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Species composition and biogeographical relationships of the Proseriata (Platyhelminthes) of the Mediterranean Sea

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SUMMARY

A revised and updated checklist of the Proseriata of the Mediterranean is presented. At least 140 species are recorded from the basin, only 76 of which have been formally described. Lack of research in entire sectors of the Mediterranean, and the recent discovery of a diverse and still undescribed sublittoral proseriate fauna, suggest that the figure given may be a minor fraction of the actual number of the species of the group. Most of the species appear endemic of the Mediterranean, with only a few species known so far from neighbouring Atlantic coasts. Analysis of the data set reveals a significant geographical structuring, with a major faunistic disjunction between Alboran Sea and the rest of the basin, and among western and eastern Mediterranean. The existence of numerous species exclusive of the Levant Sea may hint at the presence of cryptogenic species, given the exceedingly limited knowledge of tropical faunas of Proseriata and of 'microturbellarians' in general.

INTRODUCTION

The order Proseriata (Platyhelminthes: Neophora) was traditionally considered as the sister group, prevalently marine and miniaturized for life in the interstices of the sediment, of the comparatively large Tricladida (the well-known planarians) (Sopott-Ehlers, 1985). Recent upsurge of molecular data failed to confirm this assumption, and it is now clear that the two taxa are unrelated (Carranza et al., 1998; Littlewood et al., 1999; Litvaitis and Rohde, 1999). Recently, the monophyly of the Proseriata has been confirmed, as well as their basal position within the Neophora (Littlewood and Olson, 2001). However, sister group relationships of the taxon are still unclear.

The Proseriata are comprised of two suborders, the Unguiphora, including the single family Nematoplanidae, and the Lithophora, including the Monoce-

lididae, Coelogynoporidae, Archimonocelididae, Otoplanidae, and Otomesostomidae (Curini-Galletti, 2001). While most families appear monophyletic both morphologically and molecularly, the monophyly itself of the two suborders (Unguiphora and Lithophora), which is strongly supported morphologically, has not been convincingly proved by molecular data (Littlewood et al., 2000).

At present, about 400 species of Proseriata have been described, the vast majority of which occurs in marine interstitial habitats (Curini-Galletti, 2001). As most research on the group has been performed in boreal areas (particularly in Northern Europe), and knowledge of tropical faunas is particularly limited, this number is likely to represent only a minor fraction of the actual number of the species of the group. Furthermore, the recent finding of an exceedingly rich and diversified proseriate fauna, still largely undescribed, in areas of the southern hemisphere, suggests that present taxonomic arrangement might be inadequate to encompass the diversity of the group.

Proseriata are particularly common in coastal, high-energy habitats (Reise 1984, 1988; Martens and Schockaert, 1986), where they may be among the dominating organisms, characterizing entire interstitial assemblages (e.g. the "Otoplana-zone") (Remane, 1933). Proseriata are carnivorous, and their impact on meiofaunal communities might be considerable (Murina, 1981). Furthermore, it has been suggested that predation by Proseriata and other Platyhelminthes on temporary meiofauna (e.g. newly settled macrofauna larvae) may eventually structure macrofaunal communities (Danovaro et al., 1995; Watzin, 1983).

Despite the ubiquity of Proseriata, and their ecological relevance, their study, as is the case with most free-living Platyhelminthes, which necessitate of particular taxonomic expertise, has been hit by present 'taxonomy crisis'. Research on Mediterranean Proseriata, which has been fairly active, with the involvement of numerous researchers, around mid XX century, and well into the seventies (Middelburg, 1908; Palombi, 1926; Meixner, 1938, 1943; Ax, 1956a,b, 1959a,b, 1963; Riedl, 1959; Mack Fira, 1968; Lanfranchi, 1969, 1978; Ax et al., 1978) declined, at least in terms of number of researchers, in latest decades (Martens, 1984; Martens and Curini-Galletti, 1987, 1993, 1994, 1999; Curini-Galletti and Martens, 1992, 1995; Curini-Galletti and Mura, 1998), with most papers devoted to the single family Monocelididae. At present, Proseriata are among the few orders of free-living Platyhelminthes where some taxonomic research is still carried out.

The only existing checklist of the species of Proseriata of the Italian coasts included 59 species (Bello et al., 1995). Subsequent publications and recent findings made the checklist somewhat obsolete. The main aim of present contribution is thus to provide an updated (and emended) list of the Proseriata of the Mediterranean.

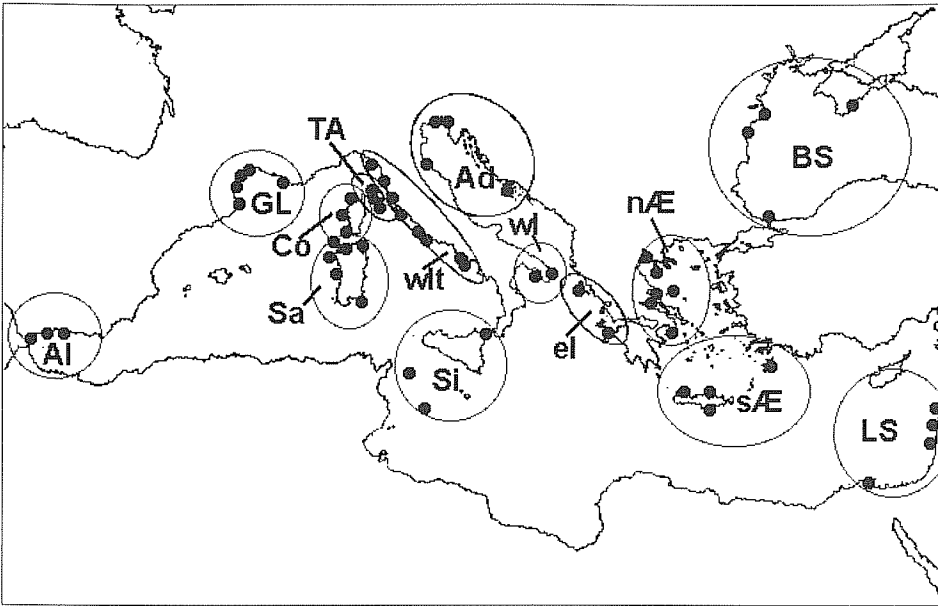


Fig. 1 - Mediterranean areas sampled for Proseriata. Reports (●) are based on literature and personal data. Sectors are abbreviated as follows: Ad = Adriatic Sea; AI = Alboran Sea; BS = Black Sea; Co = Corsica; eI = eastern Ionian Sea; GL = Gulf of Lions; LS = Levant Sea; nAE = northern Aegean Sea; Sa = Sardinia; sAE = southern Aegean Sea; Si = Sicily; TA = Tuscan Archipelago; wI = western Ionian Sea; wItr = western peninsular Italy.

MATERIALS AND METHODS

The checklist (Tab. I) is based on existing literature (most of which is cited above), with the addition of new findings by the authors and reports of a number of species still awaiting formal description, whose material is present in the first author's collection. When no reference source is quoted, species reports discussed in the text refer to unpublished data of the authors. The inclusion of such a vast bulk of undescribed species (most of which are nonetheless clearly ascribable to genus level) and unpublished distributional data has been deemed necessary in order to provide the broadest representation possible of the diversity and distribution of the Proseriata of the Mediterranean. Furthermore, it has been decided to rule out reports of taxa presently perceived as sibling species complexes, when adequate karyological and/or genetic information, necessary for proper species attribution, is lacking: This is the rationale underlying the absence of reports from many areas of the ubiquitous and generally abundant members of the *Monocelis lineata* (Müller, 1774), *M. longiceps* (Ant. Duges, 1830), and *Pseudomonocelis ophiocephala* (Schmidt, 1861) complexes.

Proseriata have been reported from quite a few Mediterranean localities (Fig. 1). Sampling efforts varied from prolonged and intensive to the collection of a single

jar of sediment, or, in cases, to single-species reports. For biogeographical analysis, stations have been grouped into areas, as far as possible (due to the limitation of the available reports) coincident with the main biogeographical sectors recognized for the Mediterranean (see for example Bianchi and Morri, 2000). The resulting sectors (Fig. 1) patently suffer from the heterogeneity of sampling effort, which has been maximum in central and northern Mediterranean, and least in southern and extreme western areas. Comparisons of faunistic composition among areas were based on Bray-Curtis similarity values (Bray and Curtis, 1957), calculated on all species within each sector (PRIMER 5 software package from Plymouth Marine Laboratory, UK). Data transformation was accomplished by the option "presence/absence". Differences among sectors were represented by non-metric multidimensional scaling ordinations (MDS). Stress values are shown for each MDS plot to indicate the goodness of representation of differences among sectors. Sectors were then grouped according to their geographical position (western/central/eastern Mediterranean). Analysis of similarity (ANOSIM, Clarke, 1993) was used to test the significance of differences among groupings. Pairwise tests among groupings were deemed significant at the 3% threshold.

RESULTS

One hundred-forty proseriate species are known at present for the Mediterranean, only 76 of which have been formally described. Of the 59 marine species reported by Bello et al. (1995), the occurrence in Mediterranean of *Invenusta aestus* Sopott-Ehlers, 1976 could not be confirmed. Furthermore, *Hypotrichina circinnata* Calandruccio, 1897 should be considered as *species dubia* (see Ax, 1956a). Number of species varies among sectors: not surprisingly, areas more intensively sampled (such as Sardinia) yielded the highest numbers of species.

Monocelididae, with 70 species, are by far the largest family, followed by the Otoplanidae, with 37 species – but, again, the ratio is probably biased by specific interests of researchers (as reflected by the number of papers devoted to each family), and the Otoplanidae may prove far richer than understood at present.

Analysis of the matrix of similarity revealed a strong and highly significant MDS structuring, with the Alboran Sea quite distinct from the rest of the Mediterranean sectors, which knit closely together (Fig. 2a). Further analyses were thus devoted to examine the relationships among the latter sectors. Removal of Sicily, which has been grossly undersampled and is deemed as exceedingly unrepresentative of the diversity of the area, and of the likewise species-poor Black Sea, resulted in a significant MDS structuring (Fig. 2b). The hypothesis of the existence of three distinct groupings of sectors (western: Co, GL, Sa, TA, wI, wIt; central: Ad, eI; eastern: LS, nÆ, sÆ) (see legend of Fig. 1 for abbreviations of

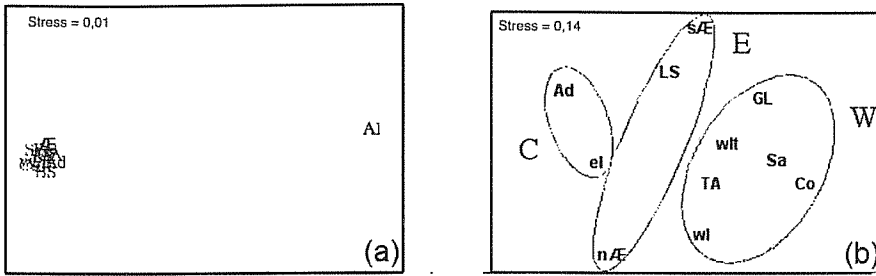


Fig. 2 - Non-metric multidimensional scaling ordinations of (a) all sectors and (b) after removal of AI, Si and BS. Abbreviations as in Fig. 1. Groupings in (b) are indicated as W (western sectors), C (central sectors), and E (eastern sectors).

sectors) was supported (ANOSIM, $R = 0.694$; $p = 0.3\%$). Pairwise tests among groupings revealed a significant difference only among western and eastern sectors (significance level 1.2%). Inclusion of wl among central sectors did not affect the significance of results (ANOSIM, $R = 0.53$; $p = 0.3\%$).

DISCUSSION

With approximately half of the species still undescribed, it is apparent that the sheer taxonomic work yet to be done on Mediterranean proseriates is daunting. Furthermore, entire sectors of the Mediterranean have been either grossly undersampled or totally neglected – such as most of the North African shores. Notwithstanding the obvious limitations of the data set, a few biogeographical and evolutionary inferences can be drawn:

The endemic component

More than 90 % of the species reported in Tab. I are known so far from the Mediterranean only. While Mediterranean proseriate fauna appears clearly distinct from the comparatively well-known North Sea fauna (cfr. Sopott, 1972), assessment of the endemicity rate of the basin is severely hampered by lack of data on Lusitanic areas. However, distinctiveness of the Alboran Sea from the rest of the Mediterranean (Fig. 2 a) may be assumed to imply that the endemism rate of the Mediterranean proseriate fauna is indeed relevant. To this, it may be added that wide ranging European species such as *Monocelis lineata* have been shown to include vast complexes of sibling species, and that Atlantic and Mediterranean populations do not appear to be conspecific (Casu et al., 2002), suggesting caution on the attribution of the same taxon to ‘similar’, geographically disjunct populations.

Many genera, which most significantly contribute to the richness of the Mediterranean fauna, are poorly represented on Atlantic coasts. The genus

Archilina Ax, 1959, of which no species are known from west European coasts, is represented by at least 12 species in the Mediterranean, whose common occurrence is a characteristic feature of shallow, low energy Mediterranean habitats (Curini-Galletti and Martens, 1990). The genus *Duplominona* Karling, 1966, widespread in the tropics, includes at least 13 species in the Mediterranean, but one species only both in the Canary Is. and in the North Sea (Ehlers and Ehlers, 1980; Martens, 1983). The striking genus *Calviria* Martens and Curini-Galletti, 1993 is only known so far from the Mediterranean, where it is represented by three species, with restricted distributions (Martens and Curini-Galletti, 1993). On the contrary, the genus *Coelogyndopora* Steinböck, 1924 is represented by 15 species on European Atlantic coasts, but by 5 species only in the Mediterranean. Ecological factors may constrain the diffusion of the genus, which appears partial to lower intertidal to upper subtidal areas, in high-energy conditions, and is particularly species-rich on the extensive sandy beaches of the North Sea (Sopott, 1972).

Mediterranean proseriate fauna is clearly not homogeneous, with a major faunistic disjunction between the Alboran Sea and the rest of the basin, and among western and eastern Mediterranean (Fig. 2 a,b). A clear west/east differentiation is also apparent in genetic studies of wide-ranging species (Casu et al., 2001, 2002). Furthermore, when phylogenetical relationships of Mediterranean species have been drawn, the existence of species pairs, with one member in western and one in eastern Mediterranean, has been documented (Martens and Curini-Galletti, 1994; Casu et al., 2001). It seems plausible to hypothesize that the different ecological conditions of the two basins, exacerbated during glacial periods, when the physical connection itself between the basins is reduced (Por, 1989), coupled with the exceedingly poor dispersal power of Proseriata, may have resulted in a genetic differentiation between western and eastern populations, in cases, eventually, leading to speciation.

The Atlantic component

Not surprisingly, a component of the Mediterranean fauna is shared with neighbouring Atlantic. This fraction, which is minor at present, is likely to increase when the Lusitanic fauna is better understood. Exemplary is the distribution of *Vannuccia campana* Ehlers and Ehlers, 1980, common and widespread in the Mediterranean, and originally described for the Canary Islands (Ehlers and Ehlers, 1980) – an area which is known so far for few samples of sediment only. Species widespread on Atlantic European coasts appear often limited to western Mediterranean, as the cases of *Nematoplana coelogyndoporoides* Meixner, 1938, only known from Alboran Sea, and *Polystyliphora filum* Ax, 1958, found in western Sardinia. In other instances, reports of Atlanto-Mediterranean, ‘variable’ species may point to the existence of sibling species

complexes, as in the case of *Monocelis lineata* cited above. *Coelogygnopora schulzii* Meixner, 1938 appears likewise exceedingly variable, and genetic studies appear indispensable to ascertain the real status of Mediterranean populations.

There are clear evidences, on the other hand, of phylogenetical relationships among Mediterranean and Atlantic taxa. Again, most evidences are from western Mediterranean. The genus *Monocelopsis* Ax, 1951, represented by few north Atlantic species, at least one of which is very common in the intertidal zone of the North Sea (Curini-Galletti and Martens, 1990) includes an undescribed species in the Alboran basin. The genera *Carenscoilia* Sopott, 1972 and *Cirrifera* Sopott, 1972, both well represented in Atlantic, include a single species each in western Mediterranean. The latter species appears to be the sister species of the boreal *Cirrifera dumosa* Sopott, 1972 (Curini-Galletti, in prep.). Sister species relationships are also hypotesizable for the Atlantic and Alboran *Nematoplana coelogygnoporoides* and *N. riegeri* Curini-Galletti and Martens, 1992, widespread in the rest of the Mediterranean (Curini-Galletti and Martens, 1992).

The Sarmatic component (?)

The genus *Promonotus* Beklemishev, 1927, as redefined by Martens and Curini-Galletti (1999), includes a clearly monophyletic unit, consisting of *P. orientalis* Beklemishev, 1927 (Aral Sea); *P. hyrcanus* Beklemishev, 1927 (Caspian Sea); *P. ponticus* Ax, 1959 (Black Sea and central-eastern Mediterranean) and *P. schultzei* Meixner, 1943 (Baltic, Atlantic and Mediterranean, excluding the easternmost sectors). All species are exclusively found in brackish water habitats. Within the complex, *P. orientalis*, *P. hyrcanus*, and *P. ponticus* share a peculiar feature (reduction to loss of distal spines in the copulatory organ), which is likely derived from a common ancestor. Species distributions and habitat make difficult to exclude Parathethys from the ancestral species' range, with speciation events following fragmentation of the Sarmatic basin. Subsequent dispersal may have resulted in present-day distributions. It is worth mentioning that the *Promonotus* species mentioned here are the only Proseriata known for Caspian and Aral seas. The Black Sea, on the contrary, harbours a rather diversified fauna, including members of the species complexes of *Monocelis lineata*; *M. longiceps* and *Pseudomonocelis ophiocephala* (Ax, 1959a; Mack Fira, 1968; Murina, 1981) not included in the checklist for the reasons mentioned above.

The Tethyan component (?)

A few Mediterranean species appear related to circumtropical or Indo-Pacific species groups. In most cases, these species are confined to the warmest portion of the Mediterranean, i.e the Levant Sea, as *Nematoplana caesarea* Curini-Galletti and

Martens, 1992, related to the Caribbean *N. caribbea* Curini-Galletti and Martens, 1992 and to an undescribed species from the Great Barrier Reef (see Curini-Galletti et al., 2002). Similarly, a new archimonocelid genus is known so far for a few species from northeastern Australia and for two species from Israel. At least one case concerns western Mediterranean: a striking new species of the genus *Polystylyphora* Ax, 1958 found in subtidal samples from the Tuscan Archipelago appears as the sister species of the Red Sea *P. marisrubri* Curini-Galletti and Martens, 1991.

There are no evidences supporting an *in situ* survival of the contingent (should it really exist, see below) during the Messinian period, and it might well derive from West African refuge areas. It is worth noting that, at the moment, proseriate fauna of the entire continental shelf of West Africa is wholly unknown.

The exotic component (?)

A possible case of introduced species is represented by the finding of *Coelogyropora biarmata* Steinböck, 1924 in the Black Sea (Ax, 1959a; Valkanov, 1957; pers. collection). The species is widely distributed in northern Atlantic, from the Baltic to New England, in marine to brackish conditions (Steinböck, 1932; Sopott, 1972; Karling, 1974; Riser, 1981; Krumwiede and Witt, 1995). The southernmost station known along European coasts is Ambleteuse (northern France)(pers. collection). The two specimens from Odessa studied by the first author appeared morphologically and karyologically undistinguishable from Baltic specimens examined; however, genetic studies aimed to assess conspecificity of populations are lacking. Provided a single species is indeed involved, the gap in distribution, given also the comparative obviousness of the species, appears difficult to explain. However, during last century, the Black Sea has been colonized by a number of exotic species, mainly from northern Atlantic (Zolotarev, 1996), and *C. biarmata* may further witness the atlantization process of the basin. It is worth noting that boreal, intertidal species of proseriates may survive for days in semi-wet sand (Sopott-Ehlers, pers. com.), and chances of their transportation in sediment used to maintain polychaetes used as bait, should be investigated.

There are so far no evidences of lessepsian migration in Proseriata. This may seem surprising, given continuity of habitat (sandy substrates are prevalent in the Suez canal for most of its length), direction of current, and present salinity range (Por, 1978). Indeed, the Levant Sea harbours a distinctive fauna, with the presence of a remarkable contingent of warm-water taxa (see above) – to the species listed, it should be added the prevalence of *Duplominona* species in shallow-water habitats, a feature shared with the Caribbean and tropical Indo-Pacific (Karling et al., 1972; Ax and Ax, 1977; Karling, 1978; Ax and Sopott-Ehlers, 1985; Martens and Curini-Galletti, 1989). None of these species are known for the Red Sea, and a ‘tethyan’ origin has been here proposed for them. However, it must

be noted that knowledge of Red Sea proseriate fauna is limited to the Eilat area. Albeit sampling has been locally intensive, the species list obtained may be considered as hardly representative of the diversity of the entire Red Sea, which might indeed harbour the 'tropical' taxa found on the levantine coast.

This case highlights the risk that, with the increase of occasions of transport, cryptogenic species (i.e. species whose geographic origin cannot be assessed, due to the absence of previous taxonomic and biogeographical knowledge) (Carlton, 1996) may become a widespread category in groups like Proseriata, which lack almost entirely of extensive, regional checklists. This may render future evolutionary and biogeographical reconstructions virtually impossible.

CONCLUSIONS

What exposed above highlights the poor state of knowledge of the Proseriate fauna of the Mediterranean. Not only, in fact, is the Mediterranean inadequately sampled (especially in southern and western-most areas), but samples are usually limited to midlittoral and upper infralittoral habitats. Recently, the examination of few jars of sediment collected inside a marine cave in north western Sardinia revealed an unsuspected species richness and diversity of Proseriata, pointing to the existence of a so far practically unexplored 'deep-water' fauna. Such unsatisfactory state of knowledge is shared with most, if not all, marine meiofaunal taxa. This lack of knowledge is particularly regrettable, considering present, widespread phenomena of 'global change'. Meiofauna taxa, characterized by short life cycles, fast metabolic rates, limited (at least in some cases) distributions, and lack of dispersal larval stages, appear as ideal candidate to follow the evolution of the process in the sea. However, for most taxa, regional faunistic inventories, which will enable to monitor future changes in species composition and distribution, are completely lacking. Furthermore, as marine conservation issues are gaining more and more importance, one may ask whether any part of the marine environment can be managed in an ecologically sustainable manner if the bulk of the fauna is ignored (Hutchings and Ponder, 2003). Without a change of policy, which favours taxonomic studies, and especially those devoted to 'inconspicuous' taxa, such as the whole of meiofauna, the issues above are unlikely to be ever addressed.

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Tab. I - Checklist of the Proseriata of the Mediterranean. See legend of Fig. 1 for abbreviations of geographical sectors.

	Al	GLSa	Co	wI	TASi	wI	Ad	eI	n/E	s/E	LS	BS
Order Proseriata Meixner, 1938												
Suborder Lithophora Steinböck, 1925												
Fam. Coelogygnoporidae Karling, 1966												
<i>Calviria solaris</i> Martens & Curini-Galletti, 1993			X	X	X	X		X				
<i>Calviria sublittoralis</i> Martens & Curini-Galletti, 1993			X	X								
<i>Calviria banyulensis</i> Martens & Curini-Galletti, 1993		X	X									
<i>Carenscoilia</i> sp. 1			X									
<i>Cirrifera</i> sp. 1			X									
<i>Coelogygnopora biarmata</i> Steinböck, 1924												X
<i>Coelogygnopora gallica</i> Sopott-Ehlers, 1976		X	X									
<i>Coelogygnopora schulzii</i> Meixner, 1938			X							X		
<i>Coelogygnopora</i> cf. <i>gynocotyla</i> Steinböck, 1924		X	X	X	X	X		X		X	X	
<i>Coelogygnopora</i> sp. 1			X									
Coelogygnoporidae n.gen. n.sp.			X									
<i>Invenusta</i> sp. 1				X	X							X
<i>Vannuccia campana</i> Ehlers & Ehlers, 1980		X	X		X	X		X	X	X		
<i>Vannuccia</i> sp. 1												X
<i>Vannuccia</i> sp. 2			X		X			X				
<i>Vannuccia</i> sp. 3												X
Fam. Archimonocelididae Meixner, 1938												
<i>Archimonocelis carmelitana</i> Martens & Curini-Galletti, 1993			X		X			X				X
<i>Archimonocelis crucifera</i> Martens & Curini-Galletti, 1993		X	X		X	X					X	X
<i>Archimonocelis mediterranea</i> Meixner, 1938				X	X							
<i>Archimonocelis meixneri</i> Martens & Curini-Galletti, 1993			X	X								
<i>Archimonocelis staresoi</i> Martens & Curini-Galletti, 1993			X	X	X	X		X		X		X
Archimonocelididae n.gen. sp. 1												X
Archimonocelididae n.gen. sp. 2												X
Fam. Monocelididae Hofsten, 1907												
Subfam. Duplomonocelidinae Litvaitis,												
Curini-Galletti, Martens & Kocher, 1996												
<i>Archilina biselenifera</i> Martens & Curini-Galletti, 1994					X							
<i>Archilina brachycirrus</i> Martens & Curini-Galletti, 1994			X	X		X						
<i>Archilina caliban</i> Martens & Curini-Galletti, 1994							X					X
<i>Archilina deceptor</i> Martens & Curini-Galletti, 1994		X	X	X	X	X			X			
<i>Archilina endostyla</i> Ax, 1959		X		X	X			X	X		X	X
<i>Archilina etrusca</i> Martens & Curini-Galletti, 1994			X	X		X	X					
<i>Archilina israelitica</i> Curini-Galletti & Martens, 1995												X
<i>Archilina palestina</i> Martens & Curini-Galletti, 1994												X
<i>Archilina selenifera</i> Martens & Curini-Galletti, 1994										X		
<i>Archilina</i> sp. 1								X				
<i>Archilina</i> sp. 2			X									
<i>Archilina</i> sp. 3			X									
<i>Archilina</i> sp. 4					X							
<i>Archiloa petiti</i> Ax, 1956		X	X		X	X	X	X				X
<i>Boreocelis filicauda</i> Westblad, 1952			X	X								
<i>Boreocelis urodasyoides</i> Ax, 1963				X	X							
<i>Boreocelis</i> sp. 1												X

Al GLSa Co wItTASi wí Ad eI n/EsÆ LS BS

<i>Nematoplana riegeri</i> Curini-Galletti & Martens, 1992		X	X			X			X	
<i>Nematoplana</i> sp. 1	X	X	X							
<i>Nematoplana</i> sp. 2									X	
<i>Nematoplana</i> sp. 3									X	
<i>Nematoplana</i> sp. 4		X								
<i>Polystyliphora filum</i> Ax, 1958		X								
<i>Polystyliphora</i> sp. 1				X						