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CLASS DIPLOPODA

Order Chordeumatida

Jörg Spelda

Bavarian State Collection of Zoology
Münchhausenstraße 21, 81247 Munich, Germany
spelda@zsm.mwn.de

Fig. Chordeumatida sp. © Endika Ussia

1. Brief characterization of the group and main diagnostic characters

1.1. Morphology

Chordeumatida is a millipede order in which the number of body rings in the adult stage is constant within a species (sometimes males have fewer rings than females). This number is mostly even and ranges from 26 to 32, depending on family or species. Most European species have 30 body rings.

As characteristics, the 'cheeks' (= the basal **mandibular lobes**) are laterally expanded, very prominent and in most species not obviously divided in separate cardines and stipetes. Only a groove at the anterior end, near the base of the antennae, is present as a remnant of the division. Body rings are open ventrally and not fused with the **sternites**. Almost all chordeumatidans have three pairs of large setae (= **macrochaetae**) on their body rings, but no other setae on them, while the head is usually densely pilose. The last antennal joint carries a unique seta with a mammillate-conic base. Above the inner **palps** of the **gnathochilarium** Chordeumatida have bi- to quadridentate styliform processes (Spelda 2001).

Chordeumatida, like the other nematophoran orders Callipodida and Stemmiulida, have two **spinners** under the dorsal part of the preanal ring (often more in Stemmiulida). The last legpairs are somewhat elongated in order to manipulate the extruded silk. Apart from a few cave species chordeumatidans have ocelli, while polydesmidans of similar habitus are always blind. The **collum** does not overlap the head (as in julidans), except in the North American family Striariidae. Except in the North American family Urochordeumatidae the last segment (= **telson**) does not have a prolonged process. The **anal valves** have 2-3 setae.

In contrast to other millipede orders, Chordeumatida have a wide range of body shapes and several taxa resemble members of other orders, especially Polydesmida. According to Verhoeff (1926-1932) six main habitus types can be recognized. These types are fixed in genera but occur independently in different families (Shear 2000), and are listed below with examples from the Iberian Peninsula.

- **Atractosoma-habitus**, with large paraterga, as wide as or wider than long, similar to those of the polydesmidan genus *Lusitaniosoma*.
- **Ochogona-habitus**, with smaller paraterga, which are usually about twice as long as wide and extend over much of the metazona (*Opisthocheiron*, *Hispaniosoma*).
- **Craspedosoma-habitus**, with the paraterga are semicircularly rounded, giving the animal the appearance of a chain of rosary beads (*Ceratosyphs*).
- **Haasea-habitus**, with only a hump instead of paraterga. The macrochaetae are usually stout and close together (*Cranogona*, *Typhlopsychrosoma*).

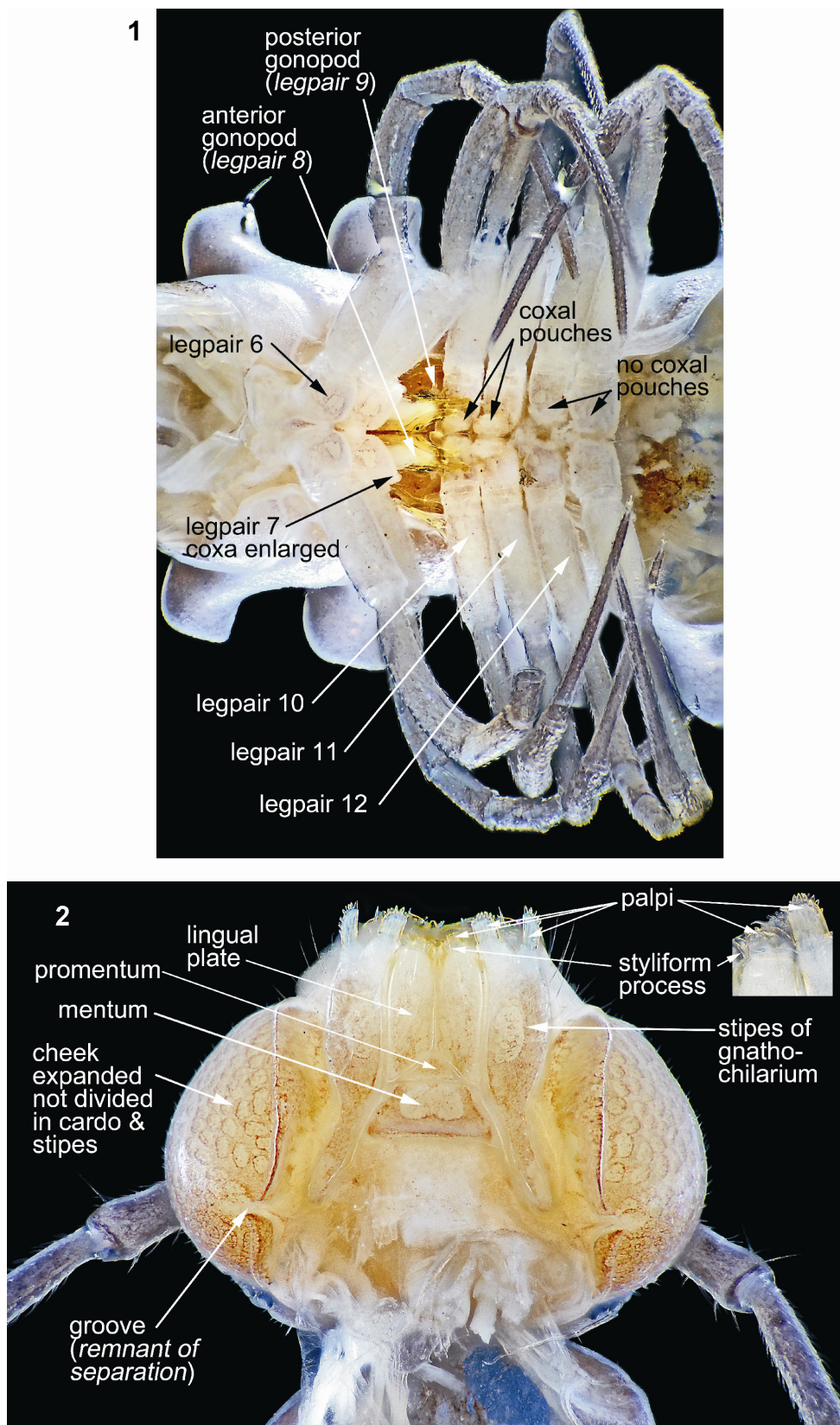


Fig. 1-2. *Atractosoma meridionale* male. 1. Body rings 6-9 ventral. 2. Gnathochilarium ventral.

- **Rhiscosoma-habitus**, with paraterga which are bent downwards (*Xystrosoma*).
- **Chordeuma-habitus**, which have a cylindrical shape and superficially resemble a short julidan millipede (at least one *Chordeuma* species in the Spanish Pyrenees).

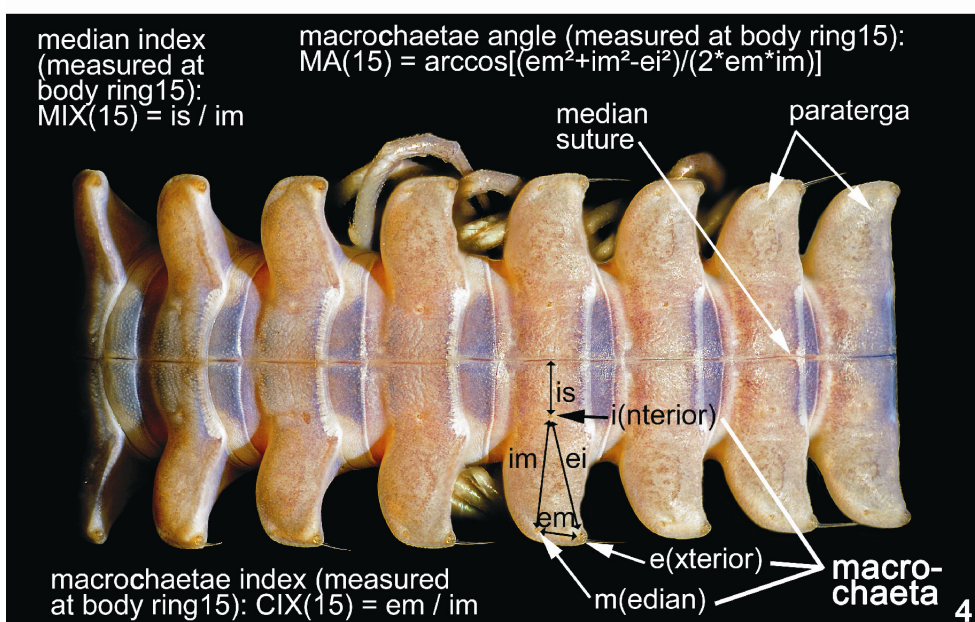
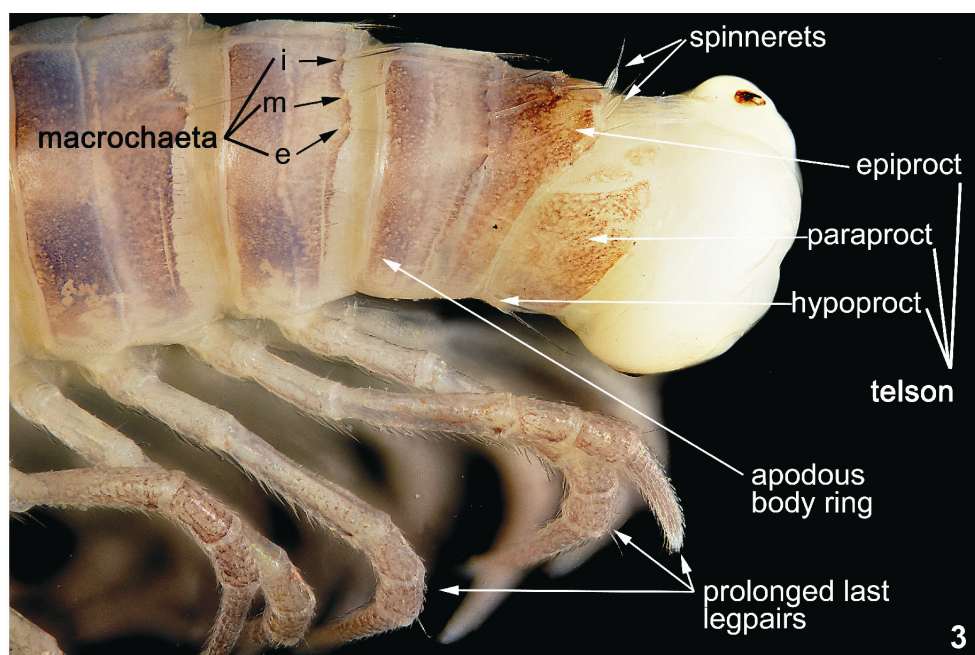


Fig. 3-4. *Atractosoma meridionale* male. 3. Last body rings lateral. 4. Midbody rings dorsal.

Chordeumatida show an enormous variation in the conformation of the male copulatory apparatus. The anterior **gonopods** of the Chordeumatida are solely of coxal origin (Shear 2000), while the posterior gonopods vary from leg-like to totally reduced. The 7th pleurotergite and the legs of the adjacent body rings are sometimes also included in the copulatory apparatus. The highest number of included legpairs is found in the family Chordeumatidae, where the second leg of ring 6 is transformed into anterior **paragonopods** and the second pair of ring 8 into posterior paragonopods. The first legpair of ring 8 is reduced. Male chordeumatidans often have a flattened frons. They have **coxal pouches** on the legs of ring 8 but not on other legs.

The female copulatory organs, the **vulvae**, are situated between the 2nd and 3rd legpair. They are simple paired structures consisting of a caudal bursa with two valves and a cranial operculum. Sometimes a postvulvar organ is present. The exerted vulvae are an easy to recognize feature of adult females, mostly species-specific and thus important for species delimitation.

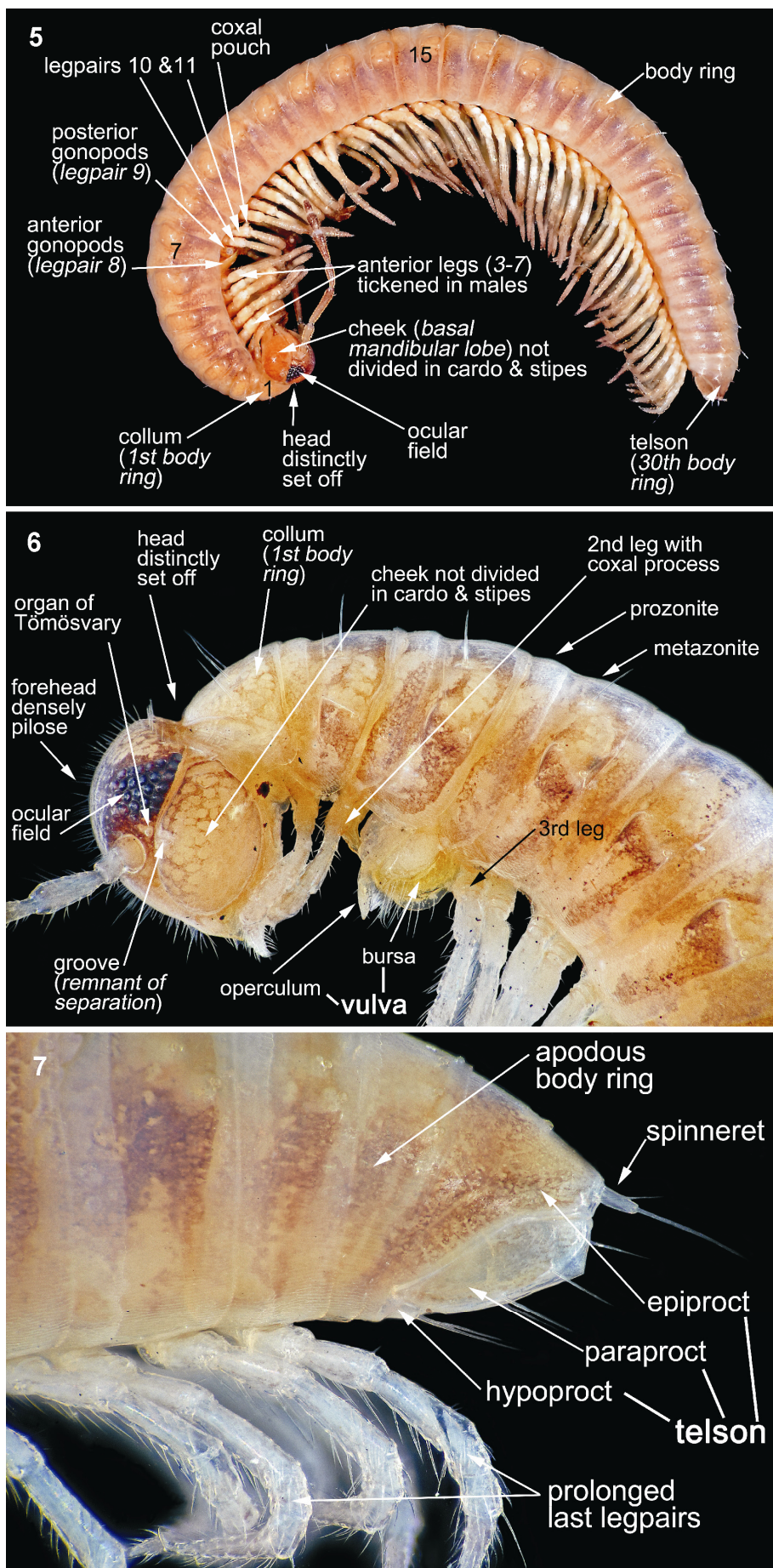


Fig. 5. *Ceratosphys amoena* habitus lateral. Fig. 6-7. *Ceratosphys picta* female: 6. Anterior part lateral. 7. Last body rings lateral.

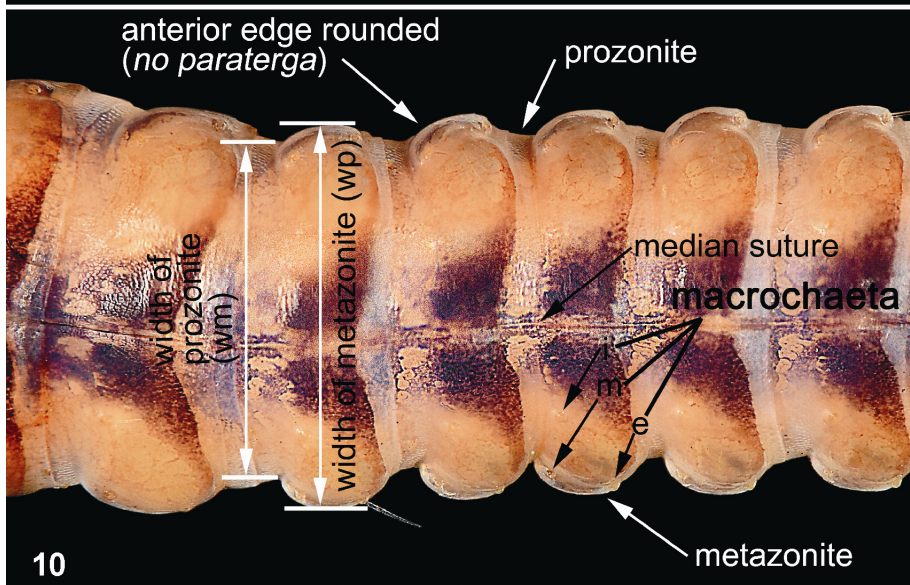
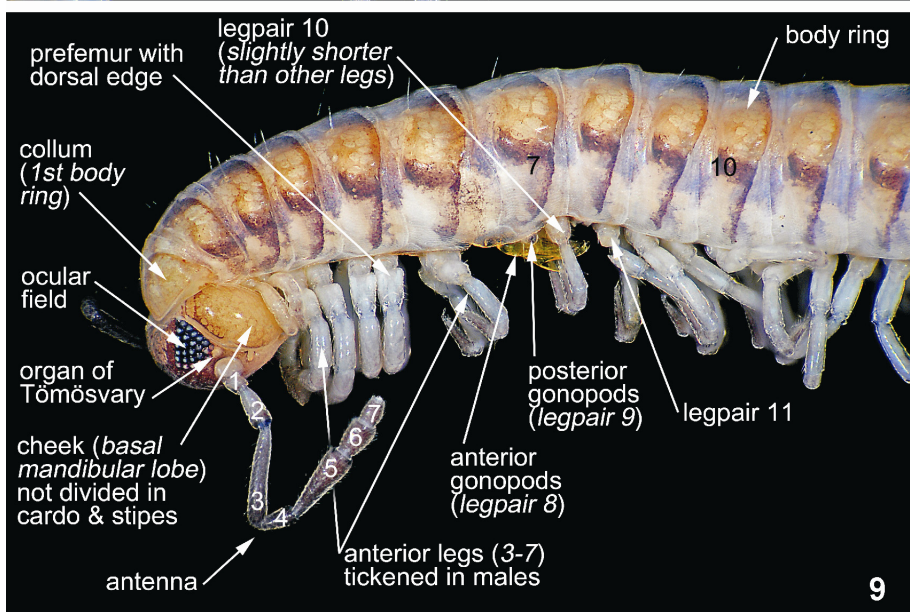
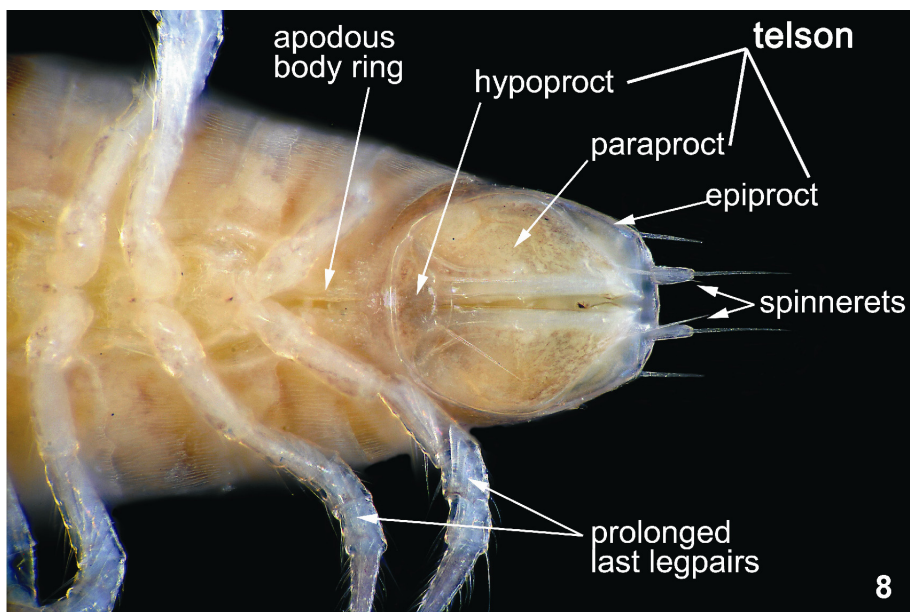


Fig. 8-10. *Ceratosphys picta*. 8. female last body rings ventral. 9. Male anterior part lateral. 10. (Craspedosoma-habitus) male midbody rings dorsal.

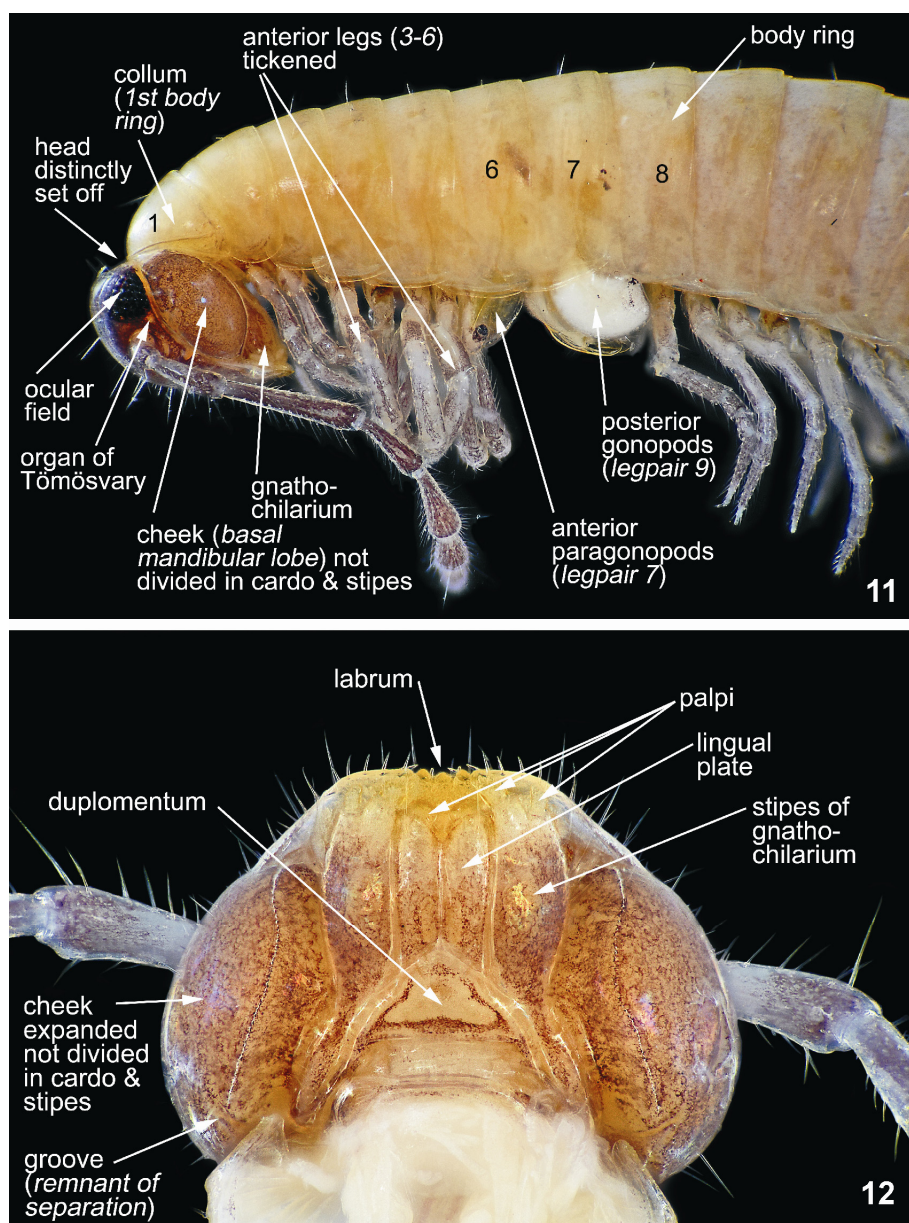


Fig. 11-12. *Chordeuma proximum*, macho: 11. Anterior part lateral. 12. Gnathochilarium ventral.

1.2. Natural History

In the lowlands Chordeumatida usually have an annual life cycle. They are short-lived there with a lifespan of about 6-8 months (Verhoeff, 1926-1932; Dunger, 1983). The juveniles hatch in late summer. First adults usually appear in autumn. Their normal activity period is from late autumn to early spring, depending on the climatic conditions. In a Mediterranean climate they are active mainly in winter, while in temperate climates they show the highest activity in late autumn and again in early spring, after frosts. In areas with snow cover they are also active in the soil below the snow (Meyer, 1990). Depending on the species Chordeumatida either mate in late autumn, lay their eggs and die before the winter, or mate and lay eggs in early spring, dying before the heat of summer. In cooler mountain conditions or in caves Chordeumatida can live two and four years (Meyer, 1990). Silk from the spinnerets is used to weave egg-nests and molting chambers. Chordeumatida seem to feed exclusively on fungi (Verhoeff, 1926-1932; Blower, 1985).

Adult males have a very short lifespan. There are several records of chordeumatidan samples of different habitus from the Iberian Peninsula lacking adult males (Verhoeff, 1893; Machado, 1946; Schubart, 1959), and the author has recognized only females in many samples.

In contrast to other millipede orders Chordeumatida lack defense glands, obviously a secondary loss, making them easy prey. However, they are usually quicker-moving than millipedes with defense glands. Chordeumatidans are also adapted to cold temperatures, being still active near the freezing point, which allows them to be active while predators are slower or immobile (personal observations). As a consequence chordeumatidans seem to be suited to life on high mountains, often above the timberline, or in cool cave systems.

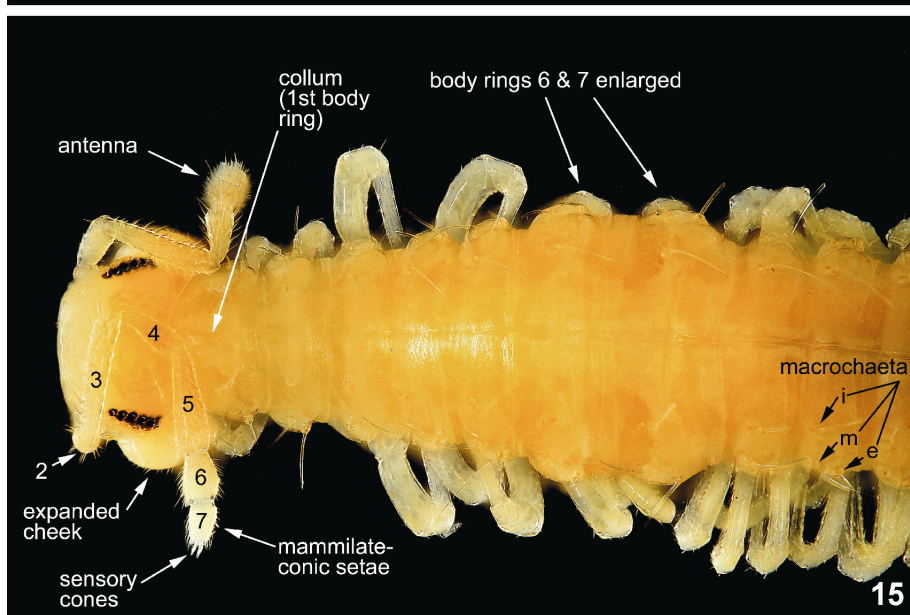
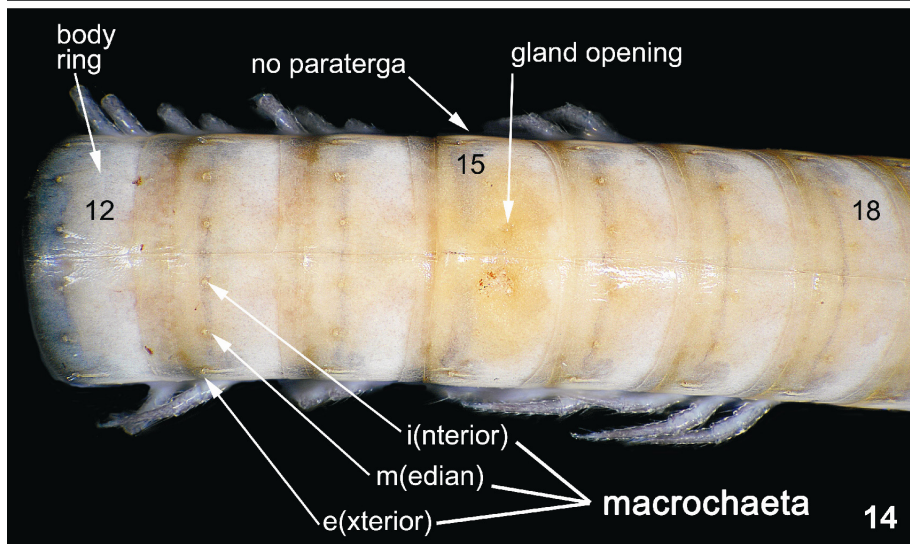
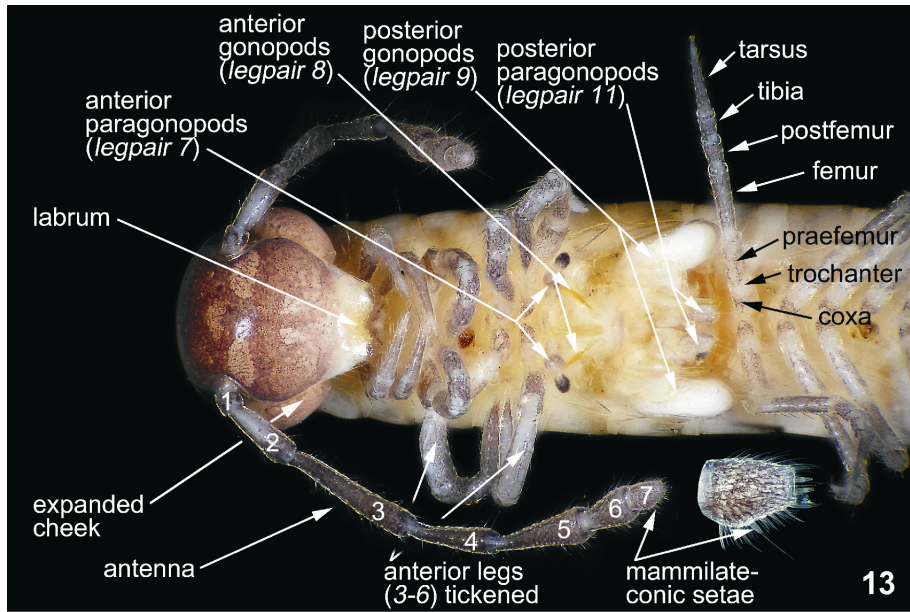


Fig. 13-14. *Chordeuma proximum*, macho: 13. Anterior part ventral. 14. (*Chordeuma-habitus*) midbody rings dorsal. Fig. 15. *Hylebainosoma nontronensis* (*Haasea-habitus*) male anterior part dorsal.

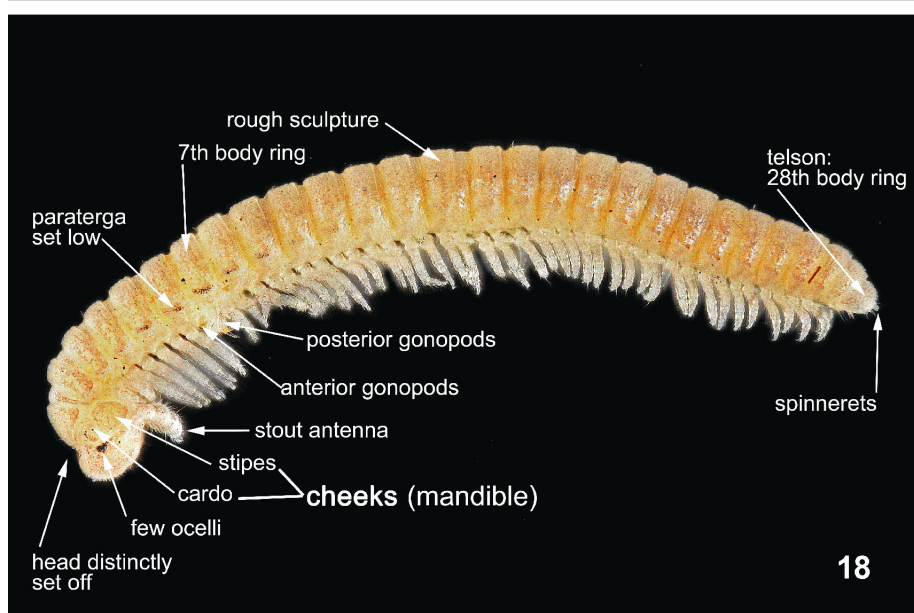
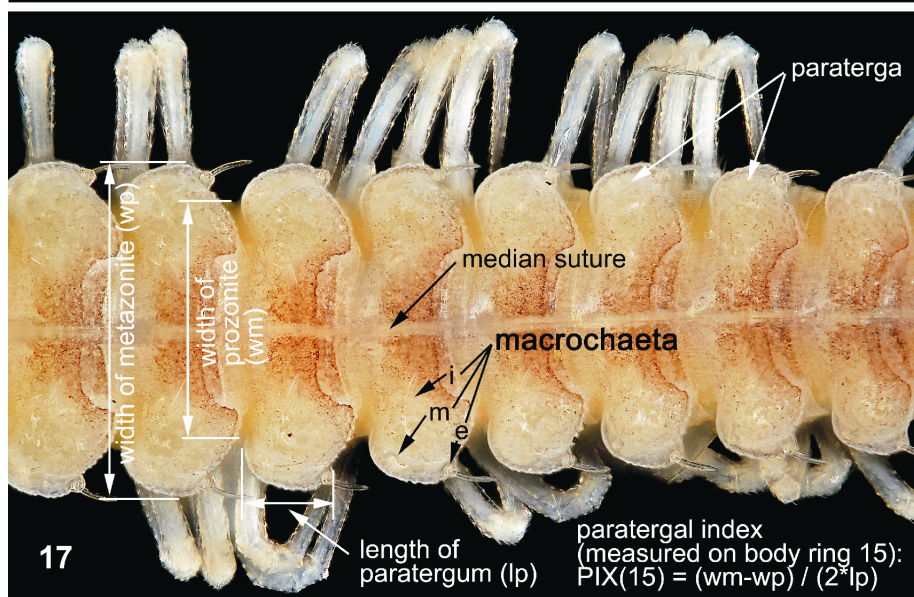
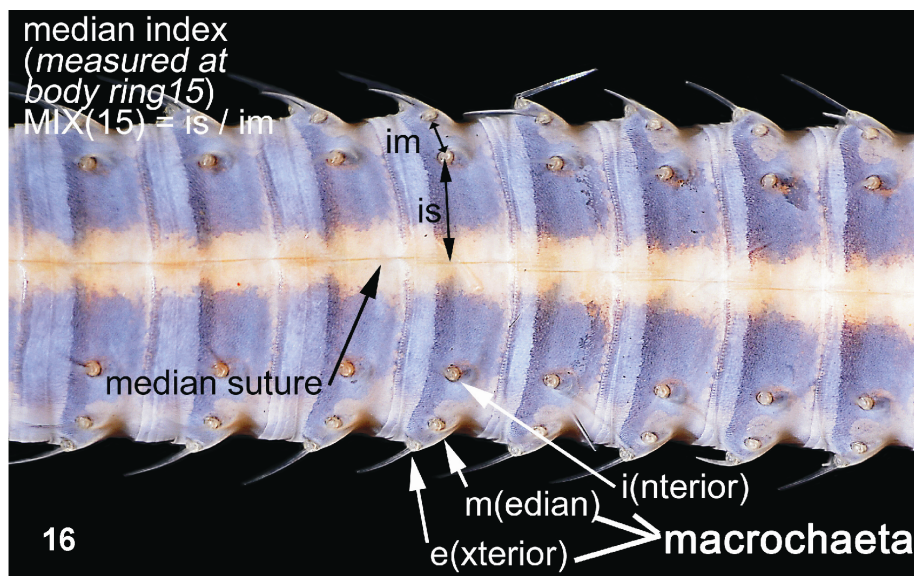


Fig. 16. *Mastigona mutabilis* (Haasea-habitus) female midbody rings dorsal. Fig. 17. *Ochogona caroli* (Ochogona-habitus) male midbody rings dorsal. Fig. 18. *Xystrosoma coiffaiti* (Rhiscosoma-habitus) male lateral.

Like many other Diplopoda most chordeumatidans are petrophilic. This means that they need stones in their environment (Verhoeff, 1926-1932, 1938). Bogs and stone-free plains are hostile areas for many species, being not populated and reacting as separating borders. Thus mountain systems are like island for chordeumatidans, allowing the study of speciation as a special case of island biogeography.

1.3. Distribution

Chordeumatida occur almost worldwide, although most species occur in the Northern Hemisphere. Only from the Afrotropical biogeographic region are there no species currently known (Shelley & Golovatch, 2011). But as the recent discovery of at least 18 species in Madagascar (Mauriès, 1994, 1997) showed, they may have been overlooked. There is also an old note of Brolemann (1920) recording the occurrence of Chordeumatida in Kenya.

1.4. importance for science and applied research

Due to the stenoecous adaptation of many species to cool and cold climatic conditions and their extremely low tendency to disperse, Chordeumatida provide excellent biogeographic indicators for mountain systems and for the reconstruction of glacial refugia (Spelda, 1996).

1.5. Endangered species

At present not much is known about the distribution of most chordeumatidan species, many of which are still only known from the type series. Nevertheless due to the high endemism in the order there may be species which are endangered because of their rarity (category R in the IUCN system).

1.6. Invasive species

As chordeumatidans have a quite small ecological amplitude, there are no really invasive species in the order. A few species have been able to extend their natural range, such as *Ceratosphys poculifer*, which can be found on arable land and which has colonised the Canary Islands (Arndt *et al.*, 2008). Among the more eastern Mediterranean species *Anamastigona pulchella* has been found in several countries in recent years, namely on Madeira (sub *Prodicus attemsi*, see Demange, 1970), in Ireland and even in Germany (Lindner *et al.*, 2010). *Haplobainosoma lusitanum* has been found in the Acores (Demange, 1970). Other chordeumatidans known from outside their natural area are *Craspedosoma rawlinsi*, *Nanogona polydesmoides* and *Melogona* species. It is quite probable that these species might be found also in the Iberian Peninsula.

2. Systematic of the group

No group of millipedes is more difficult to arrange below the ordinal level than the Chordeumatida. The internal classification of the Chordeumatida is simply chaotic (Hoffman, 1980). A thorough revision is urgently needed. The extreme complexity of the gonopods, the base of all classification within this order, has led to a fragmented system with numerous monotypic genera and monobasic families (Shear, 2000). Shear (2000) arranges the 46 families preliminarily in four suborders:

- Chordeumatidea (2 families).
- Heterochordeumatidea (10 families).
- Craspedosomatidea (29 families).
- Striariideae (5 families).

There are only a few external characters which can help to identify suprafamilial taxa, e.g. the lack of the promentum, a part of the mouthplate (gnathochilarium) in the first two suborders; the shape of the single antennomeres; the presence and shape of paraterga and the position of the 3+3 macrochaetae, which sometimes varies between higher taxa. Standard indices to describe the shape of paraterga and the position of macrochaetae have been proposed by Spelda (2001). Most families of Chordeumatida are ill-defined and rather stucked together by homologies or even shared similarities between the genera than by a clear circumscription with autapomorphies.

3. Diversity of the group in the Iberian Peninsula and Macaronesia

The Chordeumatida are the fifth largest order of millipedes, currently comprising more than 1,100 described species (Brewer *et al.*, 2012).

Chordeumatidans occur all over the Iberian Peninsula, but due to their activity peak in cold seasons and the short lifetime of males, records are rare. In recent years many species have been described, especially from caves. Taking the unexplored mountains of northern Spain (Cordillera Cantabrica) and the

species-rich Pyrenees into consideration we might expect that less than 20% of the Iberian fauna is already known. It is curious that the Spanish Pyrenees seem to harbor many fewer described species than the French Pyrenees and a recent treatment of the genus *Pyreneosoma* by Mauriès (2010) has already shown that this may not be the case generally. Promising areas for new discoveries are other central massifs higher than 2000 m, like the Sierras de Gredos, Guadarrama, de la Demanda, del Moncayo or the Picos de Urbion, while the high mountains of southern Spain have already been sampled to some extent. Beside several members of Central European families with diversity hotspots in the Pyrenees and Alps (Chordeumatidae, perhaps also Craspedosomatidae and Haaseidae) the Iberian Peninsula including the whole Pyrenees seems to be mainly inhabited by endemic families.

On the Balearic Islands endemic Chordeumatida have been discovered very recently (Mauriès, 2013). No native Chordeumatida have so far been found in Macaronesia, but *Haplobaiosoma lusitanicum* has been found in the Azores (Demange, 1970), *Anamastigona pulchella* in Madeira (Enghoff, 2008), while *Ceratophys poculifer* is now established in the Canary Islands (Arndt *et al.*, 2008).

Table I. Families of Chordeumatida occurring on the Iberian Peninsula and Macaronesia with species numbers. AZO: Azores, BAL: Balearic islands, CAN: Canary Islands, MIS: Madeira and Selvages, PEN: Iberian Peninsula. End: Endemic species.

Family	PEN		BAL		CAN		AZO		MIS	
	Sp.	End	Sp.	End	Sp.	End	Sp.	End	Sp.	End
Anthogonidae	4	3	–	–	–	–	–	–	–	–
Beticosomatidae	1	1	–	–	–	–	–	–	–	–
Anthroleucosomatidae	–	–	–	–	–	–	–	–	1	1
Chamaesomatidae	20	20	–	–	–	–	–	–	–	–
Chordeumatidae	1	1	–	–	–	–	–	–	–	–
Haplobainosomatidae	14	12	–	–	–	–	1	1	–	–
Lusitaniosomatidae	1	1	–	–	–	–	–	–	–	–
Opisthocheiridae	22	15	2	2	1	1	–	–	–	–
Vandeleumatidae	11	9	–	–	–	–	–	–	–	–

Table II. Checklist of Chordeumatida occurring on the Iberian Peninsula and Macaronesia. AZO: Azores, BAL: Balearic islands, CAN: Canary Islands, MIS: Madeira and Selvages, PEN: Iberian Peninsula. E = endemic. I = Introduced. • = Present.

Family	PEN	BAL	CAN	AZO	MIS
Anthogonidae					
<i>Anthogona variegata</i> Ribaut, 1913	•				
<i>Cranogona cornuta</i> Ribaut, 1913	• E				
<i>Cranogona espagnoli</i> Vicente & Mauriès, 1980	• E				
<i>Vascanthogona vicenteae</i> Mauriès & Barraqueta, 1985	• E				
Anthroleucosomatidae					
<i>Anamastigona pulchella</i> (Silvestri, 1898)					• I
Beticosomatidae					
<i>Beticosoma longipenis</i> Mauriès, 1990	• E				
Chamaesomatidae					
<i>Asturasoma chapmani</i> Mauriès, 1982	• E				
<i>Asturasoma fowleri</i> Mauriès, 1982	• E				
<i>Coiffaiteuma turdetanorum</i> Mauriès, 1964	• E				
<i>Krauseuma viscaianum</i> Mauriès & Barraqueta, 1985	• E				
<i>Marboreuma brouquissei</i> Mauriès, 1988	• E				
<i>Origmatogona catalonica</i> Ribaut, 1913	• E				
<i>Origmatogona jacetanora</i> Mauriès, 1964	• E				
<i>Origmatogona lagari</i> Ceuca, 1988	• E				
<i>Origmatogona tinauti</i> Mauriès, 1990	• E				
<i>Origmatogona toniperezi</i> Mauriès, 2014	• E				
<i>Scutogona ferrolensis</i> Mauriès, 2014	• E				
<i>Scutogona minor</i> Enghoff & Reboleira, 2013	• E				
<i>Scutogona mutica</i> Ribaut, 1913	• E				
<i>Scutogona oculinigra</i> Mauriès & Vicente, 1977	• E				
<i>Scutogona suboculonigra</i> Mauriès, 2014	• E				
<i>Scutogona vivesi</i> Mauriès & Vicente, 1977	• E				
<i>Vascosoma coiffaiti</i> Mauriès, 1966	• E				
<i>Xystrosoma coiffaiti</i> Mauriès, 1964	• E				
<i>Xystrosoma lusitanicum</i> Mauriès, 2014	• E				
<i>Xystrosoma vasconicum</i> Mauriès & Barraqueta, 1985	• E				
Chordeumatidae					
<i>Chordeuma vasconicum</i> Ribaut, 1913	•				

Family	PEN	BAL	CAN	AZO	MIS
Haplobainosomatidae					
<i>Haplobainosoma lusitanum</i> Verhoeff, 1900	• E			• I	
<i>Cantabrosoma rogeri</i> Mauriès, 1971	• E				
<i>Cantabrosoma serrai</i> Mauriès & Vicente, 1977	• E				
<i>Galicisoma biltoni</i> Mauriès, 2014	• E				
<i>Galicisoma desmondkimei</i> Mauriès, 2014	• E				
<i>Pyreneosoma aranense</i> Mauriès, 2010	• E				
<i>Pyreneosoma barbieri</i> (Mauriès, 1971)	•				
<i>Pyreneosoma huescanum</i> Mauriès, 2010	• E				
<i>Pyreneosoma convenarense</i> Mauriès, 2010	• E				
<i>Pyreneosoma grandicoxae</i> Mauriès, 2010	• E				
<i>Pyreneosoma ribauti</i> Mauriès, 1959	•				
<i>Turdulisoma galiciense</i> Mauriès, 2014	• E				
<i>Turdulisoma helenreadae</i> Mauriès, 2014	• E				
<i>Turdulisoma turdulorum</i> Mauriès, 1964	• E				
Lusitaniosomatidae					
<i>Lusitaniosoma machadoi</i> Schubart, 1953	• E				
Opisthocheiridae					
<i>Ceratosphys amoena</i> Ribaut, 1920	•				
<i>Ceratosphys angelieri</i> Mauriès, 1964	• E				
<i>Ceratosphys bakeri</i> Mauriès, 1990	• E				
<i>Ceratosphys deharvengi</i> Mauriès, 1978	• E				
<i>Ceratosphys escolai</i> Mauriès, 2013		• E			
<i>Ceratosphys fernandoi</i> Mauriès, 2014	• E				
<i>Ceratosphys flammeola</i> Mauriès, 2014	• E				
<i>Ceratosphys geronensis</i> Mauriès, 1963	• E				
<i>Ceratosphys hispanica</i> Ribaut, 1920	• E				
<i>Ceratosphys jabaliensis</i> Mauriès, 2013	• E				
<i>Ceratosphys mariacristinae</i> Mauriès, 2013		• E			
<i>Ceratosphys nivya</i> Ribaut, 1927	•				
<i>Ceratosphys nodipes</i> (Attems, 1952)	• E				
<i>Ceratosphys picta</i> Ribaut, 1951	•				
<i>Ceratosphys poculifer</i> (Brölemann, 1920)	• E		• I		
<i>Ceratosphys solanasi</i> (Mauriès & Vicente, 1978)	• E				
<i>Ceratosphys soutadei</i> Mauriès, 1969	• E				
<i>Ceratosphys toniserrai</i> Mauriès, 2013	• E				
<i>Ceratosphys vicenteae</i> Mauriès, 1990	• E				
<i>Hispaniosoma racovitzai</i> Ribaut, 1913	•				
<i>Marquetiella lunata</i> (Ribaut, 1920)	•				
<i>Opisthocheiron elegans</i> Ribaut, 1922	•				
<i>Opisthocheiron penicillatum</i> Ribaut, 1913	•				
<i>Sireuma nobile</i> Reboleira & Enghoff, 2014	• E				
Vandeleumatidae					
<i>Alavasoma muniesai</i> Mauriès & Vicente, 1978	• E				
<i>Guipuzcosoma comasi</i> Vicente & Mauriès, 1980	• E				
<i>Hypnosoma pallidum</i> Ribaut, 1952	•				
<i>Miniosoma litorea</i> Mauriès, 2014	• E				
<i>Strangulogona lugoensis</i> Mauriès, 2014	• E				
<i>Typhlopsychrosoma baeticaense</i> (Mauriès, 2013)	• E				
<i>Typhlopsychrosoma breuili</i> (Mauriès, 1971)	• E				
<i>Typhlopsychrosoma fradiquei</i> (Mauriès & Vicente, 1978)	• E				
<i>Typhlopsychrosoma tarraconense</i> (Mauriès, 1971)	• E				
<i>Vandeleuma hispanicum</i> Ceuca, 1967	• E				
<i>Vandeleuma vasconicum</i> Mauriès, 1966	•				

4. Current state of knowledge of the group

Chordeumatidans were known from the Iberian Peninsula as early as 1893, when Verhoeff, starting with his studies on the fauna of Portugal, recorded the presence of something he called “Atractosoma” (Verhoeff, 1893). However, he did not have males at hand, a requirement for anyone working on this group. For that reason seven years passed until the first Iberian species was described, *Haplobainosoma lusitanum*, probably the same as the species noted (Verhoeff, 1900). In the following decades the German school of myriapodologists did not add much, although Attems (1927, 1952) provided two extensive treatments of the Iberian fauna, adding a new species in the later work. It was the French school (Brölemann 1920; Ribaut 1913, 1920, 1922, 1927, 1951, 1952) that, starting with the French fauna, especially in the Pyrenees, extended their studies into the Iberian Peninsula. Studies of Iberian Chordeumatida are closely

associated with Jean-Paul Mauriès, the “*Sir of euma*” as he was recently honored with the genus *Sireuma* by Reboleira & Enghoff (2014). The name was derived because most of the Mauriès genera have the ending ‘...*euma*’ and it is an anagram of his name. Mauriès (1959, 1963, 1964a, 1964b, 1966, 1968, 1969, 1970, 1975, 1978, 1981, 1988, 1990, 2010, 2013, 2014a, 2014b) has described more than half of the 74 Chordeumatida known from the Iberian Peninsula (table II) including species he described with coauthors (Mauriès & Barraqueta, 1985; Mauriès & Vicente, 1975, 1977; Vicente & Mauriès, 1980) are also counted. A few other workers (Ceuca, 1967; Enghoff & Reboleira, 2013; Schubart, 1953; Gilgado *et al.*, 2015) have contributed descriptions or faunistics to the Iberian fauna. Quite recently an overview of the cave-inhabiting species of Andalucía has been published (Pérez Fernández, 2015)

5. Main available sources of information

5.1. General sources on taxonomy and identification

During the first quarter of the 20th century specialists tried to summarise all available knowledge about Diplopoda. This started with Verhoeff's unfinished book on German Diplopoda (1911-1914), treating many aspects beside systematics. The summarizing effort was continued by Attems (1926) and Verhoeff (1926-1932). More than half a century later Hopkin & Read (1992) published an English treatment of general aspects of Diplopoda. Special treatments of the order Chordeumatida alone have never been produced. Nevertheless the book of Brölemann (1935), treating the Chordeumatida of France provides useful help, as there is much overlap, at least in genera, in the fauna of the Pyrenees. Diplopoda in general and chordeumatidans in particular show a high degree of endemism. This has the advantage that only local or global taxonomic papers have to be checked, while treatments of local faunas even of nearby countries are not very helpful.

5.2. Keys to the families

The global keys to Chordeumatida families in Verhoeff (1926-1932) and Attems (1926a), with some changes by Attems (1959), were produced long ago and are outdated in several parts. Many families have been described since then, but no new family keys are available. Brölemann (1935) keyed the French genera but omitted a family key, but in an earlier work (Brölemann, 1932) he characterized the families by diagnoses.

5.3. Catalogs

Neither global nor local printed catalogs of Chordeumatida are available which cover the Iberian Peninsula and Macaronesia. A catalog exists only for the Nearctic fauna (Hoffman, 1999). There are two cooperating ongoing database projects by Petra Sierwald (*Millibase*) and Jörg Spelda (*SysMyr*, Spelda, 2006; Melzer *et al.*, 2011) with the aim for a global catalog but although providing information for the *Catalog of Life* (Spelda, 2007, <http://www.catalogueoflife.org/>) they have not yet reached a final state for the order Chordeumatida. The same can be said about Fauna Europaea (<http://www.faunaeur.org/>) which provides online information on European species.

6. Acknowledgement

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