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Forward without wings: Current progress and future perspectives in the study of Microcoryphia and Zygentoma

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Abstract

Since the publication of Mendes in 2002, there has been no update on the state of knowledge about Microcoryphia and Zygentoma. The organizers of the 9th International Seminar on Apterygota provided us the opportunity to review the knowledge of these orders, which are better known for their taxonomy (although many regions of the world remain unexplored) than for other aspects. Fortunately, the number of scientists interested in aspects other than taxonomy, such as biology, ecology, ethology, ultrastructure, molecular data, etc., has increased and now valuable contributions exist on all these facets. Our review includes the recent knowledge on all these topics as well as an extensive reference list for these aspects, but with a reduced number of taxonomic references.

Keywords Insecta | review | up to date knowledge | jumping bristletail | silverfish

1. Introduction

The title of this review reflects that, although Microcoryphia and Zygentoma are two orders of primitive insects that lack wings, their characteristics have not been a hindrance to achieving great levels of diversity and a wide global distribution. Moreover, the knowledge on these basal hexapods is advancing due to the work of several researchers studying their different aspects, such as anatomy, physiology, phylogeny, ecology, etc. In addition, the lack of funds (wings) has not been enough of a handicap to prevent progress in the study of these insects (forward).

Our aim is to update the knowledge in different fields of study of both orders. We may not have considered all literature references of the last years, but we believe that our overview is sufficient to provide an idea of the current knowledge achieved after the paper of our colleague Luis Mendes (2002a). This, however, was previously presented at the Xth International Colloquium on Apterygota in České Budějovice in the year 2000; therefore we begin at this point to present some then unknown aspects.

We have organized this review to reflect these different topics: taxonomy, anatomy, embryology, physiology and genomics, ecology, economic and sanitary importance, fossil record and phylogeny. At the end we suggest future research perspectives.

2. Taxonomy

Although not a purely taxonomic contribution, we wish to highlight the book *Archaeognatha* by Sturm and Machida (2001). It is an excellent monograph that summarizes the knowledge on these insects up to this date and represents a basic reference for all specialists (Fig. 1).

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Papers on taxonomy published since 2000 represent the majority of publications dealing with Microcoryphia and Zygentoma, despite the fact that the number of living scientists dedicated to this field is extremely low. An important fact is that many experts exist that are retired or close to retirement and very few young people are interested in taxonomy.

The first aspect we discuss concerns the name of one of the orders, Microcoryphia = Archaeognatha. Some specialists use the name Archaeognatha Börner, 1904 and others the name Microcoryphia Verhoeff, 1904, both published in the same year. Currently, most taxonomists use the name Microcoryphia whilst Archaeognatha is employed by phylogenetists and anatomists, depending on their schools. We believe that both can coexist, but obviously with a different taxonomic category (Archaeognatha = †Monura + Microcoryphia), i.e., Archaeognatha (monocondilic mandibles) includes †Monura (compound eyes not fused and paracercus only) plus Microcoryphia (very small head vertex due to their fused compound eyes and terminalia composed by a median paracercus and two lateral cerci). We hope that new findings on fossil records will clarify the subject providing clearer monuran characteristics.

With regard to the nomenclature of the other order, some entomologists still use the term 'Thysanura' for naming Zygentoma and Microcoryphia and others reserve the name Thysanura in a strict sense for Zygentoma. In our opinion, 'Thysanura' can be tolerated for informal, but not scientific use, although this use has been detected in high impact-factor journals. Formerly, Thysanura included the three 'apterygotan' orders with conspicuous terminalia (bristly tails, i.e., setose cerci): the Diplura (Entognatha) as well as Microcoryphia and Zygentoma (Ectognatha), which are phylogenetically clearly different, the Diplura being the sister group of Archaeognatha + Zygentoma + Pterygota; Archaeognatha being the sister group of Zygentoma + Pterygota and the Zygentoma the sister group of Pterygota (Misof et al. 2014). Thus, the use of Thysanura is confusing and, to avoid ambiguity, editors and referees should suggest the exclusive use of the name Zygentoma. In order to clarify the terminology, we encourage all scientists to use the name Zygentoma for naming the order and abandon the deprecated name Thysanura in their publications.

Having clarified the order names, we now give a short review of the scientists who have published taxonomic descriptions between 2000 and today.

Firstly, we must express our sadness at the death of Prof. H. Sturm in January 2015. We highlight his work on the courtship behaviour in several species of both orders, the description of numerous new taxa (subfamilies, genera, subgenera and species of Machiloidea) and also the edition of the aforementioned book *Archaeognatha* co-written with Prof. R. Machida.

As well as the researchers who regularly publish on the taxonomy of Microcoryphia (L. F. Mendes, V. Kaplin and our team in Spain – C. Bach, R. Molero, M. J. Notario and M. Gaju), we congratulate our Chinese colleagues Z.-S. Song and J.-Y. Zhang as well our American colleague G. D. de Jong on their addition to the team. In relation to Zygentoma, authors regularly publishing are L. F. Mendes, V. Kaplin, G. Smith, L. Espinasa and the same Spanish team.

The descriptions of Microcoryphia and Zygentoma species have evolved significantly from the very poor description of *Lepisma saccharina* Linnaeus, 1758 (Fig. 2) up to the latest made by most of the active taxonomists of these insects, which include the description of sophisticated morphological details like special sensilla or scales and their distribution on the body using light and scanning electron microscopy (SEM) (Fig. 3).

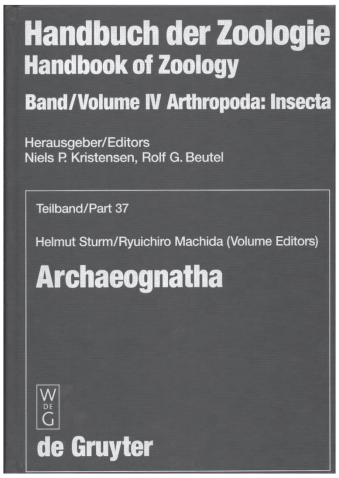
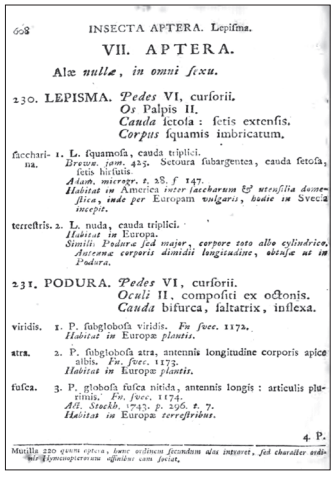


Figure 1. Cover page of the monograph on Archaeognatha, edited by Sturm & Machida (2001).


608 INSECTA APTERA. Lepisma.

VII. APTERA.

Alæ *nullæ*, *in omni sexu.*

230. LEPISMA. *Pedes* VI, cursorii.
Os Palpis II.
Cauda setosa: setis extensis.
Corpus squamis imbricatum.

saccharina. 1. L. squamosa, cauda triplici.
Brewn. jam. 425. Setoura subargentea, cauda setosa, setis bifuriis.
Adam. microgr. t. 28. *f.* 147.
Habitat in America *inter saccharum & utensilia domestica, unde per* Europam *vulgaris, hodie in* Svecia *incepit.*

terrestris. 2. L. nuda, cauda triplici.
Habitat in Europa.
Simili. Poduræ sed major, corpore toto alba cylindrico, Antennæ corporis dimidii longitudine, octofæ ut in Podura.

231. PODURA. *Pedes* VI, cursorii.
Oculi II, compositi ex octonis.
Cauda bifurca, saltatrix, inflexa.

viridis. 1. P. subglobosa viridis. *Fn. suec.* 1172.
Habitat in Europæ *plantis.*

atra. 2. P. subglobosa atra, antennis longitudine corporis apice albis. *Fn. suec.* 1173.
Habitat in Europæ *plantis.*

fusca. 3. P. globosa fusca nitida, antennis longis: articulis pluribus. *Fn. suec.* 1174.
Act. Stockh. 1743. *p.* 256. *t.* 7.
Habitat in Europæ *terrestribus.*

4. P.

Mutilla 220 *quam optica, hanc ocellorum secundum alas interest, sed character ordinis Hymenopterorum affinibus cum foeiat.*

Figure 2. Original description of *Lepisma saccharina*. Only few and very superficial characteristics are used (Linnaeus 1758).

The taxonomic novelties produced since 2000 include:
For Microcoryphia:

- The creation of the subfamily Ditriginiophthalminae (Kaplin 2000).
- Three new genera have been created: *Kerkiratrobius* (Bach de Roca et al. 2010), *Songmachilis* (Zhang & Zhou 2011) and *Turquimachilis* (Bach de Roca et al. 2013).
- The genus *Kuschelochilis* has been synonymised with *Allomachilis* (Mendes et al. 2009).
- The genera *Hybographitarsus* and *Dromadimachilis* are considered as subgenera of the genera *Graphitarsus* and *Corethromachilis*, respectively (Sturm 2001).
- Two new subgenera have been created: *Machilontus (Protomachilontus)* and *Allopsontus (Aridopsontinus)* (Kaplin 2012).
- The description of 42 new species.

For Zygentoma:

- Protrinumeridae, described as a subfamily of Nicoletiidae in 1988, is now considered as a family (Mendes 2002b) that might be more closely related to Maindroniidae and Lepismatidae than to Nicoletiidae
- Atelurinae is now considered to be a subfamily of Nicoletiidae (whereas during the last years of the 20th century it was considered to be a family) (Mendes 2002b).
- Atelurinae is now classified into five tribes (Mendes 2012).
- 22 new genera have been described (Tab. 1)
- The description of 98 new species.

In Table 2, the number of extant genera and species known in Mendes (2002a) and our data from 2014 is compared.

Table 1. New genera of Zygentoma described since the year 2000. The references of the publications are not included in the references section of this article.

Protrinemuridae	*Protrinemurella* n.g.	Mendes, 2002
	Protrinemuroides n.g.	Mendes, 2002
Nicoletiidae	*Heteronychella* n.g.	Mendes, 2001
	Protonychella n.g.	Mendes, 2001
	Rasthegotus n.g.	Mendes, 2001
	Trichotriurella n.g.	Mendes, 2002
	Olarthroceroides n.g.	Mendes, 2002
	Pseudobrinckina n.g.	Mendes, 2002
	Allotrinemurodes n.g.	Mendes, 2002
	Pseudogastrotheus n.g.	Mendes, 2003
	Allotrichotriura n.g.	Mendes et al., 2009
	Allograssiella n.g.	Mendes & Schmid, 2010
	Principella n.g.	Mendes, 2010
	Malayatelura n.g.	Mendes et al., 2011
	Ausallatelura n.g.	Smith, 2007
	Galenatelura n.g.	Smith, 2009
	Crypturelloides n.g.	Smith et al., 2011
	Acanthonima n.g.	Espinasa 2005
	Speleonycta n.g.	Espinasa et al., 2010
	Canariletia n.g.	Molero et al., 2014
Lepismatidae	*Primacrotelsa* n.g.	Mendes, 2004
	Hemikulina n.g.	Mendes, 2008

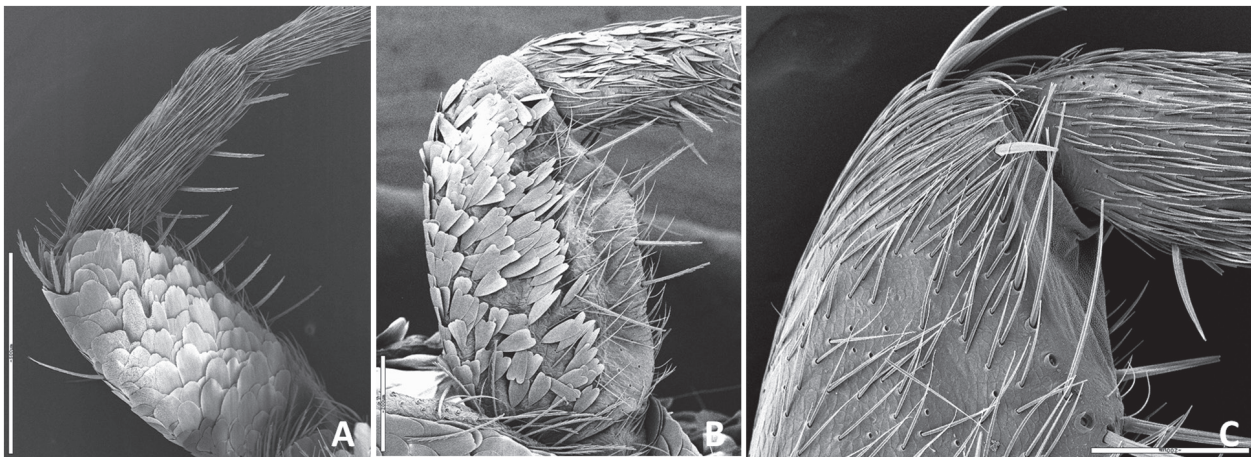


Figure 3. In modern taxonomy, the distribution, type and shape of scales and setae are useful for distinguishing species. As an example, the femora and tibiae of some Lepismatidae are compared: (**A**) *Ctenolepisma ciliata* (Dufour, 1831), (**B**) *C. nicoletii* (Lucas, 1846), (**C**) *Allacrotelsa kraepelini* (Escherich, 1905).

Table 2. Number of genera and species of Microcoryphia and Zygentoma described up to the years 2000 and 2014.

	2002		2014	
	Genera	**Species**	**Genera**	**Species**
Microcoryphia	64	493	64	(+42) = 535
Zygentoma	117	470	(+22) = 139	(+98) = 568
Total of both orders	**181**	**963**	**203**	**1103**

3. Anatomy

Some scientists have worked in this field since Mendes (2000, published in 2002a) and Sturm and Machida (2001). We can mention the papers of Dallai et al. (2001, 2004 and 2006) dealing with sperm and spermatogenesis and a review about unusual axonemes in arthropods.

A study of the circulatory system of abdominal appendages comparing the hemolymph supply of terminal filament and cerci in Archaeognatha, Zygentoma and Ephemeroptera demonstrates that this character represents a plesiomorphic state in respect to the higher insect orders (Gereben-Krenn & Pass 2000).

Bitsch & Bitsch (2002) conducted a review on the endoskeletal structures in arthropods, including comments on *Petrobius* Leach, 1809, *Lepismachilis* Verhoeff, 1910, *Nicoletia* (Gervais, 1844), *Lepisma* Linnaeus, 1758 and *Thermobia* Bergroth, 1890.

Szklarzewicz et al. (2004) described the ovarian morphology of *Petrobius brevistylis* Carpenter, 1913 and *Tricholepidion gerstschi* Wygodzinsky, 1961.

Rost-Roszkowska et al. (2010) focused on the midgut epithelium of the silverfish *Atelura formicaria* Heyden, 1855 and the way that some cells degenerate and new ones regenerate from midgut stem cells.

Matushkina (2010) studied under SEM the special integumentary 'rosette-like' sensilla, structures present in many parts of the body from different families of Microcoryphia and Zygentoma. The rosette-like sensilla were also studied by Fröhlich & Lu (2013a), who demonstrated that they are openings of epidermal glands in *Petrobius brevistylis*. The same authors studied the antennal distal chains of *P. brevistylis* (Fröhlich & Lu 2013b), focusing their work on the thinner junctions between the chains, which can be easily broken.

Mißbach et al. (2011) studied the deutocerebrum of the machilid *Lepismachilis y-signata* Kratochvil, 1945, where they did not find the mushroom bodies that were present in the brain of *Thermobia domestica* (Packard, 1873) studied by Farris (2005), who compared it with those of neopteran insects.

Blanke et al. (2014) revealed new apomorphies for Zygentoma from a comparison of the cephalic skeleto-muscular system of *Tricholepidion gertschi* Wygodzinsky, 1961 with that of other silverfish based on microtomographic studies, allowing a phylogenetic analysis with 139 cephalic characters to be performed, resulting in the monophyletic Zygentoma including *T. gertschi*. Blanke et al. (2015) furthermore revised the early evolution of the mandibles in insects by microtomographic studies of the head morphology in Microcoryphia. Their study revealed a second point of articulation of the mandibles in the region of the anterior tentorial pits.

4. Embryology, physiology and genomics

The eggs of Microcoryphia and Zygentoma usually have an oval to elliptic form. Immediately after having been laid, they are ivory or orange in colour, but after a few days take on a dark brown colour. Poprava & Rost (2004) conducted an in-depth study of the structure and ultrastructure of the egg capsule in *Thermobia domestica*, where they found a micropylar pore whilst Microcoryphia lacked this.

Masumoto & Machida (2006) described the embryonic membranes of *Lepisma saccharina,* concluding that some embryogenic traits are similar to those of archaeognathans, but considered the persistence of the amnioserosal folds to be an autapomorphy of Dicondylia.

In physiology Hansen-Delkeskamp (2001) studied electrophysiologically the taste sensilla in the antenna of *Thermobia domestica*; she suggests that the features observed represent a primitive condition in respect of those of higher insect taxa. Moreover, the metabolic rate in *Lepisma* and *Thermobia* has been studied at different temperatures by DeVries & Appel (2013), researching its relation to the ability of these species to persist for long periods without feeding, suggesting that they have some metabolic modifications compared with other insects which cannot tolerate extended starvation. We also wish to mention the contribution of Hamana et al. (2004), where polyamines of bristletail and silverfish were studied. These substances are important in the regulation of a number of cellular activities; they found that some polyamines widespread in higher insects were

also present in primitive apterygotan insects. Pick et al. (2014) have sequenced hemocyanin in adult *T. domestica*, being the second insect order where this protein has been demonstrated; moreover they study a hexamerin, suggesting the early emergence of this type of protein in hexapod evolution. Besides, molecular clock calculations using hexamerins suggest that Zygentoma and Pterygote divergence occurred 387 million years ago (which agree with the available fossil record). Finally, Marco et al. (2014) studied the adipokinetic hormones (AKH), being the first time that they were found in Zygentoma and Archaeognatha, and suggesting that they can be involved in lipid mobilization.

In genomics, four contributions described the mitochondrial genome of *Petrobius brevistylis*, *Pedetontus silvestrii* Mendes, 1993, *Atelura formicaria* and *Songmachilis xinxiangensis* Zhang & Zhou, 2011 (Podsiadlowski 2006, Zhang et al. 2008, Comandi et al. 2009 and Kun et al. 2013, respectively).

We wish to highlight the huge project 1Kite (1K Insect Transcriptome Evolution), which aims at studying the transcriptomes (i.e. the entirety of expressed genes) of more than 1,000 insect species encompassing all recognized insect orders. The subproject 'basal hexapods' coordined by A. Blanke and K. Meusemann, includes the study of 22 Archaeognatha and 13 Zygentoma species. In the project web page more information is available (http://www.1kite.org/index.html). Misof et al. (2014) made the transcriptomic study that summarizes the current state of insights of the 1Kite-project. Their results produced 'statistically robust and congruent results resolving previously controversial phylogenetic relationships', allowing the origin of insects to be estimated to the early Devonian, ca. 479 million years ago (mya) and a radiation of ectognathous insects in the early Silurian ca. 441 mya.

5. Ecology

The two orders are distributed across all terrestrial regions: Microcoryphia able to live in nearly all climatic zones (although they avoid pure deserts), and Zygentoma are not found in cold regions. Some Zygentoma have adapted to living with ants, others are strictly termitophilous or can even live in nests of wasps. We have sampled many ant nests in Spain, collecting Zygentoma and their hosts (Fig. 4). The analysis of more than 800 Zygentoma-Formicoidea relationships allows us to consider four types of silverfish according to their

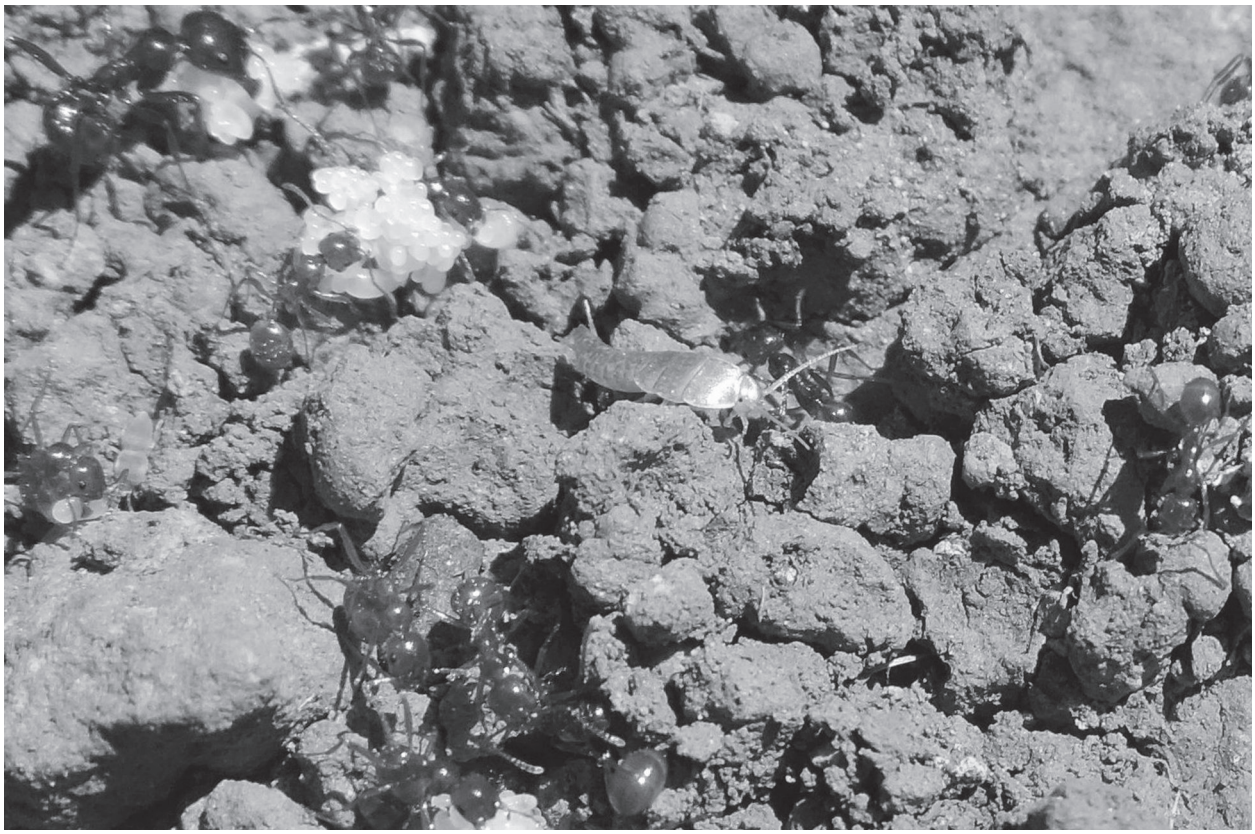


Figure 4. The myrmecophile silverfish *Neoasterolepisma spectabilis* (Wygodzinsky, 1945), a *Messor* specialist, in a nest of *Messor structor* (Latreille, 1798).

different relationships: (1) **xenomyrmecophiles** (less than 10 % of samples found in ant-nests), (2) **occasional myrmecophiles** (when they are found together with or without ants in similar proportions) and (3) **strict myrmecophiles** (more than 75 % of samples associated with ants), which can be (3A) **generalist** (living with different ant genera in similar proportions) or (3B) **specialist** (with preference for an ant genus in larger proportions, sometimes close to 100 %). A detailed study of these relationships is being prepared for publication by our team. Biogeographic remarks of the ibero-balearic fauna of myrmecophilic Zygentoma have been studied by Molero et al. (2002).

Morais & Adis (2008) studied the phenology, abundance and density of Microcoryphia in a forest in central Amazonia affected by flooding. Samples were obtained during a year by means of photo-eclectors placed on soil and trees. The two most abundant species were *Neomachilellus scandens* Wygodzinsky, 1978 and *Meinertellus adisi* Sturm, 1983. Both species showed different behaviours, *M. adisi* being a polivoltine species (immatures were found throughout the year) which lives on trees (very few specimens were captured in the soil), so that the authors considered it not to be migrant between soil and trees. On the other hand, *N. scandens* is univoltine and lives only on soil; their eggs survive during the flooding period and hatching takes place at the beginning of the unflooded period. An interesting difference with other studies affects the life cycle of *N. scandens*, which is a polivoltine species in primary and secondary forest not affected by flooding. The authors suggest horizontal migration to a new habitat as a result of deforestation.

Wachter et al. (2012) studied molecular signatures of the parthenogenetic alpine *Machilis pallida* Janetschek, 1949 in ice-free summits surrounded by glaciers (nunataks) and their peripheral areas. They suggest that refuges in these sites were more widespread than previously recognized and parthenogenesis could be acquired from different origins during the last Glacial Maximum. Finally, while parthenogenesis could have been essential to the survival of *M. pallida* within those climatic conditions, it could be a serious threat with the present climatic change. Notario-Muñoz et al. (2013) studied the life cycle and reproduction of *Machiloides tenuicornis* Stach, 1930, an interesting Meinertellidae species that is the only representative of the genus in the Palaearctic region. In the numerous samples taken, they found that 1/3 of the populations were bisexual and 2/3 only females. This suggests that *M. tenuicornis* is a species in expansion that can facultatively reproduce parthenogenetically. Could this fact also be related to Pleistocene glaciations?

6. Economic and sanitary importance

Microcoryphia have no sanitary significance, but Zygentoma –although they are not biting insects– are important in some areas because of the damage they cause in libraries and museums. Moreover, they can be the source of potent allergies.

Querner et al. (2013) published the results of monitoring some museums in Germany and Austria and found that silverfish (*Lepisma saccharina*) were among the most common pests in both countries (others being webbing clothes moths, the drugstore beetle and carpet beetles).

Tremblay & Gries (2003) tested the hypothesis that the aggregation behaviour of some dwelling silverfish is mediated, at least in part, by a pheromone and this behaviour can be used for their control. Paper discs, where the studied species remained for three days, attracted and arrested conspecifics, but frass and scales, alone or in combination, did not produce attraction, so they are not the source of the pheromone. Therefore, 'physical contact was required for pheromone recognition, indicating that the pheromone arrests rather than attracts conspecifics'. Moreover, pheromone from *T. domestica* arrests *Ctenolepisma longicaudata* Escherich, 1905, but not the common *L. saccharina*, confirming the closer phylogenetic relatedness between the long-tailed silverfish and firebrat (both are Ctenolepismatinae) than between the former and the common silverfish (which is a Lepismatinae). Woodbury (2008), studying the same species, obtained similar results but found that amber-type frass could produce the arrestment of *T. domestica* females, so it could be a source of pheromone.

Tremblay & Gries (2006) analysed the biotic and abiotic factors affecting the microhabitat selection of *T. domestica*. They conclude that 'abiotic characteristics of a shelter, coupled with the presence of conspecifics, affect microhabitat selection by firebrats'. These findings can be useful for trapping firebrats in pest management systems.

Silverfish are habitual inhabitants in human dwellings and can be an annoyance simply by their presence. For this reason, pest control companies developed traps for collecting and killing them. Sims & Naffziger (2012) developed a baiting system containing a feeding attractant and an insecticide for controlling silverfish.

In relation to sanitary troubles, in humans with rhinitis and asthma, IgE antibodies specific to indoor invertebrates have been described. Barletta et al. (2005) cloned and characterized tropomyosin from *L. saccharina*. The rLep s 1 obtained 'was able to inhibit the IgE binding to the insoluble fraction of silverfish extract and to induce histamine release by an arthropod-

allergic serum'. Boquete et al. (2008) analysed the role of silverfish in being responsible for some allergic problems, demonstrating the allergenicity of *Lepisma* through *in vitro* tests.

7. Fossil record

There have been important novelties in the study of fossils in these groups. Although new species have been described, others have been synonymized with species of other taxonomic groups.

Carbotriplura was initially described by Kukalova-Peck (1985) as an ephemeropteran (*Bojophlebia procopi*), and later Kluge (1996) viewed it as a thysanuran, perhaps close to Zygentoma because of its depressed shape. Recently Staniczek et al. (2014) considered these specimens as a new 'apterygotan' order Carbotriplurida, that may form the fossil sister group of Pterygota.

Another important synonymy concerns *Triassomachilis uralensis* Sharov, 1948. The revision of the type specimen by Sinitshenkova (2000) placed it in the ephemeropteran genus *Mesoneta* Brauer, Redtenbacher & Ganglbauer, 1889.

The revision of the early Devonian holotype of *Leverhulmia mariae* Anderson & Trewin, 2003 led Fayers & Trewin (2005) to consider it to be a hexapod incertae sedis closely related to Microcoryphia and Zygentoma. This placement is mainly based on the presence of a medial unguis on the pretarsus of the walking legs and the presence of abdominal leglets. However, because the specimen is only partially preserved its placement is not definitive, and their inclusion into insects is in doubt (Shear 2012). Nevertheless Grimaldi (2010) places *Lerverhulmia*, as a stem-group hexapod, into Ectognatha and Fayers and Trevis (op cit) suggests that it may represent the earliest 'apterous' insect (s.s.) known to date.

Rinehart et al. (2005) studied the instar sizes and growth of 25 specimens of *Dasileptus* Brongniart, 1885; they founded six group sizes (instars) which were compared with those of extant *L. saccharina* and *Petrobius* sp.

A new species of *Dasyleptus* has been described from United States (Kansas) by Engel (2009). Moreover, the period of existence of Monura has been widened from late Carboniferous – late Permian to late Triassic. Data from Central Europe can be found in the papers of Bechly & Stockar (2011) and Bashkuev & Sell (2013).

Since the year 2000, new species of Microcoryphia and Zygentoma included in amber have been described. As an example we can cite one Nicoletiidae from Dominican amber described by Mendes & Poinar (2004) and Microcoryphia and Zygentoma from Burmese amber (Mendes & Poinar 2008 and Mendes & Wunderlich 2013). Recently Riquelme et al. (2015) described a new species from Miocene Chiapas amber: *Neomachilellus (Praeneomachilellus) ezetaelenesis* Riquelme et al., 2015; the very well preserved specimens were compared with the fossil *N. (P.) dominicanus* Sturm & Poinar, 1997 and the extant species *N. (P) szeptyckii* Bach de Roca et al., 2009. Other fossils remain unstudied, such as one belonging to the Upper-Aptian/Middle-Albian age from Alava (northern Spain) (Alonso et al. 2000). A study comparing one Lepismatidae fossil preserved in Baltic amber with the extant species *Stylifera gigantea* (Escherich, 1905) was presented by us in the XIII International Colloquium on Apterygota held at Coimbra (2012).

Another way of studying palaeontology without animal remains is the analysis of the traces they leave when moving or jumping; this science is called 'ichnology'. Minter & Braddy (2006) describe traces of insects close to Microcoryphia or Zygentoma found in Lower Permian sediments: *Tonganoxichnus* (an organism close to Monurans) and *Stiaria* and their traces were compared with those of *Petrobius brevistylis*. Moreover, Getty et al. (2013) described the imprints of two living bristletails and one silverfish in sediments with different levels of water saturation and compared them with the imprints of some trace fossil organisms.

8. Phylogeny

The study of phylogeny can be conducted using different types of data, studying embryological, anatomical (s.l.) or attendant molecular variation. Most of the contributions are devoted to the general relationships of Microcoryphia (= Archaeognatha) and Zygentoma in relation to other animal phyla, Arthropoda or Hexapoda, and only a few analyze relationships within these former groups.

All studies agree with placing both orders at the base of Ectognatha, almost always with Archaeognatha as the sister group of the Dicondylia (Zygentoma + Pterygota). A phylogeny based on anatomy was conducted by Beutel & Gorb (2001 and 2006), who analysed macroscopically and structurally the different attachment structures on the tarsi of Hexapoda, with Chilopoda and Symphyla as outgroups. The results, in relation to the orders of our interest, mainly differ in the resolution of *Tricholepidion*, which remained ambiguous in the updated analysis in resolving *Tricholepidion* either as a sister group to remaining zygentomans, or as a sister group to a clade comprising remaining zygentomans and the winged insects. The latter resolution was tentatively favoured by Staniczek (2000) who conducted a study on mandibles, comparing

their musculature among the Archaeognatha, Zygentoma and Ephemeroptera. Also, Machida (2006) inferred basal hexapod relationships from their embryology and stated that Archaeognatha are plesiomorphic in the Ectognatha clade with respect to their ephemeral embryonic membrane fold, which in dicondylians is transformed into an 'amnioserosal fold-amniotic cavity system', with the Zygentoma being more primitive than Pterygota because the formation of this membrane is flexible while fixed in winged insects.

Bitsch & Bitsch (2004) carried out a review study of the phylogeny of basal hexapods among mandibulate arthropods. With regard to Zygentoma, their parsimony analysis of morphological characters favour a paraphyletic Zygentoma, with Lepismatidae more closely related to Pterygota than to *Tricholepidion*. Giribet el al. (2004) performed a combined analysis of basal hexapod relationships, analysing bibliographic morphological characters and molecular data. The results of their morphological, molecular and combined analyses also favour a sister group relationships between *Tricholepidion* and remaining Dicondylia, but with variable support. Another study (Giribet & Edgecombe 2013) reviewed the phylogenetic relationships among the major arthropod lineages, indicating, in relation to insect phylogeny, the unresolved problem of *Tricholepidion*.

Whereas most studies agree with the phylogenetic position of Zygentoma as the sister group of Pterygota within Dicondylia, Regier et al. (2004) suggested that 'Archaeognatha and Zygentoma form a monophyletic Thysanura sensu lato that forms the sister group to Pterygota'.

A review of molecular data to study the phylogeny of basal hexapods was performed by Carapelli et al. (2006). These authors pointed out 'conflicts between morphological and molecular data as well as among different data sets and analytical methods', concluding that the monophyly of each apterygotan order is almost always well supported, whereas interordinal relationships remain unclear.

Grimaldi (2010) published a review article dealing with the origin and evolution of Hexapoda. He discusses primary homology of morphological characters in the context of Atelocerata and Pancrustacea. The analysis of the basal hexapod characteristics (74 synapomorphies) and early Palaeozoic fossils provides a morphologically based phylogeny of recent lineages of Hexapoda and of early Palaeozoic fossils; Archaeognatha being the sister group of Zygentoma + Pterygota; the monophyletic Zygentoma are the sister group of Pterygota and the Devonian fossil *Leverhulmia* is a stem-group hexapod, placed between Archaeognatha and Dicondyllia clades. Finally, he suggests future lines of research, including the study of morphological synapomorphies of tracheata and homologies in living organisms, exploring phylogeny in depth using morphological and molecular characters within the basal hexapods, especially Diplura, Archaeognatha and Zygentoma, and increasing the research in fossil deposits.

With regard to the internal phylogeny of Microcoryphia, the relationships between the two extant families Machilidae and Meinertellidae seem to be clear, with the meinertellids being more evolved, among other differences, due to the reduced abdominal sternites. Machilidae are very heterogeneous: the different groups can share some characters, thereby making it difficult to analyse their relationships. Sturm & Machida (2001) provided a table with different characteristics. The work of Sturm & Machida (op. cit.) is also based on previous data from Sturm & Bach de Roca (1993) and Mendes (1998).

Koch (2003a) considered the main reasons why a cladistic analysis of Archaeognatha had not been carried out thus far. He highlighted 10 characteristics among archaeognathans and showed that there are a high number of parallelisms, which can produce an artificial phylogeny. He took into account the extinct Dasyleptidae (= Monura), which he considers to be a group of extant Microcoryphia. With regard to the exceptional presence of styli in the first abdominal segment, he reasoned that *Ditrigoniophthalmus* is the basal – most offshoot genus among the extant Machiloidea. The other two genera of the so-called palaeoforms (*Charimachilis* and *Mesomachilis*) and the remaining genera of Machilidae are considered to be paraphyletic with respect to the more evolved Meinertellidae, due to the apparent absence of unambiguous synapomorphies.

With regard to the Zygentoma, Koch (2003b) pointed out that there are some well-defined groups (Ateluridae and Maindroniidae) with unclear relationships to the families Nicoletiidae, Protrinemuridae and Lepismatidae. Based on 26 morphological characteristics, a tree of the Zygentoma families was built. He concluded that the relationships between the families are still far from being clear; this is 'due to the deficiency that current conclusions remain based on reductive traits only and include parallelisms within Zygentoma and Pterygota'.

Based on the study of spermatogenesis and sperm morphology, Dallai et al. (2004) argued that *Tricholepidion* is most closely related to Nicoletiidae and Ateluridae, this putative clade forming the sister group of Lepismatidae (Maindroniidae was not considered for the lack of spermatological data).

Tricholepidion Wygodzinsky, 1961 was originally thought to be a living fossil belonging to the Lepidotrichidae, a family formerly erected for the extinct

species *Lepidotrix pilifera* Silvestri, 1912 (from Baltic amber). Engel (2006) questioned this view in accordance with Koch (2003b) and placed *Tricholepidion* in a new family, Tricholepidiidae, that he considered to be the sister group of a clade Neozygentoma, composed of the extinct Lepidotrichidae (with *Lepidotrix* only) and all remaining zygentomans (= Euzygentoma Engel, 2006). The classification proposed by Engel (2006), however, still awaits a more thorough study of *Lepidotrix* specimens (Blanke et al. 2014)

Koch and Dolgener (2008a, 2008b) studied 18 exemplar species of the Zygentoma and combined characters of the external morphology with data on the internal anatomy in cladistic analyses. Their results favour a monophyletic Zygentoma, with *Tricholepidion* as a sister group to all remaining Zygentoma (= Euzygentoma Engel, 2006). Among the latter, Nicoletiidae and Ateluridae form a monophylum that is resolved as the sister group of a clade composed of Protrinemuridae, Maindroniidae and Lepismatidae. Whether Nicoletiidae are monophyletic or paraphyletic with respect to Ateluridae (the latter in accordance with the classification proposed by Mendes 2002b) remained ambiguous in these analyses.

Blanke et al. (2014) studied the head morphology of *Tricholepidion gertschi* by means of synchrotron micro-computer tomography and scanning electron microscopy. Their phylogenetic analysis of cephalic characters corroborates the view that Zygentoma is monophyletic and that *T. gertschi* is the sister group of Euzygentoma.

As we have seen, the internal phylogeny of Microcoryphia (= Archaeognatha) and Zygentoma is far from clear as many characteristics are shared by different genera in each order; some genera and even species are poorly described. Thus, to achieve good results in phylogeny, a deep revision of all described genera would be very useful.

9. Forward without wings

Before concluding with the future study perspectives, we wish to justify the title of our contribution. 'Forward without wings' reflects that, although these primitive insects lack wings, they have not had a problem in achieving great levels of diversity.

Moreover, we can cite some studies on Microcoryphia and Zygentoma that suggest the evolution of wings from paranotal lobes, such as that of Hasenfuss (2002), who analysed 'A possible evolutionary pathway to insect flight starting from lepismatid organization'. The same author (2008) analyzed possible steps in wing evolution and an intermediate stage of 'gliding'. Yanoviak and Yanoviak et al. (2009) demonstrated that Microcoryphia can move between trees by gliding.

Much good research on these basal insects has been carried out, as we have previously cited. Despite this considerable progress, more ways must be opened (i.e., field observations and filming of gliding, ecology and behaviour, more knowledge of genomics such as the 1KITE project, microtomography, etc.) in order to obtain the best knowledge of different aspects and discover all the secrets not yet discovered.

10. Future perspectives

We suggest the following aspects for future research of these insects:

1. It is necessary to increase the number of specialists studying taxonomy, despite the fact that the majority of literature dealing with the two orders is focused on this aspect. A proper identification is necessary not only for knowing the diversity of both orders but also for other studies, especially in phylogeny.
2. The fauna of large regions of the world has not been sufficiently studied (i.e., many countries of Central Africa, Central and South America and Asia), and that of many other regions needs a deep revision (i.e. the USA, Australia and Northern Africa). We believe that only a small proportion of species is known.
3. For the diagnosis and identification of species, the morphological characters are a great challenge. Therefore, other anatomical characteristics will be useful in providing a deeper knowledge of anatomy, biology, ecology and behaviour. The life cycle has been described in only a few species, so it is difficult to use these characteristics in the internal phylogeny of these orders.
4. New techniques are useful in increasing the knowledge of Microcoryphia and Zygentoma. Their use must be promoted. Molecular biological techniques are fundamental (DNA and RNA extractions), but using correctly identified specimens is essential. Sometimes the use of these techniques is difficult due to the scarcity of the specimens, because for their determination it is usually necessary to mount the specimen on slides.
5. New techniques such as microtomography surely have a great future.
6. Finally, there is a need for financial support. The specimens are not easy to find (they only occasionally fall into traps!). Also, it is necessary to cover many sites that have scarcely been sampled or not sampled at all. Except for a few Zygentoma, the group has no economic projection, so it is difficult to justify these studies and great effort is needed for the research.

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