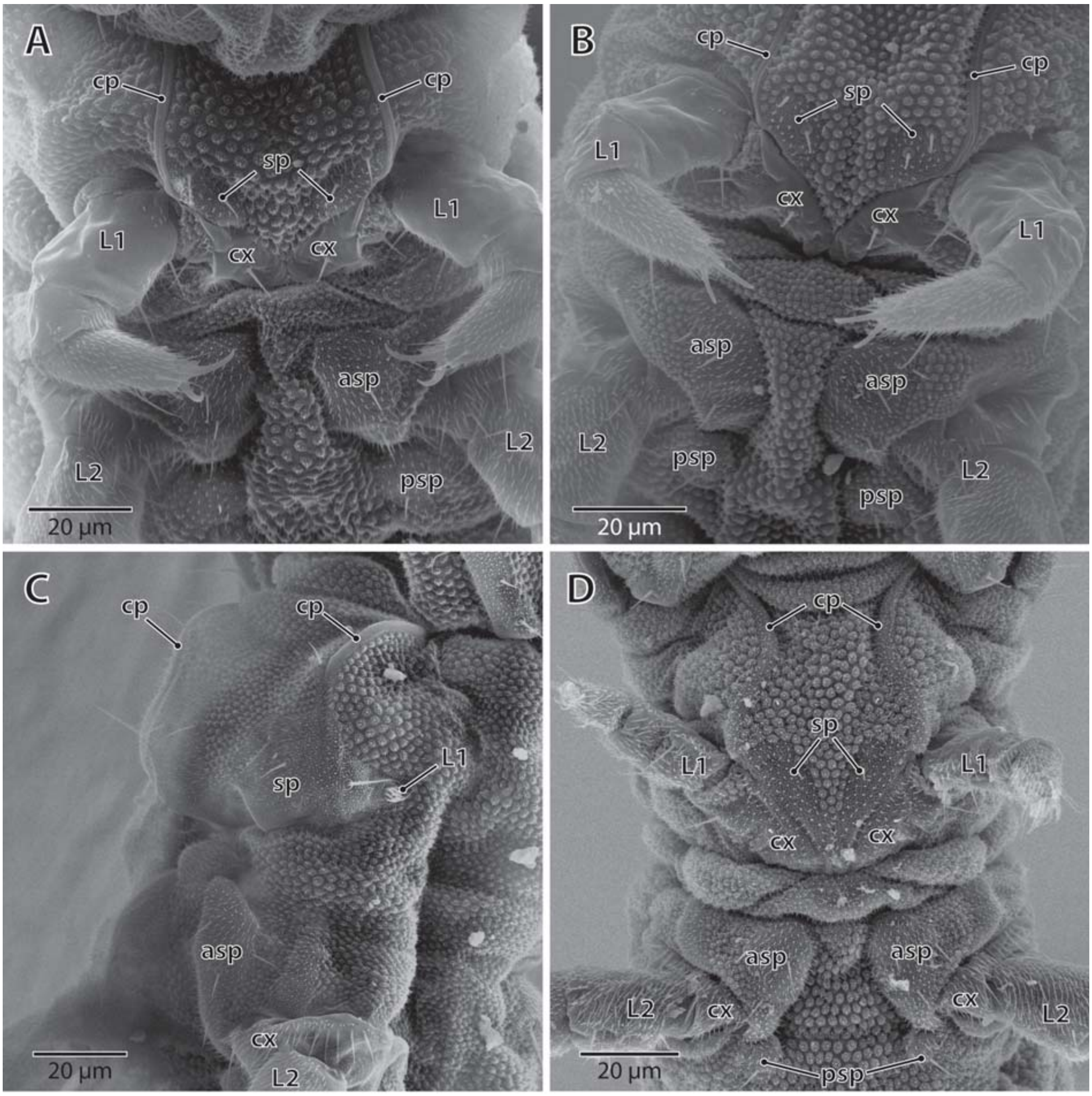

Fig. 14 SEM micrographs showing features of the first and second trunk segments in ventral view in different symphylan genera. (A) *Geophilella pyrenaica*, (B) *Parviapiciella balcanica*, (C) *Symphylella vulgaris,* (D) *Scolopendrellopsis (Symphylellopsis) subnuda*. Abbreviations: *asp*, anterior sternal plate of the second segment; *cp*, cervical plate; *cx*, coxae; *L1*, leg of the first pair; *L2*, leg of the second pair; *psp*, posterior sternal plate of the second segment; *sp*, sternal plate of the first segment.

Fig. 15 (next page) SEM micrographs showing features of the lateral side of the head in different symphylan genera. Genera which do not show intrageneric variations are represented only by one species. (A) *Scutigerella cf. immaculata,* (B) *Hanseniella cf. nivea,* (C) *Scolopendrella notacantha,* (D) *Geophilella pyrenaica,* (E) *Parviapiciella balcanica*, (F) *Symphylella vulgaris,* (G) *Scolopendrellopsis (Scolopendrellopsis) microcolpa* (museum specimen num. 9449, MfNG), (H) *Scolopendrellopsis (Symphylellopsis) subnuda*. The dorsal margin of the cephalic lobes may be vertical and pointed forwards at the articulation head-mandible (*arrows*). Abbreviations: *cl*, cephalic lobe; *mb*, mandibular base; *sp*, spiracle; *To*, Tömösváry organ.

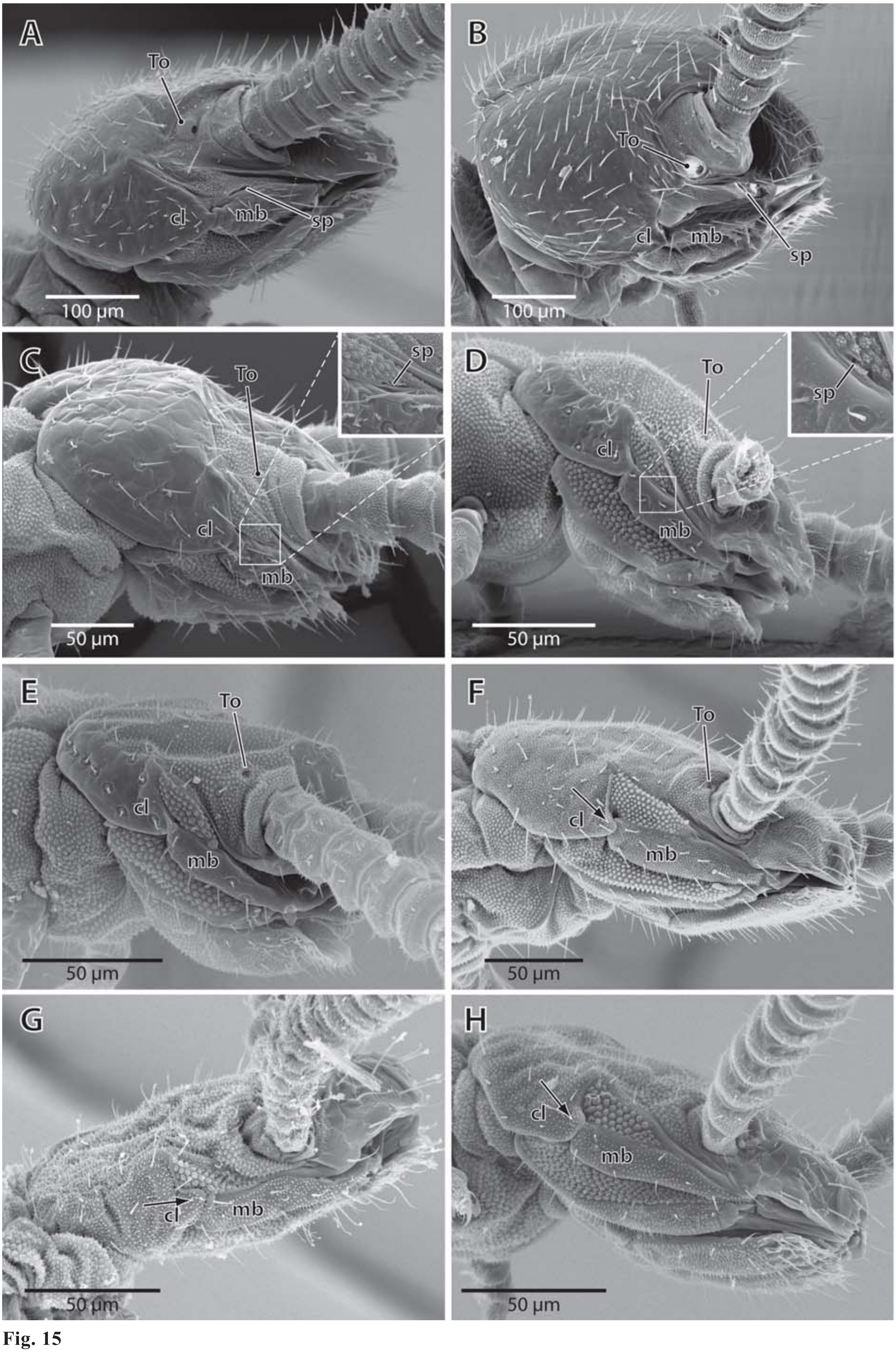
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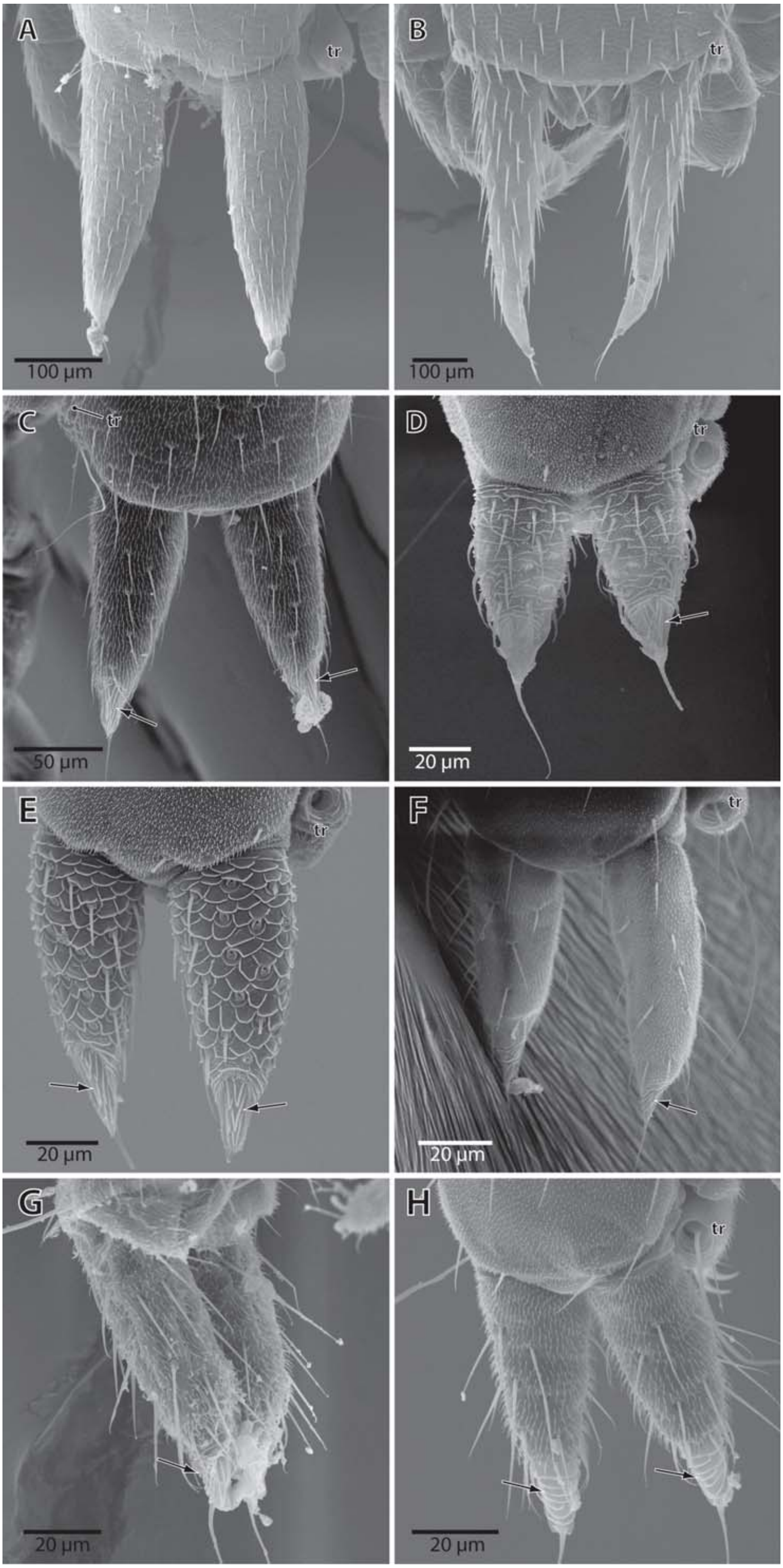
Fig. 15

Fig. 16 SEM micrographs of the cerci, with the sense calicles - or trichobothria - (*tr*) alongside, in different symphylan genera. (A) *Scutigerella cf. causeyae*, (B) *Hanseniella cf. nivea,* (C) *Scolopendrella notacantha,* (D) *Geophilella pyreanica*, (E) *Parviapiciella balcanica*, (F) *Symphylella vulgaris,* (G) *Scolopendrellopsis (Scolopendrellopsis) microcolpa* (museum specimen num. 9449, MfNG), (H) *Scolopendrellopsis (Symphylellopsis) subnuda*. Arrows point to the ridges of the terminal areas.



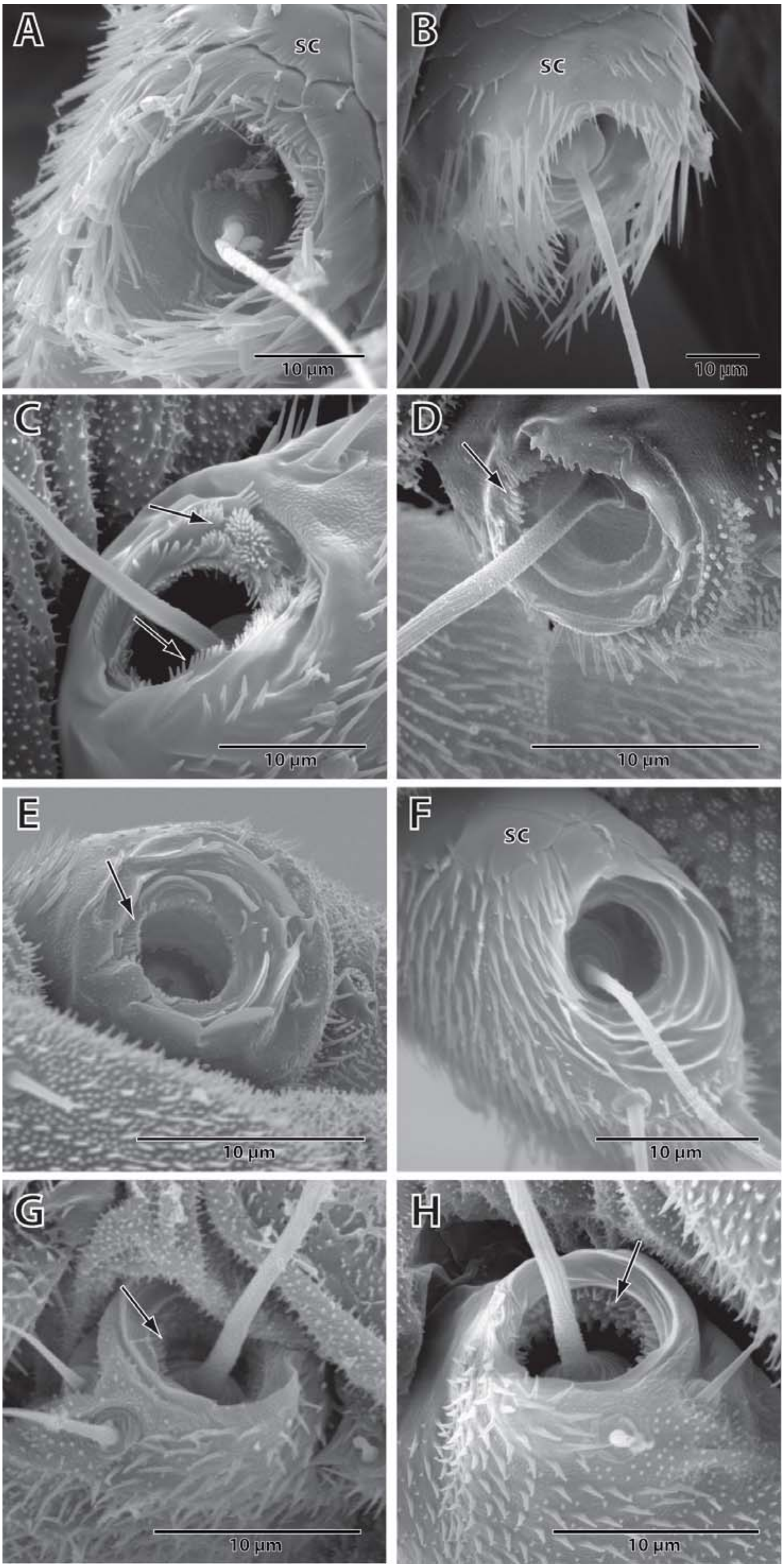


Fig. 17 SEM micrographs of the sense calicles, showing variation in the cuticular ornamentation by scales (*sc*) and in the fine structure of digitiform projections (*arrows*), in different symphylan genera. (A) *Scutigerella cf. causeyae*, (B) *Hanseniella cf. nivea,* (C) *Scolopendrella notacantha,* (D) *Geophilella pyrenaica,* (E) *Parviapiciella balcanica*, (F) *Symphylella vulgaris,* (G) *Scolopendrellopsis (Scolopendrellopsis) microcolpa* (museum specimen num. 9449, MfNG), (H) *Scolopendrellopsis (Symphylellopsis) subnuda*.

3. Key to the European genera of Symphyla

Based on the obtained results, a new key to the European genera of Symphyla is proposed, with the aim of facilitating determinations using SEM. Depending on the position of the mount, symphylan specimens do not expose all the scuta, but the head, the immediately following trunk segments and the last trunk segments with the cerci are generally visible. The proposed identification key focuses mainly in the features of the head and the first scuta. Since only the dorsal or the ventral side of the head may be fully exposed in the specimens, two keys have been elaborated for each side of the head, complemented with features of the cerci, which are generally visible from both sides. Both keys are exclusive for determination by SEM, and are applicable also to immature stages.
In addition, features of other European species not included in this study have been consulted in the literature to check the variation within the genera as accurately as possible.

KEY FOR THE DORSAL SIDE OF THE HEAD

1. Head more or less rounded (not more than 1,25 times longer than broad). Scuta well sclerotized in spread plates with rounded posterior margins (except *Hanseniella graeca*, which also shows posterior projections)…………………………………………………………………………………………....2

-. Head elongated (at least 1,25 times longer than broad), scuta either with pointed posterior projections, or reduced in size…………………......…………………………………………………………………….3

2. Head a bit longer than broad, somewhat heart-shaped. Central rod extends to the most posterior point of the head…………………………………………………………………….…………….***Scutigerella***

-. Head as broad as long or broader than long. Central rod with the posterior end in the middle of the head………………………………………………………………………………...……...….***Hanseniella***

3. Surface of the head capsule uniformly sclerotized,…………………………………………………....4

-. Surface of the head capsule heterogeneously sclerotized, with granulate areas and well sclerotized areas at the anterior part of the head, surrounding the central rod (at least its posterior half) and the posterior part plus the cephalic lobes ……………………………………………………………………...…….5

4. Surface of the head capsule smooth. Setae with a conspicuous ring-shaped basis. First scutum consisting of a pair of longitudinal rods. Cerci with longitudinal ridges in the apical part....................... ....……***Scolopendrella***

-. Surface of the head capsule completely pubescent. Frontal branches of the central rod V-shaped. Most frontal point of the head with a sclerite of smooth cuticle. First scutum transversally spread with a transversal row of setae. Cerci with transversal ridges in the apical part………..…….***Symphylella***

5. Surface of the sclerotized posterior sclerite + cephalic lobes pubescent. Cuticular reinforcement only in the posterior half of the central rod. Postantennal rods present. Cerci with transversal ridges in the apical part…………………………………………………………………….***Scolopendrellopsis***

-. Surface of the sclerotized posterior sclerite + cephalic lobes smooth. Median branches and central rod completely reinforced with cuticle, forming a cruciform structure in the middle of the head. Postantennal rods absent. Setae with a conspicuous ring-shaped basis. Cerci with a conspicuous scaly pattern and apical part with longitudinal ridges……………………………………........…....……6

6. Scuta without paired posterior projections. Cerci short (less than twice as long as broad)…… ……………………………………………………………………….…………………***Geophilella***

-. Scuta with paired digitiform posterior projections. Cerci long (more than twice as long as broad), sense calicles with folds similar to petals.....…...........………………..………........…..***Parviapiciella***

KEY FOR THE VENTRAL SIDE OF THE HEAD

1. Second maxillae with three anterior protuberances. Posterior margin clearly demarcated from the membrane behind them...2
-. Second maxillae without anterior protuberances; instead, a group of setae pointing forwards. Posterior end diffuse, not clearly demarcated with regards to the membrane behind them..............................3
2. Posterior margin of second maxillae pointed, with the exterior margin of each side very close to each other...***Scutigerella***
-. Posterior margin of second maxillae broad, with the exterior margin of each side far to each other...***Hanseniella***
3. Transversal groove of second maxillae present. Surface of second maxillare pubescent in the middle and smooth next to the exterior margins. Setae of the mouthparts with ring-shaped basis...4
-. Transversal groove of second maxillae absent. Surface of second maxillae entirely pubescent...6
4. Median groove of second maxillae short, only present in the middle.......................***Parviapiciella***
-. Median groove well developed along the entire the second maxillae.......................................5
5. Protuberance beside first-maxillary palp small. Cerci pubescent.......................***Scolopendrella***
-. Protuberance beside first-maxillary palp quite conspicuous. Cerci with a conspicuous scaly pattern ....***Geophilella***
6. First pair of legs reduced to little hairy knobs located exterior laterally to the posterior end of the cervical plate...***Symphylella***
-. First pair of legs well developed, 3-jointed and smaller than the rest, located at the posterior end of the cervical plate...***Scolopendrellopsis***

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Chapter 2

Comparative skeletomuscular anatomy of the head

Introduction

Morphological variation within Symphyla has been mainly observed in the trunk, especially in the number and morphology of scuta. These features have been the focus of a debate on a possible evolutionary trend in this group (Ravoux 1962 and Ribaut 1931 *vs.* Manton 1977 and Tiegs 1945; further information in the next chapter). In contrast, any variation in the anatomy of the head within this group has never been studied or even taken into consideration.

Skeletomuscular anatomy is an obvious source of information for comparing different taxa and for application in phylogenetic analysis (e.g. Wilson 2002). In particular, features of the cuticular cephalic endoskeleton and musculature of the mouthparts proved to be a very effective character-set for analyzing phylogenetic relationships among Arthropoda (e.g. Snodgrass 1950, Manton 1964, Koch 2001, Shultz 2007). Furthermore, the internal anatomy of the head frequently throws light upon unexpected phylogenetic relationships regarding the state of the trunk. Examples of these "evolutionary contradictions" are scutigeromorph centipedes (Manton 1958) and remipedian crustaceans (Fanenbruck 2003).

The internal anatomy of the head in Symphyla has been only partially studied in *Scutigerella immaculata* (Snodgrass 1950, Manton 1964, Ravoux 1975) and *Hanseniella agilis* (Tiegs 1940), both species belonging to the Scutigerellidae. Thus, there is a considerable gap in the knowledge of the Symphyla, especially for the Scolopendrellidae. In addition, the existing literature on symphylan sekeletomuscular anatomy largely lacks information about many non-mandibular muscles, such as the pharyngeal muscles and those related to the proximal arms of the second maxillae and to the head capsule. Additionally, some characters of the studied structures remain unclear in the existing literature. This is the case for the exoskeletal premandibular structure of the tentorium, the so called "fultural sclerites" (*sensu* Snodgrass 1950) which form the epipharyngeal, hypopharyngeal and transverse bars (*sensu* Koch 2003).

The presence of premandibular components of the tentorium is the key for translating the "swinging" movements of the tentorial complex onto the mandibular gnathal lobe to cause them to open. This mandibular mechanism has been considered the most convincing potential synapomorphy of Myriapoda (e.g. Edgecombe & Giribet 2002, Koch 2003), nevertheless their presence and function in Symphyla remain unclear. Some premandibular exoskeletal structures have been pointed out in *Scutigerella immaculata*, but their morphology and relation to the mandibular gnathal lobe are contradictory in the literature. Becker (1922 *fide* Verhoeff 1934) noted the presence of an articulation between the gnathal lobe and the epipharynx in the preoral cavity. Snodgrass (1952) added further details to this articulation, documenting the presence of a pair of sinuous epipharyngeal sclerites which have a mechanical relationship to a small process on the base of the mandibular gnathal lobe, a suggestive structure of the fultural sclerites of chilopods. Nevertheless, the isolation of this sclerite from the tentorial complex does not provide an explanation for an apparently abduction mechanism of the gnathal lobe as in Chilopoda (Koch 2003). Manton (1964) recorded a similar interaction between head and mandibular gnathal lobe without detailed explanations and illustrated it with schemes of histological sections. However, she introduced some confusion by mixing up the lateral process and the premandibular structure of the tentorium. She concluded that the “transverse processes” are required for the abduction of the gnathal lobe (referring to the lateral process of the tentorium in the present study; see below nomenclature). Soon after, Ravoux (1975) proposed a different transmission mechanism for the movements of the tentorium onto the gnathal lobe by the tangential contact between the “transverse apophysis” and the apodeme of the gnathal lobe. Neither Ravoux nor Manton mentioned any correlation between the movements of the tentorium and its articulation with the gnathal lobe, as Snodgrass did. More recently, Kluge (1999, 2000) illustrated a completely different premandibular tentorial structure in *Scutigerella carpatica*. It comprises a laminar structure above the gnathal lobes with a possible connection via condyle-like protuberances of the gnathal lobe. Unfortunately there is no further explanation in his text.

Contradictions in the literature and the possible lack of fultural sclerites in Symphyla hinder the consideration of this character as an unambiguous synapomorphy of Myriapoda (Edgecombe & Giribet 2002).

The present study provides data of the internal anatomy of the head in the Symphyla, specifically in three scolopendrellid species. In addition, two scutigerellid species are also studied, with the objective of providing further information and clarifying the contradictions in the literature by new methods in reconstruction of anatomical structures. Data on the internal anatomy of the head in the five species are compiled in a matrix of morphological characters for phylogenetic analysis. Finally, a preliminary hypothesis on the homology of muscles between Symphyla and other myriapod groups is proposed.

Material and methods

Adult specimens of two scutigerellid species, *Scutigerella causeyae* Michelbacher, 1942 from the Grunewald (Berlin, Germany) and *Hanseniella nivea* (Scopoli, 1763) from Češnjica (Slovenia), as well as three scolopendrellid species, *Scolopendrella notacantha* Gervais, 1839 from L´Estartit (Girona, Spain), *Symphylella vulgaris* (Hansen, 1903) from Pobla de Lillet (Barcelona, Spain), and *Scolopendrellopsis (Symphylellopsis) subnuda* (Hansen, 1903) from Montseny Natural Parc (Barcelona, Spain) were studied. Formaldehyde-fixed specimens of *Scolopendrella notacantha* (conserved in 70% ethanol) were donated by the Museo Nacional de Ciencias Naturales of Madrid (Spain) (identification number 20.06/88). Remaining specimens were collected at the indicated localities in 2008 by extraction from soil samples with a Kempson apparatus, fixed in Bouin's fluid (modification according Duboscq-Brazil) at room temperature for 24h and stored in 70% ethanol. Materials were postfixed with 1% osmium tetroxide for 1h at 4ºC, dehydrated in a graded acetone series and embedded into araldite via the intermedium propylenoxide. Complete series of semithin sections (0.5 µm) were made with a Jumbo-Diatome diamond knife on an Ultracut E microtome (Fa. Reichert), transferred onto slides and stained with 1% toluidine blue (modified according to Trump *et al*. 1961). Digital images of every 5 sections (2.5 µm distance between images) were taken with an Olympus BX50 light microscope equipped with a Colorview II digital camera and aligned with the software IMOD 3.11.5 (Mastronarde 1997). Three-dimensional reconstructions of the internal anatomy were produced using the software AMIRA 3.0 (TGS Template Graphics Software). All images and plates were edited with Adobe Photoshop and Adobe Ilustrator CS3 software.

Results

The following descriptions of the cephalic anatomy focus on the endoskeleton and musculature. Further to this, some structures of the first trunk segment which have a connection with the head's musculature are also described. Since the cephalic anatomy is symmetric, only one half of the head is depicted and unpaired structures are specified. Descriptions of the general anatomy are given for *Scutigerella causeyae* and only remarkable differences are depicted for the other species. In order to ease the understanding of the descriptions, a 3D-model of the head of *Scutigerella causeyae* is shown in figure 1 with a reference to series of histological sections shown in figures 4-8. Schemata for different muscle groups as well as histological sections depicting particular characters in each species are displayed in figures 2, 3, 10-21. For the muscles, a new terminology is proposed, and each muscle is described in table 1. Muscles were enumerated in ascending order, from anterior to posterior,

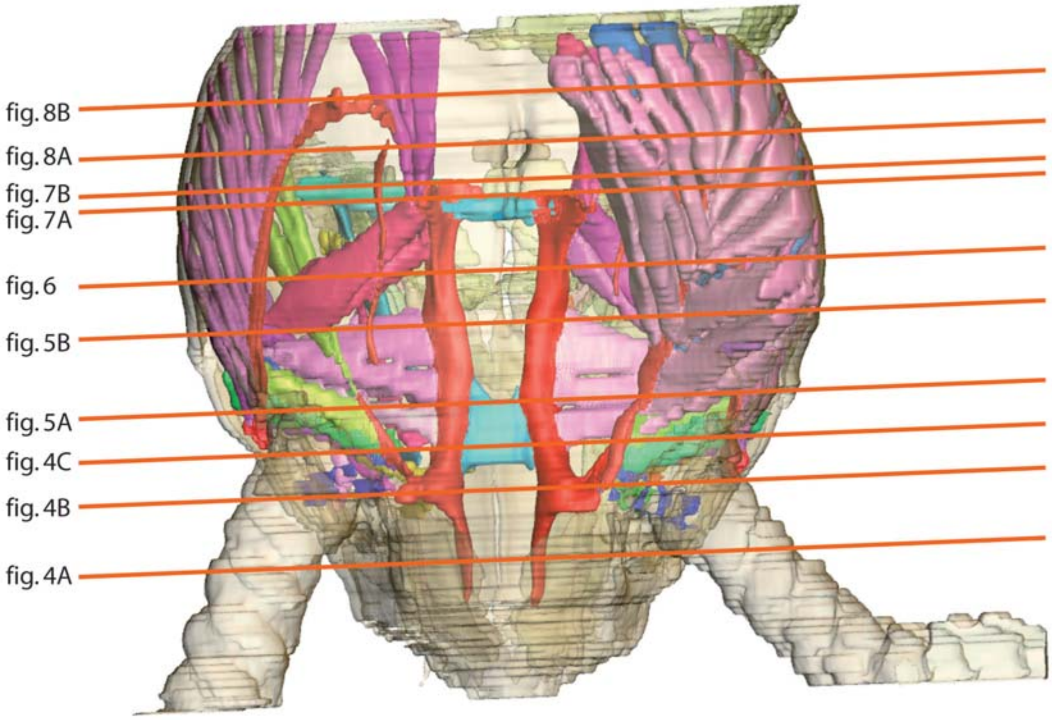


Fig. 1 3D Reconstruction of the head of *Scutigerella causeyae*, showing some structures of the inner morphology (see fig. 2). Transversal lines indicate the level of the displayed transversal sections (figs. 4-8).

mainly following the insertion points with the mouthparts and the head. Muscles composed of various units are designated with lower case letters (a, b, c…) from anterior to posterior. The description of the muscles is consistently based on a peripheral origin (O), normally in mouthparts and head capsule, and central insertion points (I) such as the tentorium or the pharynx. Significant differences between the results obtained and the descriptions of Manton (1964) and Ravoux (1975) are detailed.

The terminology for components of the tentorial complex follows Koch (2003), using the term “bars” for exoskeletal structures and “processes” for endoskeletal formations (table 2). Accordingly, the tentorial complex of the five studied genera of Symphyla corresponds to the groundplan of the myriapods: a paired posterior process, a paired hypopharyngeal bar, a paired epipharyngeal structure (a bar in other myriapods; discussed below), two frontal processes, and a paired lateral process. The presence of the transverse bar is addressed below. The general aspect of the tentorial complex of *Scutigerella causeyae* and *Symphylella vulgaris* is displayed in figure 22. Descriptive terminology of the mouthparts and the head follows Snodgrass (1952) and Manton (1964).

Scutigerella causeyae

Tentorial complex

The posterior process arises at the posterior end of the preoral chamber and extends backwards within the cephalic lumen, up to the ¾ the length of the head. It is compact at the anterior beginning (fig. 4C) but immediately posteriorly it becomes ventrally concave (fig. 5, 6). A dorsal lamina appears at the posterior end and forms the vertical terminal branch. The terminal apex ramifies into small structures among which the muscles Sp1 attach (fig. 7). Two tentorial bridges made of collagen fibres ("ligaments") interconnect the posterior processes medially (fig. 4C, 5A, 7A). The posterior tentorial bridge is not exclusively ligamentous (=collagenous) in nature, but it also comprises a cuticular branch from the interior side of each posterior process (fig. 7A, *arrow*). Anterior and posterior tentorial bridges are linked by an unpaired interpontal collagenous rod (fig. 6, *ipr*), which attaches on the anterior bridge in the middle of its dorsal surface and on the anterior margin of the posterior bridge. The interpontal rod supports the ventral pharyngeal dilator muscles Pv1 and Pv2. Between both tentorial bridges, the cerebral connection between the supral- and suboesophageal ganglia passes, always under the interpontal rod (fig. 6).

The hypopharyngeal bar arises as an anterior continuation of the posterior process, and does not support any muscle (fig. 4A, *hb*).

The premandibular lamina arises amidst the junction of the posterior process and the hypopharyngeal bar as a lateral projection which surrounds dorsally the apodeme of the mandibular gnathal lobe, with which it displays a short tangential contact (fig. 4B, *arrow*). This lateral projection is the common basis of three structures: the lateral process, frontal process and epipharyngeal lamina. The lateral process extends backwards and the frontal process upwards into the head lumen. Both are short branches that support several muscles and seem to be endoskeletal. A small ligamentous lamina connects the proximal part of the lateral process with the posterior process (fig. 4C, *arrow*). The epipharyngeal lamina is somewhat ventrally concave and extends above the mandibular gnathal lobe towards the tip of the clypeolabrum (fig. 4A, *el*). At the most anterior point, it connects to an unpaired sclerite via a less sclerotized bar. The lamina shows two cuticular reinforcements on both lateral margins, in the form of two exoskeletal bars. Each bar ventrally forms a longitudinal fold which articulates with a composite condylic outgrowth of the mandibular gnathal lobe (fig. 4A, *arrows*). The condylic outgrowth actually forms two condyles: the anterior one points forwards and outwards and articulates with the lateral fold of the epipharyngeal lamina; and the posterior one points backwards and inwards and articulates with the mesial fold of the epipharyngeal lamina.

Table 1

Head muscles in *Scutigerella causeyae*. Peripheral attachment is consistently described as origin (O), central attachment as insertion (I) of the muscles.

Abbreviation	Description (O = origin. I = insertion)	Ravoux (1975)	Manton (1964)	Figures
Mandibular basal segment				
MB1 a-e	O: medial wall, anterior. I: ventral border of the basis of the premandibular structure of tentorium. Four thick muscles parallel to each other.	-	6? (on fig. 59)	Fig. 4C
MB2 a,b	O: ventral lamina, middle; just anterior to MB3a. I: ligamentous lamina between tentorium's lateral and posterior processes.	143a	-	Fig. 4C
MB3 a,b	O: ventral lamina, middle; just posterior to MB2b and ventral to MB4. I: posterior part of the tentorium, under MB7c.	144	-	Fig. 4C, 5AB
MB4	O: ventral lamina, middle; just dorsal to MB3. I: most anterior part of tentorium's posterior process, on its ventral concavity.	140	7	Fig. 4C, 4B
MB5 a,b	O: medial wall, posterior. I: lateral process of tentorium. Parallel and ventral to MB6.	145	6	Fig. 5A, 4C
MB6 a,b	O: dorsal lamina . I: lateral process of tentorium.	143	3	Fig. 7A, 4C
MB7 a,b,c	O: ventral lamina, most posterior point. I: exterior border of the tentorium's posterior process. They lie in a flabellate form on the transversal plane.	147	4, 5	Fig. 5AB
MB8	O: posterior mandibular apodeme, ventral side of the lamina. I: posterior part the tentorium's posterior process.	146	2	Fig. 6
MB9	O: posterior mandibular apodeme, dorsal side of the lamina. I: terminal dorsal branch of the tentorium's posterior process.	146´	2	Fig. 6, 7A
Mandibular gnathal lobe				
ML1 a-e	O: antero-lateral wall of the cephalic lobe, superior plane; three more ventrally (a, b, c) and two more dorsally (d, e). I: anterior part of gnathal-lobe apodeme.	149c	8	Fig. 5, 6, 7A
ML2 a-d	O: postero-lateral wall of the head, superior plane. I: posterior part of gnatal-lobe apodeme, exterior side.	149b	8	Fig. 6, 7, 8
ML3 a-e	O: posterior wall of the head, superior plane. I: posterior part of gnathal-lobe apodeme, interior side.	149a	8	Fig. 6, 7, 8
ML4 a-i	O: lateral wall of the head, inferior plane. I: gnathal-lobe apodeme, exterior side.	149d	8	Fig. 5B, 6, 7, 8
ML5	O: posterior wall of the head, inferior plane. I: distal part of gnathal-lobe apodeme, interior side.	149d	8	Fig. 7, 8
ML6	O: posterior wall of the head, under ML5 and ML7. I: distal part of gnathal-lobe apodeme, interior side.	149d	8	Fig. 7, 8
ML7	O: posterior wall of the head, inferior plane. I: distal part of gnathal-lobe apodeme, interior side.	149d	8	Fig. 7, 8
Trachea				
T1-8	O: lateral and postero-lateral wall of the head, between both planes of ML. I: exterior side of the trachea.	148	1	Fig. 5, 6, 7, 8
First maxilla				
Mi1 a,b	O: interior side of the lacinia. I: ventral hollow of tentorium, most posterior part.	133´	II (V on fig. 58)	Fig. 4B, 6.
Mi2	O: ventral inner margin of the galea. I: anterior tentorial bridge.	137	-	Fig. 4B
Mi3	O: interior margin, anterior part. I: conjunctive-tissue lamina between tentorium's lateral- and posterior process.	130	-	Fig. 4B
Mi4 a,b,c.	O: beside exterior margin, anterior part, immediately behind the palp. I: beside interior margin, medial part. Three parallel muscles which lie by the surface of the first maxilla. Intrinsic muscle.	132	XI, (III)?	Fig. 4B, 5.
Mi5 a,b,c	O: exterior margin, medial part. I: ligamentous lamina between tentorium's lateral- and posterior process.	135a	IV, V, VI	Fig. 4C, 4A
Mi6	O: beside interior margin, medial part. I: ligamentous lamina between tentorium's lateral- and posterior process.	131	-	Fig. 5B, 4C
Mi7	O: beside interior margin, posterior part. I: tentorium's posterior process, anterior part.	134	-	Fig. 7A, 5B
Mi8	O: cardo, dorsal inner side. I: distal point of tentorium's lateral process.	135b	VII	Fig. 5B-7A
Mi9 a,b,c	O: interior margin, posterior part, beside Mi7. I: posterior part of the tentorium, more anterior than Mi10.	-	-	Fig. 6
Mi10	O: cardo´s apodeme. I: posterior part of the tentorium.	141	IX	Fig. 7
Mi11	O: cardo´s apodeme. I: posterior part of the tentorium.	150	VIII	Fig. 7
Mi12 a,b	O: proximal beginning of the galea, inner margin. I: lateral side of the head.	139	I	Fig. 4B-6B
Mi13 a,b,c	O: exterior margin, medial part. I: lateral side of the head, one (a) more anterior and two (b, c) more posterior.	136	X	Fig. 5B-7A

Table 1 (continued)

Abbreviation	Description (O = origin. I = insertion)	Ravoux (1975)	Manton (1964)	Figures
Second maxilla, anterior plate				
Mii1	O: anterior part, beside exterior margin. I: ventral side of tentorium, beside anterior tentorial bridge.	126	-	Fig. 4A-C
Mii2	O: anterior part, interior margin. I: tentorium, ventral side, beside anterior tentorial bridge.	127	-	Fig. 4A-C
Mii3	O: medial part, interior margin. I: tentorium, interior side, beside anterior tentorial bridge.	128	-	Fig. 4B
Mii4 a,b	O: medial part, interior margin, behind Mii3. I: tentorium, ventral side, beside anterior tentorial bridge.	129	only illustrated	Fig. 4B, C
Mii5	O: medial part, exterior margin. I: ligamentous lamina between tentorium's lateral- and posterior process, ventral side.	124	only illustrated	Fig. 4C
Mii6	O: posterior part, interior margin. I: anterior tentorial bridge, ventral side.	121	only illustrated	Fig. 5
Second maxilla, proximal arm				
B1 a,b,c	O: anterior part of proximal arm. I: inner margin of second-maxillar plate.	125	only illustrated	Fig. 4C, 5A
B2 a,b,c	O: anterior part. I: posterior margin of the head.	138+122	-	Fig. 5A-8B
B3 a,b,c	O: medial part. I: tentorium's posterior process, exterior side, beside anterior tentorial bridge.	-	-	Fig. 4C-5B
B4	O: medial part, behind B3. I: tentorium's posterior process, exterior side, beside anterior tentorial bridge.	-	-	Fig. A-6
B5	O: posterior distal point. I: tentorium's posterior process, most posterior part.	-	-	Fig. 7A
B6	O: posterior distal point. I: tentorium's posterior process, terminal branch.	-	-	Fig. 7B
B7	O: posterior distal point. I: posterior margin of the head.	-	-	Fig. 8
Hypopharyx				
H1	O: ventral margin of the hypopharynx. I: ventral side of tentorium, beside anterior tentorial bridge. Parallel to the Mii1 and Mii2.	-	hypoph. retractor	Fig. 4A-C
H2	O: lateral margin of the hypopharynx. I: I: tentorium's posterior process, ventral hollow. Parallel to the Mi1.	133	long hypoph. ret.	Fig. 4B-5B
Antenna				
A1	O: exterior part of basis. I: median septum, ventral side of the branch.	A1	antennal to tent. apod.	Fig. 5A-8A
A2 a,b	O: posterior part of basis. I: median septum, dorsal side of the branch.	A1´	”	Fig. 4C-8A
A3	O: exterior part of basis. I: median septum, frontal side of the branch. Small muscle which passes between A2a and A2b.	-	-	Fig. 5-7
A4 a,b	O: exterior part of basis. I: tentorium's posterior process, terminal branch.	-	-	Fig. 5, 6
A5 a,b,c	O: anterior part of basis. I: tentorium's posterior process, exterior side, very spread on the medial part.	A2	antennal to tent. apod.	Fig. 4B-6
A6	O: interior part of basis. I: tentorium's posterior process, interior side of the medial part, beside A5b	A2´	”	Fig. 4B-5B
A7	O: exterior part of basis. I: tentorium's posterior process, exterior side of the medial part, surrounded by A5c.	A3	”	Fig. 5A-6
Suspensor muscles of the tentorium (S): a = anterior, p = posterior, d = dorsal, v = ventral				
Sa1-3 (a,b,c)	O: dorsal wall of the head, anterior part, more exterior. I: frontal process of the tentorium.	sa1, sa2	tentorial protractor	Fig. 4A, B
Sa4 a-d	O: dorsal wall of the head, anterior part, more interior. I: frontal process of the tentorium.	sa3	tentorial retractor	Fig. 4C
Sd1	O: dorsal wall of the head, medial part, more exterior. I: tentorium's posterior process, terminal branch.	-	-	Fig. 7A
Sd2	O: dorsal wall of the head, medial part, more interior. I: tentorium's posterior process, interior side of the terminal branch, among the Pl3 muscles.	-	-	Fig. 7A
Sp1 a,b,c	O: posterior margin of the head, immediately under the ML8. I: tentorium's posterior process, among small laminae of the terminal brach.	116	-	Fig. 7B-8B
Sp2 a,b	O: arthrodial membrane between head and trunk. I: tentorium's posterior process, exterior side of the posterior part.	-	-	Fig. 7B-8B
Sp3 a,b	O: first trunk segment, tergal area (Ravoux 1962). I: tentorium's posterior process, posterior side.	55 Ravoux 1962	Vent.long. (up. sector)	Fig. 8
Sp4 a,b	O: third trunk segment, tergal area (Ravoux 1962). I: posterior tentorial bridge.	56 Ravoux 1962	”	Fig. 7, 8
Sp5 a,b	O: apodeme of the second pair of legs. I: tentorium's posterior process, ventral side of the posterior part.	LV_{0-II}	Vent.long. (low. sect)	Fig. 6-8
Sv1	O: apodeme of the first pair of leg. I: tentorium's posterior process, very spread on the ventral side just behind the anterior tentorial bridge.	-	-	Fig. 6
Sv2 a,b,c	O: anterior sternal plate of the opposite half of the first trunk segment. I: tentorium's posterior process, ventral side of the medial part.	-	-	Fig. 6

Table 1 (continued)

Abbreviation	Description (O = origin. I = insertion)	Ravoux (1975)	Manton (1964)	Figures
Pharyngeal dilators (P); d = dorsal, v =ventral, l =lateral				
Pd1-3 (a-e)	O: dorsal wall of the head, anterior part. I: pharynx, dorsal side of the anterior part. Three groups of five muscles each.	-	Oesophagal dilators	Fig. 4A-5A
Pd4	O: median septum. I: pharynx, dorsal side of the posterior part.	-	-	Fig. 7
Pl1	O: frontal process of the tentorium. I: pharynx, lateral side of the most anterior part. Group of several little muscles.	-	only illustrated	Fig. 4B
Pl2	O: frontal process of the tentorium. I: pharynx, lateral side of the anterior part, more posterior than Pl1. Group of several little muscles.	-	-	Fig. 4C
Pl3 a-e	O: tentorium's posterior process, interior side of the terminal branch. I: pharynx, lateral side of the posterior part.	-	-	Fig. 6-7A
Pv1	O: basis of the interpontal rod. I: pharynx, ventral side of the most anterior part. Unpaired muscle.	apd	-	Fig. 4B, C
Pv2 a-h	O: along the whole interpontal rod. I: pharynx, along the ventral side. Eight muscles unpaired	ppd	-	Fig. 4C-6
Head capsule				
C1 a,b	O: dorsal wall of the head, more exteriorly. I: dorsal wall of the head, more posterior and interior. Intrinsic muscle of the head capsule.	-	-	Fig. 8
C2 a-e	O: second trunk segment, tergal area. I: medial septum, posterior side of the branch.	LDi A, B	Dorsal long. muscle	Fig. 8B
C3	O: posterior part of the cervical plate. I: posterior margin of the head.	57a Ravoux 1962	-	
C4 a,b	O: most posterior part of the cervical plate. I: posterior margin of the head, same insertion point as C3.	57a Ravoux 1962	-	Fig. 7
C5	O: anterior sternal plate of the first trunk segment. I: posterior margin of the head, just under C3+C4.	58b Ravoux 1962	-	Fig. 7B
C6	O: trunk. I: posterior margin of the head, just under C5.	-	-	

Mandibular basal segment

The mandible of the Symphyla consists of two sclerites, a proximal one – the mandibular basal segment – and a distal one – the mandibular gnathal lobe. The mandibular basal segment, or mandibular base, is a long and concave shovel that forms the ventrolateral side of the head and closes itself distally (fig. 4A, *mb*). It is surrounded above and beneath by two flexible sleeves of conjunctival cuticle. At the posterior part, there is a dorsal lamina which hinges with a condyle of the cephalic lobe, forming the articulation head-mandible (fig. 5A, *arrow*). A ventral lamina spreads along the entire mandibular base (fig. 4B-5A, *vl*), and anteriorly supports the ventral apex of the gnathal lobe (fig. 4A, *vl*). Both laminae serve as extra-attachment surfaces for several muscles. At the posterior end of the mandibular base, a posterior mandibular apodeme is present (fig. 5B, *pma*). This apodeme arises proximally as a thick rod and projects backwards, forming a distal lamina (fig. 6, *pma*). It has no direct contact with the mandible base, since it arises directly from the arthrodial membrane immediately behind it. However, its proximity to the posterior apex must effect the mobility of the mandible.

Mandibular gnathal lobe

The mandibular gnathal lobe is moveably separated from the mandibular base. It is joined to the rest of the body via three structures:

1. postero-ventral articulation with the mandibular base, hinged to the anterior end of the mandibular-base's ventral lamina.
2. the previously mentioned condyle-like protuberances on the dorsal surface of the molar plate which match with both lateral and mesial folds of the tentorium's epipharyngeal lamina.
3. the long apodeme of the gnathal lobe which spans the cephalic lumen up to ¾ the length of the head. It arises as a thin rod with an exterior lateral hollow (fig. 4C, *gla*) and towards the posterior end becomes laminar with an irregular rounded terminal margin. It receives a great deal of large adductor muscles (ML muscles) from the head capsule that are distributed into two planes. There is also a tangential contact between the gnathal-lobe apodeme and the common basis of the premandibular structures of the tentorium (fig. 4B, *arrow*).

Trachea

The trachea opens in the articular membrane immediately above the mandibular base (fig. 4B, right, *tr*), and continues backwards into the cephalic lumen, passing between both planes formed by the ML muscles. It curves at the posterior part of the head and continues forwards. At the anterior origin, the trachea has a strong appearance, with thick cuticula (fig. 4C), but towards the end it becomes thinner (fig. 8B) and ramifies into small branches which disappear in the lumen (fig. 7, 8, *rtr*). Nine large tracheal muscles insert on the anterior part of the trachea that originate from the lateral wall of the head capsule, between both planes of the gnathal-lobe muscles.

First maxilla

The most posterior part of the first maxilla – the cardo (*sensu* Manton 1964) – forms a shovel from which dorsal wall the muscles Mi8 arise (fig. 7A). The dorsal margin of the cardo projects anteriorly, forming a short apodeme where the muscles Mi10 and Mi11 are attached (fig. 7A, *ca*). The whole construction of the first maxilla shows great mobility enabled by the several muscles that it receives from the tentorium's posterior process and the lateral wall of the head. Strikingly the muscle Mi9 has not been described thus far. It comprises three remotor muscles of the posterior part (fig. 6, right), which are possibly antagonists to the promotors of the anterior part – mainly Mi5 and Mi13. Their presence seems to be essential in completing the opposition to the pull of the anterior part of the maxilla, as explained by Manton (1964). The most anterior parts –galea and lacinia – also have extrinsic muscles – Mi1, Mi2 and Mi12 – that cause adduction of these parts. The intrinsic muscles Mi4 arise in the same point, very close to the first-maxillary palp.

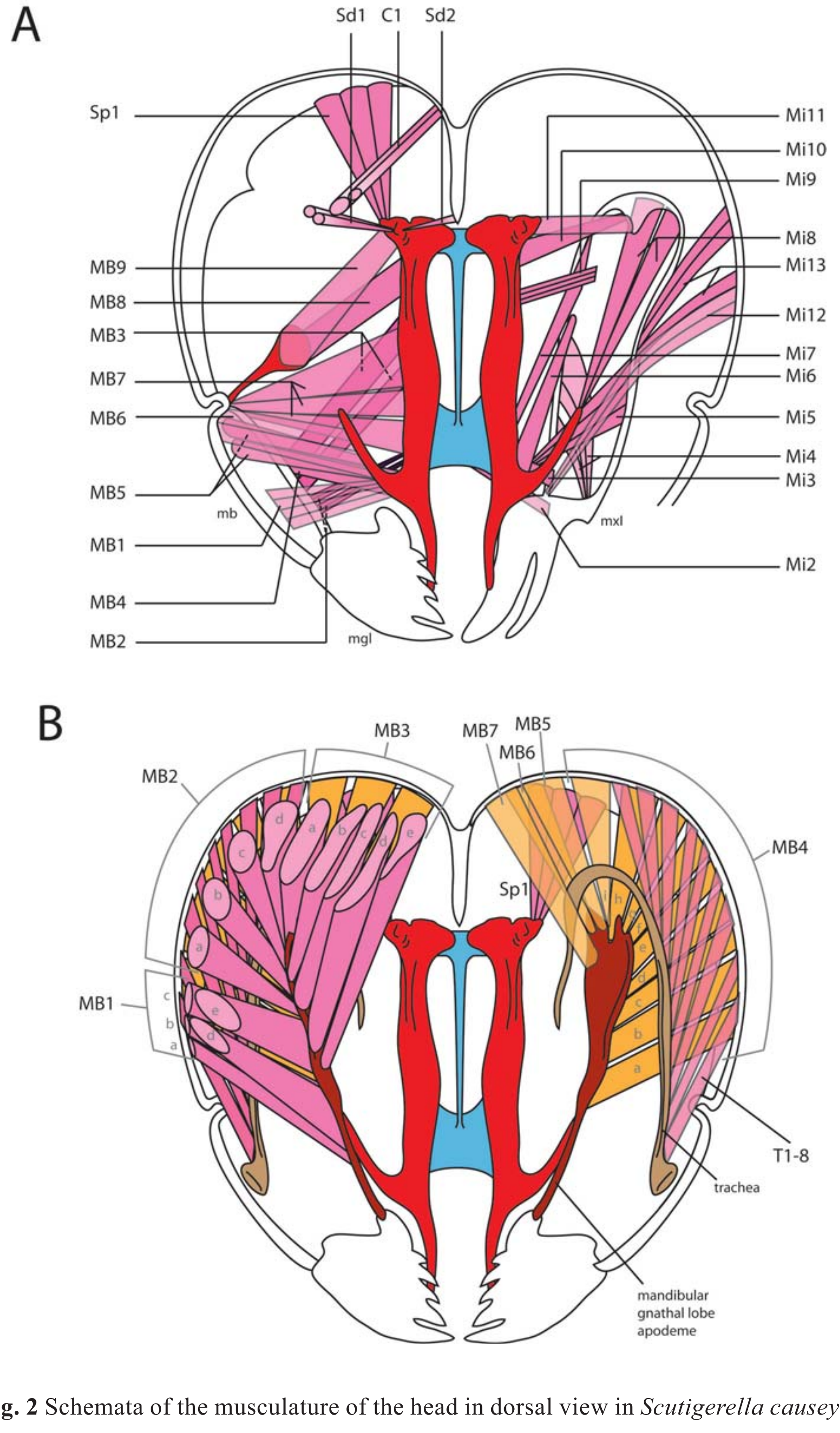


Fig. 2 Schemata of the musculature of the head in dorsal view in *Scutigerella causeyae*. Only the postmandibular part of the tentorium (in red) is depicted. A, mandibular base (*mb*) and first maxilla (*mxI*) with their related muscles (MB and Mi), and other suspensor muscles (see descriptions in table 1). B, mandibular-gnathal-lobe apodeme (in maroon) and its related muscles (ML), and tracheal apodeme (in brown) with its muscles (T).

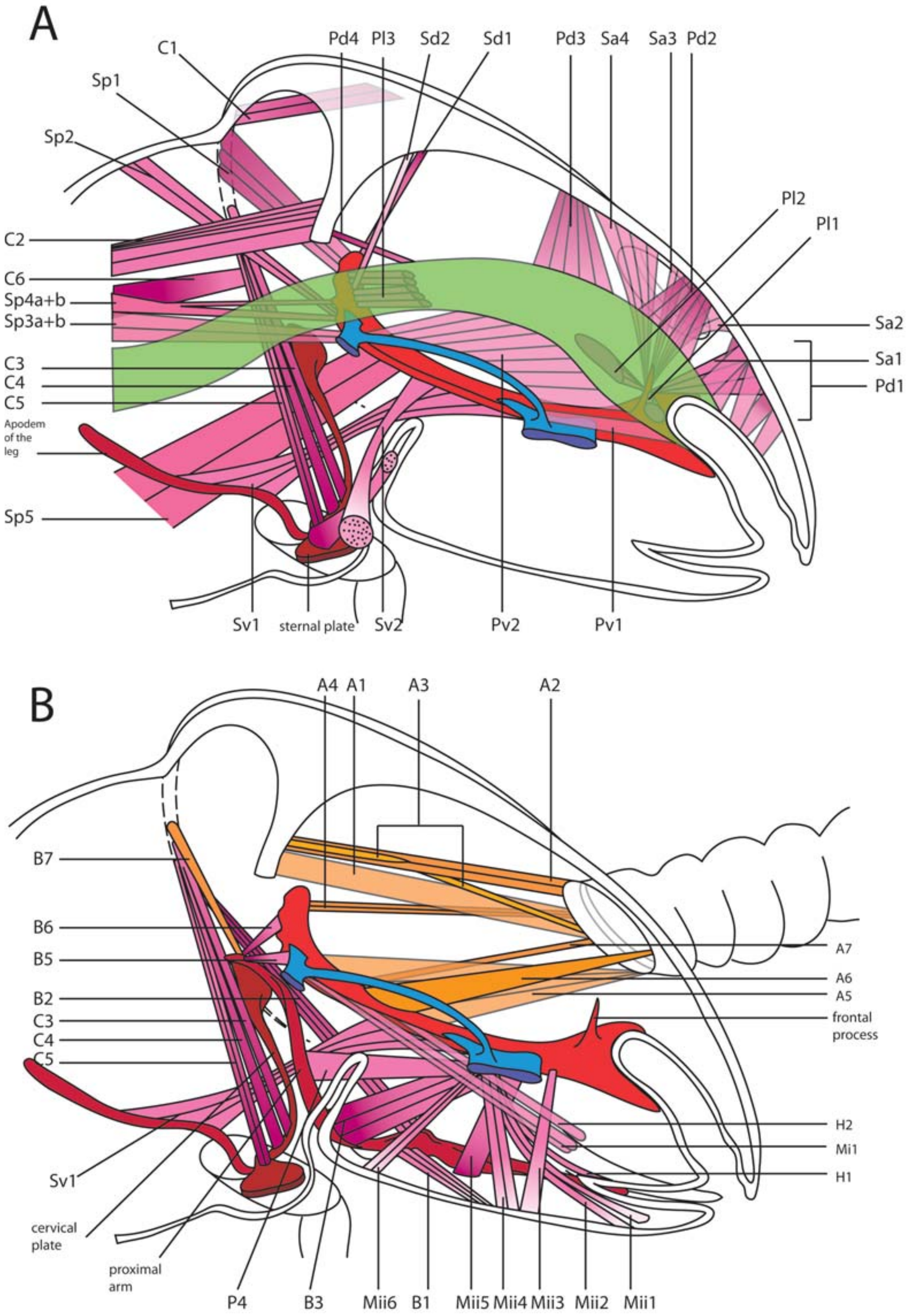


Fig. 3 Schemata of the musculature of the head in lateral view in *Scutigerella causeyae*. Only the postmandibular part of the tentorium (in red) is depicted. A, pharynx (in green), pharyngeal dilators muscles (P), suspensor muscles of the tentorium (S) and intrinsic and extrinsic musculature of the head capsule (C). B, antennal muscles (A), muscles of the anterior plate of the second maxilla (Mii), muscles of the proximal arm of the second maxilla (B) and other muscles (see descriptions in table 1).

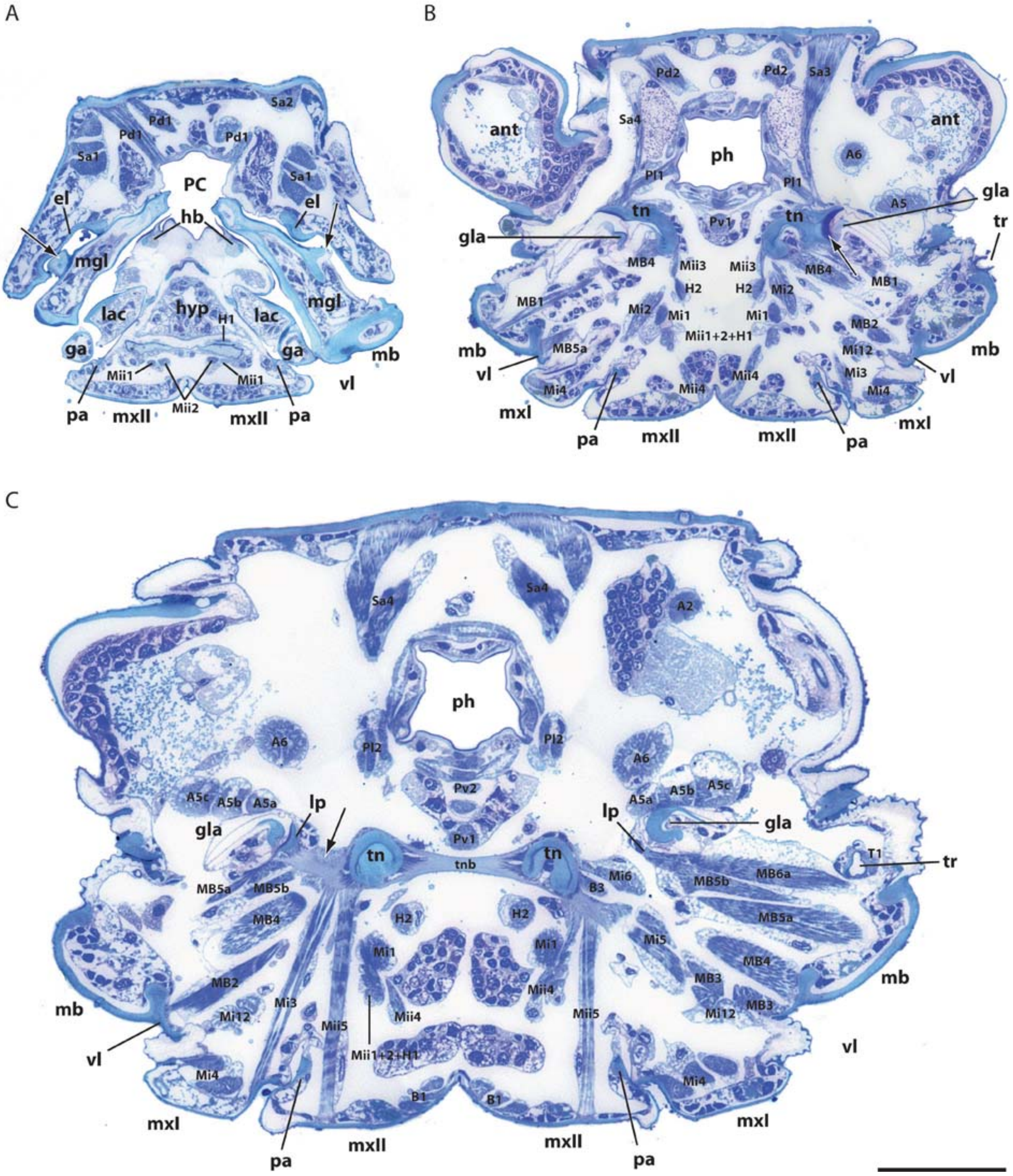


Fig. 4 *Scutigerella causeyae,* transversal sections of the head at the levels indicated on fig. 1. Muscles indicated by abbreviations listed in table 1. *Arrows*: in A, condyle-like protuberances of the mandibular gnathal lobe; in B, tangential contact between the lateral projection of the tentorium and the gnathal-lobe apodeme; in C, ligamentous lamina between the basis of the lateral process and the posterior process. Abbreviations: *Ant*, antenna; *el*, epipharyngeal lamina; *ga*, galea; *gla*, gnathal-lobe apodeme; *hyp*, hypopharynx; *lac*, lacinia; *lp*, lateral process of the tentorium; *mb*, mandibular base; *mgl*, mandibular gnathal lobe; *mxI*, first maxilla; *mxII*, anterior plate of the second maxilla; *pa*, proximal arm of the second maxillae; *PC*, preoral cavity; *ph*, pharynx; *tn*, tentorium (posterior process); *tnb*, anterior tentorial bridge; *tr*, trachea; *vl*, ventral lamina of mandibular base. Scale bar = 50 µm.

Fig. 5 & 6 *Scutigerella causeyae,* transversal sections of the head at the levels indicated on fig. 1. Muscles indicated by the abbreviations listed in table 1. *Arrow*, articulation point between the mandibular base and the cephalic lobe. Abbreviations: *dl*, dorsal lamina of the mandibular base; *gla*, gnathal-lobe apodeme; *ipr*, “interpontal rod”; *lp*, lateral process of the tentorium; *mb*, mandibular base; *Mi S*, salivary duct of the first maxilla;

Fig. 5

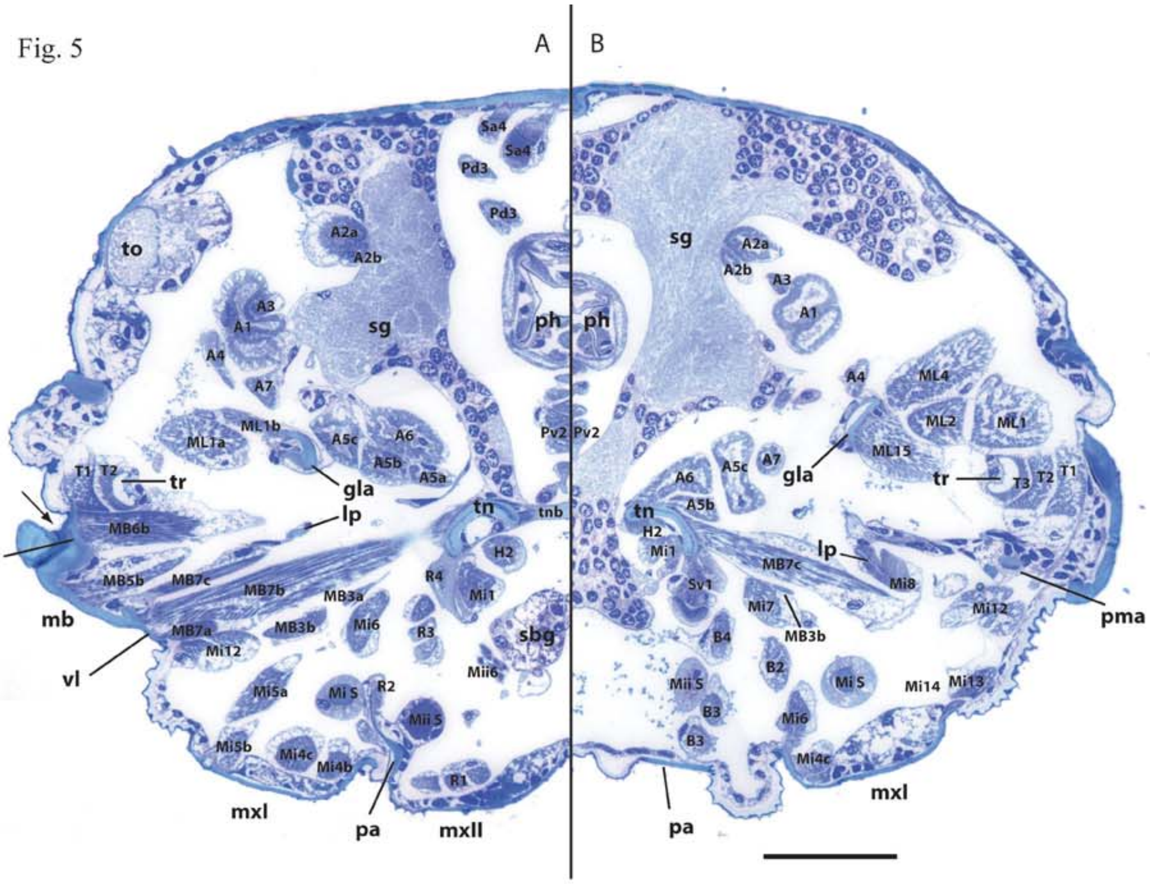
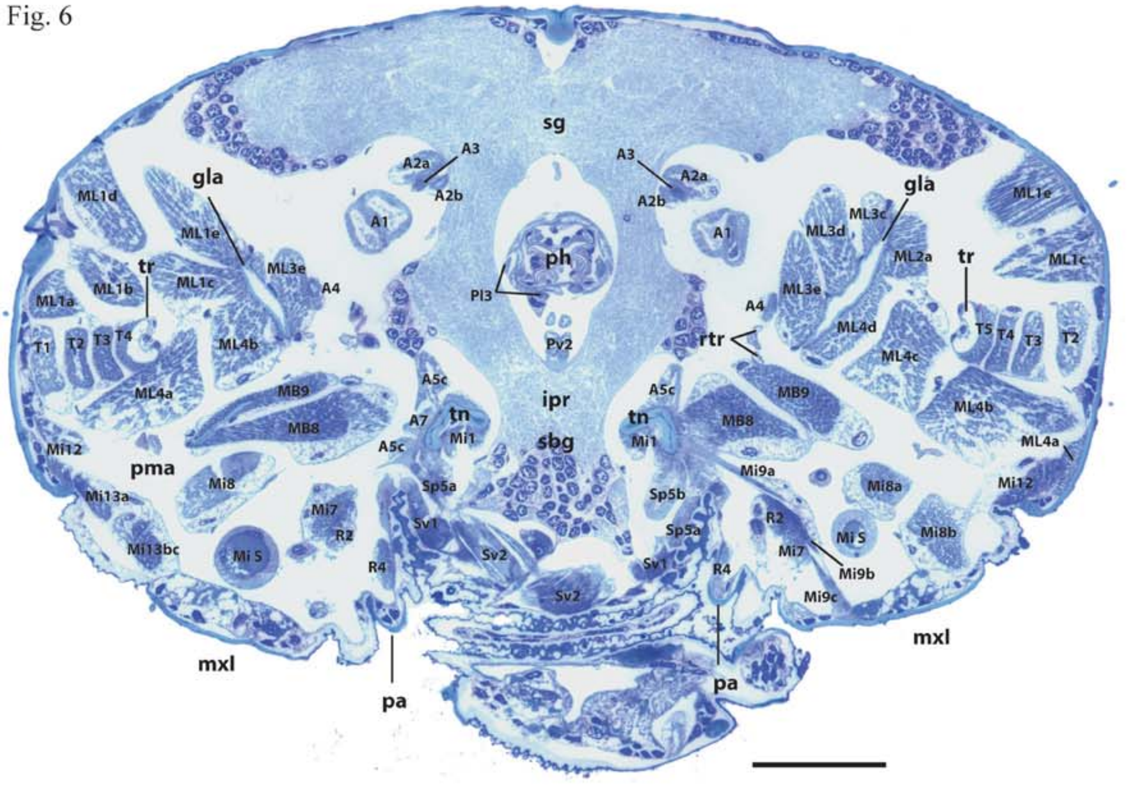


Fig. 6



Mii S, salivary duct of the second maxilla; *mxI*, first maxilla; *mxII*, anterior plate of the second maxilla; *pa*, proximal arm of the second maxilla; *ph*, pharynx; *pma*, posterior mandibular apodeme; *rtr* ramifications of the tracheae; *sbg*, suboesophageal ganglion of the brain; *sg*, supraoesophageal ganglion of the brain; *tn*, tentorium (posterior process); *tnb*, anterior tentorial bridge; *to*, Tömösváry's organ; *tr*, trachea; *vl*, ventral lamina of mandibular base. Scale bars = 50 µm.

Fig. 7

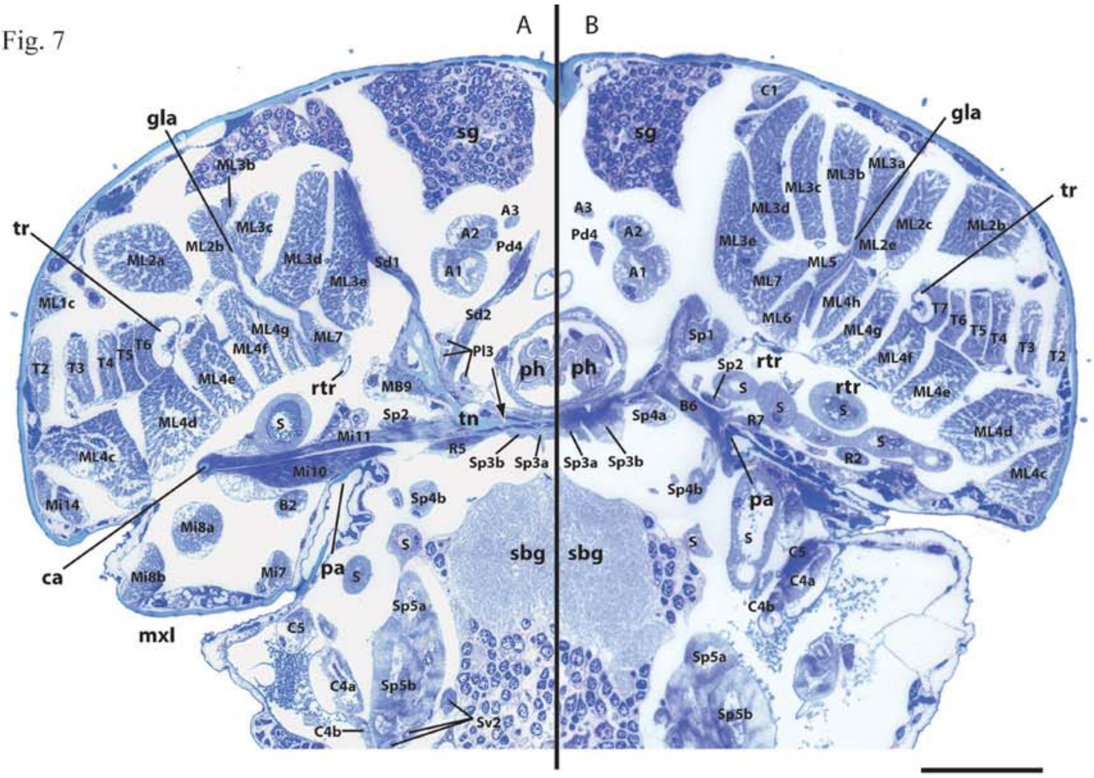


Fig. 8

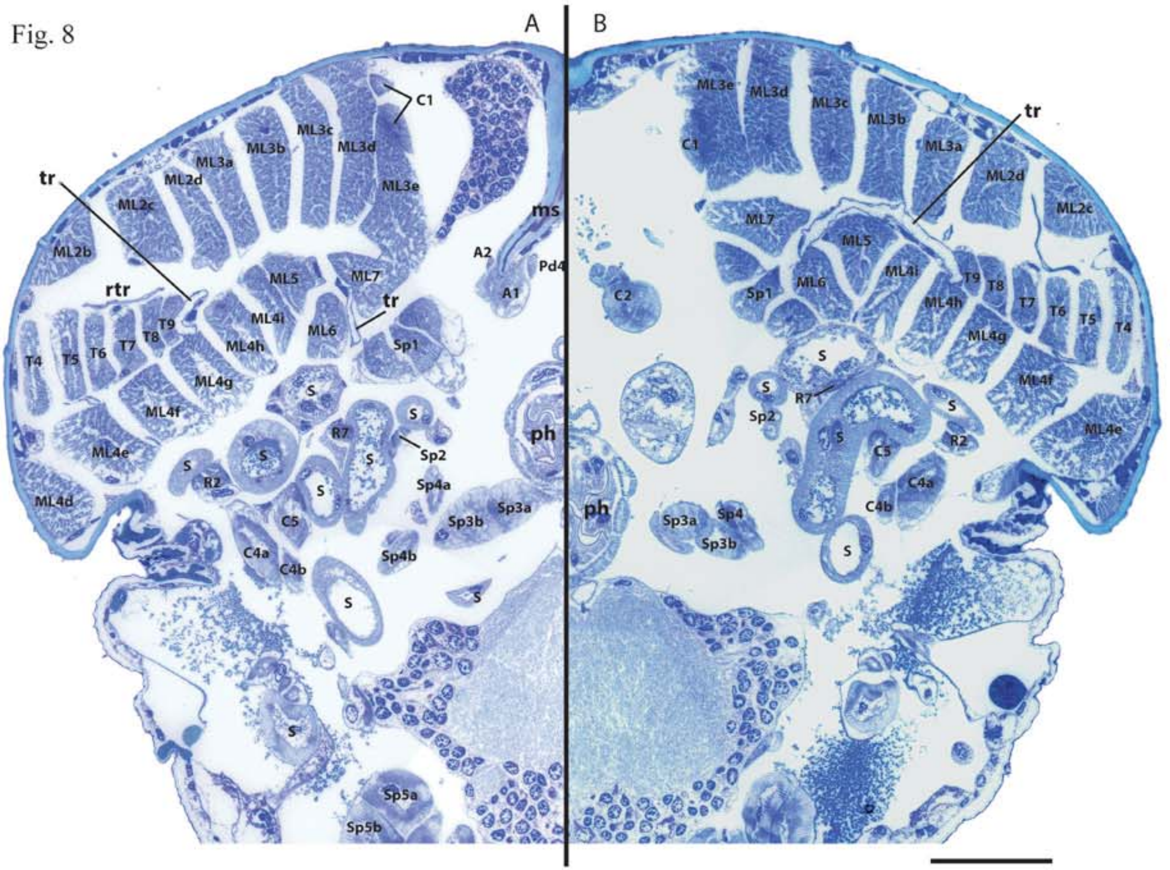


Fig. 7 & 8 *Scutigerella causeyae,* transversal sections of the head at the levels indicated on the fig. 1. Muscles indicated by the abbreviations listed in table 1. *Arrow*, cuticular reinforcement of the posterior tentorial bridge. Abbreviations: *ca*, "cardo apodeme" (distal point of the curvature of the cardo); *gla*, gnathal-lobe apodeme; *ms*, median septum; *mxI*, first maxilla; *pa*, proximal arm of the second maxilla; *ph*, pharynx; *rtr* ramifications of the tracheae; *S*, salivary duct; *sbg*, suboesophageal ganglion of the brain; *sg*, supraoesophageal ganglion of the brain; *tn*, tentorium (posterior process); *tr*, trachea. Scale bars = 50 µm.

Second maxilla

The second maxilla consists of a main anterior plate and a proximal arm, which is visible from the outside. Strikingly, the anterior origin of the proximal arm is much more anterior, at almost the same level as the anterior plates of the second maxilla (fig. 6A, *pr*). The sclerotisation of the second maxilla is differentiated into the anterior plate and the proximal arm, which extends along to the exterior margin of the anterior plate backwards and separates from it as the proximal arm *sensu stricto* (fig. 9).

The anterior plate of the second maxilla is located in the ventral part of the head and forms a functional labium. Several extrinsic muscles (Mii) are attached to the tentorium at the level of the anterior tentorial bridge.

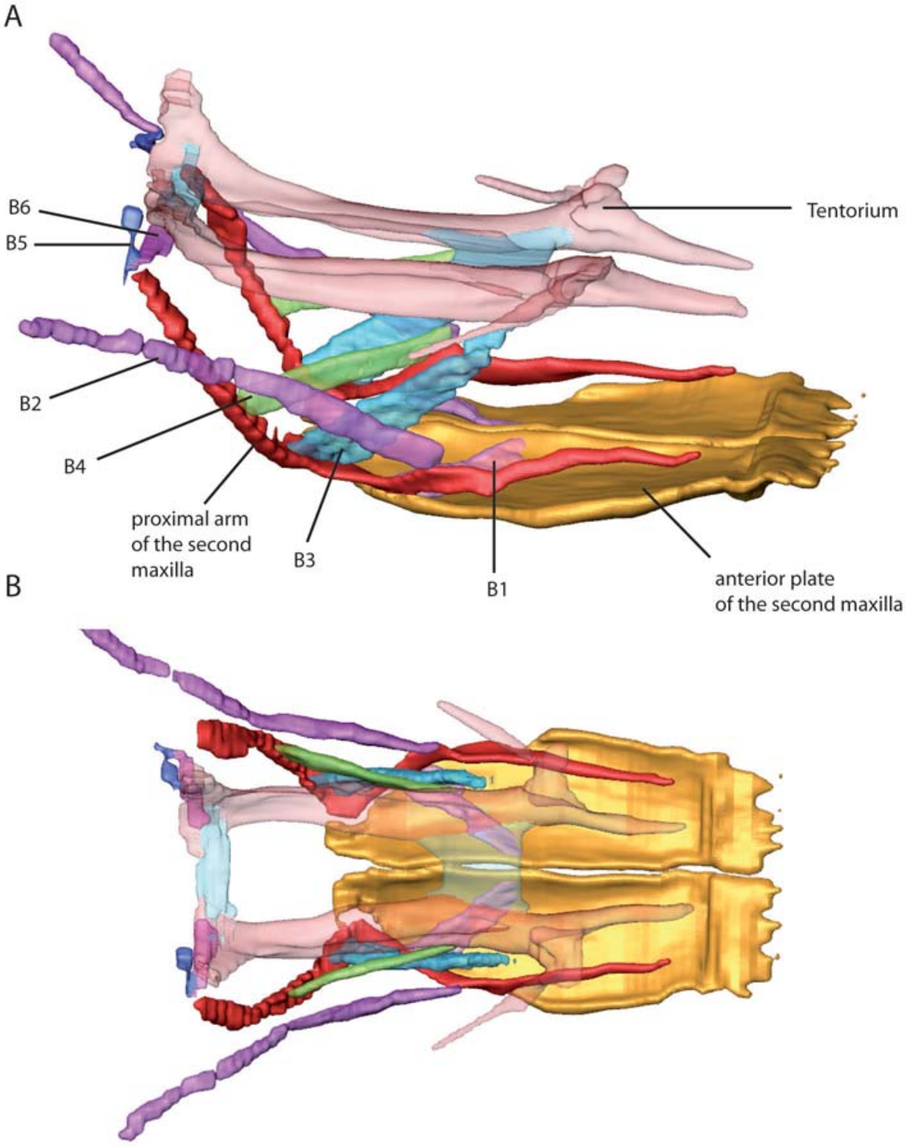


Fig. 9 3D Models showing the proximal arms (in red) of the second maxillae of *Scutigerella causeyae*, with its related muscles B1-6. The anterior plates of the second maxillae and the tentorium are also shown (in yellow). Muscles are indicated by the abbreviations listed in table 1, and their colours are the same in both diagrams. A: lateral view. B: dorsal view.

At the anterior part, the proximal arm seems to be associated with the common draining channel of both salivary ducts – corresponding to the first and second maxillae – (fig. 5A). It continues backwards as part of the ventral wall of the head. Finally it enters into the head-lumen through an invagination of the cuticle, up to level of the posterior end of the tentorium (fig 7). It is part of the superior surface of this hollow, and the inferior surface is formed by the cervical plate. Several extrinsic muscles connect the proximal arm of the second maxilla with the anterior plate – B1 – , with the tentorium at the level of the anterior tentorial bridge – B3, B4 – and the posterior one – B5, B6 –, and with the margin of the head capsule – B2, B7 (fig. 9). It is important to stress that the B1 is not an intrinsic muscle of the anterior plate, as it has been considered thus far, since it seems to play a roll in pulling the proximal arm, posibly as an antagonist muscle of B2.

Cervical plate and muscles of the head capsule.

The cervical plate (*sensu* Snodgrass 1952) arises in the hollow where the proximal arm of the second maxilla terminates. Their extremes seem to be in contact, but there is no articulation between them. The cervical plate extends backwards to the first pair of legs, and receives abductor muscles – C3 and C4 – from the posterior margin of the head capsule. Furthermore, additional abductor muscles of the head – C5 –attach to the sternal plate of the first trunk segment.

The head capsule has an intrinsic muscle – C1 – which seems to play a role against deformatory forces induced by muscles that pull the head backwards. These posterior muscles arise directly from the cephalic margin – C6 – or from the arthrodial membrane between the head and the first trunk segment (see Ravoux 1962).

Hanseniella nivea

The head of *Hanseniella nivea* is larger and more spherical than that of *Scutigerella*. It means that the most of the muscles are larger and have a stronger appearance, although the musculature is very similar to *Scutigerella*. This feature is related to a larger insertion surface in general, being accompanied by extra laminar structures in the tentorium and other apodemes of the head-musculature (see figs. 11 and 12).

Tentorial complex

The posterior process shows several cuticular projections, such as a pair of ventral laminae (fig. 10A, *vl*) and a larger dorsal lamina with a more complicated terminal ramification (fig. 10E, *arrow*). Both tentorial bridges are present, and the anterior one appears more longitudinally spread. This bridge shows a pair of ventro-lateral collagenous bars that receives several muscles from the mandible and first maxilla (fig. 10A, *ctb*). The interpontal rod is also present with some modifications: at the attachment to the anterior tentorial bridge it forms

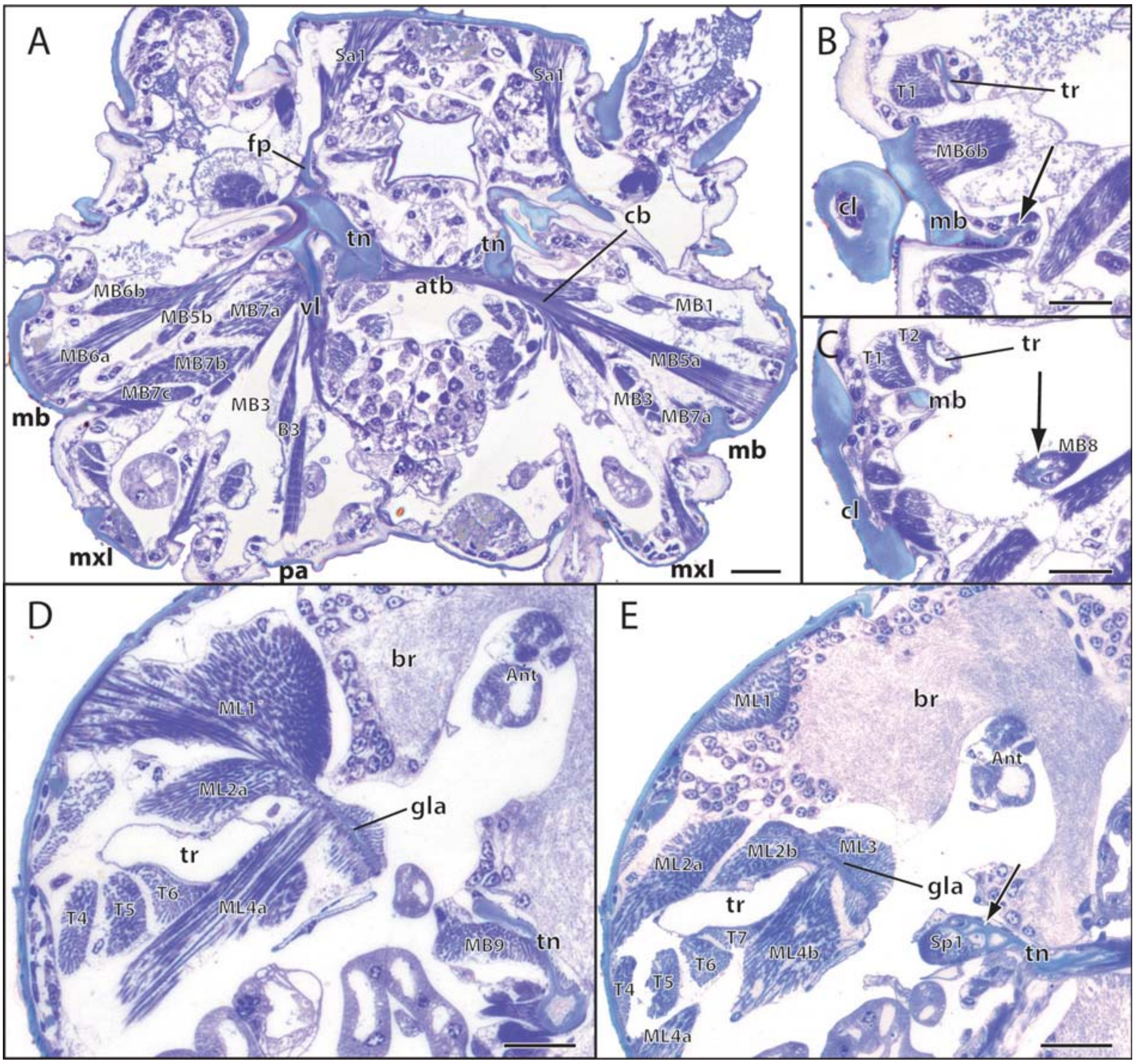


Fig. 10 *Hanseniella nivea*, transversal sections of the head at different levels, from anterior (A) to posterior (E). A, anterior part of the anterior tentorial bridge (*atb*), showing a collagenous bar (*cb*). Several mandibular muscles (*MB*) attach to the tentorium, which forms a ventral lamina (*vl*). B, articulation point between the cephalic lobe (*cl*) and the mandibular base (*mb*), where MB6b arises. The ventral projection continues behind the end of the mandible and forms the posterior mandibular apodeme (*arrow*). C, MB8 muscle arising from the posterior tentorial apodeme, which forms several laminae (*arrow*). D, ML muscles arising from the mandibular-gnathal-lobe apodeme (*gla*), and tracheal T muscles arising from the anteriorly enlarged part of the trachea (*tr*). E, tentorium (*tn*) at the posterior tentorial bridge, showing the laminae (*arrow*) where the Sp1 muscles insert. ML muscles attaching on the gnathal-lobe apodeme (*gla*) and ML1´ surrounded by components of the brain (*br*). The trachea (*tr*) forms a large chamber, from which the T muscles arise. Abbreviations: *ant*, antennal muscles; *br*, brain; *mb*, mandibular base; *mxI*, first maxilla; *pa*, proximal arm of the second maxilla; *tn*, tentorium. Scale bars = 20 µm.

a vertical lamina, and with the posterior bridge it splits into two branches. Also, it supports the ventral pharyngeal dilators Pv2, while the Pv1 is absent. The supraoesophageal ganglion of the brain lies on the anterior tentorial bridge, before passing between both bridges.

The lateral and frontal processes are notably larger than in *Scutigerella* and present a more laminar form, favouring a stronger insertion with the muscles. The epipharyngeal lamina shows no significant variations.

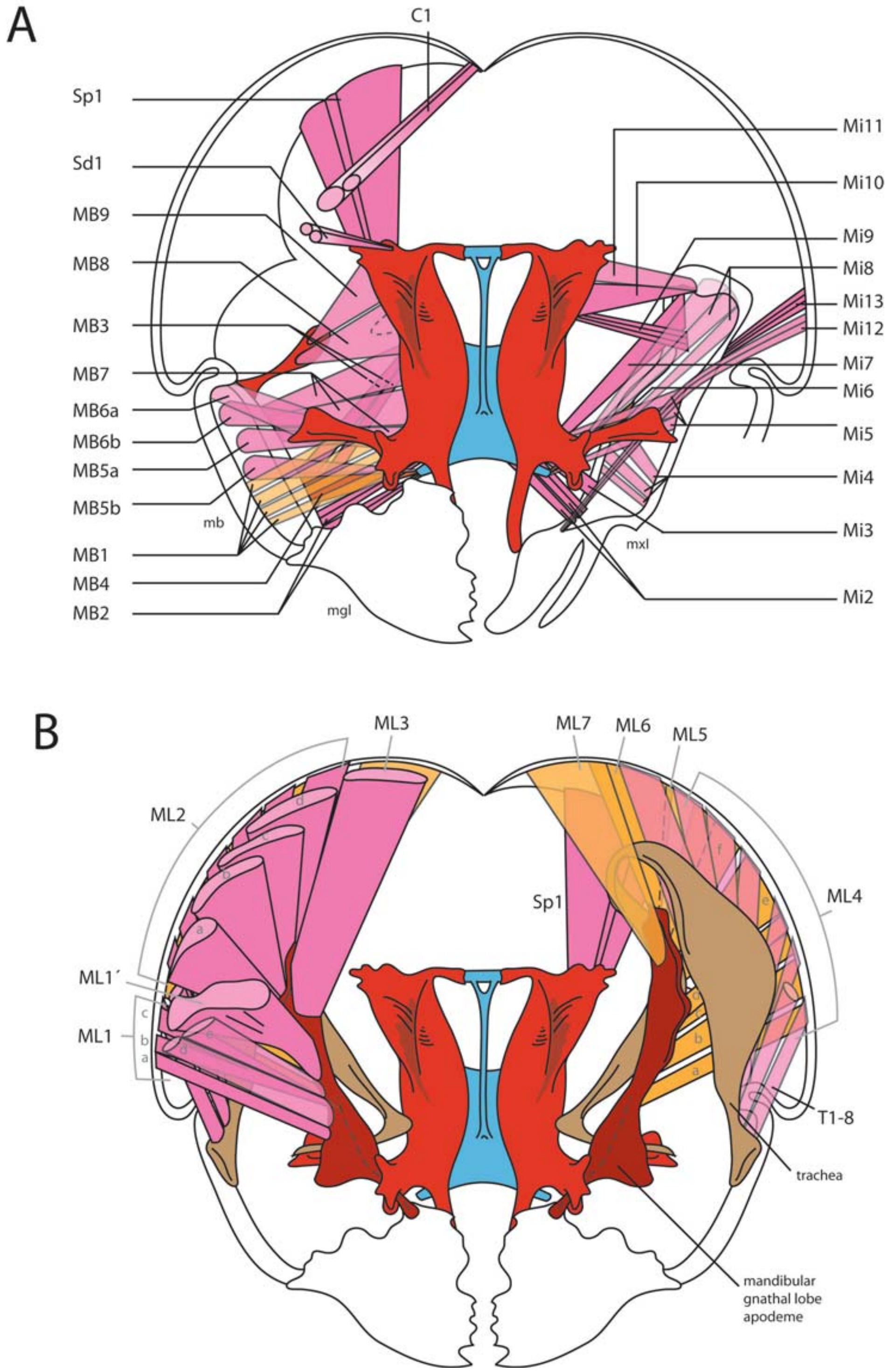


Fig. 11 Schemata of the musculature of the head in dorsal view in *Hanseniella nivea*. Only the postmandibular part of the tentorium (in red) is depicted. A, mandibular base (*mb*) and first maxilla (*mxI*) with their related muscles (MB and Mi), and other suspensor muscles (see descriptions in table 1). B, mandibular-gnathal-lobe apodeme (in maroon) and its related muscles (ML), and tracheal apodeme (in brown) with its muscles (T).

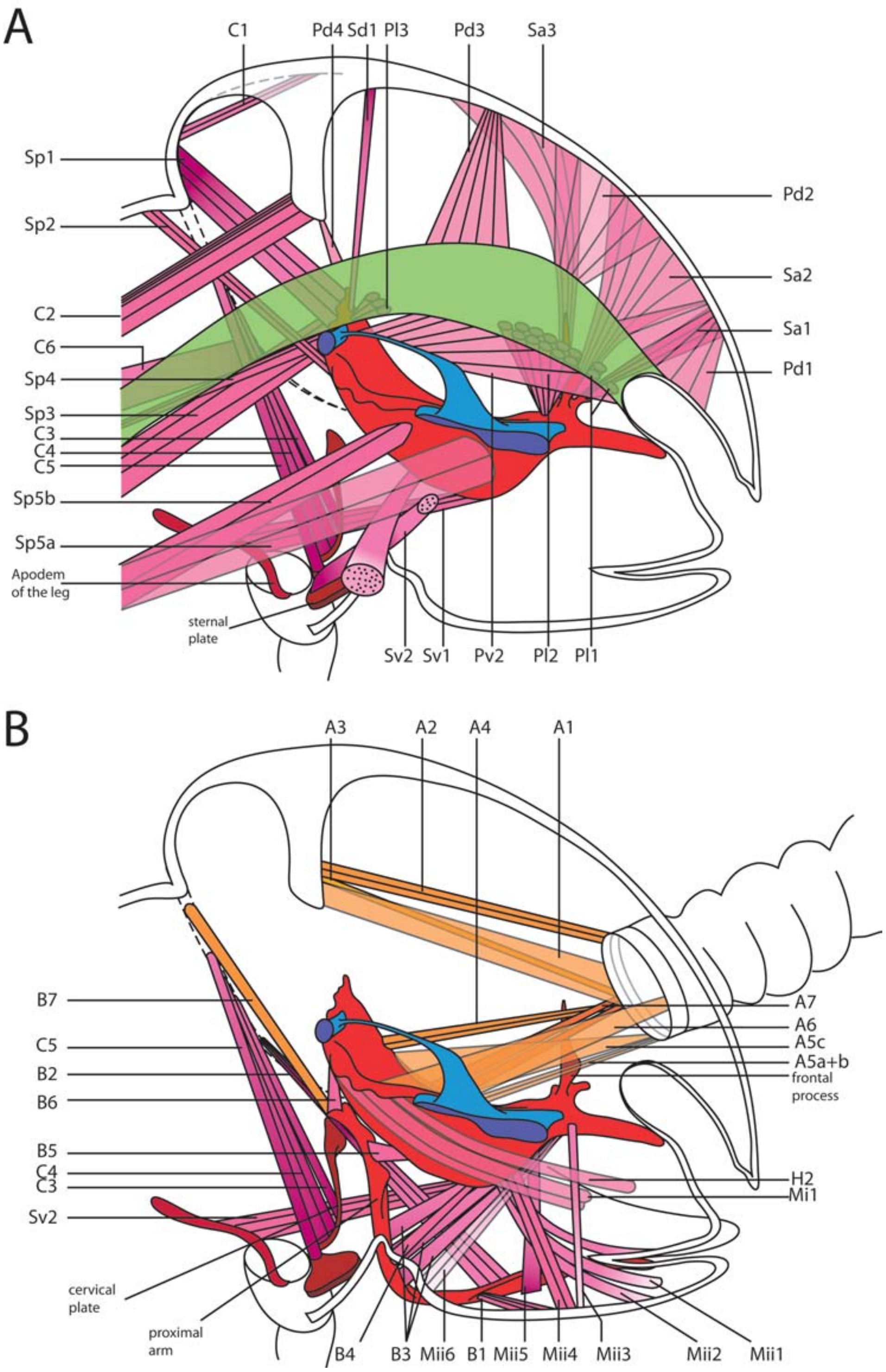


Fig. 12 Schemata of the musculature of the head in lateral view in *Hanseniella nivea*. Only the postmandibular part of the tentorium (in red) is depicted. A, pharynx (in green), pharyngeal dilators muscles (P), suspensor muscles of the tentorium (S) and intrinsic and extrinsic musculature of the head capsule (C). B, antennal muscles (A), muscles of the anterior plate of the second maxilla (Mii), muscles of the proximal arm of the second maxilla (B), and other muscles (see descriptions in table 1).

Mandibular basal segment

The mandibular basal segment of *Hanseniella nivea* forms a posterior apodeme and a ventral lamina, but no dorsal projection. Instead the mandible becomes convex interiorly at its posterior end, in which exterior concavity the anterior point of the cephalic lobe hinges (fig. 10B). The muscle MB6b arises on the dorsal part of this convexity, whereas MB6a originates from the middle wall of the mandibular base. Both muscles insert on the significantly sized lamina of the lateral process of the tentorium (fig. 10A). The muscles MB5a and MB5b take a central place in the concavity of the mandibular base, but they do not lie parallel: while MB5b attaches on the ventral side of the lateral process, MB5a inserts on the collagenous bar of the anterior tentorial bridge (fig. 10A). This collagenous bar also receives MB4 and both most anterior muscles of MB2. The muscles strands of MB1 have a more dorsal origin on the mandibular base and are attached broadly to different parts of the tentorium: both most posterior on the ventral side of the lateral process and the most anterior ones in a hollow formed between the tentorium's posterior process and the ventral lamina of the tentorium (Fig. 10A).

The ventral lamina of the mandibular base takes up the entire ventral margin of the mandibular base and extends more posteriorly, connecting to the posterior mandibular apodeme (fig. 10B, *arrow*). This apodeme has a stronger appearance in *Hanseniella*, showing a hollow cuticular bar at it base and presenting several laminae from which MB8 and MB9 arise (fig. 10C, *arrow*). Both muscles attach on the tentorium, taking up the whole exterior surface of the dorsal lamina (fig. 10D). Muscle MB8 shows a cleft near its attachment with the tentorium, through which the maxillar muscle Mi9 passes.

Mandibular gnathal lobe

There are six anterior muscles of the mandibular gnathal lobe: the five ML1 muscles and behind them, the ML1′ muscle (fig. 10D). This muscle is much larger than ML1, and extends backwards above ML2 and ML3, and through the brain (fig. 10E). On the other hand, there are only four ML2 muscles, and ML3 is represented by a single muscle. ML4 comprises four large muscles, one of which – maybe all of them – seems to be composed of two. ML5 and ML6 insert on the exterior side of the lamina of the apodeme, and ML7 is the only one of the inferior plane which inserts on the interior side.

Trachea and tracheal muscles

The trachea is much larger than in *Scutigerella* and forms a large chamber at the medial part, where eight tracheal muscles are attached (fig. 10D). When it loops to the anterior part again, it strengthens before disappearing by ramification.

First maxilla

All muscles that span the tentorium's posterior process in *Scutigerella* insert on its ventral lamina in *Hanseniella*, except Mi9, that attaches on the dorsal lamina of the tentorium. Mi6 and the most anterior Mi5 join with the tentorium through a collagenous bar of the anterior tentorial bridge. The origin points of Mi4 on the first maxilla do not have any relation to the maxillary palp, since the three muscles originate from different points of the exterior margin of the first maxilla.

The three Mi13 muscles are fused and terminate more posteriorly than both Mi12.

Second maxilla

The muscles of the anterior plate of the second maxilla that in *Scutigerella* attach to the tentorium at the level of the first tentorial bridge assemble in *Hanseniella* at the level of the anterior margin of this bridge and insert on the ventral lamina of the tentorium's posterior process.

The three muscles forming B3 are more separated from each other (fig. 10A), and B4 appears immediately behind B3c, which forms part of the same group of muscles. While B6 has the same distal position regarding the proximal arm, B5 is more anterior and attaches on the ventral lamina of the tentorium, at the level of the anterior tentorial bridge.

Antennal muscles

Remarkable differences to the state in *Scutigerella* are the presence of a pair of muscles in A4 and A7, the absence of the crossing of A3 and A2, and the distribution of the three A5 muscles, which is not regular since there is a large posterior muscle and two very small anterior ones.

Pharyngeal muscles

There are 7 muscles which form Pv2, and Pv1 is absent. The lateral pharyngeal muscles are more independent from each other. Pl1 consists of three muscles that insert on the frontal process and Pl2 is comprised of 11 muscles that attach to the tentorium's posterior process. There are only three Pl3 muscles.

Suspensor muscles of the tentorium

There is only one group of anterior suspensor muscles in *Hanseniella* (*Scutigerella*: Sa2 and Sa3). Sd2 is absent and Sp1 inserts on small laminae at the posterior end of the tentorium (fig. 10E, *arrow*). The most striking difference in the posterior suspensor muscles of the tentorium in *Hanseniella* is the separation of the two muscles which form the Sp5. They consist of two large muscles each and have different insertion areas on the interior side of the ventral lamina of the tentorium, one far more anterior than the other.

Scolopendrella notacantha

Tentorial complex

The posterior process is horizontally laminar. Ventral and dorsal laminae are present, but are not as conspicuous as in *Hanseniella*, and likewise receive several muscles. The posterior apex is laminar and does not show any ramification. Both tentorial bridges are also present but with variations: the anterior one is more longitudinally spread, while the posterior one is reduced to a small transversal rod (figs. 14, 15). Despite the smaller hollow between them, the cerebral connection between the supra- and suboesophageal ganglia passes through it. There is no interpontal rod and the pharyngeal dilators arise directly from each tentorial bridge.

The lateral process is thin at the basis but towards the posterior it becomes broader and laminar, with angular margins. Frontal process and hypopharyngeal bar are present, but considerably shorter. The epipharyngeal lamina of each half of the head join together at the most anterior part of the clypeolabrum.

Mandibular basal segment

The mandibular base of *Scolopendrella* is broader in its posterior part and most of the muscles are concentrated here, hence having a more posterior position in the mandible than in *Scutigerella* (fig. 14). These posterior muscles – MB5, MB6 and MB7 – are larger in comparison to the anterior ones – the MB1-4. In contrast, the posterior mandibular apodeme, as well as MB8 and MB9 are smaller. The dorsal lamina of the mandibular base is present, and its muscles – MB6 – attach to the broad and laminar lateral process of the tentorium. The two long MB3 muscles are not parallel. They arise from the same point in the mandible, but MB3b extends backwards to the posterior part of the tentorium while MB3a does in- and upwards, to its closest point of the tentorium. MB2 does not arise next to MB3, but more anteriorly to it, and comprises only two small muscles.

Mandibular gnathal lobe

The two superior ML1 muscles are more separated from each other, and the most anterior one is larger than the second one. The ML1′ muscle is present, composed of two large bundles. Both take the same position as ML1′ in *Hanseniella*, embedded into the brain and above the rest of the muscles (fig. 13C). There is another group of muscles, the three ML2′ which extend backwards among components of the brain. Their insertion on the head wall is more superior to the rest of the muscles (fig. 13D).

ML2 comprises two muscles and ML3 three. The inferior plane is formed by six ML4 muscles and ML5-7, which have the same arrangement as in *Hanseniella*.

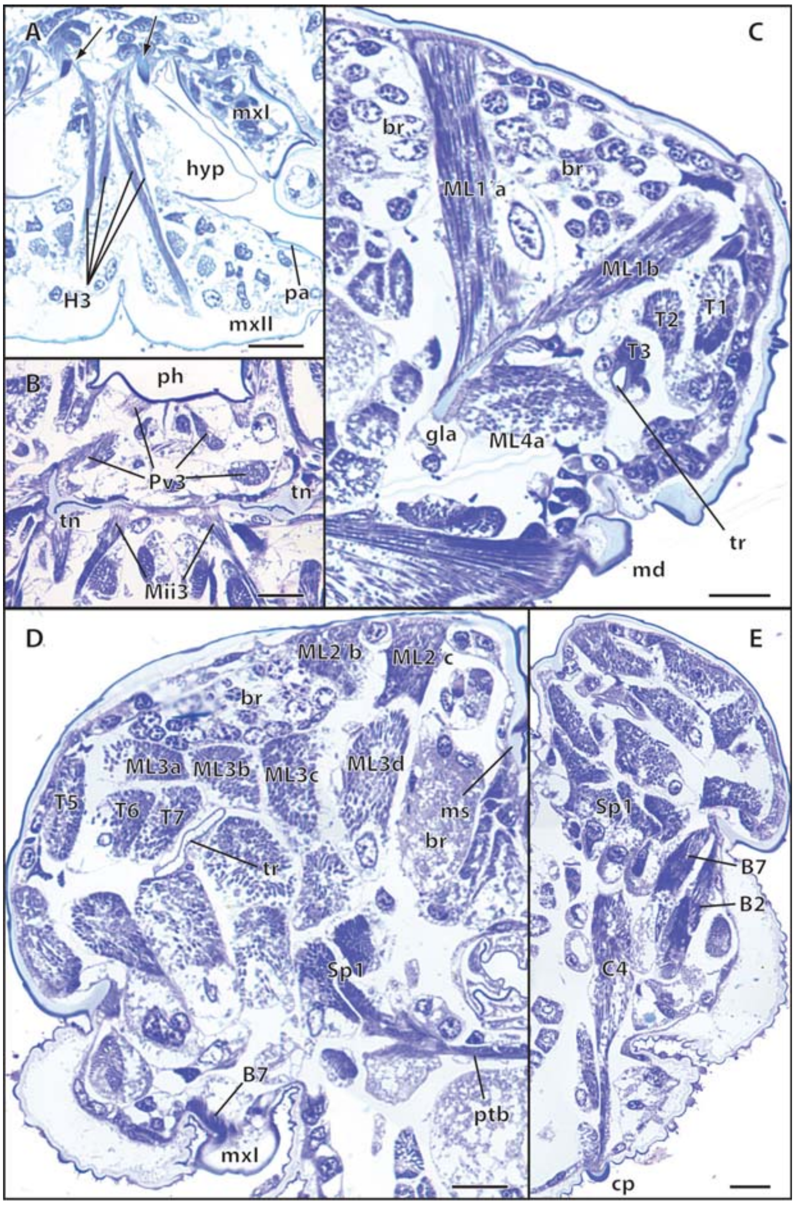


Fig. 13 *Scolopendrella notacantha*, transversal sections of the head at different levels, from anterior (A) to posterior (E). A, Hypopharynx with its apodeme (*arrow*) and the H3 muscles associated with it. B, Detail of the muscles Sv3 which connect the pharynx (*ph*) to the tentorium (*tn*), to which anterior bridge the Mii3 muscles are also attached. C, adductor muscles (*ML*) of the gnathal lobe apodeme (*gla*) and trachea (*tr*) with some tracheal muscles (*T*). D, section of the head capsule at level of the posterior tentorial bridge (*ptb*) and the median septum (*ms*), showing some adductor muscles of the gnathal lobe (*ML*), posterior muscles of the tentorium (*Sp1*), the trachea (*tr*) with tracheal muscles (*T*) and the beginning of B7 at the end of the first maxilla (*mxI*). E, posterior part of the cranium, to its wall B7 attaches, between B2 and Sp1. The cervical plate (*cp*) and C4 are also depicted. Abbreviations: *md*, mandible; *mxII*, anterior plate of the second maxilla; *pa,* proximal arm of the second maxilla. Scale bar = 10 µm.

Trachea and tracheal muscles

The trachea is not as conspicuous as in *Scutigerella* and *Hanseniella* (fig. 13C and D). It presents a broader and more laminar part in the posterior half of the first section. After the looping at the posterior part of the head, it ramifies in small branches which extend forwards. There are seven tracheal muscles, which connect the trachea to the lateral wall of the head (fig. 13C).

First maxilla

The articulation between the first maxilla and the head-capsule is not reduced to a point like it is in *Scutigerella* and *Hanseniella*, but it is more extended in a longitudinal way. Mi10 and Mi11 muscles arise from the most posterior part of the exterior margin of the maxilla, where the cardo is in contact with the margin of the head.

Mi5 and Mi6 attach on the tentorium at the most proximal part of the lateral process. The three Mi4 muscles lie similar to those in *Hanseniella*: they connect different points of the

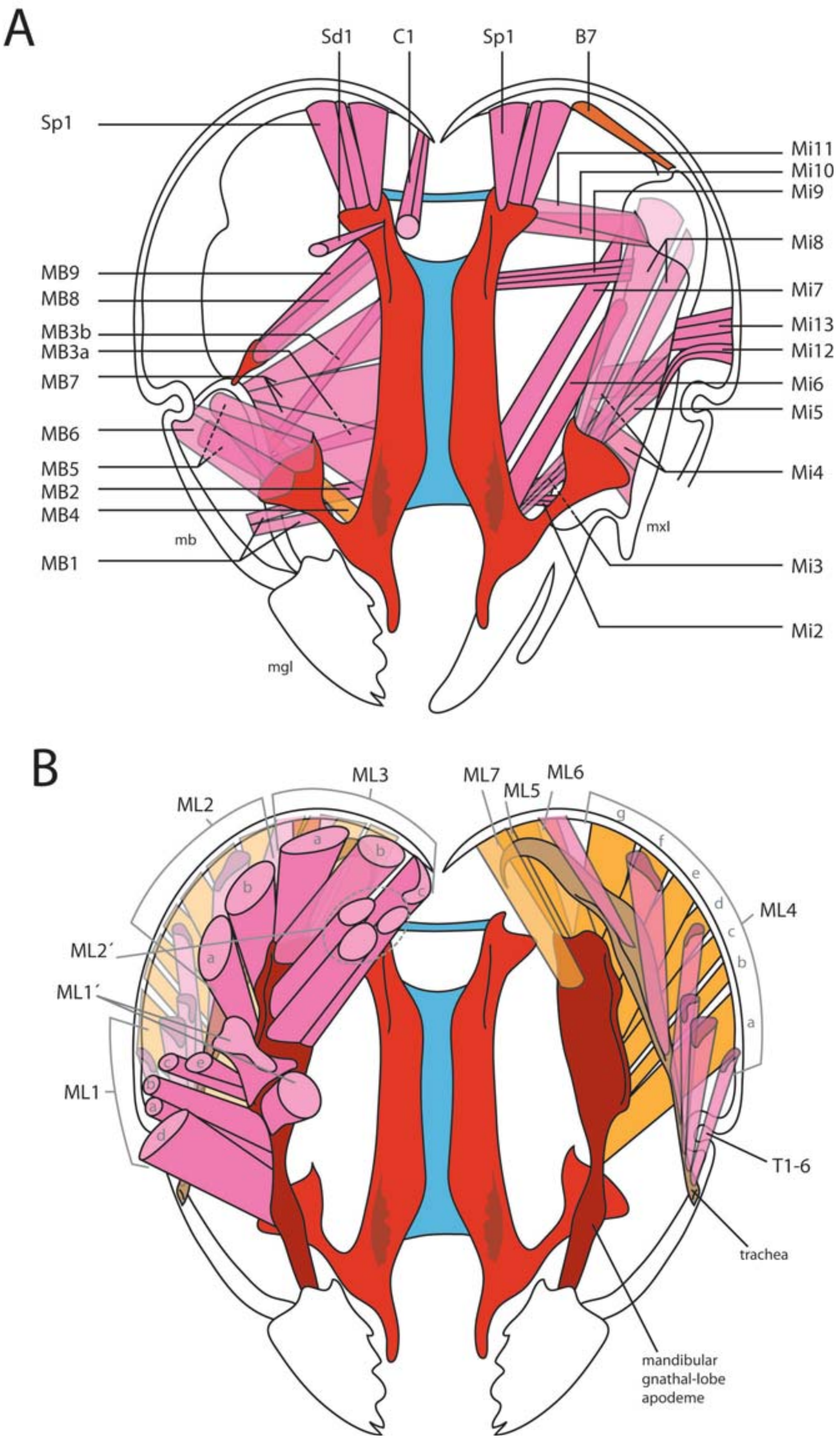


Fig. 14 Schemata of the musculature of the head in dorsal view in *Scolopendrella notacantha*. Only the postmandibular part of the tentorium (in red) is depicted. A, mandibular base (*mb*) and first maxilla (*mxI*) with their related muscles (MB and Mi), and other suspensor muscles (see descriptions in table 1). B, mandibular-gnathal-lobe apodeme (in maroon) and its related muscles (ML), and tracheal apodeme (in brown) with its muscles (T).

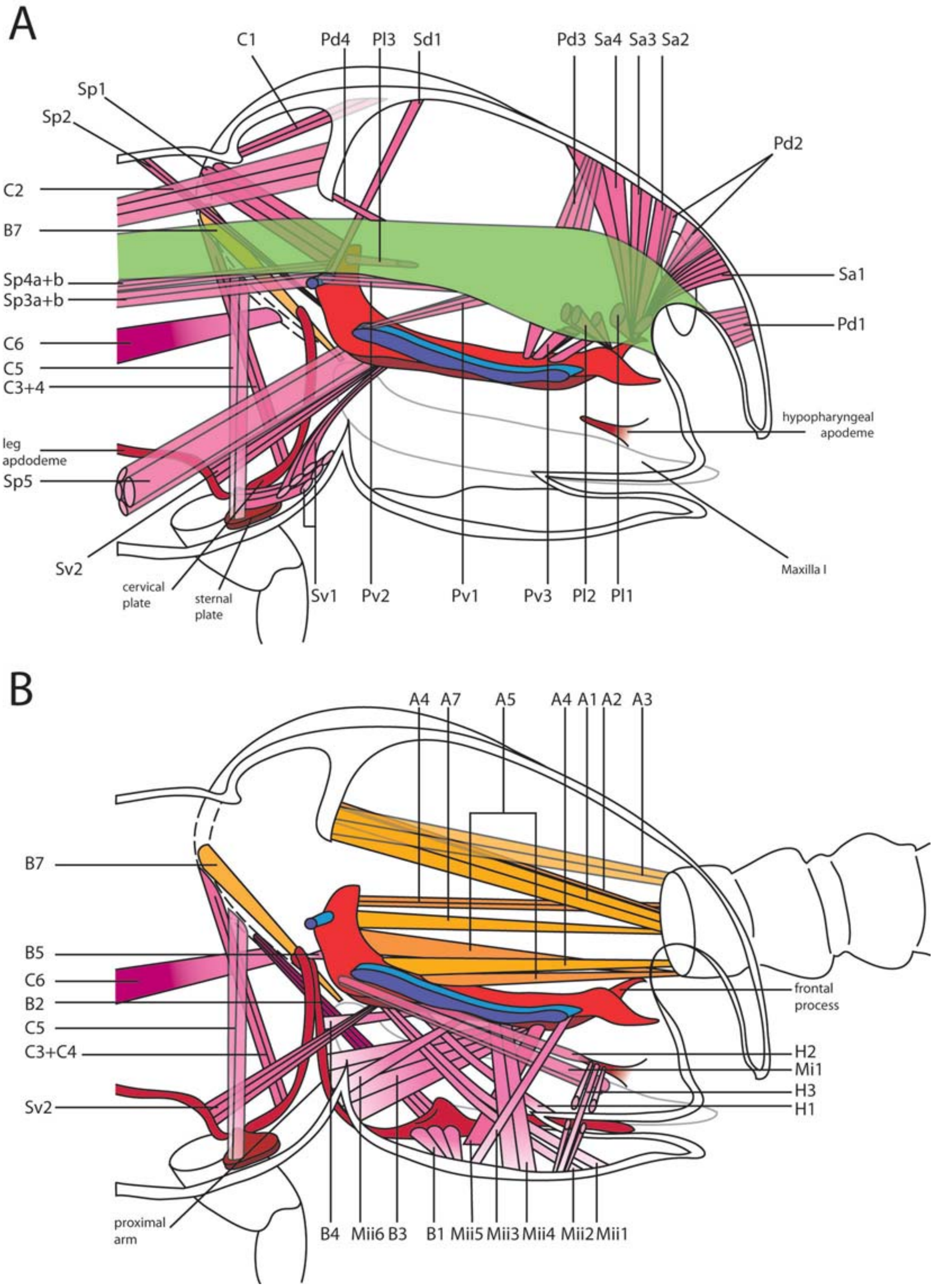


Fig. 15 Schemata of the musculature of the head in lateral view in *Scolopendrella notacantha*. Only the postmandibular part of the tentorium (in red) is depicted. A, pharynx (in green), pharyngeal dilators muscles (P), suspensor muscles of the tentorium (S) and intrinsic and extrinsic musculature of the head capsule (C). B, antennal muscles (A), muscles of the anterior plate of the second maxilla (Mii), muscles of the proximal arm of the second maxilla (B) and other muscles (see descriptions in table 1).

external margin to the internal margin of the first maxilla. The three Mi13 muscles are adjacent to each other. Strikingly, Mi12 does not arise from the interior margin, but on the exterior one, in the medial part of the first maxilla.

The posterior margin of the first maxilla is not as close to the articulation with the head as in *Scutigerella*, but it extends more posteriorly and shows a pointed termination. There is a muscle that connects this posterior part of the first maxilla with the posterior margin of the head (fig. 13D). The insertion of this muscle on the margin of the head corresponds to the position of the muscle B7 in *Scutigerella* (fig. 13E).

Hypopharyngeal muscles

H1 is parallel to Mii1 and Mii2, but not joined to them and attaches to the tentorium more anteriorly than Mii1 and Mii2, and posteriorly to B3. Strikingly, H2 arises from an apodeme which is formed at the lateral side of the hypopharynx (fig. 13A).

There is an extra group of muscles which connect this hypopharyngeal apodeme with the interior margin of the second maxilla. These three H3 muscles arise on the anterior plate of the second maxilla between Mi2 and Mi4. H3a and H3c attach to the hypopharyngeal apodeme of the other half of the head, thereby crossing each other, the ones from one half to those from the other half. H3b attaches on the hypopharyngeal apodeme of its own half of the head (fig. 13A).

Second maxilla

Mii1 has a more interior origin on the second maxilla, which means that the origin of Mii1 and Mii2 are not parallel. Their insertion on the tentorium lies much more posterior than in *Scutigerella* and *Hanseniella*, with an attachment level at the posterior margin of the anterior tentorial bridge, behind the rest of the muscles of the second-maxilla's anterior plate.

Mii3 arises more anteriorly than Mii4, and it attaches to the tentorium on the ventral side of the anterior tentorial bridge (fig. 13B).

Mii6 is not longer associated with the second-maxillary plate, but spreads from the anterior part of the tentorium to the posterior part of the head, attaching to the main fold of the ventral arthrodial membrane between head and trunk.

The three B1 muscles are relatively small and spread transversally. There are four B3 muscles. B4 seems to be absent, but it is possible that the fourth B3 muscle corresponds to B4. These four muscles have the same insertion at the tentorium, and lie parallel. B6 is absent and B7 seems to have a modified position compared to *Scutigerella*. As explained above, this muscle connects the margin of the cranium with the arthrodial membrane located immediately behind the first maxilla, and not with the proximal arm of the second maxilla (fig. 13D, E).

At the posterior limit of the head, the proximal arm of the second maxilla is not so much in a closed hollow as it is in *Scutigerella* and *Hanseniella*.

Antennal muscles

A1 presents two muscles and A3 extends parallel to them without crossing A2. Other remarkable differences are that there are only two A5 muscles and that A7 attaches to the tentorium more posteriorly than A5, close to A4.

Pharyngeal muscles

There are two Pl1 muscles and three Pl2, which arise from the frontal process of the tentorium. Close to Pl2 there are four Pv3 muscles which connect the pharynx with the dorsal side of the tentorium (fig. 13B).

Pv1 is present, since an unpaired group of three muscles connect the ventral side of the pharynx with the posterior part of the anterior tentorial bridge. There is another unpaired group of three muscles which corresponds to the Pv2 muscles, and connects the pharynx with the posterior bridge. There is only one Pl3 muscle.

Suspensor muscles of the tentorium

Sa1 is composed of eight muscles, Sa2+3 of a single large muscle, and Sa4 of two paired muscles. There are three dorsal suspensor muscles, which match to the position of Sd1.

The three Sp1 muscles have no aligned disposition, but they comprise two superior muscles and an inferior one (fig. 13D and E). The interior one of both superior muscles arises on the terminal lamina of the tentorium, while the superior-exterior- and the inferior originate below this lamina.

Sp3 and Sp4 do not insert on the same site: the first one inserts on the posterior tentorial bridge and the latter from the terminal lamina of the tentorium. Sp5 and Sv2 jointly originate from the tentorium and project backwards, until the four Sv2 muscles separate and join the basis of the apodeme of the first pair of legs. The four Sp5 muscles continue backwards, one interior muscle surrounded by three exterior ones.

Muscles of the head capsule

Both C1 muscles have a more longitudinal position, since they arise from a more interior point on the wall of the head. The median septum has no branches (fig. 13D) and receives the C2 muscles. There are three C2 muscles: an interior one and two exterior. All muscles of the posterior margin of the head have the same arrangement as in *Scutigerella*.

Scolopendrellopsis (Symphylellopsis) subnuda

The head of *Scolopendrellopsis subnuda* is very elongated and flattened. The mouth parts and the tentorium are no longer located ventrally, but more centrally relatively to the margins of the head capsule. Most of the transversal muscles which connect the mouth parts to the tentorium – MB7, MB8, MB9, Mi10 and Mi11 – are more or less aligned in one plane.

<u>Tentorial complex</u>
The tentorial complex is very similar to the one in *Scolopendrella*: laminar, with large laminar lateral processes (fig. 16A, B, *lp*). The epipharyngeal laminae of each half meet medially at the most frontal point of the clypeolabrum. The most notable difference is the absence of the posterior tentorial bridge (figs. 17, 18, 22).

<u>Mandibular basal segment</u>
MB8 and MB9 arise from the posterior mandibular apodeme, which is reduced to a small bar in the articulation between mandible and head (fig. 16C, *pma*). The dorsal lamina of the mandibular base is absent; the single MB6 muscle envelops the dorsal margin of the mandible (fig. 16B). Under MB6, there are two muscles which correspond to MB5, but they are more separated from each other than in *Scutigerella*. Both attach to the tentorium on the lamina of the lateral process, and MB6 attaches between them (fig. 16B). Under these muscles, there are two MB4 muscles instead of one, which arise from the ventral lamina of the mandible. The anterior one has the same position as in *Scutigerella*, but the posterior one is smaller and attaches to the lateral process of the tentorium, on the posterior margin next to MB5a. There are three large MB3 muscles which project backwards together and parallel to each other. MB2 comprises only two muscles which originate more anteriorly than MB3. Although the four MB1 muscles are jointed, the anterior pair attaches to the ventral side of the tentorium, while the posterior pair attaches on the base of the lateral process.
Strikingly, three muscles that connect the mandibular base to the wall of the head are present. These MB10 muscles consist of three relatively large muscles that originate from almost the entire posterior half of the dorsal margin of the mandibular base (fig. 16B). They extend upwards, parallel to each other and attach to the lateral wall of the head between the ML1 and ML1´ muscles (fig. 16C).

<u>Mandibular gnathal lobe</u>
The gnathal-lobe apodeme bends dorsally, forming a lateral fold at the anterior half of its lamina. Only the three anterior ML1 muscles are present. The MB10 muscles are positioned behind them, followed by ML1´ (fig. 16C). Both ML1´ muscles are large and have a similar insertion on the apodeme as in *Hanseniella* and *Scolopendrella*, but they do not pass through the brain. More posteriorly, ML2 and ML3 are arranged in a plane of six muscles, three

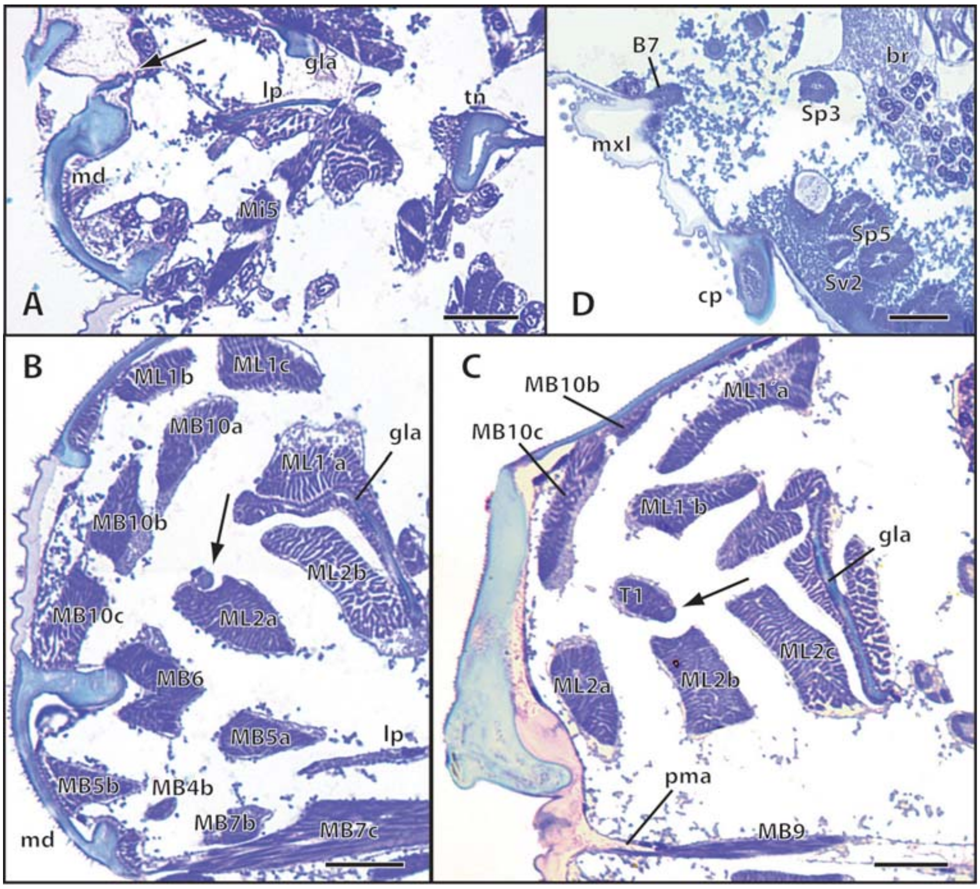


Fig. 16 *Scolopendrellopsis subnuda,* transversal sections of the head at different levels, from anterior (A) to posterior (D). A, beginning of the "tracheal" apodeme (*arrow*) from the dorsal margin of the mandibular base (*md*). Tentorium's posterior process (*tn*), laminar lateral process (*lp*) and gnathal-lobe apodeme (*gla*) also depicted. B, beginning of the MB10 muscles on the dorsal margin of the mandibular base (*md*), which is enveloped by the MB6, and "tracheal" apodeme (*arrow*) passing above the ML2 muscles. MB5a extending towards the tentorium's lateral process (*lp*). The gnathal-lobe apodeme (*gla*) shows a lateral fold. C, MB10 muscles attaching to the dorsal wall of the head more anteriorly than ML1´a and ML1´b. "Tracheal muscles" (*T*) arising from the "tracheal" apodeme (*arrow*) are also depicted, as well as MB9 arising from the posterior mandibular apodeme (*pma*). D, posterior part of the head, immediately behind the end of the first maxilla (*mxI*), where B7 arises from the arthrodial membrane. Sp3 passes backwards next to the brain (*br*). Sp5 and Sv2 muscles are also depicted, as well as the cervical plate (*cp*). Scale bars = 10 µm.

belonging to each. The muscles of the inferior plane correspond to the six ML4 muscles and ML5-7. ML7 is the only one that inserts on the interior side of the apodeme's lamina. ML6 is not located beneath ML5 and ML7, but between them.

Trachea and tracheal muscles

The trachea is absent in *Scolopendrellopsis subnuda*, but not the muscles which correspond to the tracheal muscles. These six muscles form a plane between the two planes of the ML muscles, just like in *Scutigerella, Hanseniella* and *Scolopendrella*. They originate from a

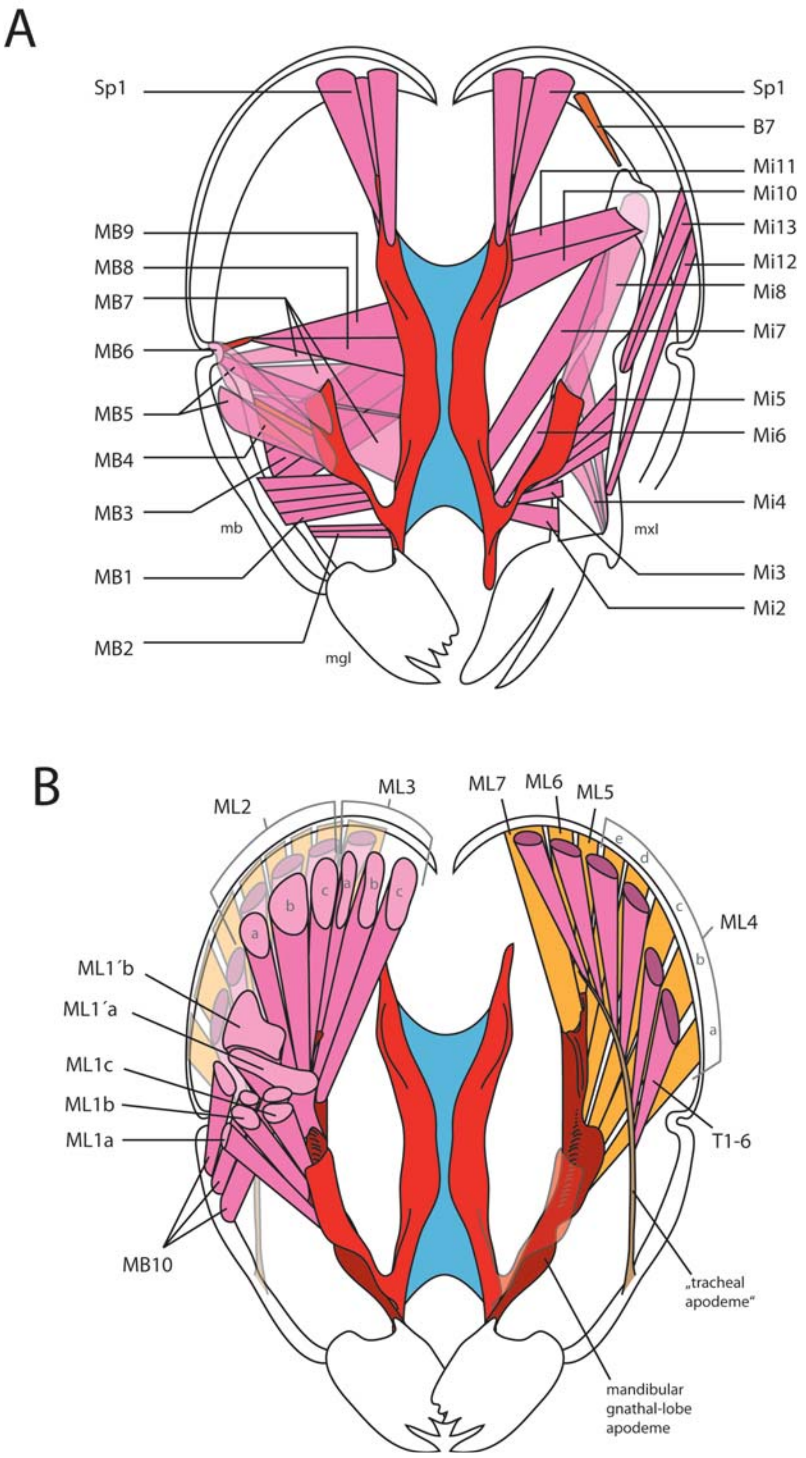


Fig. 17 Schemata of the musculature of the head in dorsal view in *Scolopendrellopsis subnuda*. Only the postmandibular part of the tentorium (in red) is depicted. A, mandibular base (*mb*) and first maxilla (*mxI*) with their related muscles (MB and Mi), and other suspensor muscles (see descriptions in table 1). B, mandibular-gnathal-lobe apodeme (in maroon) and its related muscles (ML), MB10 muscles of the mandibular base and tracheal apodeme (in brown) with its muscles (T).

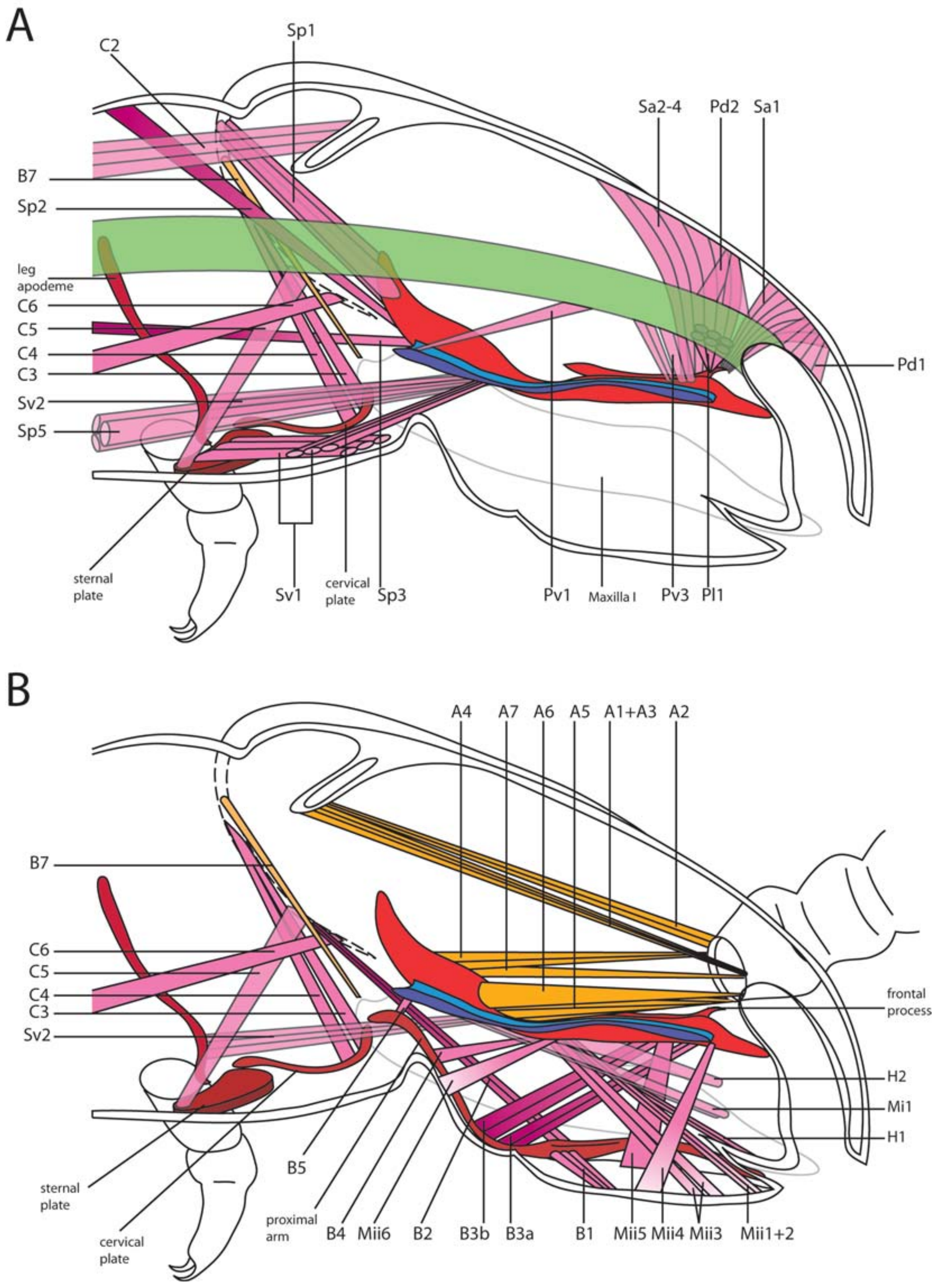


Fig. 18 Schemata of the musculature of the head in lateral view in *Scolopendrellopsis subnuda*. Only the postmandibular part of the tentorium (in red) is depicted. A, pharynx (in green), pharyngeal dilators muscles (P), suspensor muscles of the tentorium (S) and intrinsic and extrinsic musculature of the head capsule (C). B, antennal muscles (A), muscles of the anterior plate of the second maxilla (Mii), muscles of the proximal arm of the second maxilla (B) and other muscles (see descriptions in table 1).

very thin apodeme which arises from the dorsal margin of the mandible, exactly where the trachea is located in *Scutigerella* (fig. 16A, B, C, *arrow*). This cuticular apodeme differs from a trachea in the evidence that it is not hollow, but massive, and does not connect to the exterior in the form of spiracles (or stigmata). Likewise it does not continue behind the attachment of the "tracheal muscles"; any loop-forming terminal section is absent.

First maxilla

As explained above, Mi10 and Mi11 are arranged in a horizontal plane. The first one is inserted on a ligamentous bar of the only tentorial bridge, while the second one inserts on the ventral side of the tentorium's terminal lamina. Mi9 is absent. Both Mi8 muscles attach to the lamina of the lateral process, on the dorsal and ventral side respectively. Mi3, Mi5 and Mi6 insert on the tentorium at the base of the lateral process. Mi2 attaches to the ventral side of the tentorial bridge.

Mi12 arise from the exterior margin of the first maxilla, particularly close to the maxillary palp. It extends to the wall of the head capsule, next to the two Mi13 muscles.

B7 muscle shows the same position as in *Scolopendrella*. It arises from the arthrodial membrane immediately behind the first maxilla (fig. 16D), and extends upwards to the margin of the cranium, where it attaches between Sp1 and C3.

Second maxilla

Mii1 and Mii2 arise almost jointed, the first in front of the second. Both Mii4 muscles arise more anteriorly than Mii3, and they project backwards, parallel to Mii1 and Mii2. Mii3 attaches to the tentorial bridge, like in *Scolopendrella.* Mii6 has a posterior location in the second maxilla.

The proximal arm of the second maxilla does not terminate in a hollow, but remains on the ventral side of the head. B3 comprises two pairs of muscles, parallel to each other. The posterior pair attaches to the ventral side of the tentorium's posterior process, while the anterior one attaches at the base of the lateral process. B6 is absent.

The cervical plate arises much more posteriorly than the end of the proximal arm of the second maxilla, so there is no contact between them.

Antennal muscles

The A1 and A3 muscles seem to be fused together, since there is a single muscle unity composed of three bundles: two correspond to A1 and one to A3. A4 attaches on the tentorium very close to A7, but unlike *Scolopendrella*, both muscles have a more anterior location, but posterior to A5 and A6. A5 is composed of four muscles.

Pharyngeal muscles

Pd1 comprises five muscles, Pd2 only two, and Pd3 and Pd4 are absent. There are three pairs of Pl1 muscles, and Pl2 and Pl3 are absent. Pv1 is represented by only one muscle, which connects the ventral side of the pharynx with the posterior border of the tentorial bridge. The four Pv3 muscles present in *Scolopendrella* are also similarly differentiated in *Scolopendrellopsis*.

Suspensor muscles of the tentorium

There are only two groups of anterior suspensor muscles: Sa1, with 8 muscles, and Sa2-4 with 6 muscles. The Sd muscles are absent.

The three Sp1 muscles have the same arrangement on the tentorium's terminal lamina as in *Scolopendrella*: two superior and one inferior. Sp2 is present, and the Sp3 muscles are reduced to a single one which extends to the lateral part of the trunk, surrounding the brain in the anterior part (fig. 16D), since the brain passes from the dorsal to the ventral part immediately behind the tentorium. As in *Scolopendrella*, Sp5 and Sv2 originate together, and they likewise run backwards together (fig. 16D) until the three Sv2 muscles attach to the apodeme of the first pair of legs. Sp5 is a single group of three muscles, one more interior and two exterior. Sv1 is composed of three long muscles, since the first pair of legs is positioned more posteriorly relatively to the head.

Muscles of the head-capsule

C1 is absent. The arrangement of the muscles that insert on the margin of the cranium is the same as in *Scutigerella*. The only differences are that C3 and C4 attach to the cervical plate in a more anterior position, and that C5 is a single muscle that extends more backwards, due to the more posterior position of the sternal plate in *Scolopendrellopsis subnuda*.

Symphylella vulgaris

The tentorial complex and musculature of the head in *Symphylella vulgaris* is almost identical to the one observed in *Scolopendrellopsis subnuda* (figs. 19, 20), despite differences in the external morphology. The tentorium is laminar and most of the transversal muscles of the mandibular base and first maxilla are likewise more or less aligned in one plane (fig. 21C). However, there are some differences in the head-musculature which are outlined in the following.

Both anterior MB1 muscles do not attach to the tentorium's posterior process, but on the basis of the lateral process, like in *Scutigerella*. Likewise the MB2 inserts on the basis of the lateral process. The Mi10 attaches directly to the tentorium, and not on the tentorial bridge as in *Scolopendrellopsis*. The three MB10 muscles are present as well (fig. 21B).

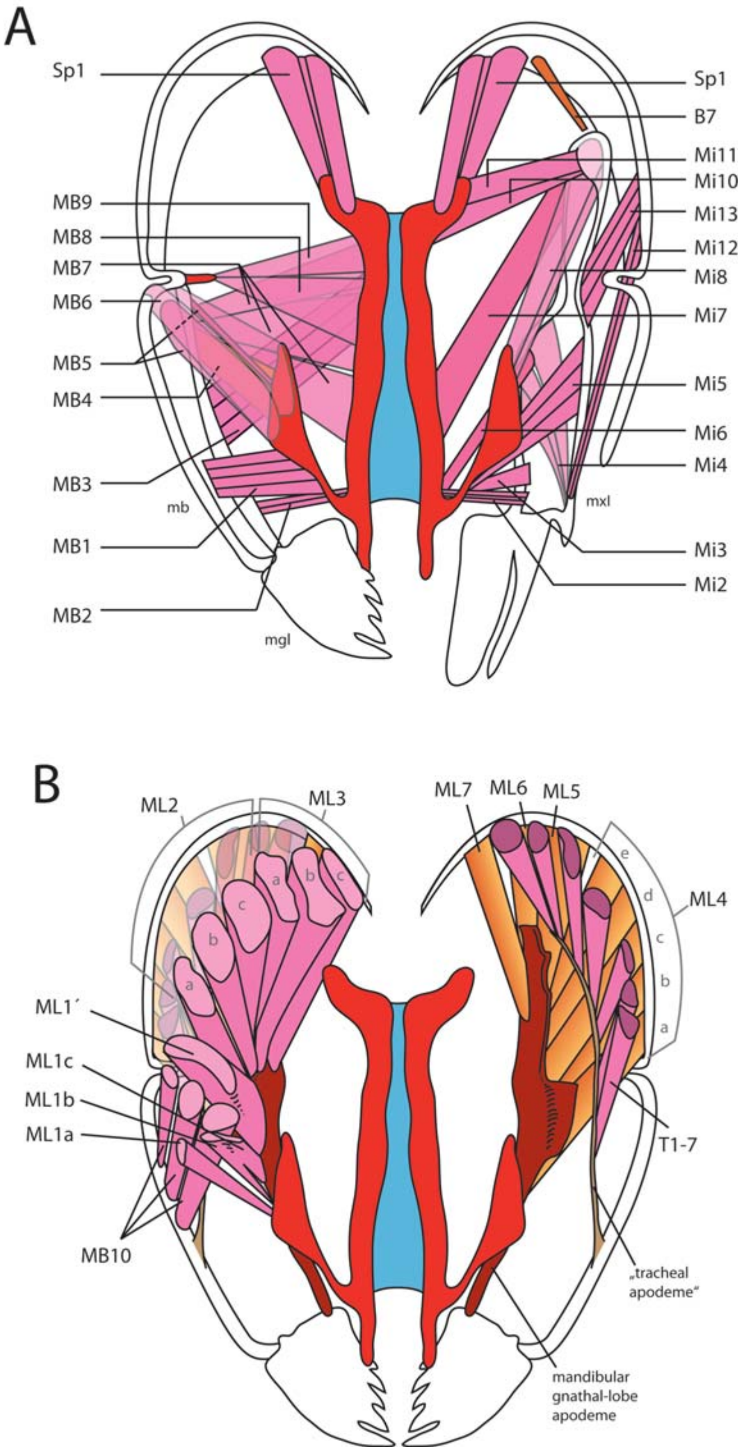


Fig. 19 Schemata of the musculature of the head in dorsal view in *Symphylella vulgaris*. Only the postmandibular part of the tentorium (in red) is depicted. A, mandibular base (*mb*) and first maxilla (*mxI*) with their related muscles (MB and Mi), and other suspensor muscles (see descriptions in table 1). B, mandibular-gnathal-lobe apodeme (in maroon) and its related muscles (ML), MB10 muscles of the mandibular base and tracheal apodeme (in brown) with its muscles (T).

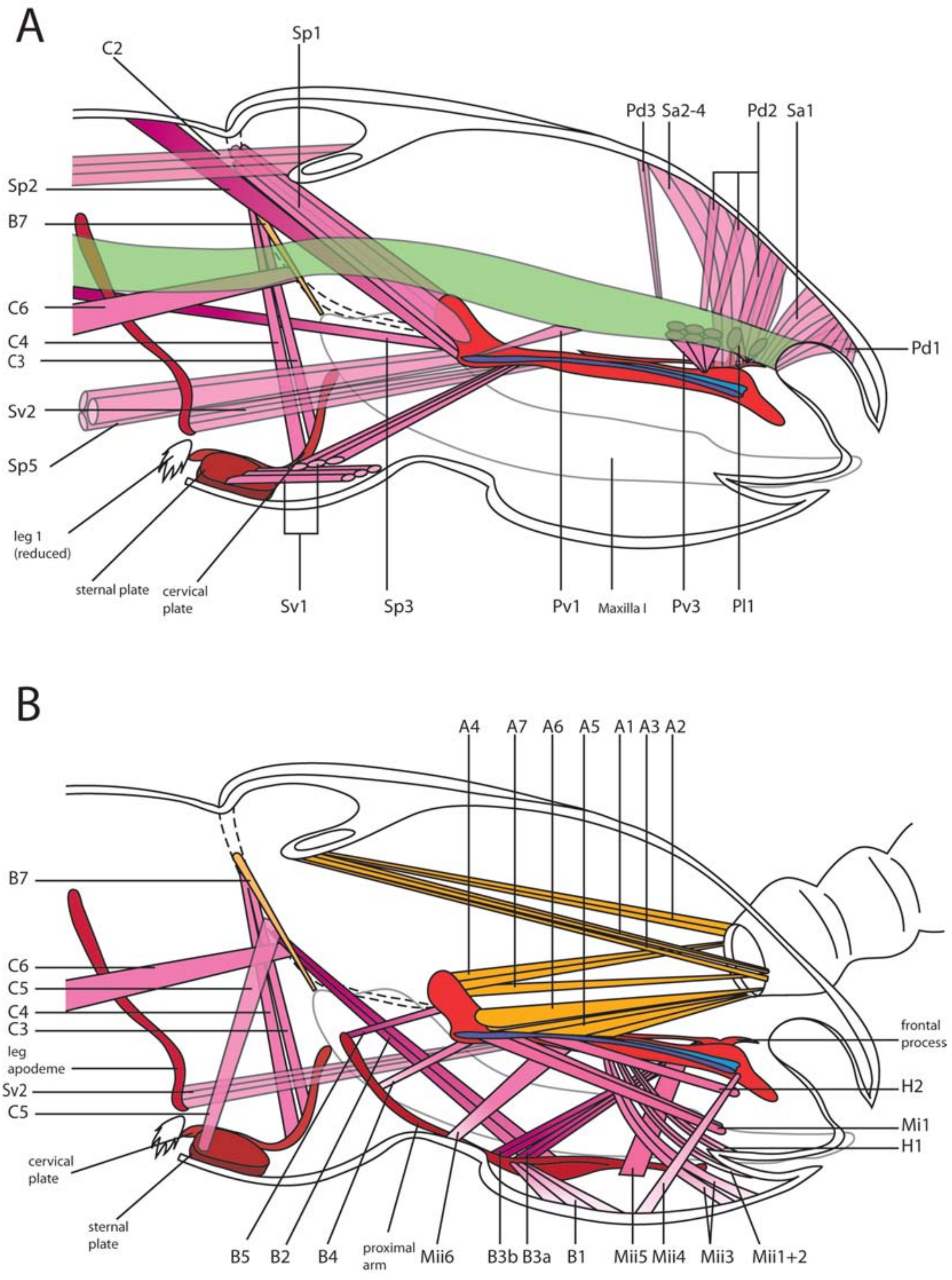


Fig. 20 Schemata of the musculature of the head in lateral view in *Symphylella vulgaris*. Only the postmandibular part of the tentorium (in red) is depicted. A, pharynx (in green), pharyngeal dilators muscles (P), suspensor muscles of the tentorium (S) and intrinsic and extrinsic musculature of the head capsule (C). B, antennal muscles (A), muscles of the anterior plate of the second maxilla (Mii), muscles of the proximal arm of the second maxilla (B) and other muscles (see descriptions in table 1).

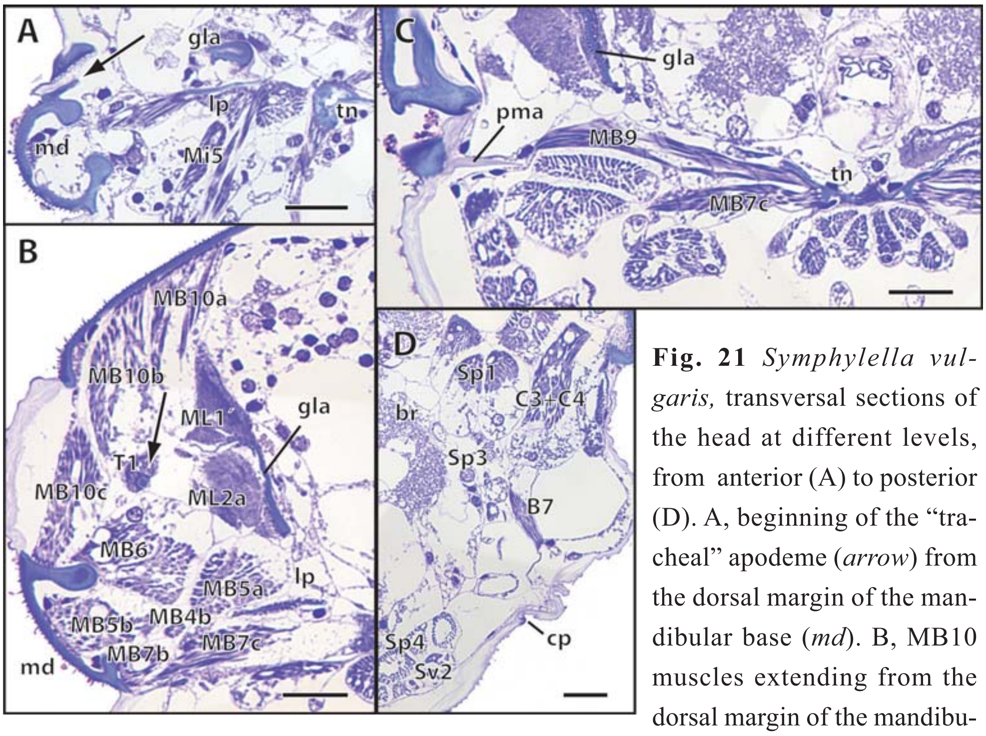


Fig. 21 *Symphylella vulgaris,* transversal sections of the head at different levels, from anterior (A) to posterior (D). A, beginning of the "tracheal" apodeme (*arrow*) from the dorsal margin of the mandibular base (*md*). B, MB10 muscles extending from the dorsal margin of the mandibular base (*md*) to the lateral wall of the head capsule, which is enveloped by MB6; the "tracheal apodeme" (*arrow*) passes above the ML2 muscles. The gnathal-lobe apodeme (*gla*) shows a lateral fold. MB5a extends towards the tentorium's lateral process (*lp*). C, laminar-like tentorium's posterior process (*tn*) and MB9 arising from the posterior mandibular apodeme (*pma*). D, posterior part of the head, immediately behind the end of the first maxilla, where B7 arises from the membrane of the head. Sp3 passes backwards next to the brain (*br*). Sp5 and Sv2 are also depicted, as well as the cervical plate (*cp*). Scale bars = 10 µm.

Two of the three ML1 muscles seem to be fused at their insertion point with the wall of the cranium, and ML1´ is represented by a single and large muscle. The trachea is absent; the "tracheal" muscles arise from a slender, massive apodeme as in *Scolopendrellopsis* (fig. 21A, B). There are seven "tracheal" muscles instead of six. B7 shows the same position as in *Scolopendrella* and *Scolopendrellopsis*, arising from the arthrodial membrane behind the first maxilla (fig. 21D). Pl1 comprises only two muscles, and Pv3 consists of six muscles. Pd3 is present. A1 and A3 lie parallel but are not fused. The A4 and the A7 also attach on the tentorium together, but attach on the terminal lamina of the tentorium much more posteriorly. Mii1 and Mii2 do not arise from the ventral side of the second maxilla, but from the dorsal side, in front of the site where the hypopharynx passes into the dorsal wall of the second maxilla. Although the legs and the sternal plates of the first trunk segment are much reduced in *Symphylella*, the arrangement of the muscles associated with them is the same as in *Scolopendrellopsis*.

Discussion

The descriptions of the musculature and the cuticular endoskeleton of the head in the five studied symphylan species enable a broader view of these features in this taxon, including the family Scolopendrellidae. The results of the present work for *Scutigerella causeyae* and *Hanseniella nivea* match with the descriptions of Manton (1964) and Ravoux (1975) for *Scutigerella immaculata*, and Tiegs (1940, 1945) for *Hanseniella agilis* respectively. Nevertheless, current methods, especially the use of software for 3D reconstructions, enable a more precise study, and some structures have been reported for the first time in the present study. The new data for the three scolopendrellids described here fill the large gap in the data of this group.

The internal anatomy of the head is pretty homogenous in the five studied symphylan species. As expected from the external morphology, *Scutigerella* and *Hanseniella* show many general similarities in the internal anatomy of the head. The head musculature of *Symphylella* and *Scolopendrellopsis* is also almost identical. *Scolopendrella* shares more features with the two scutigerellids studied thus far, but it also shows some characters in common with the other two scolopendrellids.

1. The tentorial complex

1.1. Common pattern and variations within Symphyla

In the five studied symphylan species, the tentorial complex comprises a pair of main rod-like structures, each composed of the posterior process and the hypopharyngeal bar with one or two tentorial bridges, and a lateral projection which serves as common basis for the lateral process, frontal process and an epipharyngeal lamina (fig. 22).

However, notable differences separate the five symphylans into two groups. On one hand, common features of the tentorial complex in the Scolopendrellidae are the laminar-like aspect of the posterior and lateral processes. On the other hand, the most conspicuous difference in the tentorial complex is the presence of two tentorial bridges in *Scutigerella, Hanseniella* and *Scolopendrella* (fig. 22A), while *Symphylella* and *Scolopendrellopsis* present only one (fig. 22B). This feature, thus, seems to be incongruent with the traditional classification of the two families. Because other myriapod subgroups have only one tentorial bridge (e.g. Snodgrass 1952, Manton 1964), the presence of a single bridge is likely plesiomorphic within the Symphyla and the development of the posterior bridge a potential synapomorphy of *Scolopendrella* and Scutigerellidae.

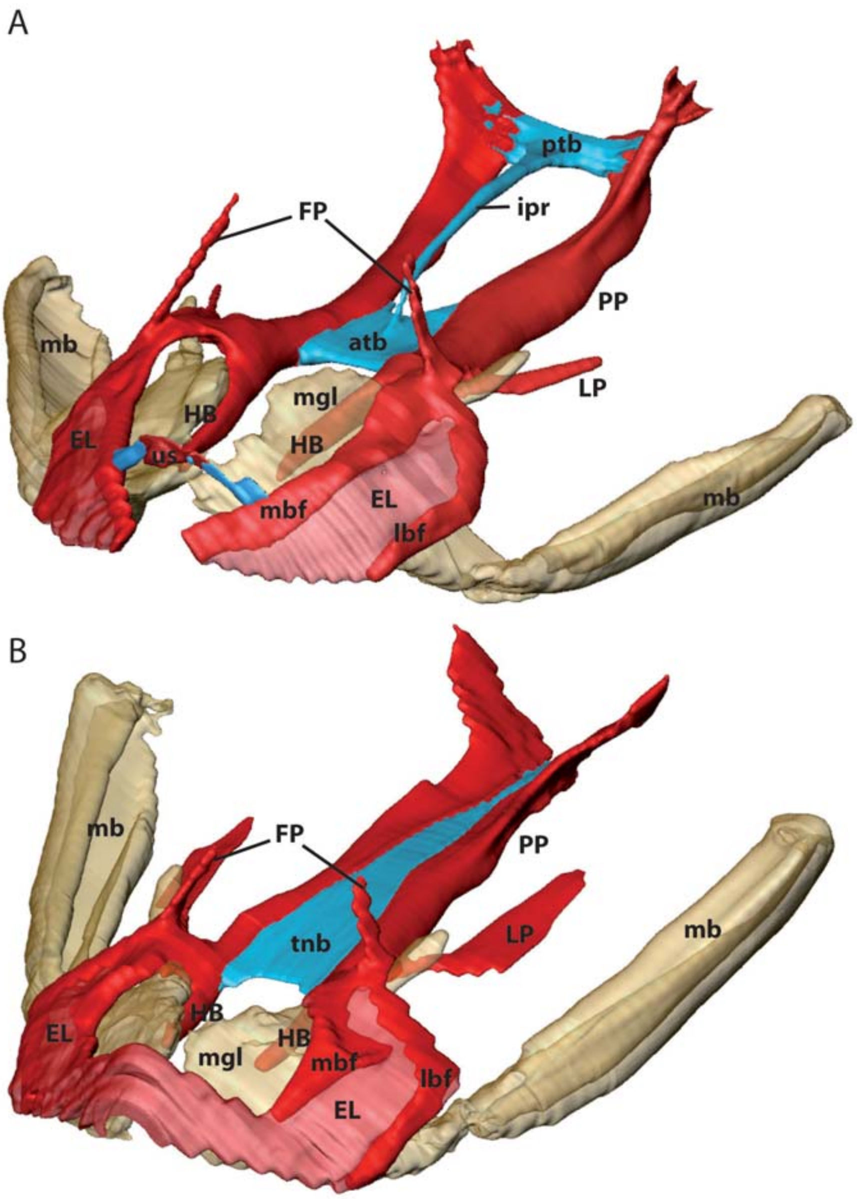


Fig. 22 3D reconstruction of the cephalic tentorium, (A) *Scutigerella causeyae* and (B) *Symphylella vulgaris*. Abbreviations: *atb,* anterior tentorial bridge; *EL,* epipharyngeal lamina with two bar-like cuticular thickenings (*mbf*, mesial bar-like fold, and *lbf*, lateral bar-like fold); *FP,* frontal process; *HB,* hypopharyngeal bar; *ipr* "interpontal rod"; *LP,* lateral process; *mb,* mandibular base; *mgl,* mandibular gnathal lobe; *PP,* posterior process; *ptb,* posterior tentorial bridge; *us,* "unpaired sclerite".

1.2. Clarification of misunderstandings in the literature

Comparisons of the obtained results with the descriptions of Snodgrass (1952), Manton (1964) and Ravoux (1975), drawing special attention to their diagrams of histological sections, enable a re-interpretation of their results (table 2). On her diagrams, Manton assigns the "lateral process" which forms a "bearing for the mandibular gnathal lobe apodeme" to the epipharyngeal bar, not clarifying where it continues. The transverse process, described by Manton as a surface sclerotization across the base of the preoral cavity which originates at the fusion between the posterior process and the hypopharyngeal process (=hypopharyngeal bar), corresponds to the epipharyngeal lamina. However, she does not specify that it has the same origin as the lateral process. On the other hand, Ravoux assigns the "transverse process of Manton" to both the lateral process and the beginning of the epipharyngeal lamina.

The descriptions of the present study clarify previous misunderstandings. Present observations of the epipharyngeal lamina correspond closely to the illustrations of Kluge (1999,

Snodgrass (1952)	**Manton (1964)**	**Ravoux (1975)**	**Present Study**
Hypopharyngeal apophysis	Hypopharyngeal process	Apophyse hypopharyngienne (a) =bras oral	Hypopharyngeal bar
Lateral epipharyngeal sclerite	"transverse process fades out into the cuticle"	Épipharynx (only illustrated)	Epipharyngeal lamina, mesial bar-like fold *(epipharyngeal bar?)*
Transverse epipharyngeal ridge (it would be only the anterior end of the epipharyngeal bar).	Transverse process	Épipharynx (only illustrated) and ap.tr (b) (=apophyse transverse?) (only shown on a diagram).	Epipharyngeal lamina, lateral bar-like fold *(transverse bar?)*
-	-	Tendon de muscles suspenseurs apophysaires antérieurs	Frontal process
Head apodemes	Anterior tentorial apodeme (=posterior process in diplopods)	Apophyse hypopharyngienne (c) (bras tentoriale or apophyse tentorial)	Posterior process
[illustrated but not designated]	-	Ap.tr. (Apophyse transverse?) (b) (=bras mandibulo-épipharyngien or "processus transverse")	Lateral process

Table 2. Terminology for the components of the tentorial complex of the Symphyla in previous descriptions and the present study.

2000). The formation of a paired epipharyngeal lamina with two strengthened bar-like folds serving as articulation points for the mandibular gnathal lobe now seems to be a common feature of symphylans.

1.2. True "fultural sclerites" in Symphyla.

The presence of an epipharyngeal lamina in Symphyla confirms the presence of "fultural sclerites" (*sensu* Snodgrass 1950), and therefore, exoskeletal components of the tentorium that transfer the swinging movements of the tentorium to the mandibular gnathal lobe. This transmission occurs through the condyle-like protuberances on the dorsal wall of the gnathal lobe, which articulate with the lateral and mesial folds of the epipharyngeal lamina.

The two cuticular reinforcements of the lamina form two bars which may correspond to the epipharyngeal and lateral bars of the other myriapods (Koch 2003, Snodgrass 1950) (fig. 23). The position of the lateral fold matches relatively well with the proposed correspondence with the epipharyngeal bar. The beginning of the lateral and mesial bars of the epipharyngeal lamina in Symphyla is very similar to the beginning of the lateral bar in Pauropoda (Koch 2003, fig. 3 and 4). However, the proposed homology of the lateral bar is doubtful and has to be taken very cautiously.

Present observations also revealed a contact between the "epipharyngeal bars" at the tip of the clypeolabrum in Symphyla, which shows a lesser grade of sclerotisation in both scutigerellids. The presence of a similar completely sclerotized contact between the two epipharyngeal bars in the chilopod *Scutigera coleoptrata* (Lewis 1981) may allow the consideration of this feature as a plesiomorphic condition too.

1.3. Tentorial mechanisms and phylogenetic implications

The presence of the same common pattern in Symphyla supports the "swinging tentorium" as an unambiguous synapomorphy of Myriapoda (Manton 1964, Boudreaux 1979). Furthermore, the presence of exoskeletal components of the tentorial complex, the "fultural sclerites", with a connection to the rest of the tentorium and with the lateral apex of the head-capsule, is confirmed. The remarkable coupling of the two condyle-like protuberances on the gnathal lobe with the articular folds of the epipharyngeal lamina is evidence of the presence of a true articulation. Based on the topology of all components, a homology hypothesis with the chilopod *Lithobius* is proposed (fig. 23). Even though there is a connection between the long apodeme of the gnathal lobe to the concavity of the common basis of the lateral process, epipharyngeal lamina and transverse bar, there is no evidence of any true articulation, as Ravoux (1975) claimed. It seems that the hinged points between the gnathal lobe and the epipharyngeal lamina play a more important role in the translation of the swinging movements from the tentorium onto the gnathal lobe than the tangential contact with the apodeme of the gnathal lobe. It allows a similar translation of the tentorial movements as occurs in Chilopoda (with the exception of Geophilomorpha). However, the presence of two articulations between the premandibular component of the tentorial complex and the gnathal lobe, instead of only one as in Chilopoda, suggests that the tentorial movements not only take part in the abduction of the gnathal lobe, but also in the adduction, as a complement of the adductor muscles (ML) of the gnathal lobe. In contrast, there are no retractor muscles attached to the "transverse bar", as occurs on the lateral bars in Chilopoda and Diplopoda. As a replacement for this muscle, the lateral process receives several retractor muscles from the posterior part of the mandibular base and maxilla I.

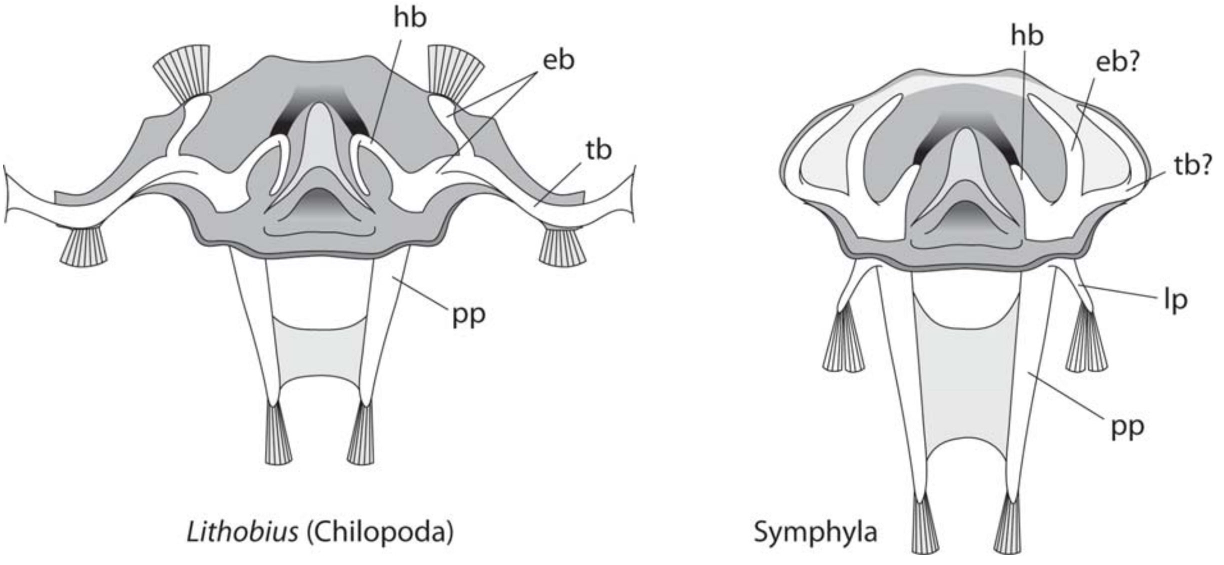


Fig. 23 Frontal view of the tentorial complex in *Lithobius* (Chilopoda) as illustrated by Snodgrass (1950, modified by Koch 2003) and corresponding components, drawn on the same illustration for direct comparison in *Sympylella* and *Scolopendrellopsis* (Symphyla). Abbreviations: *eb* epipharyngeal bar; *hb* hypopharyngeal bar; *lp* lateral process; *pp* posterior process; *tb* transverse bar.

The less pronounced hypopharyngeal bar, compared to other myriapods, does not seem to play any role in the movement of the mandibles. Since there are no muscles inserted on it, its function seems to be a simple support for the hypopharyx. The frontal processes are cuticular structures and not tendons of the transverse bar as it was suggested (Ravoux 1975). The presence of frontal processes, very likely to those in *Pauropus* and *Polyxenus* (see Koch 2003), is therefore confirmed and this feature may form a possible synapomorphy of Progoneata, although it is questionable that the frontal processes belong to the ground pattern of the tentorial complex in myriapods (Koch 2003).

2. Musculature of the head

2.1. More primitive musculature in Scolopendrellidae

An overview of the musculature of the five studied species allows some considerations about the states of the scolopendrellids compared to the scutigerellids, which are discussed in the following.

1. Lack of muscles. The muscles Sd2, ML1d,e and Mii6 are absent in the three scolopendrellids. In addition, *Symphylella* and *Scolopendrellopsis* lack Mi9, Sd1, Pv2, Pd4, Pl3 and C1. The absence of muscles may be due the smaller size of the three scolopendrellids. It could also be related to a more plesiomorphic pattern in the musculature of the Symphyla (see below).
2. Reduction of the number of muscles which form groups. This is the case of Pd3, Pd1 and Pl2 in the three scolopendrellids, and MB2, Pd1 and Pd2 only in *Symphylella* and *Scolopendrellopsis*. It could also be related to the smaller size of these species.
3. Attachment of more muscles to the lateral process instead of the posterior process of the tentorium. This shift concerns Mi5 and Mi6 in the three scolopendrellids (figs. 16A, 21A), and MB5a and Mi3 in *Symphylella* and *Scolopendrellopsis* (figs. 16B, 21B). These muscles have an important roll in the movements of the mouth parts. Compared to the state in Chilopoda, the direction of evolutionary change can be interpreted at least for MB5a. The corresponding muscle in *Lithobius forficatus* is the muscle 135 (*sensu* Rilling 1968; see homology hypothesis below), which attaches to the transverse bar of the tentorium. The attachment of this muscle to the lateral process may indicate that the lateral process evolved in Symphyla from a primitive transverse bar, as a projection of it. The shift of this muscle to the posterior process in *Scolopendrella* and both scutigerellids would then be a derivate state.
4. Attachment of muscles surrounding cuticular structures. This feature is related to the less complex nature of apodemes and other cuticular structures to which these muscles are attached, which could also be a more primitive state. This concerns Sp1 in the three scolopendrellids. In these species, the Sp1 muscles insert directly on the surface of the posterior end of the tentorium, while they insert on small laminae in

both scutigerellids (figs. 7, 10E). In *Symphylella* and *Scolopendrellopsis,* MB8 and MB9 originate from a small apodeme (figs. 17A, 16C, 21A, 21C), while in the other species they attach to the laminae of the mandibular posterior apodemes (figs. 2A, 6, 11A, 10C, 13A). Likewise, in these two genera, MB6 surrounds the dorsal margin of the mandible base and Mi8 does the same on the lamina of the lateral process of the tentorium. Topographic and functional correspondence of MB6 with the mandibular muscle 22 of the centipede *Cormocephalus nitidosus* (*sensu* Manton 1964) supports the view that this state is plesiomorphic, since Manton (1964, figure 64c) illustrates this muscle surrounding the dorsal margin of the mandibular basal lobe, similarly as MB6 does in these two symphylan genera (figs. 16B, 21B).

5. Attachment of muscles to the tentorial bridge instead of the posterior process of the tentorium. In the three scolopendrellids, the muscles Mi6 and Mii3 join the tentorial bridge (fig. 13B), as Mi2 does in *Symphylella* and *Scolopendrellopsis*. This state is generally shown by the Chilopoda and Diplopoda, since their tentorial bridge is more independent and separated from the tentorium (Snodgrass 1950, Manton 1964, Rilling 1967, Wilson 2002, Fanenbruck 2003) and thus, is considered as a plesiomorphic state. This is in agreement with the hypothesis proposed by Snodgrass (1950) for the mandibular muscles by comparison with the state in diplopods. He affirms that these muscles primarily insert on the tentorial bridge and they secondarily may shift their insertion towards the tentorium.
6. More uniform distribution of the mouthparts muscles along the tentorium. This condition is related to the smaller space between both tentorial bridges in *Scolopendrella* and the lack of the posterior one in *Symphylella* and *Scolopendrellopsis*, where this uniformity is more notable. In the scutigerellids, most of the muscles that connect the mandibles and the maxillae to the tentorium are arranged in two main groups, towards each tentorial bridge (figs. 2A, 11A). In the scolopendrellids, in contrast, the muscles spread more uniformly along the tentorium (figs. 13A, 17A, 20A). This can be clearly observed for MB8 and MB9, which have a more anterior position in *Symphylella* and *Scolopendrellopsis*, and there is no space between them and the remaining mandibular muscles. Accordingly, the arrangement of the mandibular and maxillary muscles in the scolopendrellids allows an easier homologization of the respective musculature with the corresponding muscles in other myriapod groups (see below).
7. Muscle B7 connected to the first maxillae (figs. 15, 18, 20, orange posterior muscle; 13E, 16D, 21D), while it attaches to the most posterior point of the second maxillae´s proximal arms in both scutigerellids (figs. 3B, 12B, orange posterior muscle). This feature is also shared by *Lithobius forficatus* (Chilopoda) and *Glomeris marginata* (Diplopoda), which also present a muscle from the most posterior edge of the first maxilla to the margin of the cranium (Rilling 1967, Fanenbruck 2003).

8. Presence of MB10 in *Symphylella* and *Scolopendrellopsis*. These three large muscles have an important position in relation to the mandibular mechanisms (fig. 17B, 20B). They allow a promoting movement of the mandibular bases as occurs in Chilopoda and Diplopoda with similar muscles (see Snodgrass 1950, Manton 1964, Rilling 1967, Wilson 2002, Fanenbruck 2003).
9. Absence of tracheae in *Symphylella* and *Scolopendrellopsis*. Instead, there is a pair of massive apodemes in the same position where the other studied symphylans present the tracheae (figs. 16, 21). The structure is very similar and they likewise support the "tracheal" – "T" – muscles. This could be the reason why Haase (1684 *fide* Verhoef 1934) and Ribaut (1931) mentioned the presence of tracheae in the genera *Symphylella* and *Scolopendrellopsis* respectively. These mandibular apodemes are very conspicuous in the transparent specimens mounted for light microscopy (personal observation), thus it is possible that these authors mistook the tracheae of *Scutigerella* for the mandibular apodemes located at the same position in these genera.

   The same location and the support of the same muscles proves that the superior apodeme of the mandibular base of *Symphylella* and *Scolopendrellopsis* are homologous to the tracheae of the genera *Scutigerella*, *Hanseniella* and *Scolopendrella*. Further discussion about the evolution of the tracheae in the Symphyla follows in the next chapter of this work.

2.2. Outgroup comparison

On the basis of the previous remarks, the new insights on the internal anatomy of the head in Symphyla provide a more firm ground for comparisons with other myriapod groups. With respect to the above mentioned characters, the states in *Symphylella* and *Scolopendrellopsis* seem to provide a more accurate model for such comparisons than the pattern of *Scutigerella* or *Hanseniella*, as have been used thus far (e.g. Snodgrass 1950, Manton 1964, Kluge 1999, Klass & Kristensen 2001, Fanenbruck 2003).

Despite the general difficulty to homologize the musculature in high-ranking subtaxa of arthropods (e.g. Shultz 2007) and in order to have a reference for an interpretation of the cephalic musculature in the Symphyla, a preliminary hypothesis on the homology of the muscles of the head in Symphyla, *Lithobius forficatus* and *Glomeris marginata* [as accurate representatives for Chilopoda and Diplopoda respectively (Edgecombe & Giribet 2002, Sierwald & Bond 2007)] is shown in table 3 and figure 24. This hypothesis is exclusively based on the topology criterion of Hennig (1950) and previous homology for endocuticular structures, mouth appendages and some of their muscles in different myriapod subgroups (e.g. Bitsch & Bitsch 2002, Bitsch 2001, Kraus & Kraus 1994, Koch 2003). In order to assess the topology criterion, similar origin, insertion and position relative to other muscles have been examined.

Symphylella Scolopendrellopsis	***Lithobius forficatus***	***Glomeris marginata***	**Remarks** **(O: origin; I: insertion)**
MB1 (+ MB3?)	139	md-vaa?	O: mb, anterior and medial.
MB2	138	md-vpp (ant.)	O: mb, anterior and ventral.
MB4 + MB7(a,b,c)	137 (7 muscles)	md-vpp (med. and post.)	O: mb: middle, ventral. I: tentorial bridge.
MB5 + MB6	135	- (?)	O: mb, posterior and dorsal.
MB8 + MB9	136	md-vaa?	O: mb, posterior/middle and dorsal. Fan-like spread.
MB10	131	Md-da (of the mbl)	O: dorsal margin of mb. I: lateral wall of the head.
T (6-7 muscles)	132 (8 muscles)	-	O: dorsal margin of mb. I: lateral wall of the head.
ML1(a,b,c)	134a (1 muscle + 2 rows of 5 muscles)	Md-da (of the mgl)	O: gnathal-lobe apodeme. I: lateral wall of the head.
ML1(d,e) + ML2 (+ ML3-8?)	134b (4 muscles)	-	O: gnathal-lobe apodeme. I: postero-lateral wall of the head.
-	140	md-im	Intrinsic muscle of the mandible.
?	133	?	O: mandible. I: epicranium.
H2 + Mi1	?	?	
Mi2	142a?	st-vm?	O: inner margin of mxI, anterior part.
Mi3	142b?	?	O: inner margin of mxI, anterior part
Mi4	147	-	Intrinsic muscle of the mxI, related to the Tp2 or galea area.
Mi5	-	-	
Mi6	143	?	O: inner margin of mxI, medial part.
Mi7	145	Il-vm?	O: inner margin of mxI, posterior part.
Mi8	-	-	
Mi10 + Mi11	144	st-vm?	O: outer margin of mxI, posterior part.
Mi12 or Mi13	-	st-dm	O: outer margin of mxI, medial part. I: lateral wall of the head.
Sp1	94	?	Posterior suspensor muscle from the tent. to the dorsal part of the head.
Sd1+Sd2 (not present in Symphylella and Scolopendrellopsis)	95	?	Medial suspensor muscle from the tent. to the dorsal part of the head.
Sv1 + Sv2	141 + 142 + 143	?	
Pd1	119 + 120 + 121?	?	Antero-dorsal pharyngeal dilators
Pd2	122	?	Medio-dorsal pharyngeal dilators
Pd3	123	?	Medio-dorsal pharyngeal dilators
Pd4	-	?	
Pv1 + Pv2	-	?	
Pl1 + Pl2 + Pl3	-	?	
Pl4	126 + 127	?	Lateral pharyngeal dilator arising from the posterior process of tent.
B7	141	gu-dm?	O: mxI, posterior part. I: posterior margin of head.

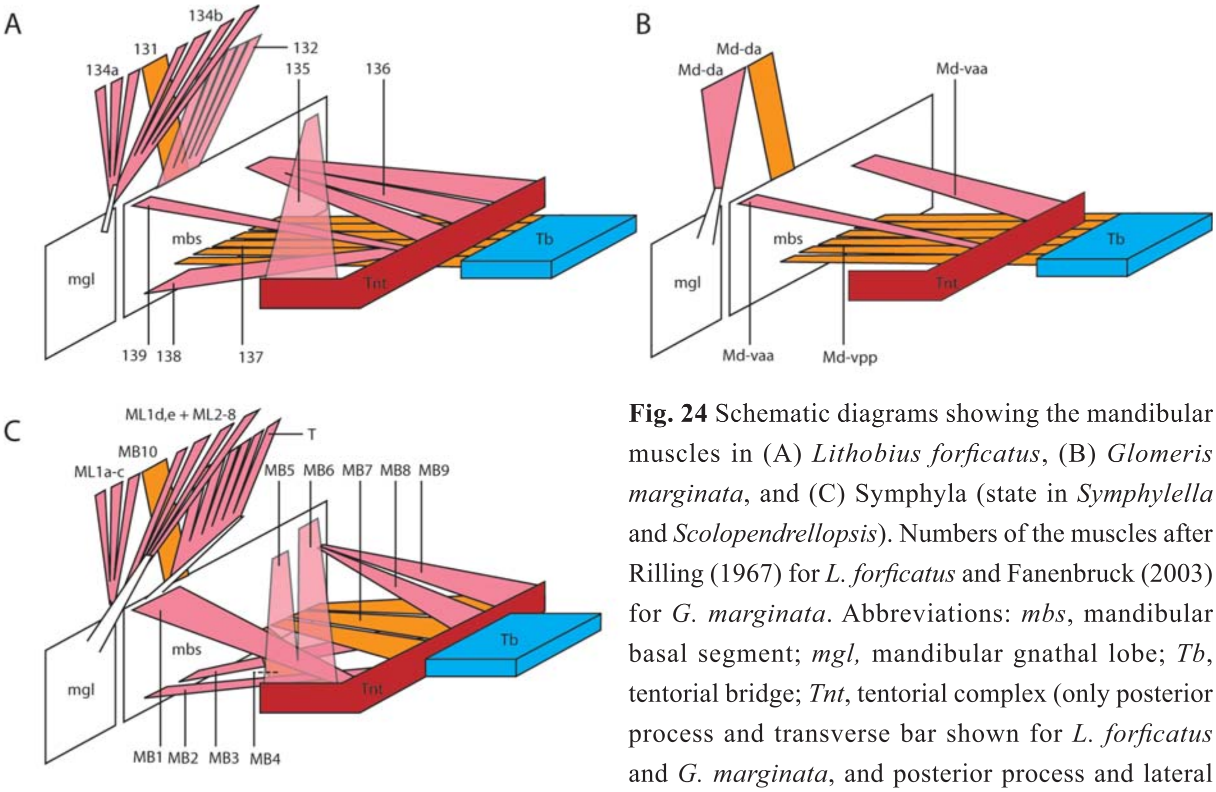


Fig. 24 Schematic diagrams showing the mandibular muscles in (A) *Lithobius forficatus*, (B) *Glomeris marginata*, and (C) Symphyla (state in *Symphylella* and *Scolopendrellopsis*). Numbers of the muscles after Rilling (1967) for *L. forficatus* and Fanenbruck (2003) for *G. marginata*. Abbreviations: *mbs*, mandibular basal segment; *mgl,* mandibular gnathal lobe; *Tb*, tentorial bridge; *Tnt*, tentorial complex (only posterior process and transverse bar shown for *L. forficatus* and *G. marginata*, and posterior process and lateral process for Symphyla).

This preliminary homologisation demonstrates that the musculature of *Symphylella* and *Scolopendrellopsis* share more similarities of the cephalic musculature with outgroups than *Scutigerella* and *Hanseniella*. Strikingly, the mandibular musculature of *Symphylella* and *Scolopendrellopsis* is more similar to *Lithobius* than to *Glomeris*. However, the comparison of the muscles of the first maxillae with those of *Glomeris* is problematic due to the participation of the first maxillae in the formation of the gnathochilarium. It was also not possible to compare the muscles of the second maxillae, since these structures are very different in *Lithobius* and *Glomeris* to those in Symphyla.

This homology also contributes to a better understanding of the evolution of the head musculature within Symphyla and reveals the state in *Symphylella* and *Scolopendrellopsis* as more plesiomorphic than in *Scutigerella* and *Hanseniella*. *Scolopendrella* seems to show an intermediate stage. However, cladistic analysis is required to determine the direction of evolutionary change. For this purpose, the homology hypothes compiled in tables 2 and 3 are used to integrate the characters of the cephalic musculature into a matrix (see Appendix II).

Table 3. Hypothesis on the homology of some cephalic muscles in Symphyla (state in *Symphylella* and *Scolopendrellopsis*), *Lithobius forficatus* (Chilopoda) and *Glomeris marginata* (Diplopoda). Data on *L. forficatus* extracted from Rilling (1967), and on *G. marginata* from Fanenbruck (2003). Abbreviations: *mb*, mandibular base; *mxI*, first maxilla; *tent*, tentorium.

2.3. Mandibular mechanisms

Snodgrass (1950) and Manton (1964) considered the Symphyla – *Scutigerella* and *Hanseniella* – together with the Diplopoda as specialized myriapods that show particular refinements regarding the mandibular mechanisms. Manton (1977) claimed that the muscular abduction of the mandibular basal segment is abandoned in Symphyla – in *Scutigerella immaculata* –, just like in Diplopoda. Instead, the mandible is assumed to abduct by the posterior process of the tentorium pushing on the sides of the gnathal lobes. However, the presence of the three large MB10 muscles and the close relationship between the T muscles and the mandibles through the superior mandibular apodeme in *Symphylella* and *Scolopendrellopsis* enable higher mobility in the mandibular base, which questions Manton's assumption. It is possible that the mandibular mechanisms in Symphyla are not as specialized as it was previously proposed, but instead very close to the myriapod ground pattern. Nevertheless, further data on the head's musculature of Pselaphognatha (Diplopoda), Tetramerocerata and Hexamerocerata (both Pauropoda), as well as more detailed studies on the mechanisms of the muscle-sets in Symphyla are required for an conclusive functional comparison of this kind.

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Chapter 3

Morphological phylogenetics of the Symphyla

Introduction

The Symphyla have represented a phylogenetically historical enigma, since Ryder proposed their name in 1882, referring to the affinity of this group to both myriapods and insects.
They have always been considered as a monophyletic group, characterized by several features, such as unpaired gonopore on the fourth trunk segment, head spiracles, absence of eyes, second maxillae united into a labium-like structure, receptacula seminis in the mouth cavity, first trunk legs reduced, tergites doubled on three or more trunk segments, presence of styli and eversible vesicles between legs, undivided tarsus and terminal paired spinnerets (e.g. Boudreaux 1979, Kraus & Kraus 1994).

Throughout history, they have variably been proposed as sister group of Chilopoda (Atelopoda-hypothesis: Boudreaux 1979), Hexapoda (Labiata-hypothesis: Snodgrass 1938; Dimalata-hypothesis: Sharov 1966; Trignatha-hypothesis: Tiegs 1947) and Diplopoda + Pauropoda (Progoneata-hypothesis; Pocock 1893) (fig. 1). Currently, most authors tend to adopt the morphological view that Progoneata form a monophyletic unit (e.g. Meglitsch & Schram 1991), either more related to Hexapoda (Labiophora-hypothesis: Kraus & Kraus 1994) or to Chilopoda within a monophyletic Myriapoda (e.g. Dohle 1980, Edgecombe 2004, Edgecombe & Giribet 2002) (fig. 1). In contrast, recent molecular analysis resolved them in new positions: as adelphotaxon of all remaining myriapod subgroups (Regier *et al*. 2005); as sister group of Diplopoda either within a myriapod clade (Gai *et al*. 2008) or as basal offshoot of Mandibulata (Podsialdlowski *et al*. 2007); as sister group of Pauropoda (Gai *et al*. 2006, Regier *et al*. 2008); or inclusively in a very basal position among the arthropods (Mallat & Giribet, 2006; Mallat *et al*. 2004, Reumont *et al*. 2009) (fig. 1). It is interesting that only a few species of Symphyla were included into all phylogenetic analyses published thus far, and they are representatives of the genera *Scutigerella* and *Hanseniella*, and eventually *Symphylella* in a few studies.

The uncertain position of the Symphyla may be affected by the lack of understanding of the phylogenetic relationships within the group, generating an inaccurate taxon sampling (Heath *et al*. 2008, Reumont *et al*. 2009). The classification of the symphylan species (chronologi-

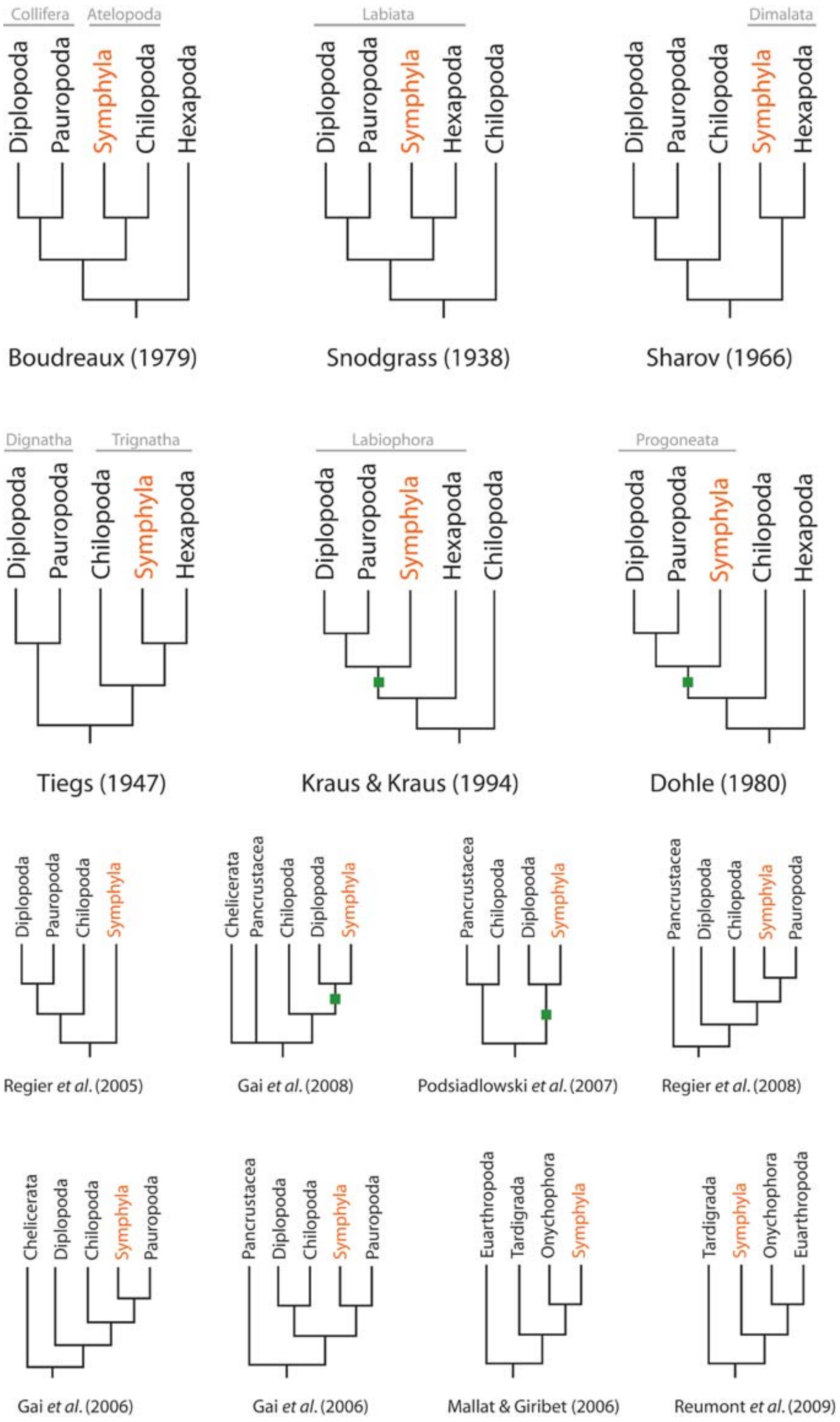

Fig 1 Alternative hypotheses of relationships between Symphyla and other myriapod and arthropod subgroups. The first six cladograms (above) are based on morphological evidences while the latter eight (below) are based on molecular analyses. Green squares indicate the group "Progoneata". Authors introducing or endorsing each hypothesis are indicated below each cladogram.

cally: Hansen 1903, Bagnal 1913, Ribaut 1913 & 1914, Attems 1926, Verhoeff 1933) led to the systematics of the different genera proposed by Edwards (1959b). The most recent revisions (Domínguez 1992, Scheller 1961, Scheller & Adis 2002) did not change this classification significantly. Accordingly, two main subgroups are still distinguished, Scutigerellidae and Scolopendrellidae, mainly based in the morphology of the margin of the sense calicles, the presence of pointed posterior projections on scuta, the size of styli, the size of first pair of legs and the body length. Likewise, variation among different genera lies mainly in the morphology and number of scuta. Only a few studies have addressed evolutionary hypothesis of these features. Ribaut (1931) and Ravoux (1962), basing their works on the correlation between tergal, pleural and sternal areas and the trunk musculature of several species of both families, proposed *Geophilella* as the most primitive symphylan, due to its high number of trunk scuta (22). They suggested a trend of fusion of couples or trios of scuta to the most advanced condition in the Scutigerellidae, which show only 15 scuta. Verhoeff (1934) proposed the same transformation series and reiterated that the scolopendrellids are more plesiomorphic than the scutigerellids. Verhoeff and Ravoux compared Symphyla with diplopods and polarised this evolutionary trend with respect this outgroup. They affirmed that both groups are closely related because of the formation of diplosegments. On the other hand, Tiegs (1940, 1945), based on embryological studies in *Hanseniella agilis*, and Manton (1966, 1977), based mainly on the musculature of *Scutigerella immaculata,* rejected the view that symphylans show diplosegments; they considered the so called “extra tergites” as duplications of the normal single dorsal sclerites. By the same token, Dallai and Afzelius (2000) suggested that the structure of the euspermatozoa of *Scutigerella* is more primitive than the one in *Symphylella* (Rosati *et al*. 1970).

So far, neither any evolutionary hypothesis, nor the validity of the classification of the Symphyla have been tested by cladistic analysis. The present work presents a cladistic study of representatives of all valid genera of Symphyla, based entirely on morphological characters of adults. The main goals of this study are: 1) to generate a hypothesis on the phylogenetic affinities among the symphylans, 2) to test the current classification, 3) to propose appropriate species for further comparative and phylogenetic studies with other myriapods, and 4) to reconstruct the ground pattern of the Symphyla and to discuss the evolution of relevant characters.

Material and Methods

1. Examined Taxa

The present analysis was undertaken by application of an exemplar approach (Yeates 1995) with 23 species representing all 14 valid symphylan genera (table 1).
The exterior morphology of eleven European species plus one Australian species – *Hanseniella agilis* – belonging to a total of seven genera was investigated in detail by SEM. Furthermore, data on the head's internal anatomy of the five studied species were also included (see previous chapter). Part of the examined taxa was collected during recent field trips

species	**source of data**	**origin of material**
Symphylella vulgaris (Hansen, 1903)	SEM, hist.	fresh collected
Symphylella elongata Scheller, 1952	SEM	loaned A.Serra (UB)
Scolopendrellopsis (Scolopendrellopsis) microcolpa (Muhr, 1881)	SEM	loaned MfNK Görlitz, num. 9449
Scolopendrellopsis (Symphylellopsis) arvernorum Ribaut, 1931	SEM	loaned C.Simón (UAM)
Scolopendrellopsis (Symphylellopsis) subnuda (Hansen, 1903)	SEM, hist.	fresh collected
Scolopendrella notacantha Gervais, 1839	SEM, hist.	fresh collected; loaned MNCN Madrid num. 20.06/88
Geophilella pyrenaica Ribaut, 1913	SEM	fresh collected
Parviapiciella balcanica (Remy, 1943)	SEM	loaned A.Serra (UB)
Scutigerella immaculata (Newport, 1845)	SEM, literature	loaned A.Serra (UB)
Scutigerella causeyae Michelbacher 1942	SEM, hist.	fresh collected
Hanseniella nivea (Scopoli, 1763)	SEM, hist.	fresh collected
Hanseniella agilis Tiegs, 1939	SEM	loaned G.Mayer (VUA)
Hanseniella graeca Remy, 1941	literature	
Millotellina (Millotellina) monteithi Naumann & Scheller 1977	literature	
Millotellina (Diplomillotellina) bidens Naumann & Scheller 1977	literature	
Scopoliella crenatus Scheller 1986	literature	
Scolopendrelloides bifida Scheller 1961	literature	
Remysymphyla hebetocornuta Scheller 1971	literature	
Symphylellina pachypoda Brölemann, 1931	literature	
Neosymphyla ghanensis Edwards & Belfield 1967	literature	
Ribautiella cathetus Scheller 2007	literature	
Ribautiella delphini Rochaix 1956	literature	
Ribautiella remyi Hinschberger 1954	literature	

Table 1. Symphylan species included into cladistic analysis. “SEM” and “hist.” indicate the species studied by SEM and histological sections. Further information on loaned material in chapter 1.

(see methodology in Chapter 1). Additional material was kindly provided by collaborators and one species belongs to a Museum's collection (besides the *Scolopendrella notacantha* specimen used for internal anatomy studies). Data on the remaining genera were compiled from the original descriptions in the literature (see reference on the name of the species, table 1). In order to obtain representation of all morphological groundplans of Symphyla in the analysis and following the *a priori* intuitive method of Yeates (1995), one species of each genus were chosen, except for those showing relevant intrageneric variation, in which case data of several species was included.

In addition, one species of each high-ranking myriapod subgroup was included in the analysis as outgroups (table 2).

2. Morphological characters

A total of 145 characters of the external morphology and internal anatomy of the head are listed and described in Appendix I and compiled into the data matrix in Appendix II.

The first 67 characters refer to the external morphology, specifically to the number and morphology of scuta (characters 1-16), morphology of the head capsule and mouthparts (characters 17-44), structures of the ventral part of the trunk segments and legs, especially sclerites of the first segments (chars. 45-58); cerci (chars. 59-62) and sense calicles (chars. 63-67). These characters were observed in the 15 available species using SEM (see methodology in the first chapter of this work) and supplemented from literature data for the remaining species, when available.

The character 68 refers to the morphology of the euspermatozoa and has been documented in only two symphylan species (Rosati *et al*. 1970; Dallai & Afzelius 2000).

In addition, 77 characters of the head's internal anatomy of the five studied species (see chapter 2) were also included. Characters 69-77 allude to the morphology of the tentorial complex, characters 78-80 to other endoskeletal structures and characters 81-145 to the

species	myriapod subgroup	source of data
Scutigera coleoptrata (Linnaeus, 1758)	Notostigmophora (Chilopoda)	Ax 1999, Brusca & Brusca 2003, Andersson 2006, Manton 1965.
Lithobius forficatus (Linnaeus, 1758)	Pleurostigmophora (Chilopoda)	Rilling 1968, Eisenbeis & Wichard 1987
Polyxenus lagurus (Linnaeus, 1758)	Penicillata (Diplopoda)	Eisenbeis & Wichard 1987, Brusca & Brusca 2003
Glomeris marginata Latreille 1802	Chilognatha (Diplopoda)	Eisenbeis & Wichard 1987, Fanenbruck 2003
Allopauropus sp.	Tetramerocerata (Pauropoda)	Personal observations, Eisenbeis & Wichard 1987
Millotauropus acostae Scheller 1997	Hexamerocerata (Pauropoda)	Scheller 1997

Table 2. Outgroups used in the cladistic analysis.

musculature of the head, especially to the mandibular and maxillary muscles. This permits to test the assumption that the tentorial complex and cephalic musculature display significant, phylogenetically informative variation. Additional data on the head's musculature in *Scutigerella immaculata* was taken from Manton (1964) and Ravoux (1975).

Data on outgroup relationships and ingroup monophyly was adopted from Kraus & Kraus (1994) and Edgecombe *et al*. (2000).

3. Cladistic analysis

Maximum-parsimony analysis of the 145-character dataset was computed with TNT (Goboloff *et al.*, 2003) using implicit enumeration. Characters were of equal weight and unordered. Nodal support was assessed in TNT by jackknifing using 1000 replicates with 36% deletion, each replicate using implicit enumeration.

In order to assess the extent to which different analysis parameters affect phylogenetic conclusions, the outcome of the unweighted analysis was evaluated using implied weighting with the "goloboff fit" criterion (Goloboff 1993) under TNT using implicit enumeration as well. Searches were conducted with *k* values 0–6.

Character optimization (Farris 1970) was explored with WINCLADA (Nixon, 2002). The most parsimonious cladograms were examined under unambiguous, fast and slow optimizations. Fast optimization – or accelerated transformation (ACCTRAN) – minimizes hypotheses of parallel acquisition of complex traits (Agnarsson & Miller 2008) by favouring eventual reversals over homoplastic gain of characters (Swofford and Maddison 1987). Vice versa, slow optimization – or delayed transformation (DELTRAN) – favours independent gains of a state rather than acquisition and reversal.

As defended by some current phylogenetic analysis on the interrelationships within Myriapoda (e.g. Edgecombe 2004): Chilopoda + [Symphyla + Dignatha (Diplopoda + Pauropoda)], cladograms were rooted using the centipede subgroups (Chilopoda) as outgroup.

Results

The data matrix comprises 131 parsimony informative characters (Appendix II). A single optimal tree was held during implicit enumeration in TNT [length 264 steps; consistency index (CI) 0.78; retention index (RI) 0.86; rescaled consistency index (RCI) 0.75] and is depicted in figure 2. Figure 3 depicts unambiguous changes on the single shortest cladogram favoured by implied character weights (Goloboff 1993), as implemented in TNT (default concavity function, $K = 2$).

Both resolutions favour a fundamental split that resolves the family Scolopendrellidae (*sensu* Edwards 1959) as a paraphyletic assemblage within which a clade composed of *Scolopendrella*, *Geophilella* and *Parviapiciella* is sister to the monophyletic Scutigerellidae. The remaining representatives of Scolopendrellidae form a monophyletic group, albeit with low support.

Besides the autapomorphies defined by Kraus & Kraus (1994) and Edgecombe *et al*. (2000) (characters 39, 52, 54, 59, 63), the monophyly of Symphyla (jackknife support = 100) receives support from two new characters: the presence of a central rod of the head (character 26) and the longitudinally spread form of the (anterior) tentorial bridge (character 70). The state of having 15 trunk tergites (character 1) will be discussed below.

Scutigerellidae is unambiguously defended as a monophylum (js = 71) based on the traditional characters absence of the subdivision of the tergites 14 and 15 (char. 2, convergent with *Remysymphyla*), absence of median branches of the head's central rod (char. 31, convergent with *Scolopendrellopsis* (*Sym.*) *arvernorum* and *Ribautiella*), 4-jointedlegs on the first trunk segment (char. 51, state 1), digitiform styli (char. 53, state 3) and sense calicles with setose margin (char. 64). Additional apomorphies of Scutigerellidae under accelerated optimization are several characters yet only observed in *Scutigerella* and *Hanseniella* by SEM, such as undivided rod of the head (char. 27, convergent with *Symphylella* and *Ribautiella cathetus*), second maxillae with posterior origin clearly delimited (char. 40) and with three terminal protuberances (char. 41), short cervical plates (char. 46), kidney-like anterior sternal plates of the second trunk segment (char. 50) and scales on the outer surface of sense calicles (car. 65, convergent with *Symphylella*), besides 19 character states of the head´s internal anatomy shared by *Scutigerella* and *Hanseniella* as well (chars. 69, 72, 76, 80, 83, 85, 97, 103, 104, 107, 108, 114, 115, 128, 130, 131, 135, 136, 137, 142, 145). These additional synapomorphies of Scutigerellidae must be taken carefully, since they have very limited sampling in the most of the included scutigerellid species.

Interrelationships within Scutigerellidae receive low jackknife values. *Scolopendrelloides* is resolved as basalmost offshoot, followed by *Hanseniella graeca* and *Scopoliella*, which are likewise resolved each as sister to the remaining scutigerellid taxa (see figs. 2 and 3). This

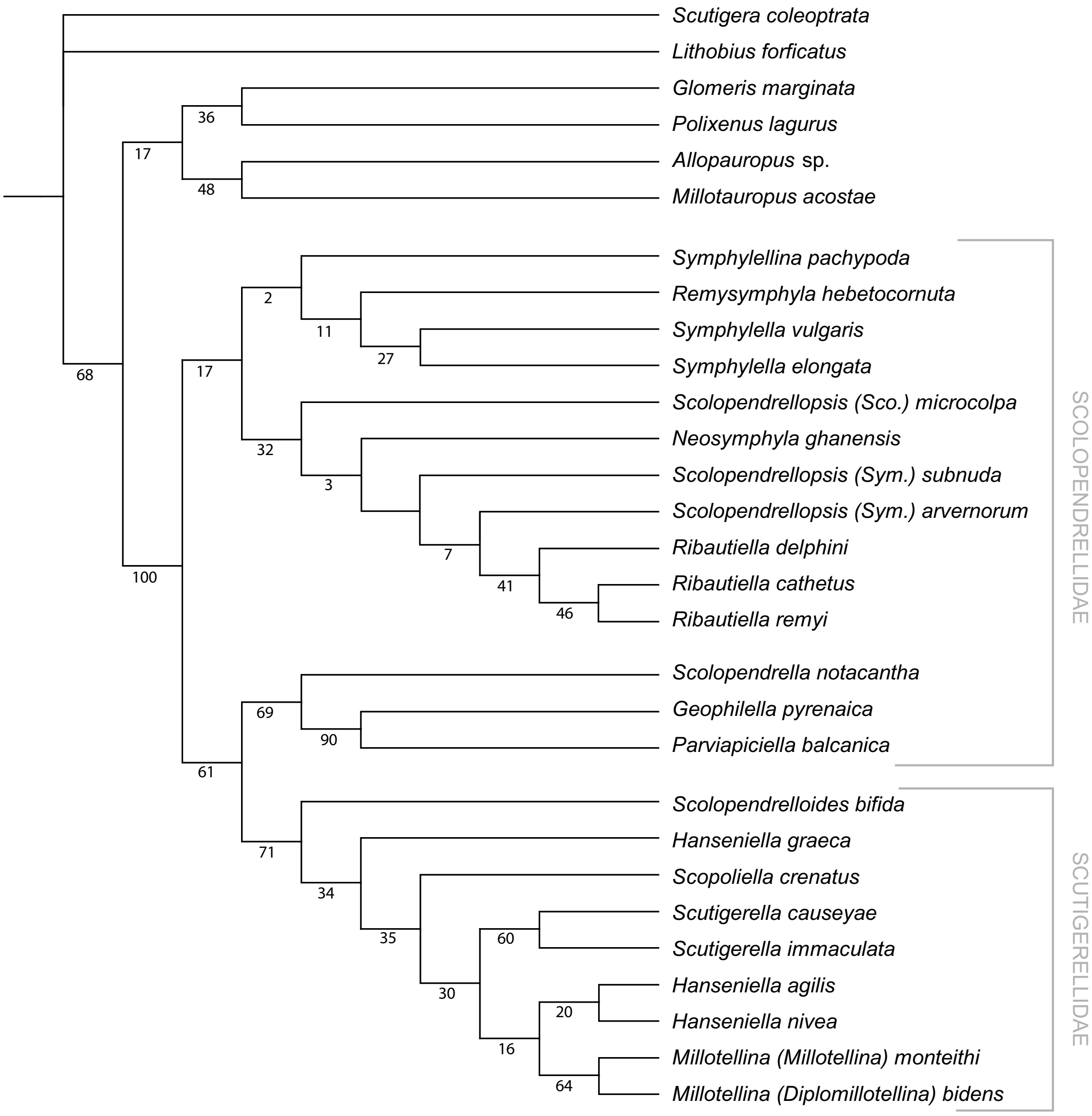

Fig. 2 Shortest cladogram (264 steps, CI 0.78 RI 0.86). Numbers below nodes are jackknife frequencies.

resolution of Scutigerellidae reveals the presence of posterior pointed projections on scuta as plesiomorphic within the group, as well as the elongated form of the head capsule. These features transform within Scutigerellidae: towards a rounded head (char. 17) and towards rounded projections on the posterior border of the scuta (char 8, state 1). The crown-group formed by *Scutigerella*, *Hanseniella* (*H. agilis* and *H. nivea*) and *Millotellina* (js = 30) is unambiguously supported by the presence of posterior branches of the head's central rod (char. 33, convergent with *Scolopendrella*) and the presence of coxal vesicles between the legs 10, besides the 3-9 (char. 55, convergent with *Geophilella*, *Parviapiciella*, *Symphylellina* and *Ribautiella*). Conditions of delayed transformation obviously locate all additional synapomorphies of Scutigerellidae that arise under fast transformation (chars. 69, 72, 76, 80, 83, 85, 97, 103, 104, 107, 108, 114, 115, 128, 130, 131, 135, 136, 137, 142, 145) in this

Fig. 3 Apomorphies optimized on shortest cladogram under implied weights ($k = 2$). Black squares are non-homoplastic changes, white squares homoplastic changes; all changes are unambiguous. Enumerated characters (upper numbers) and states (lower numbers) are described in Appendix I.

crown group, since they refer to the internal head's anatomy only observed in *Scutigerella* and *Hanseniella*.

Among the previous Scolopendrellidae, *Geophilella* unites with *Parviapiciella* with strong support (js = 90) based on a series of homoplastic characters that are shared with other scolopendrellid species: high number of scuta (chars. 3, 4, 15), pattern of sclerotisation of the scuta and head sclerites (chars. 7 and 25) and specific arrangement of the coxal vesicles between the legs 3-10 (char. 55). Characters exclusively shared by these two species are the presence of a very conspicuous scale-pattern in the cerci (char. 62) and, under accelerated transformation, presence of digitiform posterior projections on scuta (char. 10) (reduced in *Geophilella*), presence of a cuticular reinforcement in the median branches of the head's central rod (char. 32, state 3) and presence of only one group of digitiform appendages on the dorsal margin of the sense calicles (char. 67). The sister taxon of *Geophilella* and *Parviapiciella* is *Scolopendrella*. These three taxa form a monophyletic group (js = 69) which is called "Scolopendrella-group" in the following. Unambiguous autapomorphies of this group are: first scutum consisting of two longitudinal rows (char. 6, state 1), ring-shaped basis of setae in the head (char. 34), presence of a protuberance beside first-maxillary palp (char. 38), heterogeneous surface of second maxillae (char. 43) and angular shape of sternal plates of the first pair of legs (char. 49). Fast and slow optimization notably increases the number of potential apomorphies (up to 19 apomorphies under accelerated transformation).These three genera would also share the conspicuous cervical plates of smooth cuticula (char. 45, convergent with *Symphylella*), presence of digitiform appendages inside the sense calicles (char. 66, convergent with *Scolopendrellopsis*) and presence of longitudinal ridges in the apical part of cerci (char. 60).

The sister group relationship between Scutigerellidae and the "Scolopendrella-group" (js = 71) is mainly based on a series of characters of the head's internal anatomy which have been observed in *Scolopendrella*, *Scutigerella* and *Hanseniella* (chars. 71, 82, 86, 94, 112, 117, 120, 123, 124, 143). Among these, there are remarkable features which have already noted in the previous chapter of this work, such as the presence of the posterior tentorial bridge (char. 71), absence of the MB10 muscles (char. 94), presence of Mi9 (char. 112) and formation of tracheae instead of massive apodemes above the mandibular base (char. 78, only under slow optimization). Also characters of the external morphology support this clade: correspondences of the pointed projections of the scuta in *Scolopendrella*, *Scolopendrelloides* and *H. graeca* (chars. 10; 12, under fast optimisation; 13, convergent with *Symphylella* and *Remysymphyla*); presence of head spiracles (char. 18), rounded posterior part of the head (char. 36, under fast optimization), second maxillae with transversal groove (char. 42), specific arrangement of ventral sclerites on the first trunk segment (chars. 47, under fast optimization, and 48) and presence of scales on the cerci (char. 61). The presence of a long flagellum in euspermatozoa (char. 68) is located at the basis of this clade under accelerated optimization, but this character has been sampled only for *Scutigerella*.

The remaining scolopendrellids form a monophyletic group with insufficient jackknife support (js = 17). The name "Symphylellidae" is suggested for this group, in order to ease further explanations in the discussion. Unambiguous synapomorphies of "Symphylellidae" comprise the pubescence on the sclerotized sclerites of the head (char. 24, convergent with the pauropod *Allopauropus*), frontal branches of the head's central rod (char. 29), absence of muscle Sd1 (char. 105) and attachment of muscle Mi3 to the lateral process of the tentorium (char. 116). These four synapomorphies are supplemented with 25 additional characters under delayed and accelerated transformation, the most of which (17 characters) refer to the internal anatomy yet studied only in *Symphylella vulgaris* and *Scolopendrellopsis* (*Symphylellopsis*) *subnuda*. Among the additional synapomorphies of the external morphology, all of them are homoplastic (chars. 18, 20, 60), reversed (char. 6), or only observed in a few species (chars. 23, 35, 44, 67).

All groupings within "Symphylellidae" receive no significant jackknife support, and internal resolution varies when homoplastic characters are downweighted. *Symphylellina*, *Symphylella* and *Remysymphyla* cluster as the "Symphylella-group", and *Scolopendrellopsis* and *Neosymphyla* ("Scolopendrellopsis-group") form a paraphyletic group with respect to *Ribautiella*. The cladogram favoured by implied character weights (*k*=2) resolves the "Scolopendrellopsis-group" as monophylum [autapomorphies: trapezoidal first scutum (char. 6, state 3, convergent with *Ribautiella remyi*), higher number and partial sclerotisation of scuta (char. 3 and 7, convergent with *Ribautiella*, *Geophilella* and *Parviapiciella*), granulation of the head (char. 25, convergent with *Geophilella* and *Parviapiciella*) and central rod´s cuticular reinforcement (char. 28)]; and the "Symphylella-group" is favoured as paraphyletic with respect to *Ribautiella* [autapomorphies: V-shaped antero-lateral branch of central rod (char. 30) and reduction of the first pair of legs (char. 51, state 4)].

Discussion

1. Incongruence between phylogeny and the traditional classification.

The phylogenetic relationships favoured by the shortest cladograms are not congruent with the traditional classification (see Domínguez 1992, Edwards 1959b, Scheller 1961). Scolopendrellidae is not a monophyletic entity, but a paraphyletic group with *Scolopendrella*, *Geophilella* and *Parviapiciella* (the "Scolopendrella-group") closer related to Scutigerellidae. Perhaps a third family should be adopted in the classification, rendering to the Geophilellidae family of Ribaut (1914). In this case it would also include the genera *Scolopendrella* and *Parviapiciella*, besides *Geophilella*. However, although the traditional classification is clearly unsatisfactory for the phylogenetic system of the Symphyla, it is useful in descriptive taxonomy and determination, and changes are preferably not suggested.

Contradictions also exist with the nomenclature of the genera *Scolopendrellopsis* and *Hanseniella*, as they likely represent para- or polyphyletic assemblages. None of the diagnostic characters of *Scolopendrellopsis* seem to support its monophyly (see figs. 2, 3). The same is true for *Hanseniella*, particularly as some species – *H. graeca* and *H. angulosa* Hansen, 1903 (this latter non included in the analysis) – maintain apparently the plesiomorphic character of presence of posterior projections on the scuta. The polyphyly of *Hanseniella* is therefore probably the result of an inaccurate definition of this genus. Already Bagnal

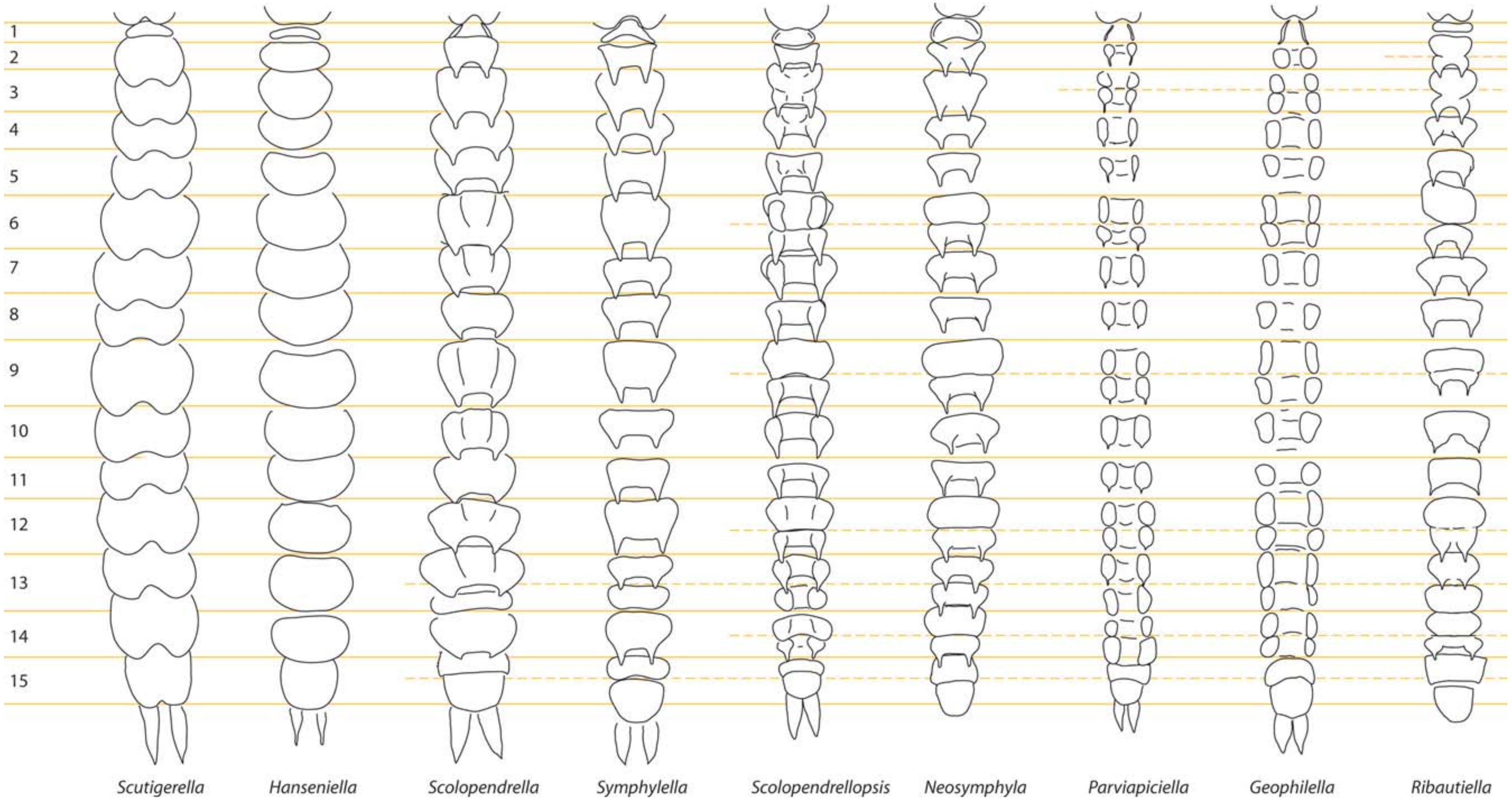

Fig. 4 Arrangement of the scuta in different symphylan genera. Numbers indicate tergal areas. For a matter of convenience, the term “tergite” is used for each “tergal area” where subdivisions can occur, increasing the total number of scuta. Broken lines indicate subdivisions of tergites. Data on *Neosymphyla* and *Ribautiella* are respectively taken from Edwards & Belfield (1967) and Allen (1998).

(1913) argued that Hanseniella consist of at least two subgenera: *Hanseniella s. str.* and *Scolopendrelloides*. Main criteria for this classification were the presence of a deep postero-median depression on the last scutum, the size of the styli and the features of some setae of the antennae. Edwards (1959b) excluded *Scolopendrelloides* form *Hanseniella* und reasoned the genus rank for the former, among others, with the shape of scuta, the first two of which are posteriorly convex in *Hanseniella* but emarginated posteriorly in *Scolopendrelloides*. According to this criterion, *H. graeca* and *H. angulosa* should no longer belong to the genus *Hanseniella*. A revision on this genus presently is premature, since *H. graeca* and *H. angulosa* are still listed under *Hanseniella* in current data bases [Fauna Europaea (Scheller 2004), BioLib (Zicha 2009), Global Name Index, etc.]. Nevertheless, further taxonomical studies are required to clarify this issue.

2. Character evolution

The results of the cladistic analyses permit reconsideration of the evolution of character systems, in which controversies have traditionally focused: number of scuta (e.g. Ribaut 1931, Ravoux 1962), distribution of tracheae (e.g. Kraus & Kraus 1994), composition of the tentorial complex (e.g. Edgecombe 2004, Koch 2003) and musculature of the mouthparts (e.g. Manton 1964). These and other characters systems are discussed in the following.

2.1. Number of the scuta

The number of dorsal scuta in the trunk varies among the different genera. However, this variation follows a pattern of subdivisions in certain tergites (Edwards & Belfield 1967, Ribaut 1931) (fig. 4), and this is the reason why the number of the scuta has been coded as several characters (see remarks of the character 1 in the Appendix I). The relationship between the distribution of the segments and scuta is complex (Ravoux 1962, Ribaut 1931) and controversies surrounding the number of the scuta exist in the literature. Basically, two confronting hypotheses for the ancestral state in the Symphyla have been proposed; species with a high number of scuta (*Geophilella, Parviapiciella, Sc. (Symphylellopsis) arvernorum* with 22 scuta and *Ribautiella* with 22 or 23) are either considered as to show the most primitive condition (Ravoux 1962, Ribaut 1931, Verhoeff 1934), or as the most derived from a more primitive state with only 15 scuta as in Scutigerellidae and *Remysysmphyla* (Manton 1966, Tiegs 1940 & 1945). Any polarization by outgroup comparison is difficult, as other myriapods either show no comparable subdivision of the tergites, or offer comparable problems with attributing the tergites to the respective body segments (e.g. Fusco 2005).

None of the two competing hypotheses for the Symphyla is supported by the shortest cladograms. Instead, the presence of 17 scuta, based on division of the tergites 14 and 15 (fig. 4) optimizes as the ancestral state maintained in *Scolopendrella*, *Symphylellina* and *Symphylella* (fig. 5). Absence of these divisions (char. 2) and the consequent condition of having 15 scuta happened twice independently: once as a synapomorphy of all scutigerellids and another as an autapomorphy of *Remysymphyla* (fig. 5, *F1*). This feature is consequently interpreted as a fusion of these last scuta. Additional subdivisions of tergites 6, 9 and 12 plus a second subdivision of tergite 14 (char. 3) increased the number of scuta to at least 21 (fig. 4) – this is revealed as homoplastic transformation in the "Scolopendrellopsis-group", *Ribautiella* and *Geophilella* + *Parviapiciella* (fig. 5, *S1*). Subdivision of the third tergite occurs in *Sc.* (*Symphylellopsis*) *arvernorum*, *Ribautiella* and *Geophilella* together with *Parviapiciella*, all of them showing at least 22 scuta (figs. 4 and 5, *S2*). *Ribautiella* shows another subdivision in the second tergite, resulting in 23 scuta (figs. 4 and 5, *S3*). In this genus, the alleged presence of 24 trunk scuta due to an additional subdivision of the first tergite is questionable. The descriptions and illustrations of this feature are not satisfactory, since the subdivisions appear in differenting grades among the species. SEM studies on this genus are required to clarify this problem.

Since it has been argued that a gradual increase or reduction of the scuta occurred within the Symphyla, the most-parsimonious resolution of symphylan phylogeny is expected to reveal an order in the evolution from highest to lowest number or vice versa. The results of the cladistic analyses do not confirm this expectation. Instead, both increases and reductions are revealed to have happened at least twice independently in different lineages, based on an original presence of 17 trunk scuta (fig. 5).

The presence of "extra scuta" in the symphylans has been regarded as a specialization correlated with subterranean life habits (e.g. Manton 1958). The scutigerellids are swift runners and, although they can sometimes be found deep in the soil (e.g. Edwards 1961), they normally live in more superficial layers (Mas 1985, personal observation). In contrast to this, scolopendrellids were described as slow-moving animals with a highly flexible trunk that facilitates to invade deeper soil layers (Mas 1985, Scheller 1982). Interestingly, *Symphylella* and *Scolopendrella* are speedy runners that are normally found in more superficial layers than *Scolopendrellopsis*, *Geophilella* and *Parviapiciella* (personal observation). It is thus likely that increases and reductions of the scuta number have been the result of an adaptation to repeated shifts towards more superficial layers on one hand, and towards deeper levels on the other, both happened several times independently in different lineages.

Strikingly, *Lithobius* also shows 17 trunk scuta, but it is not possible to affirm whether this similarity is homologous to the state in "primitive" symphylans *Scolopendrella*, *Symphylella* and *Symphylellina*, since the morphology of each segment is different. However, one of the subdivisions characteristic of these symphylan genera –the one of the last tergite – is possibly also present in *Lithobius*, since it also shows two terminal scuta that are not associated with any pedigerous segment. Nevertheless, further comparative and embryological studies are required to analyse this conclusion.

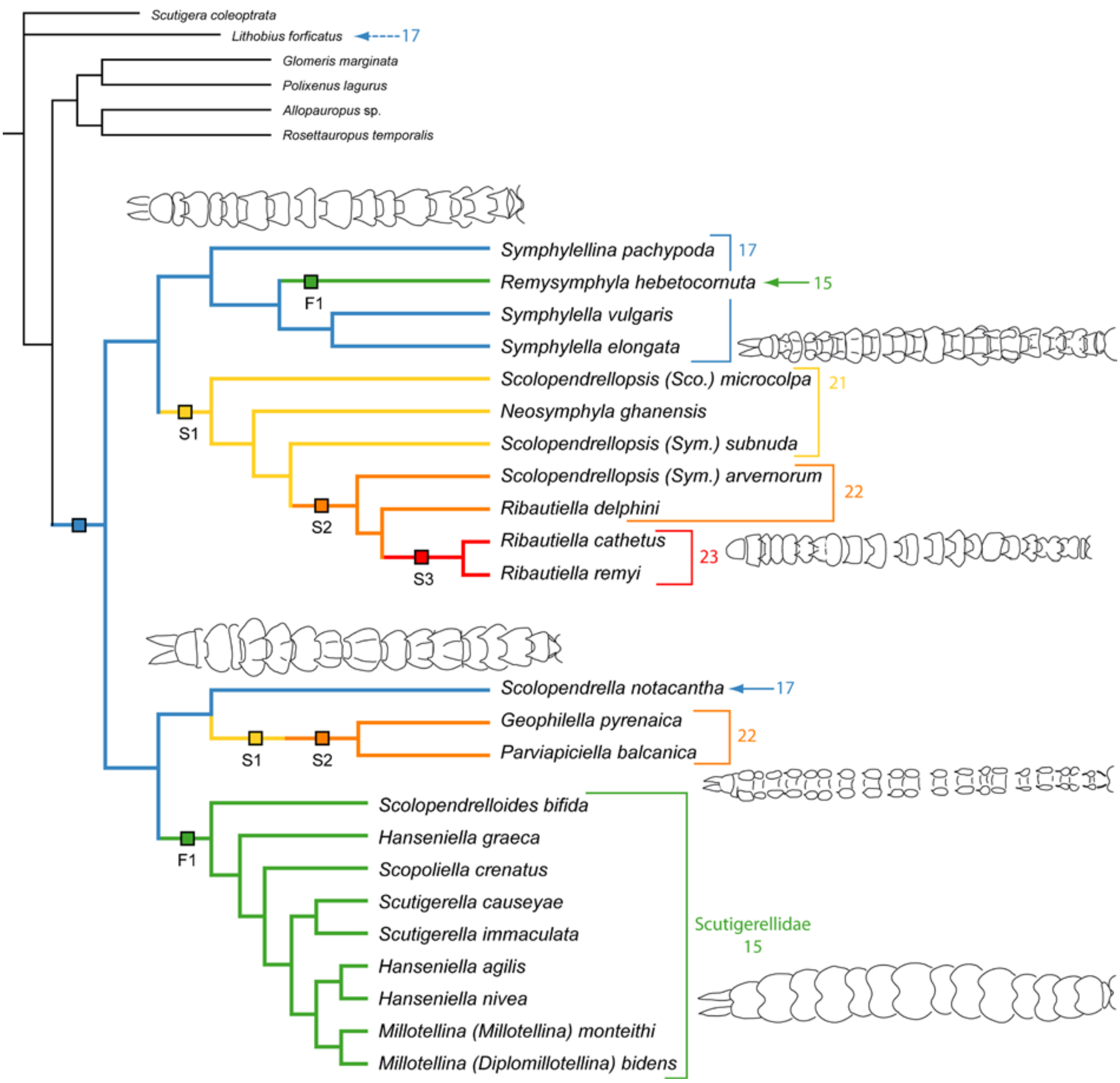

Fig. 5 Number of scuta in Symphyla and evolution of the subdivisions from a 17-scuta ground pattern (in blue). Numbers indicate the number of scuta in each clade. F1, absence (fusion) of subdivision of tergites 14 and 15 (character 2, in green); S1, subdivision of tergites 6, 9, 12 and second subdivision of tergite 14 (character 3, in yellow); S2, subdivision of tergite 3 (character 4, in orange); S3, subdivision of tergite 2 (character 5, in red). The pattern is shown in the most parsimonious cladogram.

2.2. *Morphology of scuta*

The presence of a pair of pointed projections on the posterior border of some scuta (at least one pair in each tergite from the second to the tenth; see figure 4) is widespread along the cladogram and represents a plesiomorphic character within the Symphyla. Traditionally, the first three tergites have had more weight in the taxonomy, as each genus has a specific morphology on them. This is the reason why the posterior prolongations of *Scolopendrella* have been defined as triangular (Edwards 1959a, b), similar to those of the remaining scolopendrellids. In contrast, more posterior scuta are more similar between *Scolopendrella* and basal scutigerellids (char. 10, state 0). Likewise, the morphology of the posterior scuta is considerably similar within “Symphylellidae” (char. 10, state 1), being triangular. However, the curved posterior border of the space between both projections on the fourth scuta is a character state that *Symphylella* shares with *Scolopendrella* and basal Scutigerellidae (char. 13). The presence of digitiform posterior projections is a feature present exclusively in *Parviapiciella* (char. 10, state 2).

The grade of sclerotisation changes within the Symphyla too. A weaker sclerotisation of the central parts of the tergites is convergent in *Ribautiella*, the subgenus *Symphylellopsis* together with *Neosymphyla*, and *Geophilella* together with *Parviapiciella* (char. 7). As explained above, it is likely that this partial desclerotization correlates with life habits in deeper soil layers of these representatives.

The presence of triangular projections in *Lithobius* contributes to polarise all characters referred to the morphology of the scuta (chars. 7-13). Accordingly, the "primitive" state of the symphylan scuta is very similar to the state in *Lithobius*: well sclerotized scuta with paired triangular projections showing straight borders and separated by a transversal straight area. These features are well represented in *Symphylella, Symphylellina* and *Remysymphyla*. Every variation is derived from this state in different clades and frequently convergent. Current resolution of Scutigerellidae indicates a trend of modification from the pointed projections as shown in *Scolopendrelloides* and *Hanseniella graeca* to rounded and posteriorly convex scuta in other *Hanseniella* species sampled by *H. agilis* and *H. nivea,* and *Millotellina*, with the emargination into two lobes as a transitional stage in *Scopoliella* and *Scutigerella*. The complete or partial lack of posterior projections happened independently in *Ribautiella remyi* and in *Geophilella* (char. 8, state 2).

A transversally spread first scutum optimizes as a plesiomorphy of the Symphyla and also within the Myriapoda (only under accelerated and delayed transformations), since this state of character (char. 6, state 0) is shared by *Lithobius* and several scutigerellid and scolopendrellid taxa. The same concerns the form of the last tergite, which is straight in most of the Symphyla, as well as in all outgroups.

2.3. First pair of legs

Smaller first pair of legs in relation to the rest has been observed in all Symphyla. The paraphyly of the traditional Scolopendrellidae questions the view of a gradual decrease in size within Symphyla. The 3-jointed state, less than half as long as the following pairs of legs (char. 51, state 2) optimizes as the ancestral state for Symphyla under accelerated transformation, and as ancestral for "Progoneata" under delayed transformation. The outgroup comparison, however, is hampered by the apparent absence of legs on the first trunk segment in Diplopoda and Pauropoda (Kraus & Kraus 1994). Within the Symphyla, a reduction of the first pair of legs to hairy knobs occurs in *Symphylella*, *Symphylellina* and *Ribautiella*. These taxa are grouped in a clade defined by this character (char. 54, state 2) under implied weights, but are separated under equal weights, which renders this reduction a homoplastic transformation. A secondary increase in size to 4-jointed legs optimizes as apomorphy of Scutigerellidae.

2.4. Spiracles and tracheae

The presence of a single pair of tracheal stigmata on the lateral side of the head has been traditionally regarded as an autapomorphy of the Symphyla (e.g. Edgecombe 2004, Edgecombe *et al*. 2000, Kraus & Kraus 1994). Actually, one of the names of this group is Cephalostigmata (Verhoeff 1934), a name which is sometimes used in the taxonomical rank of an order [e.g. Australian Biological Resources Study (Greenslade 2002)]. The evolutionary origin and homology of the head tracheae to tracheal systems in other arthropod taxa have been repeatedly discussed; generally, the cephalic tracheae in Symphyla is considered a derived state, acquired after the loss of pairs of tracheae in the trunk segments (Klass & Kristensen 2001, Verhoeff 1934).

In cladistic analyses, however, spiracles (or stigmata) on the membrane above the mandibular base optimize as a synapomorphy of "Scolopendrella-group" and Scutigerellidae (char. 18). This character (char. 78, see discussion in Appendix I) highlights the homology of the head tracheae to apodemes of the mandibular base. The presence of tracheae has yet only been documented in *Scolopendrella*, *Scutigerella* and *Hanseniella* whereas *Symphylella* and *Scolopendrellopsis* proved to show a massive apodeme at the corresponding position.

The tracheae of *Scolopendrella*, *Scutigerella* and *Hanseniella* support a significant number of large muscles that attach to the posterior margin of the cranium, in a similar way to the adductor muscles of the gnathal lobe. These tracheal muscles have the apparent function of suspending the tracheae, in spite of their large size. The presence of homologous muscles in *Lithobius* (the muscles 132 after Rilling 1967, see homology hypothesis in the previous chapter of this work) favours the hypothesis that the tracheal muscles had primarily a function related to the mandibular base abduction. This function seems to be maintained in at leas *Symphylella* and *Scolopendrellopsis*.

The cladograms reveal the lack of spiracles as plesiomorphic within the Symphyla. However, the absence of spiracles and tracheae in "Symphylellidae" has to be taken carefully, since is yet only documented in *Symphylella* and *Scolopendrellopsis*. Further studies in *Remysymphyla*, *Symphylellina*, *Neosymphyla* and *Ribautiella* will elucidate the present insight on the secondary evolution of the symphylan tracheae.

2.5. Mouthparts and feeding mechanisms.

Based on comparative morphology, in the previous chapter of this work, it was hypothetized that the state of the tentorial complex and mandibular mechanisms observed in *Symphylella vulgaris* and *Sc.* (*Symphylellopsis*) *subnuda* is plesiomorphic compared to the state in *Glomeris* and *Lithobius*. The cladistic analysis of these features combined with characters belonging to the outer morphology supports this interpretation.

The state of most of the characters related to the internal anatomy of the head (chars. 69-145) in *Symphylella* and *Scolopendrellopsis* are revealed as primitive not only within Symphyla, but also within Myriapoda. Some examples of these primitive features in structures associated to the feeding mechanisms observed in Symphyla and *Lithobius* are:

1. Tentorium laminar (char. 69) rather than bar-like with only one tentorial bridge (char. 71).
2. Compressed musculature of the mandibular base rather than separated into different functional groups (chars. 86 and 92).
3. Presence of dorsal muscles (MB10) arising from mandibular base (char. 94).
4. First-maxillary muscles attaching to the tentorial bridge rather than to the tentorium's posterior processes (chars. 108, 111 and 117), and absence of the Mi9 muscle (char. 112).
5. Presence of one large muscle (B7) that joins the posterior margin of the first maxillae with the posterior margin of the head (char. 145).
6. Pharyngeal dilator muscles arising directly from the tentorium's posterior process (char. 130) rather than from other specialized structures (chars. 120, 122, 123, 124, 129).

Although the morphology of the mouth parts is predominantly homogeneous in Symphyla, it is also important to take minor variations of the second maxilla into account. The presence of three distal protuberances, observed in *Scutigerella*, has been proposed as homologous to the glossae, paraglossae and labial palp of the insect's labium (e.g. Ravoux 1975, Snodgrass 1952). This homology was already questioned by Kluge (1999) and Edgecombe (2004). The shortest cladograms optimize the presence of these protuberances as an apomorphy of Scutigerellidae, and the presence of a setal area without any protuberance (char. 41) as plesiomorphic in the Symphyla.

Interestingly, *Symphylella* is the only symphylan for which predaceous behaviour was documented (Walter *et al.* 1989), while the remaining scolopendrellids are supposed to be saprophagous and scutigerellids feed on roots and other plant-materials (e.g. Scheller 1982). The optimization of typical features of *Symphylella* leads one to propose the possibility that the ancient feeding condition for Symphyla was, at least partly, predatory. Accordingly, the "particularly refinements" of the mandibular mechanism that *Scutigerella* and *Hanseniella* share with Diplopoda (Snodgrass 1952) are possibly convergent specializations to herbivorous habits. Nevertheless, the diet of most of the symphylans is still uncertain and it is probable that predatory habits are more widespread within scolopendrellids (Domínguez 1992, personal observation).

Conclusions: Evolution of the Symphyla

1. Phylogenetic interrelationships of Symphyla

The proposed phylogeny shows two or maybe three main lineages of extant Symphyla. Scolopendrellidae is revealed as paraphyletic and splits up into two groups: the “Scolopendrella-group” (*Scolopendrella* and *Geophilella* + *Parviapiciella*) and the “Symphylellidae” (remaining scolopendrellids). The “Scolopendrella-group” is closest related to the Scutigerellidae and some derived features support this sister-group relationship, such as the modification of the triangular projections on scuta, presence of a pair of spiracles on both sides of the head, presence of a posterior tentorial bridge, absence of the dorsal muscles on the mandibular base and other modifications in the musculature of the head. The “Symphylellidae” maintain more plesiomorphic features that are shared mainly with centipedes (sampled by *Lithobius*), especially referring to the morphology of the scuta and the main pattern of the musculature associated to the mouthparts. The monophyly of “Symphylellidae” has no significant support, and their present resolution – “Symphylella-group” and “Scolopendrellopsis-group” – also remains weakly supported. *Ribautiella* resolves as a more derived monophyletic group with competing relationships to either the “Symphylella-group”, or the “Scolopendrellopsis-group”, both of which are variably resolved as paraphyletic grade with respect to *Ribautiella*.

2. Biogeographical aspects in dating clades

An overview on the biogeography of each genus (Table 1 of the General Introduction of this work) illuminates an approaching on the geological age of this group. Although distributional data on Symphyla are still unsatisfactory, some genera have a subcosmopolitan distribution, such as *Scutigerella*, *Hanseniella, Scolopendrellopsis* and *Symphylella.* Strikingly, these taxa are resolved at the “crown” of different lineages in the shortest cladograms. Likewise, it is also interesting that *Millotellina*, which presents a typical disjunctive East-Gondwanan distribution, resolves also at the “crown” of Scutigerellidae. These distribution patterns are not possible to be explained sufficiently by recent expansion events, but are probably derived from an earlier continuous distribution, as was inferred for other non-flying invertebrates (e.g. Giribet & Edgecombe 2006, Wesener & VandenSpiegel 2009). This suggests that these groups were already present before the first fragmentation of Gondwana, around the Late Jurassic (Ali & Aitschison 2008) and, thus, shows that the most advanced subgroups of the Scutigerellidae, “Symphylella-group” and “Scolopendrellopsis-group” have a minimal age of about 150 million years. Likewise, the distribution of *Ribautiella*, known only from Africa and South America, indicates that this genus has a minimal age of about 100 million years, when both continents separated from each other (Ali & Aitschison 2008). However, further distributional data of the Symphyla, especially for the tropical regions, are urgently required. Moreover, molecular analyses are also necessary to test this hypothesis.

3. Taxon sampling and the symphylan ground pattern

According to the proposed phylogeny, none of the scutigerellid species represent appropriate exemplars for the symphylans, contrary to the predominant utilisation of *Scutigerella* and *Hanseniella* in phylogenetical studies. Representatives of basal offshoots in each lineage are a more accurate taxon sampling. Therefore, *Scolopendrella*, *Symphylellina* and *Scolopendrellopsis* (subgenus *Scolopendrellopsis*) presently appear to be the best representatives of the Symphyla for further phylogenetic analyses and comparative studies. An alternative to the rare genus of *Symphylellina,* which was only cited once in New Caledonia, is *Symphylella*, a relatively abundant taxon with a subcosmopolitan distribution.

The ground pattern of the Symphyla is mostly as a mix of features of the most basal taxa of each clade within the "Symphylellidae" and the "Scolopendrella-group". *Scolopendrella, Symphylella* and *Symphylellina* represent the most primitive state of presenting 17 well sclerotized scuta. *Symphylella* together with *Symphylellina* show the primitive states of the first scuta, which is smaller and spread transversally, and of the posterior projections on the rest of the scuta as paired, separated triangular projections in all scuta except 14, 16 and 17. *Scolopendrellopsis* (*Scolopendrellopsis*) and *Scolopendrella* maintained the basal state of the first pair of legs: 3-jointed and less than half as long as the following pairs of legs. The "primitive" external morphology of the head in Symphyla would be represented by *Scolopendrella*, with a completely sclerotized head capsule with smooth cuticula. Finally, *Symphylella* and *Scolopendrellopsis* share the same pattern of skeletomuscular anatomy of the head, and possibly a somewhat predaceous life habit.

4. Evolutionary history of the Symphyla

It is now evident that the first symphylans, as explained above for *Symphylella*, showed moderate subterranean and maybe predatory life habits. With regards to the evolution of the number of trunk scuta, evolutionary changes occurred independently many times in two main directions. On one hand, towards specialisation to a subterranean life in deeper layers of the substrate and feeding mainly on fungal hyphae and animal remains. Representatives of such specialization – as shown by *Scolopendrellopsis*, *Ribautiella*, *Geophilella* and *Parviapiciella* – are slow-moving symphylans which have a smaller and softer body with a more flexible trunk based on several subdivisions of the tergites, less sclerotized scuta and shorter legs (especially the first one), among other features suited to subterranean life. On the other hand, other symphylans specialised towards a life closer to the soil surface. Representatives of this specialisation – as shown by *Remysymphyla* and the Scutigerellidae – are characterized by reduction of the number of scuta by fusions and, in the case of the Scutigerellidae, adaptations to predominantly herbivorous feeding habits.

The lack of data on many characters in some symphylan genera, especially in the tropical representatives, presently remains a major problem for assessing the phylogeny of this group and implies that the proposed hypotheses, for the moment, remain preliminary. Nevertheless, the exploration of new character systems has filled a considerable gap in the knowledge of the Scolopendrellidae and is the first major step for cladistic tests of maximum congruence between different character sets. Results obtained have illuminated unexpected phylogenetic relationships and yielded astonishing new insights on the evolution of the Symphyla.

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Appendix I

Character descriptions

The following section provides a description of the characters used for cladistic analysis (see Chapter 3). There are few remarks on the characters of the cuticular cephalic endoskeleton and the cephalic musculature (69-145). Detailed information about them can be found in Chapter 2. Characters related to the external morphology are illustrated in Chapter 1. Bibliographic references can be found in the literature list of Chapter 3.

In order to facilitate a better understanding of the explanations, only names of genera are used except otherwise indicated.

1. **Number of trunk tergites:** (0) one tergite per segment; (1) one tergite for each two segments (diplotergites); (2) seven large tergites plus two smaller (genital) tergites; (3) 6 tergites; (4) 15 tergites. The terms “tergite” (subdivided into subtergites and metatergites) and “scuta” are variably used in the literature for the same structures (e.g. Ribaut 1931 vs. Scheller 1961). For a matter of convenience and on the basis of the homology of the different subdivisions (Ribaut 1931), the term “scuta” is applied on each visible tergal plate, and “tergite” to the tergal areas where subdivisions into a variable number of scuta can occur. Accordingly, all symphylans have 15 tergites, eight of which can undergo subdivisions in some species, increasing the total number of trunk scuta. Subdivisions follow a pattern in certain tergites (chapter 3, fig. 3), and it is for this reason that they are considered as independent characters, as described in the following.
2. **Subdivision of tergites 14 and 15:** (0) absent; (1) present. The tergites 14 and 15 are divided into two scuta each in all scolopendrellids, increasing the number of scuta to at least 17, except in *Remysymphyla*, which have 15 scuta. The absence of this subdivision – the resulting presence of 15 trunk scuta –is shared by all scutigerellids and *Remysymphyla*.
3. **Subdivision of tergites 6, 9 and 12, and second subdivision of tergite 14:** (0) absent; (1) present. *Geophilella*, *Parviapiciella*, *Scolopendrellopsis* and *Ribautiella* present these subdivisions, increasing the number of trunk scuta to at least 21 (chapter 3, fig. 3).
4. **Subdivision of tergite 3:** (0) absent; (1) present. The third trunk tergite is subdivided in the genera *Geophilella*, *Parviapiciella* and *Ribautiella*. In the species of *Sc. (Symphylellopsis)*, this subdivision is clearly demarcated only in *Sc. (Symphylellopsis) arvernorum*. However, *Sc. (Symphylellopsis) subnuda* also shows a subdivision of this same tergite, but the components are hardly demarcated (chapter 1, fig. 8).
5. **Subdivision of tergite 2:** (0) absent; (1) present. The subdivision of the second tergite is characteristic of the genus *Ribautiella*. However, Rochaix (1956) pointed out that the subdivision of the second tergite in *R. delphini* is not very apparent. Accordingly, he showed this tergite without any division in his diagram.
6. **Shape of first scutum:** (0) transversally extended; (1) two longitudinal cuticular rods; (2) indicated only by a row of setae; (3) trapezoidal; (4) divided into two susbtergites; (5) absent.

Most of the symphylan species have a well developed and smaller first scutum compared to remaining scuta. The name “rudimentary” has been frequently assigned to the first scutum in the literature, with regards to the other scuta. A truly rudimentary first scutum is found in *Millotellina* and *Scolopendrelloides*, where it is reduced to a little tergal area which is not sclerotized and bears a row of setae. The first scutum of *Ribautiella delphini* is divided into two subergites. The first tergite in *Scolopendrella*, *Geophilella* and *Parviapiciella* consists of two longitudinal rods of smooth cuticula (chapter 1, fig. 6).

7. **Strenght of scuta 2-14:** (0) completely sclerotized; (1) only the lateral parts well sclerotized. The fact that the scuta show different grades of sclerotisation among the genera was proposed by Domínguez (1992) as a morphological character relevant for the systematics of the Symphyla. Only the lateral parts of the scuta present a thicker sclerotisation in *Geophilella*, *Parviapiciella*, *Scolopendrellopsis*, *Neosymphyla* and *Ribautiella*, while the central area is thinner and similar to the non-sclerotized pleural sides of the trunk segments.

8. **Posterior margin of scuta 2-14:** (0) with pointed projections in some scuta; (1) with rounded projections in all scuta; (2) with no projections in all scuta. Traditionally, this character was used to distinguish the two families (e.g. Edwards 1959b; Scheller 1961). In most Scutigerellidae all scuta except the latter are equipped with posterior rounded or emarginated margins, while the scolopendrellids generally show a pair of pointed projections in some scuta. Such pointed projections also occur in some scutigerellids. This is the case of *Scolopendrelloides* and some species of *Hanseniella*, such as *H. graeca* and *H. angulosa* (the latter not included in the analysis). Vice versa, some scolopendrellid species, such as *Geophilella* and *Ribautiella remyi* do not show any posterior projection in the scuta. Within the outgroups, *Lithobius* form similarly pointed projections in the tergites 9, 11 and 13, while *Scutigera* is characterized by rounded projections in all scuta.

9. **Posterior border of rounded projections:** (0) straight; (1) emarginated into two lobes. The shape of the posterior border of the scuta is a major diagnose for the genera of the family Scutigerellidae (e.g. Edwards 1959b). Most *Hanseniella* species (such as *H .agilis* and *H. nivea*) and *Millotellina* have non-lobulated, rounded and posteriorly concave projections, while *Scutigerella* and *Scopoliella*, as well as the outgroup *Scutigera*, show two lobes.

10. **Shape of pointed projections of tergites 4-14:** (0) small pointed projections from a rounded exterior border of the scuta; (1) triangular projections; (2) digitiform. Among the scuta which present pointed projections, the first two (on tergites 3 and 4) have a distinctive morphology in each genus and, thus, are difficult to compare between the different genera. It is for this reason that the comparison of the morphology of the pointed projections is exclusively applied on the scuta of the tergites 4-14. For details of the morphology of scuta 2 and 3, see character 14. Although the presence of the triangular projections have been considered as characteristic for all scolopendrellids (Edwards 1959b, Scheller 1961), the shape of the posterior projections in *Parviapiciella* clearly differs from the triangle-shaped projections of the rest of the scolopendrellids, since they are digitiform projections that arise directly from the rounded scuta. Likewise, the posterior projections of *Scolopendrella* cannot be accepted as triangular, since they are more similar to the small pointed projections of *Hanseniella graeca* and the

Scolopendrelloides (only in the posterior scuta).The projections of the outgroup *Lithobius* are triangular.

11. **Shape of triangular projections:** (0) with straight borders; (1) with rounded borders that make the triangular projections somewhat funnel-like. *Symphylella*, *Symphylellina* and *Sc. (Scolopendrellopsis)*, as well as *Lithobius*, show clearly triangle-shape projections with straight borders. In contrast, the triangular projections of *Sc. (Symphylellopsis)*, *Ribautiella* and *Neosymphyla* have a more irregular shape, with rounded borders that make them funnel-like.

12. **Posterior margin of tergal area between the posterior pointed projections of scuta 2 and 3:** (0) straight; (1) rounded, concave; (2) angular. All scolopendrellid species with posterior projections in the scuta (except *Scolopendrella*) have a tergal area between the projections with a straight posterior margin. The posterior projections of *Lithobius* are similarly separated. Instead, *Scolopendrella* and *H. graeca* have a rounded concavity between the projections. The angle formed between them is an autapomorphy of *Scolopendrelloides*. This character is not applied to *Lithobius*, since it only refers to the anterior tergites, which devoid projections in *Lithobius forficatus*.

13. **Posterior margin of tergal area between the projections of scutum 4:** (0) straight; (1) curved, concave. From scutum 4 to 14, *Scolopendrelloides* does not present the distinctive angle between both posterior projections, but a rounded concave border, as in *Scolopendrella* and *Scolopendrelloides*.

14. **Posterior prolongations in the anterior scutum of tergite 14:** (0) absent; (1) present. The presence of the triangular prolongations on scutum 17 is the main difference between *Neosymphyla ghanensis* and *Sc. (Symphylellopsis) subnuda* (Edwards & Belfield 1967) (chapter 3, fig. 3).

15. **Posterior prolongations in the posterior scutum of tergite 14:** (0) absent; (1) present. The lack of triangular prolongations on scutum 18 was the main reason for the erection of the monotypic genus *Parviapiciella*, which differs in this regard from *Scolopendrellopsis* (Mas & Serra 1995).

16. **Shape of last scutum:** (0) with deep cavity beneath middle of posterior margin of last tergite; (1) with posteromedian projection between cerci; (2) straight (neither deep cavity, nor median projection). The presence of a deep cavity beneath the middle of the caudal margin is a distinctive diagnostic character to identify the genus *Scutigerella*. However, *Scolopendrelloides* is also characterised by a deep posterior depression in the last scutum (Edwards 1959b), which is here considered to be homologous to the state in *Scutigerella*. The presence of a disciform projection in the corresponding position is a diagnostic character for the genus *Scopoliella*. Strikingly, *Ribautiella remyi* sows a similar postero-median projection in the last scuta.

17. **Shape of the head capsule:** (0) rounded; (1) elongated; (2) subtriangular; (3) oval; (4) cuadrangular, flattened. Previous descriptions of the shape of the head capsule vary considerably for the same species (e.g. Hansen 1903 *vs.* Domínguez 1991). The reason for this is the mounting of the animals for light microscopy (personal observation). The SEM-micrographs show the true shape of the head, pointing out a remarkable difference between both studied scutigerel-

lids - *Scutigerella* and *Hanseniella* - which have a rounded head, and the observed scolopendrellids - *Scolopendrella*, *Geophilella*, *Symphylella*, *Scolopendrellopsis* and *Symphylellopsis* - which have an elongated head (chapter 1, figs. 9, 10). An elongated head was also described in *Scolopendrelloides* and *Symphylellina*. The rest of the scutigerellid species were described having a rounded head.

18. **Spiracles in the arthrodial membrane above the mandibular base:** (0) absent; (1) present. There is a pair of tracheal spiracles in the head of *Scutigerella*, *Hanseniella*, *Scolopendrella* and *Geophilella*. In these latter two, the opening of the tracheae is almost hidden by a fold of the arthrodial membrane above the superior margin of the mandible basal segment (chapter 1, fig. 15, "*sp*"). These structures are definitively absent in the other studied species, which contrasts with the previous assumption that this character is an autapomorphy of the Symphyla (e.g. Kraus & Kraus 1994, Edgecombe 2004). This feature is only well described in *Scutigerella immaculata* (Ravoux 1975) and *Hanseniella agilis* (Tiegs 1941) in the literature. Ribaut (1931) and Becker (1922 *fide* Verhoeff 1934) mentioned spiracles in the genera *Symphylellopsis* and *Symphylella* respectively, but there is no detailed description about these structures. It is likely that these authors misinterpreted a massive mandibular apodeme as tracheae and spiracles (see character 78).

19. **Tömösváry's organ:** (0) ringed organ set on a triangular sclerite lateral to the clypeus; (1) large and horseshoe-shaped at basis of the antennae; (2) pseudoculus; (3) a sphaerical chamber with a small rounded opening to the exterior. The Tömösváry's organ (or temporal organ) is widespread in atelocerates (Klass & Kristensen 2001). Its general structure varies among the myriapod subgroups (Haupt 1979).

20. **Position of the chamber of Tömösváry's organ:** (0) external (protuberance with an orifice); (1) internal, opening to exterior through a tube or a little chamber. The Tömösváry's organ is present in all symphylans, but its external appearance varies among the different genera (chapter 1, fig. 15, "*To*"). In *Scutigerella*, *Hanseniella* and *Scolopendrella*, it has an external position, and the chamber is visible from the outside as a protuberance on the head with the exterior opening. In contrast, in the other studied species, it has a more internal location. In *Geophilella*, *Parviapiciella* and *Symphylella*, only the exterior opening is visible, and in *Scolopendrellopsis* it is not visible at all, since it is covered by little cuticular spines, although it is present in both genera (personal observation on histological sections). The Tömösváry's organ is described and illustrated in most of the species in the literature, but only from the view of the mounts for light microscopy, which does not match with the real exterior appearance (personal observation). Only more detailed descriptions of this organ were therefore used in this analysis. This is the reason why data on the Tömösváry's organ in *Scopoliella*, *Ribautiella remyi* and *Ribautiella delphini* were not included in the matrix.

21. **Eyes:** (0) present; (1) absent. Eyes are present in the chilopods *Scutigera* and *Lithobius* and in the diplopods *Polyxenus* and *Glomeris*, while all members of the Symphyla and Pauropoda are blind.

22. **Antennae:** (0) moniliform; (1) branched. Terminally branched antennae are an autapomorphy of the Pauropoda. All other myriapods have monoliform antennae.

23. **Postantennal cuticular row:** (0) absent; (1) present. *Symphylella*, *Scolopendrellopsis* and *Symphylellopsis* show a bar of smooth cuticula on the base of the antennae, which distinguishes it from the setose or papilate cuticula of the head (chapter 1, figs. 8, 10, "*pr*").

24. **Cuticular ornamentation of sclerotized sclerites of the head:** (0) entirely smooth; (1) pubescent; (2) the sclerites of the head capsule pubescent and mouthparts smooth. The sclerotized sclerites of the head capsule as well as the mouthparts are smooth in *Hanseniella*, *Scutigerella*, *Scolopendrella*, *Geophilella* and *Parviapiciella*, and in the outgroups *Scutigera*, *Lithobius* and *Glomeris*. In contrast, *Symphylella*, *Scolopendrellopsis* and *Symphylellopsis*, as well as *Allopauropus* and *Millotauropus*, show a pubescence on these sclerites (chapter 1, figs. 9-12, 15). *Polyxenus* shows pubescence on the head capsule but not on the mouthparts, which are smooth.

25. **Pattern of sclerotisation of the head:** (0) uniform, as sclerotized as the mouthparts; (1) granulated except for the posterior part, which is as sclerotized as the mouthparts. While the head capsule of *Hanseniella*, *Scutigerella*, *Scolopendrella* and *Symphylella* have a regular surface, *Geophilella*, *Parviapiciella*, *Scolopendrellopsis* and *Symphylellopsis* present a more sclerotized posterior part which is differentiated from the rest of the granular surface of the head capsule and largely distinct in lateral view of the head (chapter 1, fig. 15).

26. **Central rod of the head:** (0) absent; (1) present. It is present in all representatives of the Symphyla.

27. **Shape of central rod of the head:** (0) undivided (unbroken); (1) divided (with break in the middle); (2) composed of posterior part only; (3) composed of anterior part only. The interruption of the central rod in the middle is traditionally another diagnostic character for the Scolopendrellidae (Edwards 1959b). However, the central rod is not interrupted in *Symphylella* and *Ribautiella cathetus*. In addition, it is only composed of the posterior part in *Scolopendrelloides bifida* (Scheller 1961) and of anterior part in *H. agilis and H .nivea* (chapter 1, figs. 9, 10, "*cr*").

28. **Central rod's cuticular reinforcement:** (0) present along the entire rod; (1) only present in the posterior half. A rod of smooth cuticula is present in the species which has a granulate surface of the head, as a cuticular reinforcement of the central rod. It is present along the entire length of the rod in *Geophilella* and *Parviapiciella*, while it is only present in the posterior half of the rod in *Scolopendrellopsis* (chapter 1, fig. 10, *arrow*).

29. **Frontal branches of central rod:** (0) absent; (1) present as a regular line. The frontal branches are present in *Remysymphyla*, *Neosymphyla*, *Ribautiella remyi* and *R. delphini*, *Symphylella* and *Scolopendrellopsis* (chapter 1, fig. 10, "*fb*"). The outgroup *Lithobius* shows a similar structure (despite it lacks central rod), a transversal cuticular groove between the antennae which is interpreted as homologous to the frontal branches of the central rod in Symphyla.

30. **Shape of frontal branches:** (0) straight; (1) V-shape. *Scolopendrellopsis* shows straight frontal branches of the head's central rod. The transversal line of *Lithobius* shows also this morphology. *Symphylella*, *Symphylellina*, *Remysymphyla* and *Ribautiella* have V-shaped frontal branches (chapter 1, fig. 10, "*fb*").

31. **Median branches of central rod:** (0) absent; (1) present. They are present in *Scolopendrella*, *Geophilella*, *Parviapiciella*, *Sc. (Scolopendrellopsis)*, *Sc. (Symphylellopsis) subnuda* and *Symphylella*, as well as in *Remysymphyla* and *Neosymphyla* (chapter 1, figs. 9, 10, "*mb*").

32. **Shape of median branches:** (0) deep groove arising from the central row; (1) more exterior grove, without contact with the central row; (2) soft line; (3) reinforced with two branches of smooth cuticula. The median branches are formed by a deep groove that arises from the central row in *Sc. (Scolopendrellopsis) microcolpa* and *Sc. (Symphylellopsis) subnuda*. In *Scolopendrella* they are also grooves, but without contact with the central row. In *Symphylella* and *Remysymphyla* they are a soft line without pubescence in the cuticula. Strikingly in *Geophilella* and *Parviapiciella* they are reinforced with two branches of smooth cuticula which, with the cuticular reinforcement of the central rod, form a cruciform structure in de middle of the head capsule (chapter 1, figs. 9, 10, "*mb*").

33. **Posterior branches of central rod:** (0) absent; (1) present. In spite of the position of the posterior branches of *Hanseniella nivea*, they were considered as posterior branches since they point diagonally forwards, like those in *Scutigerella* (chapter 1, fig. 9, "*pb*").

34. **Ring-shaped margin of setae in the head:** (0) absent; (1) present. All studied scolopendrellid species show a ring-shaped margin at the base of some setae in different parts of the body, such as on the tergites or on the cerci. Only *Scolopendrella*, *Geophilella* and *Parviapiciella* show this feature of the setae on the head (chapter 1, figs 9-12, 15).

35. **Cuticular border of cephalic lobe behind the head-mandible articulation:** (0) diagonal and straight; (1) vertical and angular at the inferior part. The border of the cephalic lobe just behind the articulation with the mandible is diagonal in *Scutigerella*, *Hanseniella*, *Scolopendrella*, *Geophilella* and *Parviapiciella*, following more or less the shape of the cephalic lobe. On the other hand, it is vertical in *Symphylella* and *Scolopendrellopsis*, bestowing a more angular appearance on the cephalic lobe, and presenting a protuberance on the most superior part of the margin (chapter 1, fig. 15, *arrow*).

36. **Shape of the posterior part of the head capsule:** (0) rounded; (1) flattened; (2) not visible (stuck to the trunk or covered by the first tergite). Independent of the shape of the head in dorsal view, in lateral view the head of *Scolopendrella* shows more similarities to *Scutigerella* and *Hanseniella*, since the posterior part is rounded, while it is flattened in the rest of the studied scolopendrellids (chapter 1, fig. 15).

37. **Mandibular base forming side of head:** (0) absent ; (1) present. In Symphyla and Diplopoda, the mandibular basal segment (or basal plate) is a prominent component of the head capsule (Edgecombe 2004).

38. **Protuberance beside the first-maxillary palp:** (0) absent; (1) present. *Scolopendrella*, *Geophilella* and *Parviapiciella* show a protuberance on the lateral side next to the palp of the first maxilla (chapter 1, figs. 11, 12, *arrow*).

39. **Second maxillae:** (0) two separated sclerites with articulations; (1) fused, forming a functional labium; (2) fused, forming an unpaired subtriangular plate; (3) absent or integrated into a gnathochilarium. The second maxillae are fused together forming a functional labium in all

symphylans (chapter 1, figs. 11, 12, "*m*"). They are separate appendages with articulations -telopodites- in Chilopoda. *Polyxenus* shows vestigial articulations (Kraus & Kraus 1994). In Pauropoda the second maxillae form an unpaired plate, since the "Kehlplatte" of Millotauropus was considered to be the same structure as the subtriangular plate of *Allopauropus*, according to the fig. 16 of Kraus & Kraus (1994). This consideration that the second maxillae simply form an unpaired subtriangular plate as a synapomorphy of the Pauropoda is supported by the affirmation made by these authors.

40. **Origin of second maxillae:** (0) clearly delimited; (1) gradual. The anterior plates of the second maxillae in the observed scutigerellid consist of two well sclerotized sclerites clearly differentiated from the thin cuticula located behind them. In contrast, the studied scolopendrellids do not show such a sclerotisation in the second maxillae, and the posterior limit is gradual with the cuticula behind them (chapter 1, figs. 11, 12). The second maxillae are clearly delimited by their sclerotized pieces in both chilopods and in *Glomeris*. In contrast, this sclerotisation is not as conspicuous in *Polyxenus* (Kraus & Kraus 1994, fig 10) and in *Allopauropus* (personal observation). It is for this reason that the origin of the second maxillae is considered as gradual for these two taxa in this study.

41. **Three terminal protuberances in second maxillae:** (0) present; (1) absent. These anterior structures have been homologized with the glossae, the paraglossae and the maxillary palps of the insects (e.g. Ravoux 1975). This homology is questionable (e.g. Edgecombe 2004). They are absent in all studied scolopendrellids (chapter 1, figs. 11, 12, "*tp*").

42. **Transversal groove of second maxillae:** (0) absent; (1) present. *Scutigerella*, *Hanseniella*, *Scolopendrella*, *Geophilella* and *Parviapiciella* present a transversal groove that separates the setae-bearing part, which itself presents a group of setae pointing forwards, from the rest of the second maxillae (chapter 1, figs. 11, 12, "*tg*"). *Symphylella* and *Sc.(Symphylellopsis)* lack this groove, as well as both pauropods. The entirely different morphology of the second maxillae in chilopods and diplopods makes this character inapplicable to these groups.

43. **Second maxillae's surface:** (0) uniform; (1) exterior half smooth and interior half pilose. Both studied scutigerellid genera have a smooth cuticula on the second maxillae, and *Symphylella*, *Scolopendrellopsis* have a pilose surface. *Scolopendrella*, *Geophilella* and *Parviapiciella* show a smooth cuticula in the exterior part of the second maxillae, while the interior part has a pilose surface(chapter 1, figs. 11, 12, *broken line*).

44. **Anterior origin of the proximal arms of the second maxillae:** (0) in the main plates of the second maxillae; (1) only conspicuous behind the maxilla II. In *Scutigerella*, *Hanseniella*, *Scolopendrella*, *Geophilella* and *Parviapiciella*, the proximal arms of the second maxillae extend from the inside of the main plates of the second maxillae backwards (chapter 1, figs. 11, 12, "*pa*"). In *Symphylella* and *Sc.(Symphylellopsis)* they apparently originate behind the posterior end of the anterior plates, although they are present as a much thinner structure inside of the head (personal observation on the histological cuts).

45. **Structure of cervical sclerites:** (0) thin cuticula, not very conspicuous; (1) thick and smooth cuticula, very conspicuous. The cervical sclerites are very conspicuous in *Scolopendrella*,

Geophilella and *Parviapiciella*. Furthermore, *Symphylella* has a thick cervical sclerite of smooth cuticula (chapter 1, figs. 13, 14, "*cp*").

46. **Length of cervical sclerites:** (0) short; (1) long. The cervical sclerite is much longer in the studied scolopendrellids than in the scutigerellids (chapter 1, figs. 13, 14, "*cp*").

47. **Sternal plates of first pair of legs:** (0) meeting medially; (1) separated medially. The sternal plates of the first trunk segment are separated in all studied species except in *Sc.(Symphylellopsis)*. In this species they meet medially and have an elongated form. In *Symphylella*, the sternal plates are different and difficult to homologize with the sternal plates in other genera (chapter 1, figs. 13, 14, "*sp*").

48. **Coxae of first pair of legs:** (0) meeting medially; (1) separated medially; (2) absent; (3) coxosternites of the maxillipeds. The coxae of the first pair of legs meet medially in all studied symphylans, except in *Sc. (Symphylellopsis)* and *Symphylella* (chapter 1, figs. 13, 14, "*cx*"). *Allopauropus*, *Polyxenus* and *Glomeris* have the first pair of legs reduced (Kraus & Kraus 1994). Furthermore, the chilopods present a modified first pair of legs in the maxillipeds.

49. **Shape of coxae of first pair of legs:** (0) regular; (1) angular, more or less triangular. *Scolopendrella*, *Geophilella* and *Parviapiciella* have more or less triangular coxae on the first pair of legs (chapter 1, figs. 13, 14, "*cx*").

50. **Shape of anterior sternal plate of the second segment:** (0) kidney-like; (1) more or less rounded; (2) absent. The studied scutigerellids show a kidney-like anterior sternal plate at the second pair of legs (chapter 1, fig. 13, "*asp*").

51. **First pair of legs:** (0) 5-6-jointed; (1) 4-jointed, more than half as long as following pairs; (2) 3-jointed, less than half as long as following pairs; (3) 2-jointed, strongly reduced; (4) unsegmented hairy knobs; (5) absent. The reduction of the legs to 3 segments is characteristic for the scolopendrellids. Within them, the genera *Symphylella* and *Ribautiella* are characterised by the total reduction of the first pair of legs to hairy knobs. In addition, the genus *Remysymphyla* is characterised by the partial reduction of the first pair of legs, in different grades among the species. The first pair of legs has been taken for absent in Diplopoda and Pauropoda (Kraus & Kraus 1994).

52. **Styli at the basis of legs 3-12:** (0) absent; (1) present. The presence of the styli at the basis of the legs 3-12 is shared by all symphylans.

53. **Shape of styli:** (0) conical; (1) spiny; (2) rounded; (3) digitiform. Although the styli of the Scutigerellidae are described in the literature as "conical", in this study they were differentiated from the conical styli of *Remysymphyla* and *Ribautiella remyi* as "digitiform". The other two included *Ribautiella* species - *R. delphini* and *R. cathetus* - have rounded styli. The rest of the Scolopendrellidae present very small styli covered by numerous setae.

54. **Coxal vesicles at basis of legs:** (0) absent; (1) present. The presence of coxal vesicles is also shared by all symphylans.

55. **Arrangement of coxal vesicles:** (0) between legs 3-10; (1) between legs 3-9. The coxal vesicles are absent between legs 11 in some of the selected species, without any taxonomical criterion.

The presence of the coxal vesicles between legs 11 is the main character to separate the genus *Symphylellina* from *Symphylella* (Brölemann 1931).

56. Sternal appendages associated with at least some of legs 5-11: (0) absent; (1) present. These structures are the main diagnostic character for the genus *Millotellina* (Scheller 1977).

57. Type of sternal appendages: (0) unpaired; (1) paired. This is the main character that separates the genus *Millotellina* into two subgenera (Scheller 1977).

58. Position of the gonopore: (0) opisthogoneate; (1) progoneate. Progoneaty (the anterior position of the genital opening) is one of the main synapomorphies that defines the taxon Progoneata (e.g. Kraus & Kraus 1994, Edgecombe 2004). It is shared by all symphylans, as well as by the Pauropoda and Diplopoda.

59. Cerci: (0) absent; (1) present. The presence of cerci, or spinnerets, is exclusively shared by all symphylans.

60. Apical part of cerci: (0) without terminal ridges (non striated); (1) with transverse ridges; (2) with longitudinal ridges. The scutigerellids - except *Scopoliella* - do not show any ridge at the apical part of the cerci, while the scolopendrellids *Scolopendrella*, *Geophilella* and *Parviapiciella* show longitudinal ridges (chapter 1, fig. 16 *arrows*). The rest of the scolopendrellids and *Scopoliella* have transversal ridges.

61. Scales on cerci: (0) absent; (1) present. Some scutigerellids form scales in some parts of the body, and also on the cerci. The scolopendrellids *Scolopendrella*, *Geophilella* and *Parviapiciella* also have scales on the cerci (chapter 1, fig. 16).

62. Shape of the scales on cerci: (0) regular; (1) very conspicuous. The scaly cuticular pattern of the cerci was another diagnostic character for the erection of the genus *Parviapiciella*. This feature is shared with *Geophilella* (Mas & Serra 1993) (chapter 1, fig. 16).

63. Trichobothria with basal bulbus on 12th trunk segment: (0) absent; (1) present. The trichobothria with basal bulbus, or sense calicles, is one of the synapomorhies which support the group Progoneata (e.g. Kraus & Kraus 1994, Edgecombe 2004). Nevertheless, the presence of a pair of trichobothria on the last segment of the trunk is only shared by symphylans.

64. Margin of calicles of trichobothria: (0) smooth; (1) setose. This is the first diagnostic character that Edwards (1959b) introduced to separate the two symphylan families: "paired sense calicles with many setae irregularly distributed around margin of pit" for Scutigerellidae, and "paired sense calicles without setae around margin of pit" for Scolopendrellidae. This character is only valid for the observation of mounts by light microscopy, since the SEM-micrographs show a more complicated structure which varies in the different genera (chapter 1, fig. 17). Nevertheless it was included into the analysis exactly as it was described in the literature.

65. External scales on the outer surface of trichobothria: (0) absent; (1) present. The SEM-micrographs show the scales on the outer surface of the trichobothria in *Hanseniella*, *Scutigerella* and *Symphylella* (chapter 1, fig. 17, "*sc*"). The description of *Ribautiella cathetus*, as well as the detailed schemata of this structure, enabled the inclusion of this feature in the analysis. This species shows a smooth surface on the outer margin of the sense calicles.

66. **Digitiform appendages inside the sense calicles of trichobothria:** (0) absent; (1) present. All studied scolopendrellid species except *Symphylella* show digitiform appendages in the sense calicles (chapter 1, fig. 17, *arrows*).

67. **Arrangement of digitiform appendages in sense calicles of trichobothria:** (0) one row in the entire margin; (1) one row only in the dorsal part; (2) several rows inside the calicle. *Scolopendrella* shows one row of digitiform appendages on the margin of the sense calicles, and also in the exterior. *Geophilella* and *Parviapiciella* only have one row of few digitiform appendages in the dorsal part of the margin. *Sc.(Scolopendrellopsis)* and *Sc.(Symphylellopsis)* present several rows inside the calicle (chapter 1, fig. 17, *arrows*)

68. **Flagellum of euspermatozoa (macrosperm):** (0) short; (1) long. Dallai & Afzelius (2000) described the spermatozoa of the "primitive type" in *Scutigerella*, which are characterized by a short sperm head with a bilayered acrosome. Although they did not identify the species, this feature was applied to both included *Scutigerella* species. In contrast, Rosati et al. (1970) described elongated spermatozoa for *Symphylella vulgaris*.

69. **Shape of the tentorium:** (0) bar-like; (1) laminar-like. The three studied scolopendrellids have a laminar tentorium, while the two scutigerellids show one that is bar-like. The outgroups (Chilopoda and Diplopoda) also show a laminar tentorium.

70. **Anterior tentorial bridge:** 0. longitudinally compressed; (1) longitudinally extended. Among the studied symphylans, only *Scutigerella*, as the outgroups, show a longitudinally compressed anterior tentorial bridge.

71. **Posterior tentorial bridge:** (0) present; (1) absent. The presence of two tentorial bridges (anterior and posterior) is one of the most striking features that *Scolopendrella* only shares with the scutigerellids. The outgroups (Chilopoda and Diplopoda) only present a single tentorial bridge, as *Symphylella* and *Scolopendrellopsis*.

72. **Lateral process of tentorium:** (0) bar-like; (1) extended plate-form.

73. **Dorsal lamina at the medial part of tentorium:** (0) absent; (1) present.

74. **Dorsal process at the posterior part of tentorium:** (0) only at the end, cylindrical; (1) extended, plate-like.

75. **Ventral lamina of the tentorium:** (0) absent; (1) present on the medial part; (2) present on the posterior part.

76. "**Interpontal ligamentous rod":** (0) absent; (1) present.

77. **Inner lamina at the medial part of tentorium:** (0) absent; (1) present

78. **Apodeme of the superior arthrodial membrane of mandible base:** (0) differentiated as trachea arising above mandibular margin; (1) massive apodeme arising from mandibular margin; (2) absent. In addition to the presence or absence of the tracheae in the outer morphology of the head, the study of the internal anatomy has illuminated that in *Symphylella* and *Sc. (Symphylellopsis)*, the homologues to the tracheae in *Scutigerella*, *Hanseniella* and *Scolopendrella* are massive apodemes which support the same muscles (T-muscles) (chapter 2, figs. 18, 21).

79. Mandibular gnathal-lobe apodeme: (0) a straight vertical lamina; (1) a vertical lamina bent to the exterior.

80. Median septum: (0) bifurcated; (1) simple.

81. Attachment of muscles MB9 and MB8 on the mandible: (0) investing the lamina of the posterior mandibular apodeme; (1) among laminae of the posterior mandibular apodeme; (2) pointed contact with the posterior mandibular apodeme.

82. Attachment of muscle MB6 on the mandible: (0) on the dorsal projection of the mandibular base; (1) surrounding the border of the mandibular base.

83. Insertion of muscle MB7 on the tentorium: (0) The three muscles aligned on the same plane; (1) MB7a on the dorsal lamina of the tentorium, MB7b on the middle part, and MB7c on the ventral lamina of the tentorium.

84. Insertion of muscle MB5b on the tentorium: (0) under the lateral process; (1) on the exterior border of the lateral process.

85. Arrangement of muscles MB5a and MB5b: (0) next to each other; (1) one above the other.

86. Insertion of muscles MB8 and MB9 on the tentorium: (0) behind the other mandibular muscles; (1) at the same level of , or more anterior than, other mandibular muscles. The more anterior position of these muscles in *Symphylella* and *Scolopendrellopsis* give, like in the outgroups (Chilopoda and Diplopoda), the appearance of a more compressed mandibular musculature.

87. Insertion of muscle MB5a on the tentorium: (0) under the basal part of the lateral process; (1) on a ligamentous bar of the anterior tentorial bridge; (2) under the exterior border of the lateral process.

88. Insertion of muscle MB5a on the mandibular base: (0) on the middle part of the mandibular base; (1) under the ventral border of the mandible.

89. Insertion of muscle MB4 on the tentorium: (0) on the ventral side of the lateral process; (1) on a ligamentous bar of the anterior tentorial bridge.

90. Insertion of muscle MB2 on the tentorium: (0) on the ventral side of the posterior process; (1) on the basal part of the lateral process; (2) on a connective-tissue bar of the anterior tentorial bridge.

91. Composition of muscles MB2: (0) 4 muscles; (1) 1 muscle.

92. Arrangement of muscles MB2 and MB3: (0) aligned when arising from the mandible; (1) not aligned, very distant when arising from the mandible; (2) fused as only one muscle.

93. Insertion of muscle MB1 on the tentorium: (0) on the ventral side of the basal part of the lateral process; (1) on the inner part of the ventral side of the posterior process.

94. Muscles MB10: (0) absent; (1) present. These three muscles are absent in *Scutigerella*, *Hanseniella* and *Scolopendrella*. In contrast, they are present in *Symphylella* and *Scolopendrellopsis*, as well as in the outgroups (Chilopoda and Diplopoda), and provide a higher mobility in the mandibular base.

95. **Muscles ML1:** (0) 5 muscles; (1) 3 muscles; (2) 11 muscles.

96. **Muscles ML2:** (0) 4 muscles; (1) 3 muscles; (2) 2 muscles.

97. **Muscles ML3:** (0) 5 muscles; (1) 1 large muscle; (2) 3 muscles.

98. **Muscles ML4:** (0) 8 muscles; (1) 4 large (doubled) muscles; (2) 7 muscles; (3) 5 muscles.

99. **Attachment of muscles ML5 and ML6 on the gnathal-lobe apodeme:** (0) on the inner side; (1) on the outer side.

100. **ML6:** (0) under ML5 and ML7; (1) between ML5 and ML7.

101. **ML1´:** (0) absent; (1) a single muscle; (2) two muscles.

102. **ML2´:** (0) absent; (1) present.

103. **Muscles Sp1:** (0) arise among small laminae at the posterior end of the tentorium. Lying parallel; (1) one arises under and two on the superior lamina of the tentorium, and do not lie parallel (two above and one below).

104. **Muscle Sd2:** (0) present; (1) absent.

105. **Muscle Sd1:** (0) present; (1) absent.

106. **Muscle Sd1:** (0) 2 muscles; (1) 1 muscle.

107. **Insertion of muscle Sp2 on the tentorium:** (0) on the lateral side; (1) at the posterior end, on the interior side.

108. **Insertion of muscle Mi10 with the tentorium:** (0) on the lateral side of the posterior process; (1) on the ventral side of the dorsal lamina; (2) on the tentorial bridge.

109. **Attachment of muscle Mi8 on the first maxilla:** (0) in the concavity of the maxilla I; (1) on the exterior border.

110. **Insertion of muscle Mi8 on the tentorium:** (0) on the distal point of the lateral process; (1) on the posterior side of the basis of the lateral process; (2) on and under the lamina of the lateral process.

111. **Insertion of muscle Mi7 on the tentorium:** (0) on the posterior process, behind the lateral process; (1) on the ventral lamina, at level of the lateral process; (2) on the tentorial bridge.

112. **Muscle Mi9:** (0) present; (1) absent.

113. **Arrangement of muscles Mi5 at the insertion on the tentorium:** (0) at the same point, while the three muscles lie together; (1) at different points, the three muscles do not lie together.

114. **Insertion of muscles Mi5 on the tentorium:** (0) on the lateral side of the posterior process; (1) on the basis of the lateral process.

115. **Insertion of muscle Mi6 on the tentorium:** (0) on the lateral side of the posterior process; (1) on the tentorial bridge; (2) on the intersection between the posterior process and the lateral process.

116. **Insertion of muscle Mi3 on the tentorium:** (0) on the lateral side of the posterior process; (1) on the interior border of the basis of the lateral process.

117. **Insertion of muscle Mi2 on the tentorium:** (0) two on the ventral side of the posterior process and one to the ventral side of the tentorial bridge; (1) only on the ventral side of the tentorial bridge.

118. **Muscle Mi4:** (0) parallel muscles in a longitudinal way; (1) not parallel, more or less transversal.

119. **Insertion of muscles Mi1 and H2 on the tentorium:** (0) on the ventral side of the posterior process; (1) in the ventral hollow of the posterior process.

120. **Muscle Pv2:** (0) present; (1) absent.

121. **Muscle Pv2:** (0) a series of muscles that arise from the "interpontal bar"; (1) three muscles that arise from the anterior tentorial bridge.

122. **Muscle Pv1:** (0) present; (1) absent.

123. **Muscle Pd4:** (0) present; (1) absent.

124. **Muscle Pl3:** (0) present; (1) absent.

125. **Muscle Pd3:** (0) 5 muscles; (1) less than 5 muscles; (2) absent; (3) more than 5 muscles.

126. **Muscle Pd2:** (0) 5 muscles; (1) 2 muscles; (2) more than 5 muscles.

127. **Muscle Pd1:** (0) 5 muscles; (1) 4 muscles; (2) 3 muscles; (3) 2 muscles.

128. **Muscle Pl2:** (0) 5 muscles; (1) 3 muscles; (2) absent.

129. **Muscle Pl1:** (0) 2 muscles; (1) 3 muscles; (2) absent.

130. **Muscle Pv3:** (0) present; (1) absent.

131. **Muscle B3:** (0) 3 muscles; (1) 4 muscles.

132. **Muscle B3:** (0) 1 group; (1) 2 groups.

133. **Insertion of muscles Mii1 and Mii2 on the tentorium:** (0) on the ventral side of the posterior process; (1) on the inner side of the ventral lamina; (2) on the exterior side of the ventral lamina.

134. **Insertion of muscle Mii2 on the tentorium:** (0) among the other maxilla-II muscles; (1) more posterior to the other maxilla-II muscles.

135. **Attachment of muscle Mii2 on the second maxilla:** (0) more exteriorly than Mii1; (1) more posteriorly than Mii1, as interior as Mii1.

136. **Insertion of muscle Mii3 on the tentorium:** (0) on the interior side of the bar; (1) on the tentorial bridge.

137. **Muscle Mii6:** (0) present; (1) absent.

138. **Arrangement of muscle A3:** (0) passes between the two A2 muscles; (1) does not pass between the two A2 muscles.

139. **Muscles A5:** (0) 3 muscles; (1) 4 muscles; (2) 2 muscles.

140. **Insertion of muscle A7 on the tentorium:** (0) on the dorsal point of the dorsal lamina; (1) on the lateral side.

141. **Insertion of muscle A5 on the tentorium:** (0) on the lateral side; (1) on the horizontal medial lamina.

142. **Insertion of muscle A7 on the tentorium:** (0) at the level of A5; (1) behind A5.

143. **Muscle C1:** (0) present; (1) absent;

144. **Arrangement of muscle C1:** (0) diagonal outwards; (1) longitudinal.

145. **Attachment of muscle B7:** (0) to the posterior end of the proximal arms of the second maxilla; (1) to the posterior part of the first maxilla.

Appendix II

Data matrix representing the 145 morphological characters coded for the relationships of Symphyla and myriapod outgroups [the six first taxa: *Scutigera coleptrata* (Chilopoda), *Lithobius forficatus* (Chilopoda), *Glomeris marginata* (Diplopoda), *Polyxenus lagurus* (Diplopoda), *Allopauropus* sp. (Pauropoda) and *Millotauropus acostae* (Pauropoda)] as described in Appendix I. Question marks (?) indicate missing data; dashes (-) indicate inapplicable character states.

	0000000001	1111111112	2222222223	3333333334	4444444445
	1234567890	1234567890	1234567890	1234567890	1234567890
Scutigera coleoptrata	2----5011-	-----2400-	00?000--0-	---0-10-00	1-0----3-1
Lithobius forficatus	0----000-1	0-0--2400-	00?000--10	---0-10-00	1-0----3-1
Glomeris marginata	1----502--	-----2301-	00?000--0-	---0-21-3?	1-0----2-2
Polyxenus lagurus	1----502--	-----2301-	00?200--0-	---0-21-01	1-0----2-2
Allopauropus sp.	3----502--	-----2202-	11?100--0-	---0-20-21	100----2-2
Millotauropus acostae	0----502--	-----22?2-	11?100--0-	---?-?0-2?	?0?----???
Millotellina (Mill.) monteithi	400002010-	-----20?30	1000?10-0-	0-10??1?1?	??????????
Millotellina (Dipl.) bidens	400002010-	-----20?30	1000?10-0-	0-10??1?1?	??????????
Scolopendrelloides bifida	40000200-0	-21--01?30	10?0?12?0-	0-00??1?1?	??????????
Scopoliella crenatus	400000011-	-----10?3?	10?0?10?0-	0-00??1?1?	??????????
Hanseniella graeca	40000000-0	-11--20?3?	10???1??0-	0-0?????1?	??????????
Hanseniella agilis	400000010-	-----20130	1000013-0-	0-00001010	0100001000
Hanseniella nivea	400000010-	-----20130	1000013-0-	0-10001010	0100001000
Scutigerella causeyae	400000011-	----100130	1000010-0-	0-10001010	0100001000
Scutigerella immaculata	400000011-	-----00130	1000010-0-	0-10001010	0100001000
Scolopendrella notacantha	41000100-0	-110121130	1000011-0-	1111001111	1110111011
Geophilella pyrenaica	41110112--	---0021131	100011100-	1301011111	1110111011
Parviapiciella balcanica	41110110-2	---0021031	100011100-	1301011111	1110111011
Sco. (Sco.) microcolpa	41100310-1	0000121031	1011111110	1000111011	100?01????
Sco. (Sym.) subnuda	41100310-1	1000121031	1011111110	1000111011	1001010101
Sco. (Sym.) arvernorum	41110310-1	1000121031	1001111100	0-00111011	1001010101
Symphylella vulgaris	41000000-1	0010121031	1011010-11	1200111011	10011102-1
Symphylella elongata	41000000-1	0010121031	1011010-11	1200111011	10011102-1
Symphylellina pachypoda	41000000-1	0000121?31	10???11??1	??0???1?1?	??????????
Ribautiella cathetus	41111010-1	1000121?31	10?1?1000-	0-0???101?	??????????
Ribautiella remyi	41111312--	---0011?3?	10???11?11	0-0???1?1?	??????????
Ribautiella delphini	41110410-1	1000121?3?	10???11?11	0-0???1?1?	??????????
Remysymphyla hebetocornuta	40000?00-1	001--21?31	10?1?11011	120???101?	??????????
Neosymphyla ghanensis	41100310-1	1001121??1	10???11?10	1?0???1?1?	??????????

					1
	5555555556	6666666667	7777777778	8888888889	9999999990
	1234567890	1234567890	1234567890	1234567890	1234567890
Scutigera coleoptrata	00-0-0-00-	--0----1??	?----?-2??	??????????	??????????
Lithobius forficatus	00-0-0-00-	--0----110	1----0-2--	-1---1--10	?2112-----
Glomeris marginata	50-0-0-10-	--0----?10	1----0-2--	-?---1--??	??11?-----
Polyxenus lagurus	50-0-0-10-	--0----?1?	1----0-???	??????????	??????????
Allopauropus sp.	50-0-0-10-	--0----???	1----?-???	??????????	??????????
Millotauropus acostae	50-0-0-10-	--0----???	?----?-???	??????????	??????????
Millotellina (Mill.) monteithi	1131110110	1011??????	??????????	??????????	??????????
Millotellina (Dipl.) bidens	1131011110	1011??????	??????????	??????????	??????????
Scolopendrelloides bifida	113110-110	0-11??????	??????????	??????????	??????????
Scopoliella crenatus	113110-111	1011??????	??????????	??????????	??????????
Hanseniella graeca	1????0-110	??11??????	??????????	??????????	??????????
Hanseniella agilis	113100-110	101110-???	???????0??	??????????	??????????
Hanseniella nivea	113100-110	101110-?01	0011111000	1000001012	0000000000
Scutigerella causeyae	113100-110	101110-000	0000010000	0000000000	0000001110
Scutigerella immaculata	113100-110	101110-000	0000010000	00??00?00?	?0?000111?
Scolopendrella notacantha	211110-112	1010010?11	0111201001	0010100000	?100022210
Geophilella pyrenaica	211100-112	1110011???	??????????	??????????	??????????
Parviapiciella balcanica	211100-112	1110011???	??????????	??????????	??????????
Sco. (Sco.) microcolpa	211110-111	0-10012???	??????????	??????????	??????????
Sco. (Sym.) subnuda	211110-111	0-10012?11	1101101111	2111112100	1211112311
Sco. (Sym.) arvernorum	211110-111	0-10012???	??????????	??????????	??????????
Symphylella vulgaris	411110-111	0-1010-111	1101101111	2111112101	1201112311
Symphylella elongata	411110-111	0-1010-???	??????????	??????????	??????????
Symphylellina pachypoda	411100-11?	0-10??????	??????????	??????????	??????????
Ribautiella cathetus	410100-111	0-100?????	??????????	??????????	??????????
Ribautiella remyi	410100-110	0-10??????	??????????	??????????	??????????
Ribautiella delphini	412100-111	1010??????	??????????	??????????	??????????
Remysymphyla hebetocornuta	310110-111	0-10??????	??????????	??????????	??????????
Neosymphyla ghanensis	21?110-111	0?10??????	??????????	??????????	??????????

	1111111111	1111111111	1111111111	1111111111	11111
	0000000001	1111111112	2222222223	3333333334	44444
	1234567890	1234567890	1234567890	1234567890	12345
Scutigera coleoptrata	??????????	??????????	??????????	??????????	?????
Lithobius forficatus	---00-?2--	21--1010?1	-11132?220	??????????	??1-1
Glomeris marginata	---????2--	??????????	??????????	??????????	????1
Polyxenus lagurus	??????????	??????????	??????????	??????????	?????
Allopauropus sp.	??????????	??????????	??????????	??????????	?????
Millotauropus acostae	??????????	??????????	??????????	??????????	?????
Millotellina (Mill.) monteithi	??????????	??????????	??????????	??????????	?????
Millotellina (Dipl.) bidens	??????????	??????????	??????????	??????????	?????
Scolopendrelloides bifida	??????????	??????????	??????????	??????????	?????
Scopoliella crenatus	??????????	??????????	??????????	??????????	?????
Hanseniella graeca	??????????	??????????	??????????	??????????	?????
Hanseniella agilis	??????????	??????????	??????????	??????????	?????
Hanseniella nivea	1000000011	101-100110	0100001011	0010000000	00000
Scutigerella causeyae	0000000100	0000000000	0000000001	0000000101	10000
Scutigerella immaculata	??000??100	0?00000000	0000000??1	00000001??	??00?
Scolopendrella notacantha	2111011200	0001200100	1000103100	1021111020	11011
Geophilella pyrenaica	??????????	??????????	??????????	??????????	?????
Parviapiciella balcanica	??????????	??????????	??????????	??????????	?????
Sco. (Sco.) microcolpa	??????????	??????????	??????????	??????????	?????
Sco. (Sym.) subnuda	10111-1?02	0101211001	-011212120	1100111011	011-?
Sco. (Sym.) arvernorum	??????????	??????????	??????????	??????????	?????
Symphylella vulgaris	20111-1202	0101211001	-011212100	1100111010	011-1
Symphylella elongata	??????????	??????????	??????????	??????????	?????
Symphylellina pachypoda	??????????	??????????	??????????	??????????	?????
Ribautiella cathetus	??????????	??????????	??????????	??????????	?????
Ribautiella remyi	??????????	??????????	??????????	??????????	?????
Ribautiella delphini	??????????	??????????	??????????	??????????	?????
Remysymphyla hebetocornuta	??????????	??????????	??????????	??????????	?????
Neosymphyla ghanensis	??????????	??????????	??????????	??????????	?????

Summary

The Symphyla are the smallest subgroup of the myriapods, with about 200 species which are representatives of the soil fauna. Some of their features and their cosmopolitan distribution corroborate the view that they are geologically old. However, their phylogenetical relationships to other arthropods are still unclear, and the main reason is the lack of understanding of their phylogeny.

In this study, the external morphology of 15 species representing the seven European genera has been studied in detail by scanning electron microscopy. New data on distribution and taxonomy, including new diagnostic characters, are especially provided for the subgroup Scolopendrellidae. Variation in some morphological features of the head, first segments, sense calicles and cerci has led to the development of a new key to the European genera, which facilitates determinations of this taxonomically difficult group.

The internal anatomy of the head has been investigated in representatives of five genera and the skeletomuscular anatomy of three scolopendrellids is described for the first time. Detailed data on the tentorial complex confirms of the presence of "fultural sclerites" in Symphyla, which supports the monophyly of Myriapoda. The tentorial complex and musculature of the scolopendrellid *Scolopendrella* presents more similarities to the Scutigerellidae than to *Symphylella* and *Scolopendrellopsis* (the other two studied Scolopendrellidae). These latter two genera show features that – compared to the state in other myriapod subgroups – seem to be plesiomorphic, such as the presence of a laminar tentorium with only one bridge, the absence of tracheae in the head, as well as the presence of large dorsal muscles of the mandibular base. These characters are shared with other myriapod subgroups and show that the musculature of mouthparts in Symphyla is not as specialized as has been previously assumed to date.

Data on the external morphology and internal anatomy was compiled in a character matrix –completed from the literature for the remaining genera. After cladistic analysis, the shortest cladograms are incongruent with the traditional classification of the two families. The family Scutigerellidae is retrieved as a monophylum while Scolopendrellidae is resolved as a paraphyletic group with respect to the Scutigerellidae. The scolopendrellids *Scolopendrella*, *Geophilella* and *Parviapiciella* form a monophyletic group with the Scutigerellidae characterised by the presence of tracheae in the head and two tentorial bridges, among other synapomorphies. The remaining Scolopendrellidae form a monophyletic group without significant support, the resolution of which varies under different character weightings. Among other considerations, the proposed phylogenetic hypothesis supports the view that

increase and reductions of the number of trunk scuta happened several times in the evolution of the Symphyla, possibly as adaptations to different subterranean life habits. To unravel the phylogenetic position of the Symphyla among Arthropoda, the genera *Scolopendrella*, *Scolopendrellopsis* and *Symphylellina* are revealed as the most accurate taxon sampling for this group as they seem to maintain most of the ancestral states of the Symphyla according to the shortest trees revealed in this study.

Zusammenfassung

Die Symphyla, die Vertreter der Bodenfauna sind, bilden mit etwa 200 Arten die artenärmste Teilgruppe der Myriapoda. Einige ihrer Merkmale und ihre kosmopolitische Verbreitung lassen auf ein hohes geologisches Alter schließen. Ihre Stellung im System der Arthropoda ist jedoch unklar. Der wichtigste Grund dafür ist, dass bis heute kein phylogenetisches System für die Symphyla vorliegt.

In dieser Arbeit wurde die äußere Morphologie von 15 Arten, die alle sieben bekannten europäischen Gattungen repräsentieren, mittels Rasterelektronenmikroskopie studiert. Insbesondere für die Teilgruppe Scolopendrellidae werden neue diagnostische Merkmale sowie neue Verbreitungsdaten mit Bemerkungen über ihre Taxonomie vorgestellt. Neu entdeckte Merkmale der Morphologie des Kopfes, der ersten Segmente, Trichobothrien und Cerci führen zu einem neuen Bestimmungsschlüssel, der die Bestimmung dieser taxonomisch schwierigen Gruppe erleichtert.

Für fünf Genera wird exemplarisch die innere Kopfanatomie dargestellt. Zum ersten Mal werden die Muskulatur und das Kopfinnenskelett (Tentorium) bei den Scolopendrellidae anhand von 3 Arten beschrieben. Detaillierte Daten über den tentorialen Komplex bestätigen die Existenz von „fultural sclerites“ und dieses wiederum unterstützt die Monophylie der Myriapoda. Die Scolopendrellide *Scolopendrella* zeigt mehr Ähnlichkeiten mit den Scutigerellidae als mit *Symphylella* und *Scolopendrellopsis* (die beiden anderen hier untersuchten Scolopendrelliden). Letztere zeigen Merkmale, die als Plesiomorphien interpretiert werden, insbesondere die Ausbildung eines laminaren Tentoriums mit nur einer einzigen Tentorialbrücke, das Fehlen von Tracheen im Kopf und Vorhandensein von großen dorsalen Muskeln am proximalen Mandibelgrundglied. Diese Merkmale werden mit anderen Teilgruppen der Myriapoda geteilt und zeigen, dass die Muskulatur der Mundwerkzeuge bei den Symphyla nicht so spezialisiert ist, wie bislang angenommen wurde.

Mit den neuen Daten zur äußeren Morphologie und inneren Kopfanatomie wurde eine Merkmalsmatrix zusammengestellt und mit Literaturdaten für die restlichen Gattungen ergänzt. Mittels kladistischer Analyse werden Kladogramme generiert, die inkongruent mit der traditionellen Klassifikation der zwei Familien sind. Die Scutigerellidae erweisen sich als monophyletische Gruppe, während sich die Scolopendrellidae als paraphyletisch herausstellen. Die Scolopendrelliden-Gattungen *Scolopendrella*, *Geophilella* und *Parviapiciella* sind näher mit den Scutigerellidae verwandt als mit den restlichen Teilgruppen der Scolopendrellidae. Diese Hypothese wird vor allem durch zwei apomorphe Merkmale gestützt: die Bildung von Tracheen im Kopf, sowie die Existenz von zwei ligamentösen Brücken im Tentorium. Im

Gegensatz dazu bilden die restlichen Scolopendrellidae eine monophyletische Gruppe ohne nennenswerte Unterstützung, deren Topologie in Abhängigkeit von der Merkmalsgewichtung variiert. Neben anderen Schlussfolgerungen unterstützt die neue phylogenetische Hypothese die Annahme, dass Veränderungen in der Anzahl der Rückenplatten mehrfach unabhängig in der Evolution der Symphyla erfolgt sind, wahrscheinlich als Ausdruck der Anpassung an verschiedene unterirdische Lebensweisen. Nach der vorliegenden Untersuchung sind Vertreter der Gattungen *Scolopendrella*, *Scolopendrellopsis* und *Symphylellina* besonders geeignet, um die Stellung der Symphyla innerhalb der Arthropoda zu untersuchen, da sie viele ursprüngliche Merkmale bewahrt haben.

Curriculum Vitae

For reasons of data protection,
the curriculum vitae is not included in the online version

Publications

Escuer, M., Labrador, S., Campos-Herrera, R., Rivera, Y., Cuadrea, L., Cedenilla, O., Domínguez, M. & Gutiérrez C. 2006. *Preliminary study of cropping management effect on nematode communities in La Rioja (Northern Spain).* XXVIII European Society of Nematologists (ESN) International Symposium. Abstracts book (p.138). Blagoevgrad, Bulgary.

Gutiérrez, C., Escuer, M., Simón, C., Campos-Herrera, R., Labrador, S., Gómez-Ros, J.M., Domínguez, M., Cuadra, L. y Cedenilla, O. 2007. *Preliminary study of the edaphic biodiversity as indicator system of the soil conservation.* (*"La biodiversidad edáfica como sistema bioindicador del estado de conservación del suelo. Estudio preliminar."*) I Congreso Nacional Sobre Cambio Global. Comité Español de Investigación, Cambio Ambiental Global (ceiCAG). Abstracts book (p.78). Madrid, Spain.

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Domínguez Camacho, M. & Koch, M. 2008. Towards a phylogenetic system of the Symphyla. *Peckiana*, 6: 103.

Domínguez Camacho, M. & Koch, M. 2009. Phylogeny and evolution of the Symphyla (Myriapoda). Systematics 2009. Abstract book (p. 44). Leiden, Netherlands.

Fellowships and grants

- February 2010 Synthesys grant of the European Union-funded Integrated Activities for the Royal Museum of Central Africa in Tervuren (Belgium).
- 01.10.2007-31.11.2009 PhD fellow of the DAAD (German Academic Exchange Service) and "La Caixa" Foundation.
- 01.12.2006-30.05.2007 UAM Travel Award for the Teaching and Investigation Staff, at the Free University Berlin ("Beca de Movilidad Internacional para el Personal Docente e Investigador de la Universidad Autónoma de Madrid").
- 01.10.2005-30.09.2007 UAM Postgraduate fellow ("Beca de Inicio de Estudios de Programas de Postgrado, de la Universidad Autónoma de Madrid").
- 01.09.2003-31.08.2004 Socrates-Erasmus fellow of the *Comunidad de Madrid*, at the Freie Universität Berlin (Alemania).
- 20.06-19.08.1998 Ruta Quetzal BBVA Expedition Award, to Venezuela and Trinidad and Tobago.

Research and teaching experience

- 01.10.2007 – present. Animal Systematics and Evolution Lab, Free University Berlin (Germany)
- 2007 – present. Volunteer collaborator as taxonomist on myriapods at the Natural History Museum of Madrid and the Animal Biodiversity Resources Centre of the University of Barcelona (Spain).
- 01.10.2005-30.06.2006 Teaching assistant for Zoology at the Biology Department of the Universidad Autónoma de Madrid (Spain).
- 01.09.2005-31.05.2006 Research collaboration at the Environmental Sciences Centre of the CSIC (Spanish National Research Council), in the project (transl.) "Study of the cropping management effect in the edaphic fauna biodiversity from La Rioja (Spain)", under supervision of Dr. Carmen Gutiérrez.
- 21.06-09.07.2004 / 02-13.08.2004 Volunteer collaborator at the Paleontology Department of the Natural History Museum of Berlin (Germany), under supervision Dr. David Unwin.
- 03-31.05.2004 Volunteer collaborator at the Animal Systematics and Evolution Laboratory of the Free University Berlin (Germany), in the project "Synthesis of ascorbic acid in invertebrates" under supervision of Dr. Dietmar Glaubitz.
- 05-30.04.2004 Volunteer collaborator at the Animal Systematics and Evolution Laboratory of the Free University Berlin (Germany), in the project "Comparative Genomics and Animal Evolution", under supervision of Dr. Lars Podsialdlowski.
- 15.10.2003-27.02.2004 Volunteer collaborator at the Animal Systematics and Evolution Laboratory of the Free University Berlin (Germany), in the project "Comparative Ultrastructure and Development of the coelomic cavities of the Metazoa", under supervision of Prof. Dr. Thomas Bartolomaeus.
- 01-21.07.2003 Volunteer collaborator in the dinosaurs palaeontology site Las Hoyas (Cuenca, Spain), under supervision of Dr. José Luis Sanz.

Non-academic courses

- 27-28.10.2008 Workshops "Digital drawing methods for taxonomy" and "Delta, descriptive language in taxonomy" at Natural History Museum of Berlin, organised by the Youth Systematics (*JuSys*) of the German Biological Systematics Association (*GfBS*).
- 09-13.10.2006 Workshop "Cladistic Methods in Phylogenetics", at Free University Berlin (Germany).
- 12-30.07.2004 Marine Biological Course in Kristineberg Marine Research Station (Sweden).
- 22-24.07.2003 Palaeontology Course (transl.) "The first living organisms" at the Cuenca Auditory (Spain) and organised by Dr. José Luis Sanz and the Juan de Valdés Institute.

- 01-05.11.2000 Environmental Education Course in Pedro Bernardo (Avila, Spain) and organised by the YMCA.
- 28.03-13.04.2000 Astronomy and Astrophysics Course at the Planetarium of Madrid (Spain).

Attendance at congresses and conference cycles

- 10-14.08.2009 Systematics 2009 1st meeting of Biosyst / 7th Biennial Conference of the Systematics Association at National Herbarium of the Netherlands and National Museum of Natural History Naturalis, Leiden (Netherlands).
- 04-06.03.2009 International Congress "Celebrating Darwin: From *The Origin of Species* to Deep Metazoan Phylogeny" at Humboldt University Berlin (Germany) and organised by the Deutsche Forschungsgemeinschaft (DFG).
- 24-26.10.2008 "Systematik und Taxonomie im 21. Jahrhundert" JuSys Meeting 2008 at the Natural History Museum of Berlin (Germany) and organised by the Youth Systematics (*JuSys*) of the German Biological Systematics Association (*GfBS*).
- 21-25.07.2008 14th International Congress of Myriapodology, at Staatliches Museum für Naturkunde de Görlitz (Germany) and organised by the *Centre International de Myriapodologie*.
- 18-19.06.2007 International Meeting "The Evolution of the Animals: a Linnean Tercentenary Celebration", at The Royal Society (London, United Kingdom) and organised by Dr. Tim Littlewood and Dr. Max Telford.
- 21-25.11.2005 Technical Conferences (transl.) "New methodological techniques applied to the environmental systems study: the stabile isotopes" at the Universidad Autónoma de Madrid (Spain) and organised by Ecology Department and the Stabile Isotopes Laboratory of the Interdepartmental Research Service of the UAM.
- 21-24.11.2005 Seminar (transl.) "Thinking about the Evolution: History, Epistemology and Present" at the Universidad Autónoma de Madrid (Spain) and organised by Dr. Máximo Sandín and Dr. Andrés Galera in collaboration with the UAM and the CSIC.
- 10-11.02.2005 Conferences cycle (transl.) "The Dinosaurs in the XXI Century" at the Cosmo-Caixa Museum (Barcelona, Spain) and organised by "La Caixa" Foundation.
- 08.11-05.12.2002 Conferences cycle (transl.) "Adaptative radiations: highlights in the Evolution" at the Universidad Autónoma de Madrid (Spain) and organised by the Biology Students' Association.

Other information

- Student representative in the Department Council, Faculty Board and University Senate at the Universidad Autónoma de Madrid (2000-2005).
- Advanced musical skills: theory and piano, until 7th degree.
- Keyboard-player of the music group "Ad-Astra" (2000-2005).
- Membership to the theatre group "El Apagón" (1996-2003).
- Prize for the best actor-music player at the Youth Theatre Contest of Madrid in 1999.
- Advanced skills in drawing and fine arts; membership of an art studio (1990-1996).
- First prize at the Natural Drawing Contest "Amizoo", organised by the Bararida Zoo (Venezuela) in August 1998.
- First prize for the best short story at the Literary Contest "Alborada" of the Comunity of Madrid, in 1999.