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Abstract

In the last years the knowledge concerning the early splits among hexapod lineages steadily increased but some relationship hypotheses are still questioned. Only few potential apomorphies are mentioned to support the monophyly of Diplura and Zygentoma, respectively. Therefore additional characters are needed to confirm the validity of these taxa. Two casually mentioned antennal characters are evaluated in this respect: (i) The extrinsic antennal musculature of Diplura is reported to contain a muscle inserting at the base of the second antennomere. In all other basal hexapods the entire extrinsic antennal musculature seemingly inserts at the first antennomere (scape of Ectognatha). (ii) The antennae of Zygentoma are mentioned to have a dicondylic articulation, whereas the latter is monocondylic in all remaining basal hexapods.

The extrinsic antennal musculature and the articulation of antennae of representatives of all basal hexapod groups were investigated. Aims of this study are: (i) to describe these structures in detail in Collembola, Diplura, Zygentoma and Archaeognatha, (ii) to investigate whether these character systems can provide additional support for the monophyly of Diplura and/ or Zygentoma, and (iii) to test whether these two character systems are informative for the reconstruction of phylogenetic relationships among basal hexapods. In order to answer these questions the extrinsic antennal musculature was 3D reconstructed based on semi-thin section series. The antennal articulation was investigated using light microscopy and SEM.

The analysis of the antennal articulation proved to be difficult. The applied methods did not allow to analyse the antennal articulation in all investigated representatives of the basal hexapod groups. In Zygentoma the articulation of the basal antennal segment to the head capsule is not very distinct and could not be definitely clarified with the applied methods. Muscles of the extrinsic antennal musculature insert at the base of the second antennomere in all examined Diplura. Since a comparable insertion could be detected to be likewise present in representatives of Collembola this character, however, does not give support to monophyletic Diplura. A thorough investigation of this character in potential outgroups of hexapods thus is necessary to evaluate whether the shared state of Collembola and Diplura is an old plesiomorphy or may represent a potential synapomorphy supporting the monophyly of Entognatha. Another interesting result is that only in archaeognathans muscles are build up of fibres that originate at the homolateral and heterolateral anterior tentorium. This may be a potential synapomorphy supporting the monophyly of Archaeognatha.

1. Introduction

Despite increasing knowledge regarding the earliest branchings in the tree of Hexapoda in the recent years, some phylogenetic hypotheses still remain but weakly supported. The traditional view joins Protura, Collembola and Diplura in the taxon Entognatha based on the presence of oral folds enclosing the mandibles and first maxillae as the most distinctive synapomorphic character (Hennig, 1969). Protura and Collembola are regarded as sister-groups within Entognatha forming the taxon Ellipura. Synapomorphic characters shared by these two orders are the absence of cerci, the more pronounced entotrophic condition, the presence of unpaired pretarsal claws and of the linea ventralis (Kristensen, 1981). The monophyly of Ellipura and the position of Protura in the hexapod tree are still questioned by morphological and molecular studies (Dallai, 1980, 1989; Bitsch and Bitsch, 1998; D'Haese, 2002; Giribet et al., 2004; Luan et al., 2005; Dallai et al., 2010; von Reumont et al., 2009, 2012) because of some peculiar morphological features of Protura like the anamorphic development, the lack of antennae, the presence of 12 abdominal segments in the adults, the position of the genital opening between the 11th and 12th abdominal segments, as well as peculiarities in sperm axonemal ultrastructure (Dallai, 1980, 1994) and mesoderm segregation (Machida and Takahashi, 2003). The traditional view regards the Entognatha as the sister-taxon of the Ectognatha (Hennig, 1969), a taxon which is characterised by the presence of external mouthparts, with exposed mandibles and maxillae (ectotrophic condition) (Kristensen, 1997; Klass and Kristensen, 2001; Wheeler et al., 2001). These Ectognatha comprise the two remaining apterygotan taxa Archaeognatha and Zygentoma along with the Pterygota. The articulation of mandibles is monocondylic in Archaeognatha and they are regarded as the most ancient lineage among Ectognatha, representing the sister-group of Zygentoma+Pterygota. The latter taxa have a dicondylic articulation of mandibles and are therefore called Dicondylia (cf. Carapelli et al., 2006).

An alternative hypothesis places Diplura as the sister-group of Ectognatha (Kukalová-Peck, 1987), thus dismissing the monophyly of Entognatha. The author described the presence of a semi-entotrophic condition in the fossil japygid *Testajapyx thomasi* and suggested that the entognathous condition of modern Diplura is a secondary acquisition, parallel, but independent, from that found in Parainsecta (= Ellipura).

Based on a study of the female reproductive system of basal hexapods yet another hypothesis concludes that Diplura might represent a paraphyletic assemblage (Stys and Bilinski, 1990). The Campodeina are considered as the sister-group of the Ellipura, sharing the existence of meroistic ovarioles, compared to the panoistic ovarioles of Japygina. Ovaries of Protura are, however, regarded as secondarily panoistic, derived from a meroistic polytrophic condition. Furthermore, ovaries of Protura, Collembola and Campodeina are sac-shaped, whereas those of Japygina are arranged in a

segmental way, which provoked Stys and Bilinski (1990) to propose a still unresolved polytomy among Japygina, Ectognatha and an assemblage of Campodeina+Ellipura.

Moreover the monophyly of some taxa of basal hexapods are still debated. The support of monophyletic Diplura is based only on a few morphological characters which are in addition inconsistent with other characters and there are also just a few potential apomorphies known that support the monophyly of Zygentoma. Typical regressive apomorphies of Diplura are the complete loss of all visual organs and loss of anterior tentorial arms. Other potential synapomorphies of campodeids and japygids are a unique position of the gonopore located in both sexes between VIII and IX, a trochanteral femur-twisting muscle, a femur-tibia pivot joint and a peculiar interlocking of galea and superlingua (Kristensen, 1997). While there is much known about the Campodeidae and the Japygoidea not all above mentioned characters have been investigated in the other families Anajapygidae, Projapygidae and Procampodeidae which are very rarely collected. Usually the non-japygoid Diplura are grouped into the taxon Campodeina. Although this taxon (Procampodeidae+Campodeoidea) seems to be a reasonable working hypothesis (Bareth et al., 1989), anajapygid, octostigmatid and projapygid affinities still remain questionable. In addition, the evidence for monophyly of Diplura needs to be pondered against the possibility of a closer relationship between one of their subgroups and another hexapod taxon. The Campodeoidea have some potential synapomorphies in common with Ellipura: the absence of abdominal spiracles, non-metameric embryonic ovaries- the latter condition regarded plesiomorphic in the adults at the hexapod level (Stys et al., 1993) and ovarioles with linear meroism (Stys and Bilinski, 1990). There are other problems concerning the monophyly of Diplura or Entognatha, respectively. One of those problems relates to the very different head configuration in the Diplura and Ellipura which raised questions whether the entognathy types in these two groups belong to the same transformation series (Kraus, 1997). Another line of argument provoked Kukalová-Peck (1987) to include the Diplura in the Insecta. Kukalová-Peck's main reason for joining the Diplura with the Insecta is that the abdominal limb bases including the trochanter are integrated in the trunk wall. In Ellipura the trochanter supposedly stays non-incorporated.

Each of the two main dipluran lineages shares similarities with true insects not shown by the other. The Campodeidae have in common with the Archaeognatha a particular sperm modification, viz. a 4+5 grouping of the peripheral singlets in the axoneme. A condition not present in Zygentoma or basal pterygotes (Kristensen, 1997). The Japygidae have in common with the Insecta the probably apomorphic (paedomorphic) 'metameric' configuration of ovaries in the adult (Stys et al., 1993).

Despite this Kristensen (1997) believes that there is enough support for monophyletic Diplura (at least the Campodeoidea+ Japygoidea) to be considered as a reasonable working hypothesis. Regarding their phylogenetic affinity he believes that at present time an unresolved basal trichotomy of Ellipura, Diplura and Ectognatha should be maintained.

The monophyly of the taxon Zygentoma is likewise not strongly supported and a possible paraphyly in terms of the Pterygota has also been suggested several times (Kristensen, 1981, 1991). This suggestion is based on an undocumented statement made by Boudreaux (1979) that in the family Lepidotrichidae, which consists of a single species *Tricholepidion gertschi*, parts of the ligamentous cephalic endoskeleton are retained, whereas in all other Dicondylia a cuticular tentorium exists. So, *T. gertschi* could be the sister group of all other Dicondylia (Kristensen, 1997). But Kristensen's opinion (1997) is that although the lamellar tendon is retained in *T. gertschi*, *T. gertschi* should still be included in a monophyletic taxon Zygentoma which is supported by the following synapomorphies: markedly widened apical segment of labial palp (distinctive throughout the Nicoletiidae, Lepismatidae and *T. gertschi*), absence of superlinguae, which are still well developed in Ephemeroptera and must therefore be attributed to the dicondylan ground pattern (Kristensen, 1997) and sperm conjugation (known from *T. gertschi* (Wygodzinsky, 1961), Lepismatidae and Nicoletiidae (Jamieson, 1987)).

Despite the reported apomorphies the monophyly of Diplura and Zygentoma is still weakly supported from morphology and therefore additional characters are needed to further support their monophyly. Such new characters might be present in the extrinsic antennal musculature of basal hexapods, where single muscles differ in insertion sites. In Diplura muscles insert not only at the first but also at the second antennomere, whereas in the remaining basal hexapod groups only muscles inserting at the first antennomere were mentioned (Imms, 1939).

The present study aims to show whether this character can be used to provide additional support for the monophyly of Diplura, and whether extrinsic musculature can deliver information for the reconstruction of phylogenetic relationships among basal hexapods. Furthermore there is reported from literature that the Zygentoma have an allegedly dicondyllic antennal articulation whereas the remaining basal hexapod groups have a monocondyllic one (Chaudonneret, 1950). This unique character state may provide another useful apomorphy to support the monophyly of Zygentoma.

2. Material and Methods

2.1. Material

Most specimens were fixed in Duboscq Brazil (Böck, 1989) before carried over and stored in 70% ethanol. Only some specimens used for whole mounting after maceration were directly fixed in 70% ethanol. Representatives of all groups of primarily wingless insects with antenna were collected at the following sites:

Collembola

- *Sminthurus viridis* – Breitenfurt, clover field, 03/05.08.2004 (Duboscq Brazil)
- *Pogonognathellus flavescens* – Breitenfurt, mixed manure, 03.-05.08.2004 (Duboscq Brazil)
- *Tetrodontophora bielanensis* – High Tatra (Duboscq Brazil)

Diplura (Campodeidae)

- *Campodea augens* – Vienna Woods, 11.2008 (Duboscq Brazil)

Diplura (Japygidae)

- *Catajapyx aquilonaris* – Florisdorfer Aupark, Vienna, 21st district, 12.11.1989 (Duboscq Brazil)
- *Catajapyx aquilonaris* – Arzthgasse 73, Vienna, 21st district, 25.9.2010 (70% ethanol)

Archaeognatha

- *Lepismachilis ysignata* – Lainzer Tiergarten, Vienna 13th district, 08.08.2004 (Duboscq Brazil)
- *Lepismachilis ysignata* – Lainzer Tiergarten, Vienna, 13th district, 5.10.2006 (Duboscq Brazil)
- *Machilis hrabei* – Nasenweg, Vienna, 19th district, 20.10.2004 (Duboscq Brazil)

Zygentoma

- *Lepisma saccharina* – Vienna 8th district, 24.10.2004 (Duboscq Brazil)
- *Lepisma saccharina* – Biocenter department evolutionary biology 3rd floor, Althanstraße 14, Vienna, 9th district, 23.5.2010 (70% ethanol)

- *Atelura formicaria* – Breitenfurt, Lower Austria, 11.7.2009 (Duboscq Brazil)
- *Ctenolepisma lineata* – flat in Engerthstraße 137/7/14, Vienna, 2nd district, 27.10.2010 (70% ethanol)

2.2. Semi-thin sections

Semi-thin section series of 1µm thickness were made with a Reichert Ultracut Om U3, stained with a mixture of 1% azure II and 1% methylene blue in a 1% aqueous borax solution (Richardson et al., 1960), diluted 1:20 in Aqua bidest., for approximately 40 seconds at 80° Celsius and analyzed with a Nikon Microphot – FXA microscope.

2.3. 3D Reconstruction

All semi-thin sections were digitised with a Nikon DS – Fi1 digital camera on a Nikon Microphot – FXA microscope using tenfold magnification and saved with a resolution of 2560x1920.

Consecutively image processing was performed in Photoshop CS4 and 7. The images were minimized to half their size, changed in contrast and brightness, the picture quality reduced from 12 to 8 and minimized to a resolution of 656x492. Renaming of the images was done in ACDSee 7. The 3D reconstruction was conducted with the program Amira 4.1 and 5.4.0. At first the processed and renamed images got aligned in the “Slice Aligner” of Amira using the automatic alignment tool implemented in the software. A manual correction between single sections was performed where alignment mistakes occurred. Structures were labelled in the “Image Segmentation Editor” of Amira, and the surface was subsequently generated and smoothed.

2.4. Whole mounts

The antennal articulations were investigated by creating whole mounts. Specimens were decapitated, the antennae cut off to the base and the heads fixed in 70% ethanol. For maceration of the head tissue a potassium hydroxide tablet was added and put onto a heating plate adjusted to 60°C for 60 to 90 minutes, till all the tissue was dissolved. Subsequently heads were transferred into glass bowls with 70% denatured ethanol. The embedding medium Marc Andre II was then put on an object slide with hollow grinding and each head was embedded into it. After this a cover slip was placed over the embedded head.

2.5. SEM samples

Heads were washed 3 times with 70% ethanol and then dehydrated in a series of ethanol with ascending concentration starting with 80% ethanol, then 90%, 96% and 100% absolute ethanol. The heads were put into small bottles with snap on caps and left in each alcohol stage for twenty minutes. The last step in 100% absolute ethanol was repeated three times before heads were left overnight in 100% ethanol. After an additional step in 100% absolute ethanol heads were transferred into HMDS (Hexamethyldisilazane) for 30 minutes. Then the snap on caps were opened a crack and the heads dried overnight under the exhaust hood. After the drying process they were put onto small stubs with graphite adhesive tapes and got sputter coated with gold.

2.6. Terminology of the extrinsic antennal musculature

The extrinsic antennal muscles were termed after the system of Stefan von K  ler (1963) in a slightly modified way. In figures and in the text muscles were abbreviated with a capital M for *Musculus* and a number. For example: in *Lepismachilis ysignata* there are 13 extrinsic antennal muscles abbreviated M1 to M13. This kind of abbreviation was used in all investigated species but does not imply homology between the same number among different species.

3. Results

For clarity the extrinsic musculature of the antennae is divided into musculature which originates at the head capsule or endoskeletal structures. The position of insertion on the antennomere is used to subdivide the extrinsic musculature of the antennae.

3.1. *Sminthurus viridis*

Sminthurus viridis has segmented antennae with 4 antennomeres which own all intrinsic musculature. The last antennomere is additionally annulated. The antennal articulation could not be seen in *Sminthurus viridis* but in Collembola it seems that a monocondylic ventral articulation is present in general (cf. *Tetodontophora bielanensis*, fig.3).

In *Sminthurus viridis* muscles originate at the head endoskeleton and at an endoskeletal structure that may represent the terminal branches of the tentorial trabecula.

There are 8 pairs of extrinsic antennal muscles grouped after their insertion on the first and second antennomere:

1. Muscles inserting at the ventral base of the first antennomere:

The muscle *Musculus tentorio-scapalis ventralis* (M1) originates at the lateral arm of the pseudotentorium lateral to M3 and inserts at the ventral lateral edge of the base of the antenna (fig.2).

2. Muscles with a lateral insertion:

The muscle *Musculus tentorio-scapalis lateralis* (M2) has its origin at the body of the pseudotentorium behind M4 and inserts at the posterior lateral margin of the base of the antenna (fig.1).

3. Muscles with a medial insertion:

There is a muscle *Musculus tentorio-scapalis medialis* (M3) that has its origin behind M6 and inserts at the ventral inner lateral edge of the base of the antenna (fig.2).

4. Muscles with a dorsal insertion:

The muscle *Musculus tentorio-scapalis dorsalis 1* (M4) has its origin at the lateral margin of the pseudotentorium below M6 and inserts at the dorsal (posterior) margin of the first antennomere (fig.1).

Another muscle *Musculus trabeculus-scapalis dorsalis 2* (M5) has its origin possibly at the so called terminal branches of the tentorial trabecula and inserts also at the posterior (dorsal) basal margin of the first antennomere, above M4 (fig.1).

5. Muscles with an insertion at the second antennomere:

The muscle *Musculus tentorio-pedicellaris medialis 1* (M6) originates from the middle of the lateral arm of the pseudotentorium and is running through the whole first antennomere to insert in the middle of the basal margin of the second antennomere (fig.1).

Another muscle *Musculus tentorio-pedicellaris medialis 2* (M7) has its origin behind M2 and passes through the entire length of the first antennomere to insert also in the middle of the basal margin of the second antennomere (fig.2).

The muscle *Musculus trabeculus-pedicellaris medialis 3* (M8) has its origin at an endoskeletal structure that could be the terminal branches of the tentorial trabecula and passes as well through the first antennomere to insert in the middle of the basal margin of the second antennomere (fig.2).

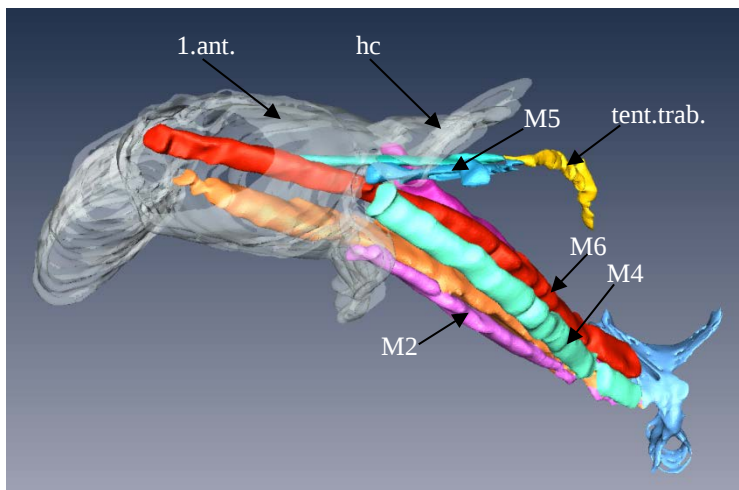


Fig. 1: Dorsal view of the left antenna of *Sminthurus viridis*, 1.ant.= 1.antennomere, hc= head capsule, tent.trab = terminal branches of tentorial trabecula

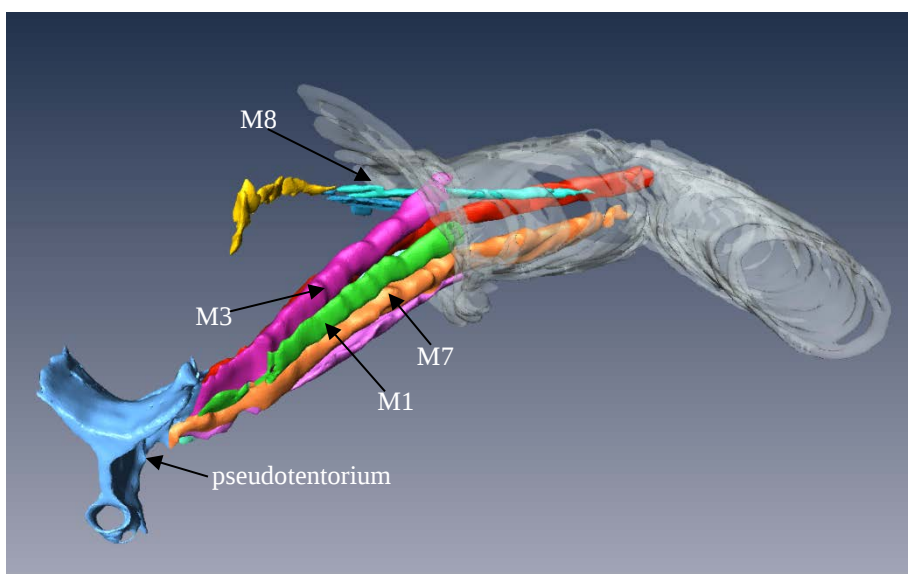


Fig. 2: Ventral view of the left antenna of *Sminthurus viridis*

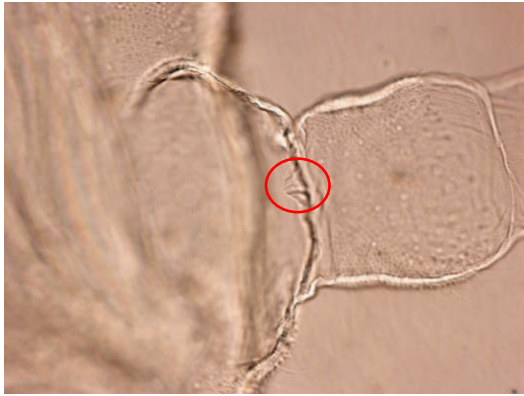


Fig. 3: Ventral antennal articulation (red circle) of *Tentrodontophora bielanensis*

3.2. *Catajapyx aquilonaris*

Catajapyx aquilonaris owns the segmented type of antennae, which is composed of several antennomeres having their own musculature. The antennal articulation could not be observed in *Catajapyx aquilonaris* and *Campodea augens* but in Diplura or at least in Japygidae the antennal articulation should be in a dorsal position (Chaudonneret, 1950).

In *Catajapyx aquilonaris* extrinsic muscles originate on the head endoskeleton and on the head capsule.

There are 8 pairs of extrinsic antennal muscles grouped after their insertion at the first and second antennomere:

1. Muscles with a lateral insertion at the first and second antennomere: three muscles insert at the first and two of them at the second antennomere.
 - a. The muscle *Musculus tentorio-scapalis lateralis 1* (M1) arises from the anterior lateral part of the endosternum and inserts at the outer lateral basal margin of the first antennomere (fig.5).
 The muscle *Musculus tentorio-scapalis lateralis 2* (M2) arises from the posterior part of the dorsal arm of the endosternum behind M8 and inserts in the same position like M1 (fig.5).
 Another muscle *Musculus tentorio-scapalis lateralis 3* (M3) arises from the middle of the dorsal arm of the endosternum partly behind M1 and inserts lateral to M2 (fig.5).
 - b. The muscle *Musculus tentorio-pedicellaris lateralis 1* (M4) has its origin at the hypopharyngeal apodeme of its side and passes through the entire length of the first

antennomere to insert at the outer lateral basal margin of the second antennomere (fig.4).

Another muscle *Musculus tentorio-pedicellaris lateralis 2* (M5) has its origin at the anterior lateral part of the endosternum between M1 and M6 and is also running through the first antennomere to insert at the outer lateral basal margin of the second antennomere like M4 (fig.5).

2. Muscles with a medial insertion:

The muscle *Musculus tentorio-scapalis medialis* (M6) has its origin at the anterior lateral part of the endosternum and inserts at the inner lateral basal margin of the first antennomere (fig.4).

3. Muscles with a dorsal insertion: two muscles insert at the dorsal base of the first antennomere. The muscle *Musculus cranio-scapalis dorsalis 1* (M7) has its origin in the middle of the side-wall of the head and inserts in the middle of the dorsal basal margin of the first antennomere (fig.4).

Furthermore the muscle *Musculus tentorio-scapalis dorsalis 2* (M8) arises from the posterior part of the dorsal arm of the endosternum and inserts behind M7 in the same position (fig.4).

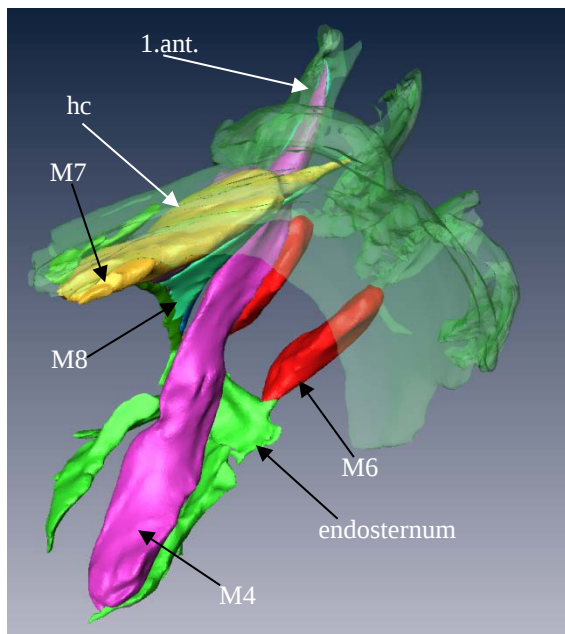


Fig. 4: Dorsal view of the left antenna of *Catajapyx aquilonaris*, 1.ant.= 1.antennomere, hc= head capsule

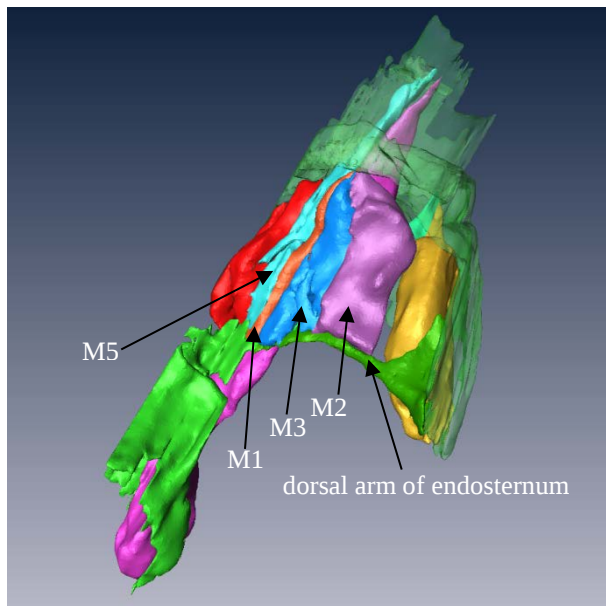


Fig. 5: Lateral view of the left antenna of *Catajapyx aquilonaris*

3.3. *Lepismachilis ysignata*

Lepismachilis ysignata owns the annulated type of antennae, where only the first two antennomeres contain muscle insertions. The first two articles are called scape and pedicel. Those two articles carry a flagellum composed of several in number varying annulated antennomeres. The monocondylic antennal articulation is found in a ventro-lateral position in *Lepismachilis ysignata* and *Machilis hrabei* (fig.8 and 9).

In *Lepismachilis ysignata* the extrinsic antennal musculature originates at the head endosekeleton.

There are 13 pairs of extrinsic antennal muscles which can be distinguished into 3 groups according to their points of insertion on the base of the scape: those with a ventral, a lateral and a dorsal insertion.

1. Muscles with a ventral insertion: all in all seven extrinsic muscles insert at the ventral base of the scape.

The muscles *Musculus tentorio-scapalis ventralis 1 and 2* (M1, M2) have their origin at the front of the anterior tentorial plate and insert at the anterior (ventral) basal margin of the scape (fig. 6 and 7).

The two muscles *Musculus tentorio-scapalis ventralis 3 and 4* (M3, M4), of very different thickness, insert also at the anterior (ventral) basal margin of the scape. They have their origin on the one hand on the middle part of the anterior tentorial plate (*Musculus tentorio-scapalis ventralis 3*) and on the other hand on the posterior part of the anterior tentorial plate (*Musculus*

tentorio-scapalis ventralis 4). Additionally, fibres of those muscles are attached to the heterolateral anterior tentorial plate. These muscles are therefore “hemichiasmatic” (fig.6). Another muscle *Musculus tentorio-scapalis ventralis* 5 (M5) inserts at the anterior (ventral) basal margin of the scapula behind the muscle M4 and has its origin at the posterior half of the anterior tentorial plate (fig.6).

The next muscle *Musculus tentorio-scapalis ventralis* 6 (M6) originates at the anterior part of the anterior tentorial plate below the muscles M1 and M2 and inserts also at the anterior (ventral) basal margin lateral to the previous muscle (fig. 6).

The following muscle *Musculus tentorio-scapalis ventralis* 7 (M7) arises from the anterior part of the anterior tentorial plate lateral to M5 and has its insertion at the anterior (ventral) basal margin below M1 and M2 (fig.6 and 7).

2. Muscles with a lateral insertion: altogether four extrinsic muscles insert at the lateral base of the scapula.

The muscle *Musculus tentorio-scapalis lateralis* 1(M8) inserts at the outer lateral basal margin of the scapula and originates at the anterior part of the anterior tentorial plate (fig.7).

Musculus tentorio-scapalis lateralis 2 (M9) inserts below the preceding and has its origin at the posterior half of the anterior tentorial plate (fig.7).

Another muscle *Musculus tentorio-scapalis lateralis* 3 (M10) has its origin in the middle of the anterior tentorial plate and inserts at the outer lateral margin below the previous muscle (fig.7).

The following muscle *Musculus tentorio-scapalis lateralis* 4 (M11) inserts above M10 and has its origin at the posterior half of the anterior tentorial plate lateral to M9 (fig.7).

3. Muscles with a dorsal insertion: all in all two extrinsic muscles insert at the dorsal base of the scapula.

The muscle *Musculus tentorio-scapalis dorsalis* 1 (M12) inserts at the posterior (dorsal) basal margin of the scapula and has its origin at the middle part of the anterior tentorial plate (fig.6 and 7).

The next muscle *Musculus tentorio-scapalis dorsalis* 2 (M13) is a very voluminous muscle with its origin at the posterior part of the anterior tentorial plate lateral to M3 and inserts in the same position like the previous muscle (fig.6 and 7).

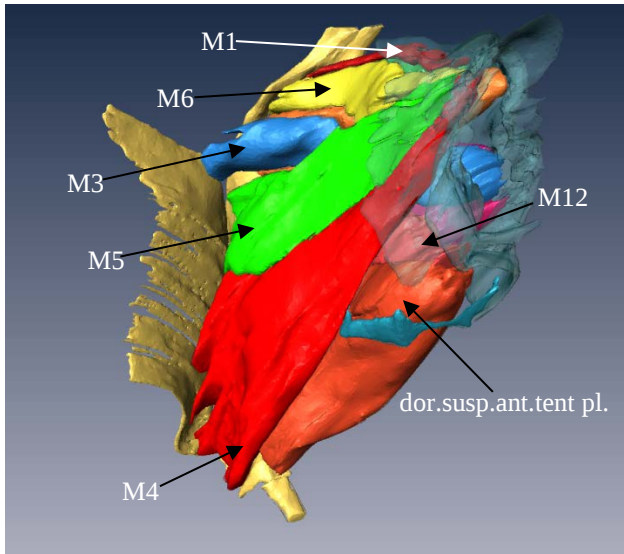


Fig. 6: Dorso-lateral view of the right antenna of *Lepismachilis ysignata*, dorsal suspensor of the anterior tentorial plate= dor.susp.ant.tent.pl.

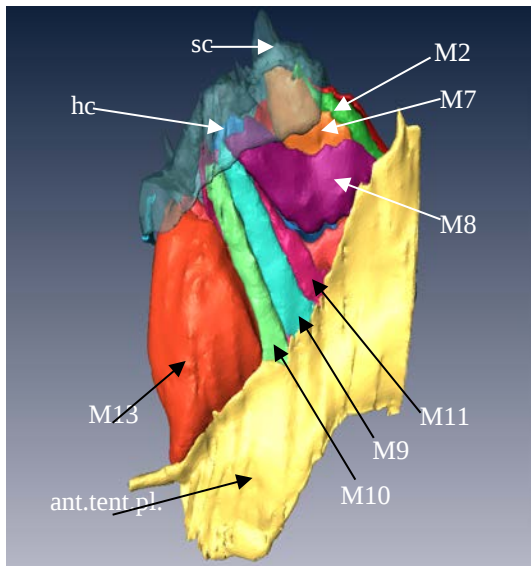


Fig. 7: Ventro-lateral view of the right antenna of *Lepismachilis ysignata*, sc= scape, hc= head capsule, anterior tentorial plate= ant.tent.pl.

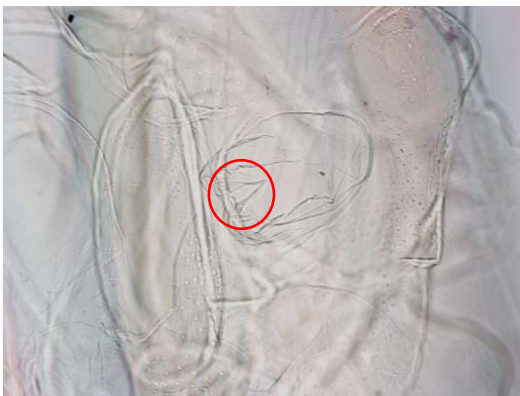


Fig. 8: Overview ventro-lateral antennal articulation (red circle) of *Machilis hrabei*



Fig. 9: Detail ventro-lateral antennal articulation (red circle) of *Machilis hrabei*

3.4. *Lepisma saccharina*

Lepisma saccharina owns also the annulated type of antennae. The first two antennomeres are called scape and pedicel. Thereupon follows a flagellum with annulated antennomeres, which has no musculature. Only the first two articles own musculature. The dicondylic antennal articulation could not be found in the investigated species of *Lepisma saccharina*, *Ctenolepisma lineata* and *Atelura formicaria*. In general a dicondylic antennal articulation should be in a dorsal and ventral position in Zygentoma. A dorsal one could be found in *Lepisma saccharina* and a ventral one in *Atelura formicaria* but not in a single individual both joints could be definitely demonstrated (fig.12 and fig.13).

In *Lepisma saccharina* the extrinsic musculature of the antennae originates on the head endoskeleton.

There are 9 pairs of extrinsic antennal muscles forming three groups regarding their insertion on the scape:

1. Muscles with a ventral insertion: there are three muscles that insert at the ventral base of the scape.

The muscle *Musculus tentorio-scapalis ventralis 1* (M1) has its origin at the outer side of the anterior arm of the anterior tentorium and inserts at the anterior (ventral) basal margin of the scape (fig.10).

The two muscles *Musculus tentorio-scapalis ventralis 2 and 3* (M2, M3) have their origin at the posterior part of the anterior tentorium and insert at the scape with the previous one (fig.10).

2. Muscles with a lateral insertion: also three muscles insert at the lateral base of the scape.

The muscle *Musculus tentorio-scapalis lateralis 1* (M4) has its origin at the anterior tentorium in a latero-anterior position to M1 and inserts at the ventral outer lateral margin of the scape (fig.11).

Two other muscles *Musculus tentorio-scapalis lateralis 2 and 3* (M5, M6) have their origin at the dorsal surface of the anterior tentorium next to M7 and insert in the same position as M4 (fig.11).

3. Muscles with a dorsal insertion: there are as well three muscles that insert at the dorsal base of the scape.

The muscle *Musculus tentorio-scapalis dorsalis 1* (M7) originates at the dorsal surface of the anterior tentorium behind M1 in a latero-posterior position and inserts at the posterior (dorsal) basal margin of the scape (fig.11).

Another muscle *Musculus tentorio-scapalis dorsalis 2* (M8) originates at the posterior end of the posterior suspensor and inserts at the posterior basal margin of the scape with the previous one (fig.10).

The following muscle *Musculus tentorio-scapalis dorsalis 3* (M9) arises from the posterior part of the anterior tentorium lateral to M2 and inserts also at the posterior (dorsal) basal margin of the scape with the previous ones (fig.10 and 11).

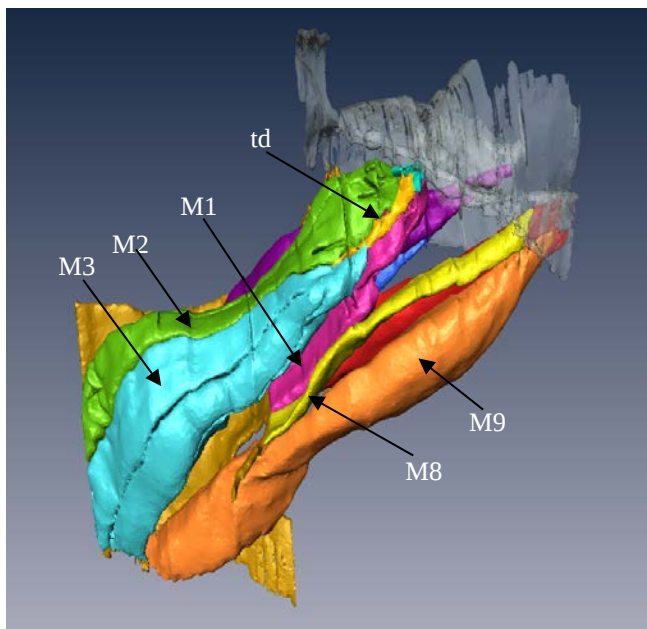


Fig. 10: Dorsal view of the right antenna of *Lepisma saccharina*, td= tendon

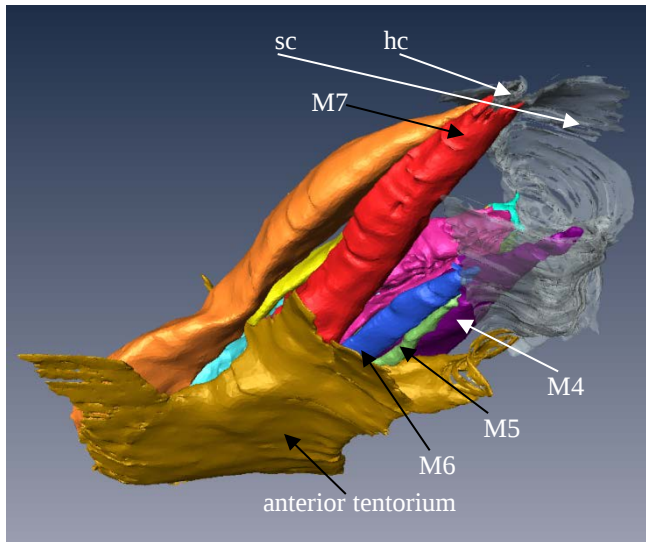


Fig. 11: Ventro-anterior view of the right antenna of *Lepisma saccharina*, sc= scape, hc= head capsule

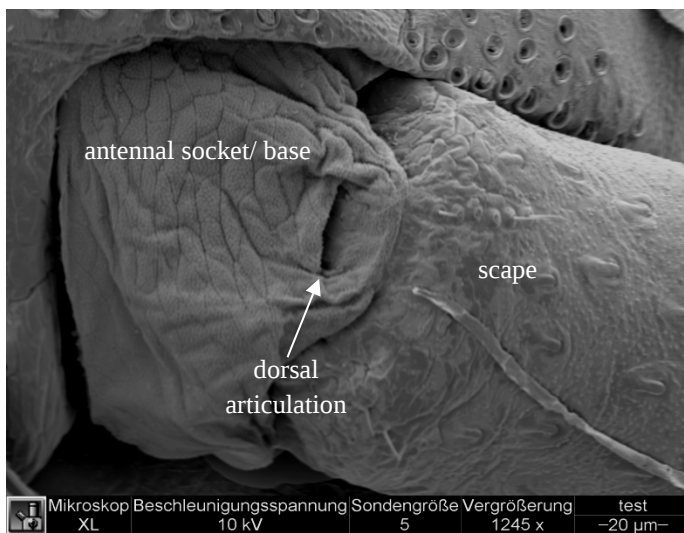


Fig.12: Dorsal articulation of the antenna of *Lepisma saccharina*

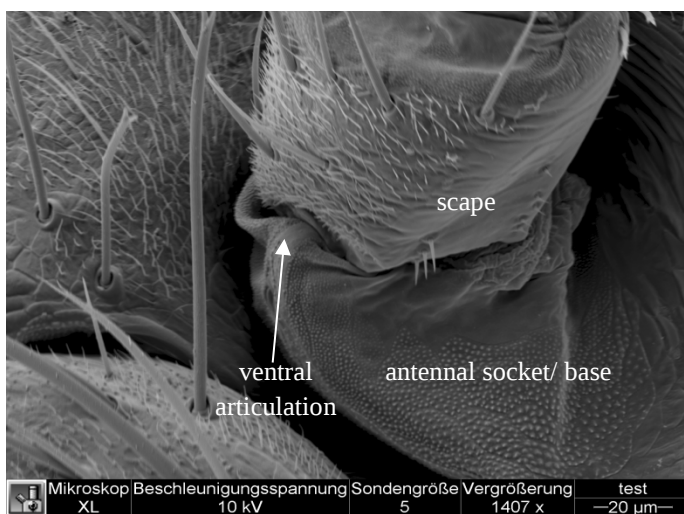


Fig.13: Ventral articulation of the antenna of *Atelura formicaria*

4. Discussion

4.1. Muscle definition and problems of homologisation

In some cases homologisation of muscles turned out to be difficult since authors differ in their assessment of what is an individual muscle. Thus it is hard to say whether a certain muscle of one author corresponds to that of a different author, or whether the latter distinguished portions of a muscle to be separate muscles. In this study a muscle is defined by being distinct from origin till insertion site from neighbouring muscles. For example in the collembolan *Anurida maritima* two muscles described in literature are assessed to correspond to a single muscle of *Sminthurus viridis*. In this case it is likely that in *A. maritima* two bundles of a single muscle were counted as two distinct muscles by Denis (1928).

An initial aim of the study was to test whether the extrinsic antennal musculature and the articulation of the first antennomere can be used as phylogenetic characters to reconstruct the earliest splits within the hexapod tree. The big differences among the investigated taxa, along with the restricted taxon sampling of the present study requires as a first step comparisons within each subgroup to determine the variation within each studied main lineage, i.e. Collembola, Diplura, Archaeognatha and Zygentoma. In the next chapters the proposed homologisations of the extrinsic muscles are summarised in comparative tables.

4.2. Extrinsic antennal musculature of Collembola

There are only a few studies until now which considered the extrinsic antennal musculature of Collembola, actually just Denis (1928) and Imms (1939). There seems to be a big variability within Collembola concerning the extrinsic antennal musculature. A comparison is hampered, since it seems questionable whether Imms actually has really seen all muscles because of the preliminary character of his study. But even within their own studies both Imms (1939) and Denis (1928) report considerable differences in the number and relationships of the extrinsic antennal muscles among different subgroups of Collembola. In Poduromorpha 8 or 5 pairs of muscles and in Entomobryomorpha 11 or 7 pairs of muscles are found. Another study conducted by Altner (1988) concerning the scolopidial organs in the first antennal segment in *Allacma fusca* (Collembola, Sminthuridae) deals with the musculature of the first antennomere. The author reports that the musculature differs strongly from the description of Imms (1939) in that it is not possible to discriminate extrinsic from intrinsic muscles.

In *S. viridis* our study revealed a total of 8 pairs of extrinsic antennal muscles. This number exactly mirrors the number of extrinsic antennal musculature described in *Anurida maritima* by Denis (1928). Like in *S. viridis* all muscles, labelled I, II, III, IV, V, VI, VII and VIII originate at the cephalic endoskeleton (Denis, 1928). Nevertheless only 6 pairs of muscles of *S. viridis* which originate at the tentorium seem to be homologous to the 8 pairs in *A. maritima* (Tab.1). Even though the origins differ in that M1 originates at the lateral arm of the pseudotentorium and VII and VIII at the medial arm of the pseudotentorium M1 may be homologous to the muscles VII and VIII of *A. maritima* because of corresponding insertions on the ventral base of the first antennomere. The two muscles of Denis (1928) are mentioned to originate in close vicinity to each other. They run parallel along their entire length to insert commonly with muscle II at the ventral antennal base. Thus they may be assessed to be two portions of the same muscle. It should be noted, however, that no subdivision could be discerned in the muscle M1 of *S. viridis*. Although M2 originates at the body of the pseudotentorium and the muscle III at the lateral arm of the pseudotentorium the muscle M2 may be homologous to the muscle III of *A. maritima* because of the comparable insertions on the posterior lateral margin of the base of the antenna. Even though the origins are not corresponding in that muscle M3 attaches to the lateral arm of the pseudotentorium and the muscle II to the side edges of the pseudotentorium the matching insertions on the ventral inner lateral edge of the base of the antenna indicate homology of the muscle M3 with the muscle II of *A. maritima*. Although again the origins differ in that muscle M4 attaches to the lateral margin of the pseudotentorium and the muscles V and VI to the lateral arm of the pseudotentorium the muscle M4 may be homologous to the muscles V and VI since both muscles insert at the dorsal margin of the first antennomere. The origins of the two other muscles are also different in that muscle M6 originates at the lateral arm of the pseudotentorium and muscle I at the lateral edges of the pseudotentorium. Despite that the muscle M6 seems to be homologous to the muscle I of *A. maritima*, even though M6 inserts at the second antennomere and the muscle I is mentioned to just penetrate the antenna. The same applies for muscle M7 that may be homologous to muscle IV, although again there is only mentioned that the muscle IV enters the antenna and not where it inserts. But since those two muscles are the only ones that pass into the antenna they are thought to be homologous to the muscles M6 and M7 of *S. viridis*.

Tab.1: proposed homologisation of extrinsic musculature within Collembola

Present study	Denis (1928)	Denis (1928)	Denis (1928)	Imms (1939)	correspondences
<i>Sminthurus viridis</i>	<i>Anurida maritima</i>	<i>Onychiurus fimetarius</i>	<i>Tomocerus catalanus</i>	<i>Orchesella villosa</i>	
M1	VII and VIII	VII and VIII	ventral group X, V, VII, IX?	group II f, g, e, h?	insert at ventral lateral edge of the base of the antenna
M2	III	III	VI	?	insert at posterior lateral margin of the base of the antenna
M3	II	?	?	?	insert at ventral inner lateral edge of the base of the antenna
M4	V and VI	V and VI	dorsal group Y, I, II, VIII?	group I dorsal muscles a, b, c, d?	insert at dorsal margin of the first antennomere
M5	?	?	?	Extensor of antenna?	originate at the terminal branches of the tentorial trabecula or medio-dorsal apodeme formed by extensions of the tentorium?
M6	I	I	lateral group III	?	insert at basal margin of the second antennomere
M7	IV	I	lateral group IV	?	insert at basal margin of the second antennomere
M8	?	?	?	?	

In *A. maritima* Denis (1928) grouped muscles according to their origin. A comparison of origins shows little correspondences between *S. viridis* and *A. maritima*, in that the muscles of *S. viridis* originate at different positions on the pseudotentorium in comparison to the muscles of *A. maritima*, whereas the insertions are comparable between these two species. Therefore the above mentioned homologisations are based on the comparison of the insertions alone, leaving the hypotheses somewhat ambiguous. In addition there is a difference concerning the tentorium of *S. viridis* and *A. maritima*. In *A. maritima* a medial arm of the tentorium is present which could not be recognised in *S.*

viridis. The corresponding muscles in *S. viridis* originate either at the body of the pseudotentorium or lateral arm of the pseudotentorium.

In two cases two muscles of *A. maritima* are homologised with a single muscle in *S. viridis*. This can be explained by either a reduction of muscles in Symphypleona, or by the already mentioned problem that two muscles in *A. maritima* may be interpreted as portions or bundles of a single muscle. The muscles M6, M7 and M8 of *S. viridis* are running through the entire length of the first antennomere to insert at the basal margin of the second antennomere. Two such muscles with their origin at the tentorium are also present in *A. maritima* called I and IV but it is only said that they penetrate the antenna without mentioning where they insert (Denis, 1928).

Further there are two muscles in *S. viridis* which do not have their origin on the pseudotentorium or tentorial arms. They have their origin on an endoskeletal structure that could be the terminal branches of the tentorial trabecula (dorsal region of the head). Those muscles are named M5 and M8. Although the terminal branches of the tentorial trabecula of *A. maritima* are described and also muscles originate there not one of them is mentioned in particular. In *A. maritima* those muscles form a large bundle on each side of the head and are directed laterally to the cavity of the antenna in which they enter (Denis, 1928). Judging from this description only the muscle M8 of *S. viridis* is comparable to those muscles with their origin on the terminal branches of the tentorial trabecula since muscle M5 does not enter the antenna but instead inserts at the base of the first antennomere.

In *Onychiurus fimetarius* Denis (1928) mentioned 5 pairs of extrinsic antennal muscles. Those are labelled III, V, VI, VII and VIII. All of them have their origin at the ‘corne anterieure du tentorium’ and their insertions are either at the dorso-lateral, dorsal or ventro-lateral base of the antenna. There is a muscle I that enters the antenna and originates at the outside of the lateral arm of the tentorium (Denis, 1928). A comparison of the muscles of *S. viridis* and *O. fimetarius* is based on the insertions of the muscles, since the origins in *O. fimetarius* and *S. viridis* on the pseudotentorium are quite different compared to each other. In *O. fimetarius* all muscles except muscle I originate at the ‘corne anterieure du tentorium’, a structure not recognised in *S. viridis*. The muscles of *S. viridis* originate either at the body or at the lateral arm of the pseudotentorium. The following 4 pairs of muscles of *S. viridis* may be homologised to muscles of *O. fimetarius* (Tab.1). The muscle M1 is potentially homologous to the muscles VII and VIII of *O. fimetarius* because of corresponding insertions on the ventral lateral edge of the base of the antenna. The next muscle M2 could be homologous to the muscle III because of their matching insertions at the posterior lateral margin of the base of the antenna. According to their corresponding insertions at the dorsal (posterior) margin of the first antennomere the muscle M4 may be homologised to the muscles V and VI. The muscles M6 or M7 with origin at the tentorium and insertion at the second antennomere both may be homologous to the muscle I even though Denis (1928) just mentions that the muscle I penetrates the antenna and not where it inserts. Additionally

Denis (1928) considers the muscle I of *O. fimetarius* to be homologous to the muscle I of *A. maritima* and therefore M6 seems to be the most probable homolog to the muscle I of *O. fimetarius*.

For the muscles M1 and M4 applies the same as in *A. maritima* and therefore the same explanations as already mentioned above. In *O. fimetarius* only the muscle I is described to penetrate the antenna in comparison to *S. viridis* where three muscles pass through the first antennomere to insert at the base of the second antennomere. In *O. fimetarius* the terminal branches of the tentorial trabecula are not mentioned in the text as a site of origin of extrinsic muscles. But similar muscles with origin at the terminal branches of the tentorial trabecula are figured by Denis (1928) and therefore the muscle M8 of *S. viridis* seems to be comparable with those of *O. fimetarius*.

In *Tomocerus catalanus* 11 pairs of extrinsic antennal muscles are described (Denis, 1928). Those are classified into 3 groups a ventral composed of the muscles X, V, VII, IX, a dorsal with the muscles Y, I, II, VIII, a lateral composed of the muscles III, IV and a muscle called VI inserted at the dorso-lateral limit of the base of the antenna. Concerning the origins of the ventral and dorsal group it is not mentioned where they start from, the lateral originates from the lateral face of the tentorial body and the muscle VI arises at the level where the medial anterior arm leaves the tentorial body (Denis, 1928). The muscles of *S. viridis* and *T. catalanus* are compared based on their insertions because of very different origins on the tentorium. The following muscles of *S. viridis* may be homologous to those of *T. catalanus* (Tab.1). The origins of the ventral and dorsal group could not be compared with origins of the muscles of *S. viridis* since it is not mentioned where they are attached to. Therefore M1 may be homologous to the ventral group X, V, VII and IX of *T. catalanus* because of matching insertions on the ventral lateral edge of the antenna. Although the muscle M2 originates at the body of the pseudotentorium and the muscle VI at the level where the medial anterior arm leaves the tentorial body M2 may be homologised to the muscle VI due to their insertions on the posterior lateral margin of the base of the antenna. M4 may be homologous to the dorsal group Y, I, II, VIII based on the corresponding insertion at the dorsal (posterior) margin of the first antennomere. The muscle M6 attaches to the lateral arm of the pseudotentorium and M7 to the body of the pseudotentorium in contrast to the lateral group of *T. catalanus* which originates from the lateral face of the tentorial body. Despite this the muscles M6 and M7 that pass through the first antennomere and insert at the base of the second antennomere could be homologous to the lateral group III and IV, respectively although it is not mentioned where they insert just that they pass directly into the first antennomere.

The correspondences concerning the ventral and dorsal group seem not that convincing since the ventral and dorsal group of *T. catalanus* are composed of 4 muscles and those of *S. viridis* only of one muscle. This could be related to a reduction from 4 to 1 muscle, which seems not very probable. The muscles of the lateral group of *T. catalanus* also pass through the first antennomere like the two muscles M6 and M7 of *S. viridis*. A third one with origin at the terminal branches of the tentorial trabecula like in *S. viridis* is not mentioned in *T. catalanus*.

In *T. catalanus* muscles have their origin at the terminal branches of the tentorial trabecula (dorsal region of the head) but there is nothing particular to say about those dorsal muscles. Their group is homologous to those of other Collembola (Denis, 1928). Judging from this description only the muscle M8 of *S. viridis* is comparable to those muscles with their origin at the terminal branches of the tentorial trabecula since muscle M5 does not enter the antenna but instead inserts at the base of the first antennomere.

Denis (1928) did not attempt a comparison of the extrinsic antennal muscles of *T. catalanus* with those of the studied Poduromorphes *A. maritima* and *O. fimentarius*. Denis (1928) just states what is special about the antennal musculature of *T. catalanus*.

In *Orchesella villosa* 7 pairs of extrinsic antennal muscles are present (Imms, 1939). Those are divided into two main groups a dorsal and ventral one. Group I encompasses the dorsal muscles called a, b, c, d and group II is chiefly composed of a depressor of the antenna, separated into a dorsal and a ventral component called f and g. There are two more muscles belonging to group II called e and h. Another muscle called Extensor of the antenna is mentioned but not belonging to any of these two groups (Imms, 1939). The muscles of group I and group II of Imms correspond with the muscles of group II and group I of Denis in *T. catalanus*, respectively (Imms, 1939). The muscles of *S. viridis* are compared with *O. villosa* based on their insertions since the origins are too different from each other. The following muscles of *S. viridis* may be homologous to those of *O. villosa* (Tab.1). M1 could be homologous to group II f, g, e, h due to their insertions on the ventral lateral edge of the antenna. The same applies for the muscle M4, which may be homologised to group I the dorsal muscles a, b, c, d because of the corresponding insertion on the dorsal (posterior) margin of the first antennomere. Those correspondences seem not that convincing since the dorsal and ventral group of *O. villosa* are composed of 3 and 4 muscles, respectively, which is also the case in *T. catalanus* and those of *S. viridis* only of a single muscle, which may be explained by a unlikely reduction of muscles from 4 to 1. The extensor muscle of *O. villosa* may be comparable with muscle M5 of *S. viridis* since the origins are corresponding in that the extensor muscle originates on a medio-dorsal apodeme formed by extensions of the tentorium and muscle M5 at the terminal branches of the tentorial trabecula. This time the insertions are not corresponding. The extensor muscle inserts at the ventral border of the first antennomere close to the origin of the depressor of segment II in contrast to the muscle M5 which inserts at the posterior (dorsal) basal margin of the first antennomere.

There are no muscles reported by Imms (1939) to pass through the first antennomere like in *S. viridis* and the other three described species.

In summary it seems easier to compare *S. viridis* with *A. maritima* and *O. fimentarius*, both representatives of Poduromorpha, than with the entomobryomorph species *T. catalanus* and *O. villosa*. In the studies used for comparison just the extrinsic antennal musculature with tentorial origin were described, while those that originate at the dorsal region of the head or terminal branches of the

tentorial trabecula are mentioned but not described in detail. A comparison with such muscles in *S. viridis* is therefore reliable only to a limited extent. Since the origin at the tentorium likewise seems to have readily changed during evolution even the latter homologisations remain ambiguous. This high variability in origin demands for homology hypotheses mainly based on insertions, which is usually handled this way. Most of the head muscles are designed to serve the cephalic limbs and their insertions did not change at all or just a little. The origins however change several times very significantly in connection with the intensification, extensification or change of function. A change of origin from head capsule to the tentorium or vice versa is not unusual (von K  ler, 1963).

4.3. Extrinsic antennal musculature of Diplura

There is little described concerning the extrinsic antennal musculature of Diplura. Only one study of Imms (1939) deals explicitly with representatives of Diplura, one japygid *Japyx* sp. and one campodeid *Campodea lubbocki*, respectively. In the japygid species 4 pairs of muscles and in the campodeid species 5 pairs of muscles are found which are named after their function. In total 8 pairs of extrinsic antennal muscles are found in *C. aquilonaris*. Those are compared with *Japyx* sp. and *C. lubbocki* described by Imms (1939).

Homologisation seems to be reasonable in 4 pairs of muscles of *C. aquilonaris* when compared to the data of Imms (1939) (Tab.2). M1 may be homologous to Imms' flexor of *Japyx* sp. because of corresponding insertions on the outer lateral basal margin of the first antennomere in close vicinity to the origin of the flexor of the second antennomere. No such muscle is mentioned in *C. lubbocki*, which however possesses the flexor of the second antennomere. In M4 both origin and insertion correspond to Imms' long flexor of segment 2 of *Japyx* sp.. Both muscles have their origin at the hypopharyngeal apodeme and insert at the outer lateral basal margin of the second antennomere at the same location like the flexor of the second antennomere. In *C. lubbocki* the insertion corresponds to that of M4 but the origin is different in that Imms' long flexor of segment 2 attaches to the transverse bar of the tentorium and not to the hypopharyngeal apodeme. M6 can be homologised with the extensor because of corresponding insertions at the inner lateral basal margin of the first antennomere. M7 corresponds in origin and insertion with the levator in *Japyx* sp.. Both originate in the middle of the cephalic side-wall and insert in the middle of the dorsal basal margin of the first antennomere. In *C. lubbocki* the internal levator seems most likely to be homologous to M7, while the external levator seems to have no corresponding muscle in japygids.

Tab.2: proposed homologisation of extrinsic musculature within Diplura

Present study	Imms (1939)	Imms (1939)	correspondences
<i>C.aquilonaris</i>	<i>Japyx</i> sp.	<i>C.lubbocki</i>	
M1	Flexor		insert at outer lateral basal margin of the first antennomere
M2	?	?	
M3	?	?	
M4	Long Flexor of Segment 2	Long Flexor of Segment 2	originate at hypopharygeal apodeme (<i>Japyx</i> sp.), insert at outer lateral basal margin of the second antennomere (<i>Japyx</i> sp. and <i>C. lubbocki</i>)
M5	?	?	
M6	Extensor	Extensor	insert at inner lateral basal margin of the first antennomere
M7	Levator	Internal Levator	originate in the middle of the side-wall of the head (<i>Japyx</i> sp.), insert at middle of the dorsal basal margin of the first antennomere (<i>Japyx</i> sp. and <i>C. lubbocki</i>)
M8	?	?	
?		External levator	
?		Depressor of the antenna	

In *C. aquilonaris* two muscles M4 and M5 are running through the entire length of the first antennomere to insert at the outer lateral margin of the second antennomere. M4 originates at the hypopharygeal apodeme of the opposite side, such that the muscles of the two sides form a chiasma. This muscle is also described by Imms (1939) and termed there Long Flexor of Segment 2, but not mentioned to be a chiasmatic muscle. No second muscle is mentioned by Imms (1939) to insert at the base of the second antennomere. In *C. aquilonaris* the muscular nature of M5 could be confirmed solely on one side. In *Campodea augens* (Campodaeidae) also two extrinsic muscles were observed to insert at the base of the second antennomere (fig.14, unpublished data). Additionally 4 muscles are discovered in *C. aquilonaris* which are not described in *Japyx* sp.. Those muscles are M2, M3 M5 and M8. Maybe the methods applied by Imms did not allow to discern all, or several muscles have been assessed to represent a single muscle.

With the exception of the levator muscle which originates in the middle of the cephalic side wall all other muscles of *Japyx* sp. have their origin at the hypopharygeal apodeme (Imms, 1939). This is not

the case concerning the muscles of *C. aquilonaris*. Only the origins of the muscles entitled levator and Imms' long flexor of segment 2 are congruent with those of the muscles M7 and M4. All other muscles of *C. aquilonaris* originate at the dorsal arm of the endosternum or at the endosternum itself. The muscles external levator and depressor of *C. lubbocki* are not comparable with any of the muscles of *C. aquilonaris*.

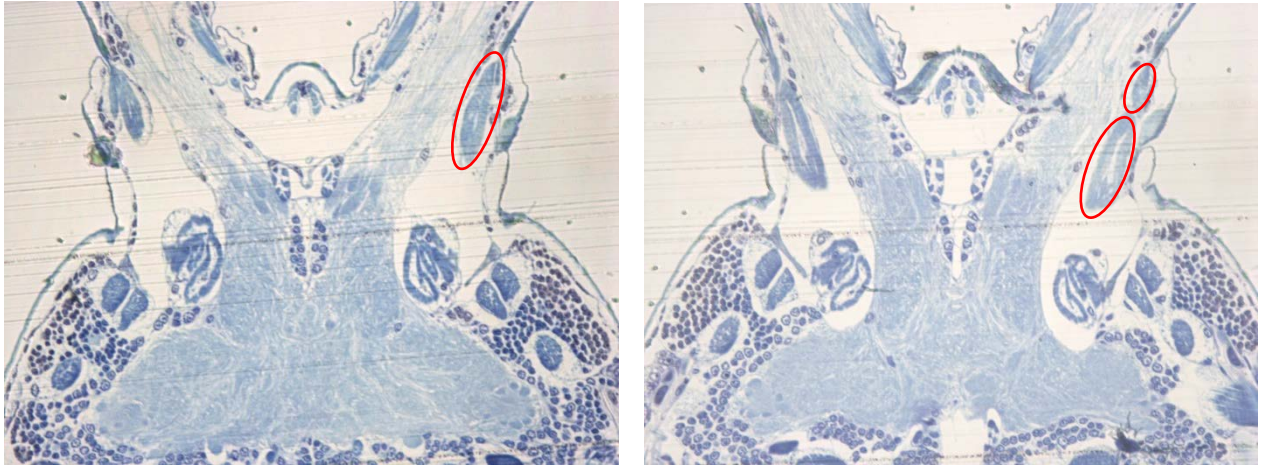


Fig. 14: semi-thin sections of the antennae of *Campodea augens*, showing two muscles inserting at the outer lateral basal margin of the second antennomere (red circle)

4.4. Extrinsic antennal musculature of Archaeognatha

At present there is not much information available concerning the extrinsic antennal musculature of Archaeognatha. There is only the study of Bitsch (1963) that reports 9 extrinsic muscles to be present in *Lepismachilis ysignata*, *Petrobius brevistylis*, *Machilis burgundiae* and *Dilta denisi* whereupon Bitsch just described the extrinsic muscles in detail for the species *L. ysignata* but added that in general the same applies for the other examined species.

The 13 pairs of extrinsic antennal muscles reported from *L. ysignata* by the present study contrast with only 9 pairs of extrinsic antennal muscles mentioned for the same species by Bitsch (1963). Bitsch (1963) labelled his muscles mds1, mds2, mds3, mds4 (depressor muscles), mfs1, mfs2, mfs3 (flexor muscles), and mls1 and mls2 (levator muscles). The following 8 pairs of muscles are in all probability homologous to the muscles described by Bitsch (1963) (Tab.3). M1 and M2 are homologised with mds1 and mds2 because of the corresponding origin at the front of the anterior tentorial plate and insertion at the anterior (ventral) basal margin of the scape. M3 and M4 are homologous to the muscles mds3 and mds4 due to the origin on the middle part of the anterior tentorial plate and posterior part of the anterior tentorial plate, respectively. All insert at the anterior (ventral) basal margin of the scape. M8 may be homologous to the muscles mfs1 and mfs2 because of the origin at

the anterior part of the anterior tentorial plate and the insertion at the outer lateral basal margin of the scape. M9 corresponds both in its origin on the posterior half of the anterior tentorial plate, and its insertion below muscle M8, to mfs3. M12 is homologous to mls1 since sharing corresponding origins on the middle part of the anterior tentorial plate and the insertion at the posterior (dorsal) basal margin. M13 corresponds to mls2 by originating at the posterior part of the anterior tentorial plate and inserting commonly with M12 or mls1, respectively.

Tab.3: proposed homologisation of extrinsic musculature within Archaeognatha

Present study	Bitsch (1963)	correspondences
<i>L. ysignata</i>	<i>L. ysignata</i> , <i>Petrobius brevistylis</i> , <i>Machilis burgundiae</i> , <i>Dilta denisi</i>	
M1	mds1	originate at the front of the anterior tentorial plate, insert at anterior (ventral) basal margin of the scape
M2	mds2	originate at the front of the anterior tentorial plate, insert at anterior (ventral) basal margin of the scape
M3	mds3	originate on the middle part of the anterior tentorial plate, insert at the anterior (ventral) basal margin of the scape
M4	mds4	originate on the middle part of the anterior tentorial plate, insert at the anterior (ventral) basal margin of the scape
M5	?	
M6	?	
M7	?	
M8	mfs1 and mfs2	originate at anterior part of the anterior tentorial plate, insert at the outer lateral basal margin of the scape
M9	mfs3	originate at posterior half of the anterior tentorial plate, insert below muscle M8 at the outer lateral basal margin of the scape
M10	?	
M11	?	
M12	mls1	originate on the middle part of the anterior tentorial plate, insert at posterior (dorsal) basal margin
M13	mls2	originate on the posterior part of the anterior tentorial plate, insert in the same place as M12

Bitsch (1963) mentioned two muscles to originate at the anterior part of the anterior tentorial plate and insert to the outer lateral basal margin of the scape. In this study we described a single muscle (M8) with corresponding attachment sites, which however is build up of two distinct portions. There is also a slight difference in the position of insertions of the muscles M3 and M4 compared to the muscles

mds3 and mds4, but since only fibres of these two muscles attach to the heterolateral anterior tentorial plate it is assumed that they correspond to the muscles mds3 and mds4 of Bitsch (1963). The remaining 5 pairs of reconstructed muscles: M5, M6, M7, M10 and M11 are not described by Bitsch (1963). Either these muscles were not recognised by the author due to their slenderness, or not perceived as separate muscles but merged with other muscles.

4.5. Extrinsic antennal musculature of *Zygentoma*

There is not much described regarding the extrinsic antennal musculature of *Zygentoma*. A study of Chaudonneret (1950) deals with the extrinsic antennal muscles of *Thermobia domestica*. There 7 pairs of muscles are discovered and form two groups the protractors and retractors.

9 pairs of extrinsic antennal muscles described in the present study for *L. saccharina* contrast to the 7 pairs of muscles mentioned for *T. domestica* and labelled pas (Muscle protracteur antérieur du scape), pps (Muscle protracteur postérieur du scape), ras (Muscle retractor antérieur du scape), rms (Muscle retractor moyen du scape), rps (Muscle retractor postérieur du scape), ravs (Muscle retractor accessoire ventral du scape) and rads (Muscle retractor accessoire dorsal du scape) (Chaudonneret, 1950). A comparison allows to homologise 7 pairs of muscles nearly unambiguously (Tab.4). M1 is homologous to pas (Muscle protracteur antérieur du scape) because of matching attachment sites on the outer side of the anterior arm of the anterior tentorium and anterior (ventral) basal margin of the scape. M2 and M3 are homologised to the muscle pps (Muscle protracteur postérieur du scape) due to corresponding attachment sites on the posterior part of the anterior tentorium and anterior (ventral) basal margin of the scape with the previous muscle. M4 may be a homolog to ravs (Muscle retractor accessoire ventral du scape) by sharing the origin at the anterior tentorium in a latero-anterior position to M1 and insertion at the ventral outer lateral margin of the scape. M7 is homologous to ras (Muscle retractor antérieur du scape) because of corresponding origins at the dorsal surface of the anterior tentorium behind M1 in a latero-posterior position and insertion at the posterior (dorsal) basal margin of the scape. M8 is homologous to rms (Muscle retractor moyen du scape) due to matching origins at the posterior end of the posterior suspensor, and insertions at the posterior basal margin of the scape commonly with M7 (ras). M9 is homologous to rps (Muscle retractor postérieur du scape) because of corresponding origins at the posterior part of the anterior tentorium lateral to M2 and their common insertion at the posterior (dorsal) basal margin of the scape together with M7 and M8.

Tab.4: proposed homologisation of extrinsic musculature within Zygentoma

Present study	Chaudonneret (1950)	correspondences
<i>L. saccharina</i>	<i>T. domestica</i>	
M1	pas	originate at outer side of the anterior arm of the anterior tentorium, insert at anterior (ventral) basal margin of the scape
M2, M3	pps	originate at posterior part of the anterior tentorium, insert at anterior (ventral) basal margin of the scape
M4	ravs	originate at anterior tentorium in a latero-anterior position to M1, insert at ventral outer lateral margin of the scape
M5	rads?	
M6	rads?	
M7	ras	originate at dorsal surface of the anterior tentorium behind M1 in a latero-posterior position, insert at the posterior (dorsal) basal margin of the scape
M8	rms	originate at posterior end of the posterior suspensor, insert at posterior basal margin of the scape
M9	rps	originate at posterior part of the anterior tentorium lateral to M2, insert at posterior (dorsal) basal margin of the scape with M7 and M8
?	rads	

The muscle pps is mentioned as a single muscle by Chaudonneret (1950) in *T. domestica* but homologised with two muscles M2 and M3 of *L. saccharina*. The latter can also be judged as two distinct portions of a single muscle as in *T. domestica* since in close vicinity to each other over their entire length.

The insertion of the muscle ravs (Muscle retracteur accessoire ventral du scape) in *T. domestica* and M4 in *L. saccharina* are slightly differing from each other. In addition the description of that muscle in *T. domestica* deviates from the muscle in *L. saccharina*. In *T. domestica* ravs originates next to the muscle pas, latero-anterior to him and its insertion on the ventral edge of the scape, just behind the ventral articulation of the antenna (Chaudonneret, 1950). The corresponding muscle M4 in *L. saccharina* does not fit that description completely. A really big difference concerns the thickness of those two muscles. In *T. domestica* it is a very thin muscle with a clear striation on its proximal half while its distal portion is tendinous and even chitinous (Chaudonneret, 1950) compared to the muscle in *L. saccharina* which is not that thin and does not show the other mentioned characteristics. Therefore it's not certain that those two muscles are homologous to each other.

Another muscle described in *T. domestica* called rads (Muscle retracteur accessoire dorsal du scape) is “missing” in *L. saccharina* whereas in *L. saccharina* two muscles M5 and M6 are found, which lack in *T. domestica*. These muscles were either not recognised as separate muscles, or merged with other muscles, or were not recognised as muscles at all. Alternatively M5 and M6 were merged by Chaudonneret (1950) and homologous to the muscle rads of *T. domestica*. This explanation, however, seems very unlikely. While the muscles correspond in their origin, the insertion of M5 and M6 differs from rads in that M5 and M6 insert at the ventral outer lateral margin of the scape in contrast to the insertion of rads at the dorsal margin of the scape, just behind the dorsal articulation of the antenna. Additionally rads is described as more slender than ravs, and to be constituted by a single narrow fiber. While M5 and M6 are also slender muscles they are not composed of only a single fibre.

4.6. Comparison of extrinsic antennal musculature among primarily wingless insects and outgroup comparison

A comparison among extrinsic antennal muscles of Collembola, Diplura, Archaeognatha and Zygentoma is hampered by (i) big differences in the number of muscles, (ii) problems concerning homologisation of the head endoskeletons, and (iii) problematic comparisons regarding insertion sites. Some remarkable points can nonetheless be concluded (1) Only Collembola and Diplura possess muscles that do not solely originate at the respective tentoria, but at the terminal branches of the tentorial trabecula (dorsal region of the head) or the head capsule, respectively. This circumstance needs to be treated with caution since the terminal branches of the tentorial trabecula in Collembola are also interpreted as a part of the tentorium (Denis, 1928). (2) Only in Collembola and Diplura extrinsic muscles insert at the second antennomere. In Archaeognatha and Zygentoma all muscles originate on the anterior tentorium and anterior tentorial plate, respectively, and insert at the base of the scape. Another interesting point can be mentioned concerning the muscles of Archaeognatha. Only in archaeognathans muscles are build up of fibres where some originate at the homolateral, others on the heterolateral anterior tentorium. This may be a putative synapomorphy which supports the monophyly of Archaeognatha. On the other hand, likewise in Diplura a whole muscle originates at the heterolateral cephalic endoskeleton, so interpretations have to be taken with care.

Since in Collembola and Diplura muscles insert at the second antennomere this character cannot be used as a synapomorphy to support the monophyly of Diplura. Whether this state is plesiomorphic or apomorphic should become apparent by an outgroup comparison.

Since a few years a close relationship between Crustacea and Hexapoda forming a clade called Pancrustacea (Zrzáý & Stys, 1997) or Tetraconata (Dohle, 2001) is suggested by molecular studies (Turbeville et al., 1991; Ballard et al., 1992; Friedrich and Tautz, 1995 and 2001; Shultz & Regier, 2000; Giribet et al., 2001; Hwang et al., 2001; Regier and Shultz, 2001; Nardi et al., 2003; Carapelli et

al., 2007) but is also supported by morphological character complexes (Averof & Akam, 1995; Osorio et al., 1995; Whittington, 1995; Dohle, 2001; Richter, 2002; Strausfeld & Andrew, 2011). Most authors assume that crustaceans are paraphyletic and Hexapoda are sister group of a crustacean subgroup. Which subgroup of Crustacea is forming the sister group to the Hexapoda is still uncertain.

Based on the outgroup comparison the polarisation of characters pertaining to the extrinsic antennal musculature are ambiguous. Different groups of Crustacea are suggested as the sister group to the Hexapoda by molecular and morphological studies. Molecular studies suggest: Branchiopoda (Regier and Shultz 1997; Regier et al., 2005; Mallatt and Giribet, 2006; Timmermans et al., 2008), Copepoda or Branchiopoda (Mallatt et al., 2004, Mallatt and Giribet, 2006; von Reumont et al., 2009), a clade of Remipedia and Cephalocarida (Regier et al., 2008), Remipedia (Ertas et al., 2009; Regier et al., 2010; von Reumont et al., 2012), Malacostraca + Branchiopoda (Cook et al., 2005). Groups proposed by morphological studies contain: Malacostraca (Harzsch, 2002; Sinakevitch et al., 2003), Branchiopoda (Schram and Koenemann, 2004) or Remipedia and Malacostraca (Fanenbruck et al., 2004; Fanenbruck and Harzsch, 2005; Harzsch, 2006; Strausfeld, 2009). Dependent on which of these taxa is chosen as outgroup, an extrinsic muscle inserting to the second antennomere might be both plesiomorphic and apomorphic. Generally little data is available concerning the extrinsic antennal musculature of Crustacea. In Boxshall (2004) the remipede crustacean *Speleonectes tulumensis* is figured with a muscle that seems to extend into the second antennomere. No reference is given in the text concerning this muscle. If extrinsic antennal muscles insert at the second antennomere in all Remipedia, Collembola and Diplura this would argue for a plesiomorphic condition. At the same time the absence of such a muscle would be an apomorphic condition supporting monophyly of Ectognatha.

On the other hand it cannot be ruled out at present stand that the evolution of such a muscle is a synapomorphy of Entognatha, however with a remaining ambiguity due to the lack of antenna in Protura. Hence, no definite conclusion can be drawn regarding that character. Further investigations concerning the extrinsic antennal muscles of Crustacea would be an interesting issue and useful in helping to determine the polarisation of this character.

The applied methods unfortunately did not allow to analyse antennal articulations in all subgroups of primarily wingless insects. Chaudonneret (1950) mentioned that Zygentoma are the only group of primarily wingless hexapods possessing a dicondylic antennal articulation between scape and head capsule. In this study it was possible to visualise a dorsal articulation in *L. saccharina* and a ventral one in *A. formicaria*, but unfortunately it was not possible, with neither SEM nor light microscopy, to observe both articulations in the same individual of the same species. In the remaining groups a monocondylic articulation is reported but in different positions. The dicondylic articulation has been assumed as the plesiomorphic condition for hexapods by Chaudonneret (1950). This seems to be a highly unparsimonious hypothesis. It would demand for multiple independent losses, with only Zygentoma retaining the plesiomorphic condition. It seems more plausible that a monocondylic

articulation is plesiomorphic and the dicondylic joint an apomorphy of Zygentoma. Since the dicondylic articulation could not be confirmed clearly in any zygentoman specimen it is not possible to draw conclusions concerning the antennal articulation. Nevertheless it would be a potentially interesting character for further investigations using different methods and could be a continuative exciting issue.

5. References

- Altner, H. (1988). The scolopidial organs in the first antennal segment in *Allacma fusca* (Collembola, Sminthuridae). *Zoomorphology* 108: 173-181.
- Averof, M., Akam, M. (1995). Insect-crustacean relationships: insights from comparative developmental and molecular studies. *Philosophical Transactions of the Royal Society B* 256: 183-235.
- Bäcker, H., Fanenbruck, M., Wägele, J.W. (2008). A forgotten homology supporting the monophyly of Tracheata: the subcoxa of insects and myriapods re-visited. *Zoologischer Anzeiger* 247:185-207.
- Ballard, J. W., Olsen, G. J., Faith, D. P., Odgers, W. A., Rowell, D. M. and Atkinson, P. W. (1992). Evidence from 12S ribosomal RNA sequences that onychophorans are modified arthropods. *Science* 258: 1345–1348.
- Bareth, C., Conde, B. and Pages, J. (1989). Les procampodeides, des diploures peu connus. in 3rd International Seminar on Apterygotes (Ed. R. Dallai). University of Sienna. pp. 137-144.
- Bitsch, J. (1963). Morphologie céphalique des Machilides (Insecta, Thysanura). *Annales des Sciences Naturelles Zoologie et Biologie Animale* 5:501-706.
- Böck, P. (1989). *Romeis Mikroskopische Technik*. 17th edn. Urban und Schwarzenberg. München.
- Bitsch, C., Bitsch, J. (1998). Internal anatomy and phylogenetic relationships among apterygote insect clades (Hexapoda). *Annales de la Société Entomologique de France* 34: 339–363.
- Boudreaux, H.B. (1979). *Arthropod Phylogeny: with Special Reference to Insects*. John Wiley and Sons. New York.
- Boxshall, G.A. (2004). The evolution of arthropod limbs. *Biological Reviews* 79: 253-300.
- Carapelli, A., Nardi, F., Dallai, R., Frati, F. (2006). A review of molecular data for the phylogeny of basal hexapods. *Pedobiologia*. 50: 191-204.

Carapelli, A., Liò, P., Nardi, F., Van Der Wath, E., Frati, F. (2007). Phylogenetic analysis of mitochondrial protein coding genes confirms the reciprocal paraphyly of Hexapoda and Crustacea. *BMC Evolutionary Biology* 7:1-13.

Chaudonneret, J. (1950). La morphologie céphalique de *Thermobia domestica* (Packard) (Insecte, Aptérygote, Thysanoure). *Annales Sciences Naturelles Zoologie et Biologie Animal* 12(11 sér): 145-302.

Cook, C.E., Yue, Q., Akam, M. (2005). Mitochondrial genomes suggest that hexapods and crustaceans are mutually paraphyletic. *Proceedings of the Royal Society of London B* 272: 1295-1304.

Dallai, R. (1980). Considerations on Apterygota phylogeny. *Bolletino di zoologia* 47: 35–48.

Dallai, R. (1989). Are Protura really insects? In: Simonetta, A.M., Morris, S.C. (Eds.), *The Early Evolution of Metazoa and the Significance of the Problematic Taxa*. Cambridge University Press. Cambridge. pp. 263–269.

Dallai, R. (1994). Recent findings on apterygotan sperm structure. *Acta Zoologica Fennica* 195: 23-27.

Dallai, R., Mercati, D., Bu, Y., Yin, Y. W., Callaini, G., Riparbelli, M. G. (2010). The spermatogenesis and sperm structure of *Acerentomon microrhinus* (Protura, Hexapoda) with considerations on the phylogenetic position of the taxon. *Zoomorphology* 129: 61–80.

Denis, J. R. (1928). Études sur l'anatomie de la tête de quelques Collembolés suivies de considérations sur la morphologie de la tête des Insectes. *Archives de zoologie Experimentale et Générale* 68: 1-291

D'Haese, C.A. (2002). Were the first springtails semiaquatic? A phylogenetic approach by means of 28S rDNA and optimization alignment. *Proceedings of the Royal Society B* 269: 1143-1151.

Dohle, W. (2001). Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name 'Tetraconata' for the monophyletic unit Crustacea + Hexapoda. In: Deuve, T. (Ed.) *Origin of the Hexapoda*. *Annales de la Société Entomologique de France (N.S.)* 37: 85-103.

Ertas, B., von Reumont, B.M., Wägele, J., Misof, B., Burmester, T. (2009). Hemocyanin suggests a close relationship of Remipedia and Hexapoda. *Molecular Biology and Evolution* 26: 2711-2718.

Friedrich, M., Tautz, D. (1995). Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. *Nature* 376: 165-167.

Friedrich, M., Tautz, D. (2001). Arthropod rDNA phylogeny revisited: a consistency analysis using Monte Carlo simulation. In: Deuve, T. (Ed.) *Origin of the Hexapoda*. *Annales de la Société Entomologique de France (N.S.)* 37: 21-40.

Fanenbruck, M., Harzsch, S., Wägele, J.W. (2004). The brain of Remipedia (Crustacea) and an alternative hypothesis on their phylogenetic relationships. *Proceedings of the National Academy of Sciences* 101: 3868-3873.

Fanenbruck, M., Harzsch, S. (2005). A brain atlas of *Godzilliognomus frondosus* Yager, 1989 (Remipedia, Godziliidae) and comparison with the brain of *Speleonectes tulumensis* Yager, 1987 (Remipedia, Speleonectidae): implications for arthropod relationships. *Arthropod Structure & Development* 34: 343-378.

Giribet, G., Edgecombe, G.D., Wheeler, W.C. (2001). Arthropod phylogeny based on eight molecular loci and morphology. *Nature* 413:157-161.

Giribet, G., Edgecombe, G.D., Carpenter, J.M., D'Haese, C.A., Wheeler, W.C. (2004). Is Ellipura monophyletic? A combined analysis of basal hexapod relationships with emphasis on the origin of insects. *Organisms Diversity & Evolution* 4: 319-340.

Harzsch, S. (2002). The phylogenetic significance of crustacean optic neuropils and chiasmata: a re-examination. *Journal of Comparative Neurology* 453: 10-21.

Harzsch, S. (2006). Neurophylogeny: architecture of the nervous system and a fresh view on arthropod phylogeny. *Integrative and Comparative Biology* 46: 162-194.

Hennig, W. (1969). *Die Stammesgeschichte der Insekten*. Frankfurt am Main: Waldemar Kramer.

Hwang, U.W., Friedrich, M., Tautz, D., Park, C.J., Kim, W. (2001). Mitochondrial protein phylogeny joins myriapods with chelicerates. *Nature* 413:154-157.

Imms, A. D. (1939). On the antennal musculature in insects and other arthropods. *Quarterly Journal of Microscopical Science* 81: 273-320.

Jamieson, B.G.M. (1987). The Ultrastructure and Phylogeny of Insect Spermatozoa. Cambridge University Press. Cambridge.

von K ler, S. (1963). Entomologisches W rterbuch. AkademieVerlag, Berlin.

Klass, K.D., Kristensen, N.P. (2001). The ground plan and affinities of hexapods: recent progress and open problems. Annales de la Soci t  Entomologique de France (N.S.) 37: 265-298.

Kraus, O. (1997). Phylogenetic relationships between higher taxa of tracheate arthropods. In: Fortey, R.A., Thomas, R.H. (Eds.). Arthropod Relationships. Systematic Association Special Volume Series 55. Chapman & Hall, London: pp. 295–303.

Kristensen, N.P. (1981). Phylogeny of insect orders. Annual Review of Entomology 26: 135-157.

Kristensen, N. P. (1991). Phylogeny of extant hexapods. In: D. F. Waterhouse, P. B. Carne and N. I. D. (Eds.). Insects of Australia: A Textbook for Students and Research Workers. Ithaca, NY, Cornell University Press: pp. 281-293.

Kristensen, N. P. (1997). The groundplan and basal diversification of the hexapods. In: R. A. Fortey and R. H. Thomas (Eds.). Arthropod relationships. London, Chapman & Hall: pp. 281-293.

Kukalov -Peck, J. (1987). New Carboniferous Diplura, Monura and Thysanura, the hexapod groundplan, and the role of thoracic side lobes in the origin of wings (Insecta). Canadian Journal of Zoology 65: 2327-2345.

Luan, Y., Mallatt, J.M., Xie, R., Yanng, Y., Yin, W.Y. (2005). The phylogenetic position of three basal-hexapod groups (Protura, Diplura and Collembola) based on ribosomal RNA gene sequences. Molecular Biology and Evolution 22:1579–1592.

Machida, R., Takahashi, I. (2003). Embryonic development of a proturan *Baculentulus densus* (Imadat ): Reference to some developmental stages (Hexapoda: Protura, Acerentomidae). Proceedings of the Arthropod Embryological Society of Japan 38: 13-17.

Mallatt, J.M., Garey, J.R., Shultz, J.W. (2004). Ecdysozoan phylogeny and Bayesian inference: first use of nearly complete 28S and 18S rRNA gene sequences to classify the arthropods and their kin. Molecular Phylogenetics and Evolution 31: 178-191.

Mallatt, J.M., Giribet, G. (2006). Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. *Molecular Phylogenetics and Evolution* 40: 772-794.

Nardi, F., Spinsanti, G., Boore, J.L., Carapelli, A., Dallai, R., Frati, F. (2003a). Hexapod origins: monophyletic or paraphyletic? *Science* 299: 1887-1889.

Osorio, D., Averof, M. and Bacon, J. P. (1995). Arthropod evolution: great brains, beautiful bodies. *Trends in Ecology and Evolution* 10: 449-454.

Regier, J. C., Shultz, J.W. (1997). Molecular phylogeny of the major arthropod groups indicates polyphyly of Crustaceans and a new hypothesis for the origin of hexapods. *Molecular Biology and Evolution* 14: 902-913.

Regier, J. C., Shultz J.W. (2001). Elongation factor-2: a useful gene for arthropod phylogenetics. *Molecular Phylogenetics and Evolution* 20: 136-148.

Regier, J. C., Shultz, J. W., Kambic, R. E. (2005). Pancrustacean phylogeny: hexapods are terrestrial crustaceans and maxillopods are not monophyletic. *Proceedings of the Royal Society B* 272: 395-401.

Regier, J. C., Shultz, J. W., Ganley, A. R. D., Hussey, A., Shi, D., Ball, B., Zwick, A., Stajich, J.E., Cummings, M.P., Martin, J.W., Cunningham, C.W. (2008). Resolving arthropod phylogeny: exploring phylogenetic signal within 41 kb of protein-coding nuclear gene sequences. *Systematic Biology* 57: 920-938.

Regier, J. C., Shultz, J. W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J. W., Cunningham, C. W. (2010). Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* 463: 1079-1083.

von Reumont, B.M., Meusemann, K., Szucsich, N.U., Dell'Amplio, E., Gowri-Shakar, V., Bartel, D., Simon, S., Letsch, H.O., Stocsits, R.R., Luan, Y.-X., Wägele, J.W., Pass, G., Hadrys, H., Misof, B. (2009). Can comprehensive background knowledge be incorporated into substitution models to improve phylogenetic analyses? A case study on major arthropod relationships. *BMC Evolutionary Biology* 9: 119.

von Reumont, B. M., Jenner, R. A., Wills, M. A., Dell'Ampio, E., Pass, G., Ebersberger, I., Meyer, B., Koenemann, S., Iliffe, T. M., Stamatakis, A., Niehuis, O., Meusemann, K. (2012). Pancrustacean Phylogeny in the Light of New Phylogenomic Data: Support for Remipedia as the Possible Sister Group of Hexapoda. *Molecular Biology and Evolution* 29:1031-1045.

Richardson, K. C., Jarett, L. and Finke, E. H. (1960). Embedding in epoxy resins for ultrathin sectioning in electron microscopy. *Stain Technology* 35:313–323.

Richter, S. (2002). The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea. *Organisms Diversity & Evolution* 2: 217-237.

Schram, F. R., Koenemann, S. (2004). Are the crustaceans monophyletic? In: Cracraft, J., Donoghue, J. (Eds.), *Assembling the Tree of Life*. Oxford University Press: pp. 319-329.

Shultz, J. W., Regier, J. C. (2000). Phylogenetic analysis of arthropods using two nuclear protein-encoding genes supports a crustacean + hexapod clade. *Proceedings of the Royal Society B Biological Science* 267: 1011–1019.

Sinakevitch, I., Douglass, J. K., Scholtz, G., Loesel, R., Strausfeld, N. J. (2003). Conserved and convergent organization in the optic lobes of insects and isopods, with reference to other crustacean taxa. *Journal of Comparative Neurology* 467: 150–172.

Strausfeld, N. J. (2009). Brain organization and the origin of insects: an assessment. *Proceedings of the Royal Society B* 276: 1929–1937.

Strausfeld, N. J., Andrew, D. R. (2011). A new view of insect-crustacean relationships I. Inferences from neural cladistics and comparative neuroanatomy. *Arthropod Structure & Development* 40: 276-288.

Stys, P., Bilinski, S. (1990). Ovariole types and the phylogeny of hexapods. *Biological Reviews* 65: 401–429.

Stys, P., Zrzavy, J., Weyda, F. (1993). Phylogeny of the Hexapoda and ovarian metamerism. *Biological Reviews* 68: 365-379.

Timmermans, M.J.T.N., Roelofs, D., Marien, J., van Straalen, N.M. (2008). Revealing pancrustacean relationships: phylogenetic analysis of ribosomal protein genes places Collembola (springtails) in a monophyletic Hexapoda and reinforces the discrepancy between mitochondrial and nuclear DNA markers. *BMC Evolutionary Biology* 8: 83.

Turbeville, J. M., Pfeifer, D. M., Field, K. G. & Raff, R. A. (1991). The phylogenetic status of the arthropods, as inferred from 18S rRNA sequences. *Molecular Biology and Evolution* 8: 669-686.

Wheeler, W. C., Whiting, M. F., Wheeler, Q. D., Carpenter, J. M. (2001). The phylogeny of the extant hexapod orders. *Cladistics* 17: 113-169.

Whittington, P. M. (1995). Conservation *versus* change in early axonogenesis in arthropod embryos: a comparison between myriapods, crustaceans and insects. In: Breidbach, O. & Kutsch, W. (Eds.) *The Nervous System of Invertebrates: an Evolutionary and Comparative Approach*. Birkhäuser, Basel: pp. 181-219.

Wygodzinsky, P. (1961). On a surviving representative of the Lepidotrichidae (Thysanura). *Annals of the Entomological Society of America* 54: 621-627.

Zrzavy, J. & Stys, P. (1997). The basic body plan of arthropods: insights from evolutionary morphology and developmental biology. *Journal of Evolutionary Biology* 10: 353-367.

Appendix

Zusammenfassung

Die Kenntnisse bezüglich der frühen Verzweigungen innerhalb der basalen Hexapoda sind in den letzten Jahren stetig angestiegen, aber einige Verwandtschaftsverhältnisse sind noch immer nicht eindeutig geklärt. Nur einige potentielle Apomorphien werden genannt, die eine Monophylie von Diplura beziehungsweise Zygentoma unterstützen. Es werden daher weitere Merkmale benötigt, um die Validität dieser Taxa zu bestätigen. In der vorliegenden Arbeit werden zwei Merkmale der Antennen untersucht: (i) Die extrinsische Antennenmuskulatur, die laut Literatur bei den Diplura nur einen Muskel besitzt, der an der Basis des zweiten Antennenglieds ansetzt und die bei allen anderen basalen Hexapoda am ersten Antennenglied (Scapus der Ectognatha) zu inserieren scheint. (ii) Die Gelenkung der Antennen an der Kopfkapsel: Während diese bei den Entognatha und den Archaeognatha monocondyl ist, gibt es Hinweise auf eine dicondyle Gelenkung bei den Zygentoma.

Die extrinsische Antennenmuskulatur und die Antennengelenkung wurden bei Vertretern aller Gruppen der basalen Hexapoda untersucht mit folgenden Zielen: (i) genaue Beschreibung der Strukturen bei Collembola, Diplura, Archaeognatha und Zygentoma, (ii) sind diese Merkmalssysteme Apomorphien der Diplura und/ oder Zygentoma, (iii) die Merkmalssysteme auf ihre Brauchbarkeit für phylogenetische Fragen hin zu untersuchen. Die extrinsische Antennenmuskulatur wurde anhand von Semidünnschnittserien 3D rekonstruiert und die Antennengelenkung mittels Lichtmikroskopie und REM untersucht, um diese Fragen beantworten zu können.

Die Analyse der Antennengelenkung erwies sich als schwierig, da die angewandten Methoden es nicht zuließen die Antennengelenkung in allen Gruppen der basalen Hexapoda zu analysieren. Die Gelenkung des basalen Antennenglieds mit der Kopfkapsel ist bei den Zygentoma nicht stark ausgeprägt und konnte daher nicht eindeutig geklärt werden. Muskeln der extrinsischen Antennenmuskulatur setzen bei allen untersuchten Diplura am zweiten Antennenglied an. Da eine vergleichbare Insertion auch bei Vertretern der Collembola nachgewiesen werden konnte ist dieses Merkmal für die Monophylie der Diplura hinfällig. Eine gründliche Untersuchung potentieller Außengruppen der Hexapoda ist notwendig um feststellen zu können, ob dieser gemeinsame Zustand bei Collembola und Diplura eine alte Plesiomorphie oder eine potentielle Synapomorphie darstellt, welche die Monophylie der Entognatha unterstützt. Als ein weiteres Ergebnis zeigte sich, dass nur bei Archaeognathen Muskeln aus Fasern aufgebaut sind, die am homolateralen und heterolateralen vorderen Tentorium entspringen und damit als eine potentielle Synapomorphie die Monophylie der Archaeognathen unterstützen könnten.

Curriculum vitae



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Career history

July 2002 Central Library Vienna
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March 2010 Storage work Company Pharmawell
Consignment
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Scientific publications

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Szucsich Nikolaus U. , Böhm Alexander, Jellinek Verena, Pass Günther,
Morphology and the earliest splits within the hexapod lineage -
Refinement of morphological concepts to choose among conflicting
hypotheses (Poster contribution at the IXth European Congress of
Entomology, Budapest, Hungary)