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Global diversity of ostracods (Ostracoda, Crustacea) in freshwater

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Abstract There are close to 2,000 subjective species and about 200 genera of Recent non-marine Ostracoda. Together, Cyprididae (1,000 spp.) and Candonidae (c. 550 spp.) represent more than 75% of the extant specific diversity; the remaining 11 families comprise the other 25% of the species. The Palaearctic region has the highest absolute non-marine ostracod diversity, followed by the Afrotropical. The Australian region has the highest relative endemicity. About 90% of the species and 60% of the genera occur in one zoogeographical region only. This means that all the biological mechanisms which lead up to efficient dispersal and which are present in at least part of the non-marine Ostracoda (e.g. brooding, drought-resistant eggs, parthenogenesis) have not induced common cosmopolitan distributions in ostracods. Several habitats are hotspots for ostracod diversity and endemicity. For example, it appears that the ancient lakes hold up to 25% of the total ostracod diversity. Other speciation-prone habitats are groundwater, temporary pools and Australian salt lakes; in the latter two instances, cladogenesis has often been paralleled by gigantism. The present ostracod diversity results from 9 to 12 separate invasions of the non-marine habitat, starting about 400 Myr ago. Genetic diversity can be very different in different species, mostly, but not always, related to reproductive mode.

Keywords Ostracoda · Freshwater · Species · Genera · Ancient lakes

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Freshwater Animal Diversity Assessment

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Introduction

Mussel-shrimps, or Ostracoda, are small, bivalved Crustacea. Their calcified carapaces have an average length of c. 1 mm and completely envelop the reduced body (Fig. 1). Ostracods are very common in most inland waters, where they abound in the benthic and periphytic animal communities, but they also occur in marine, interstitial and even (semi-) terrestrial environments. Ostracoda are of great interest as a model group in various ecological and evolutionary studies. This is mainly so because the

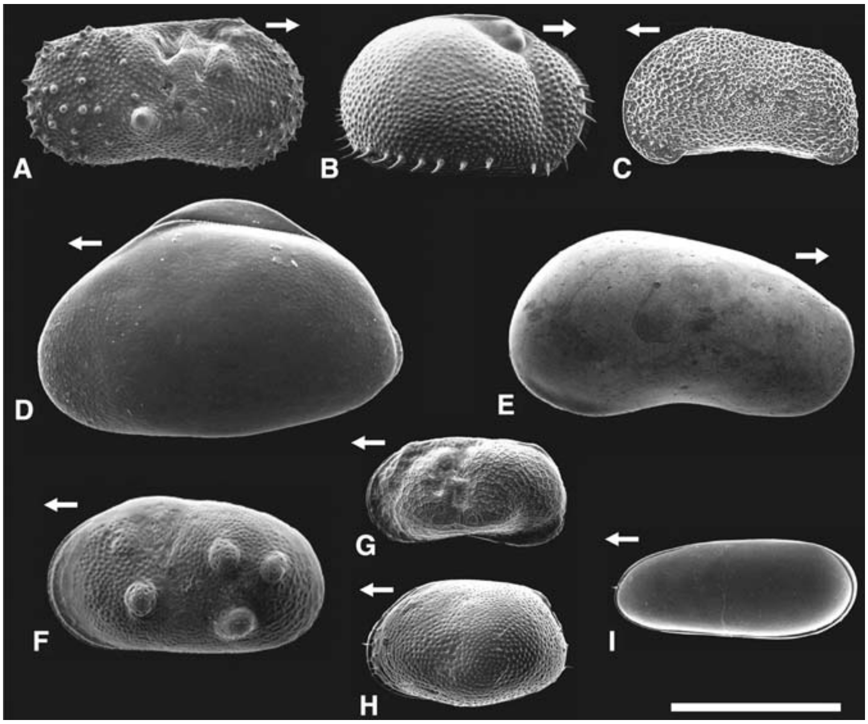

Fig. 1 External views of carapaces of main extant non-marine ostracod groups. A, *Ilyocypris* (Ilyocyprididae, Cypridoidea); B, *Centrocypris* (Notodromadidae, Cypridoidea); C, *Potamocypris* (Cyprididae, Cypridoidea); D, *Cyprinotus* (Cyprididae, Cypridoidea); E, *Candona* (Candonidae, Cypridoidea); F, *Cyprideis* (Cytherideidae, Cytheroidea); G, *Limnocythere* (Limnocytheridae, Cytheroidea); H, *Metacypris* (Limnocytheridae, Cytheroidea); I, *Darwinula* (Darwinulidae, Darwinuloidea). Scale bar = 0.5 mm

calcified valves of non-marine ostracods can be very common in lake sediments and this adds a real-time frame to the evolution of ostracod lineages as well as of their biological traits. At present, ostracods are popular model organisms for research on the evolution of reproductive modes (Martens, 1998a) and as proxies for climate and ecosystem changes (Holmes & Chivas, 2002).

There are three main lineages of recent non-marine ostracods (Fig. 2), all belonging to the Podocopida. All three originated in the Palaeozoic and are between 450 and 360 million years old. The Cytheroidea are mostly marine, but have several non-marine incursions of which the Limnocytheridae are the most common. The Darwinuloidea, with one extant family, are fully non-marine, but have only about 30 extant species. The largest group, the Cypridoidea, comprises 4 families.

In spite of their general presence in aquatic habitats, there still appears to be some aversion towards the study of Ostracoda, when compared to other meiobenthic crustaceans. This has two main reasons. Firstly, correct specific and even generic identification of ostracods generally requires a full dissection. To acquire the skills to do this properly can easily take several months. Secondly, there are almost no identification books or illustrated specific keys (with few exceptions, mostly e.g. Meisch, 2000 for western Europe), so that identification of animals from most zoogeographical regions requires a full set of copies of all (original) descriptions, which are often difficult to track down.

The present article sets out to analyse the extant specific and generic diversity of non-marine Ostracoda, based on literature reviews. However, there are still large numbers of undescribed species, either because certain regions have been unexplored (e.g. the Amazon floodplain), or because known endemic faunas have not yet been described (e.g. Lake Malawi, from which dozens of new, but thus far undescribed, species are known, Martens, 2003), or because many cryptic species remain unrecognized

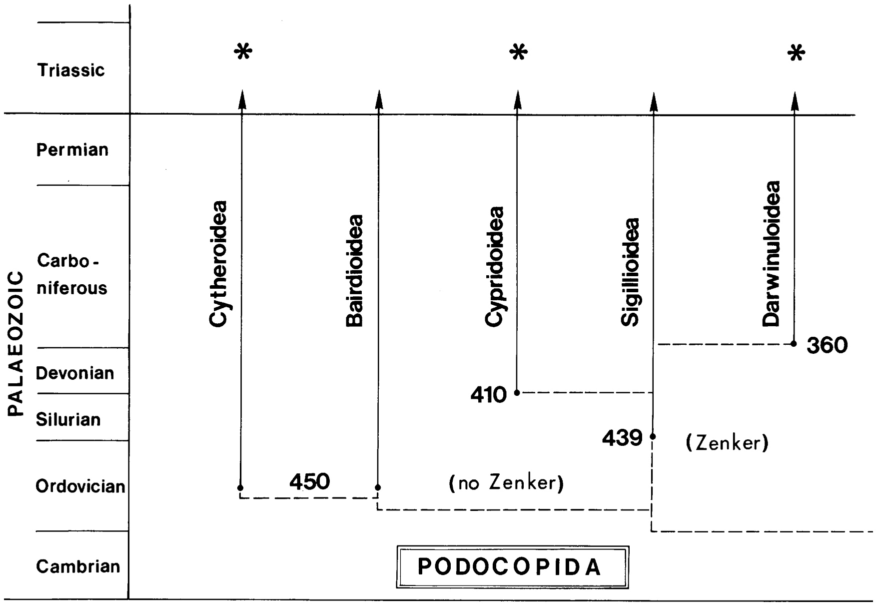

Fig. 2 Origin of the main ostracod lineages in the Podocopida. Asterisks indicate the three lineage with non-marine radiations. Zenker/no Zenker refers to presence or absence of Zenker organ in males. (After Martens, 1998a)

(e.g. in the Lake Baikal *Cytherissa* species flock, Schön & Martens, unpublished). The present survey is therefore only a snapshot in time.

The present data are compiled from the Cologne Database (Kempf, 1980a, b, 1991a, b and subsequent unpublished up dates). These lists include all Phanerozoic non-marine ostracod genera and species, both living and fossil. Moreover, these lists are fully objective, i.e. all published combinations of generic and specific names are included, while also synonymies are listed independently. Extraction of the information needed for the present article, therefore, required four steps. Firstly, Recent taxa had to be separated from fully fossil ones, as the present analyses deal with Recent (extant) taxa only. Secondly, the objective nomenclatorial lists had to be converted into subjective lists, i.e. lists with *real* number of described species in the most recent nomenclature. This is a cumbersome and continuously ongoing process, for which a good deal of the literature has to be consulted, unless revisions and/or checklists are available (e.g. Meisch, 2000 for western Europe, Martens, 1984 for Africa and Martens & Behen, 1994 for South America). Thirdly, the distribution of these subjective taxa over the different zoogeographical regions needed to be plotted. Again, primary literature had to be consulted, but this survey will require constant updating. Finally, rates of endemicity were determined. Endemic here means that the species/genus occurs in one zoogeographical region only. Endemicity can be much narrower (e.g. occurring in one lake only), but for the present analysis the unit of endemicity is the zoogeographical region.

Several other caveats exist:

1. Several (semi-) terrestrial species of Ostracoda are known, which either occur in leaf-litter, or in mosses in splash zones of waterfalls. Although some of these taxa have meanwhile also been found in fully lacustrine conditions (e.g. *Terrestricythere*), we here classify them as 'limnoterrestrial' (see Balian et al., this volume).
2. Also in view of the agreements set for all the chapters in the present volume, non-free-living species were not included in the surveys. Therefore, the c. 200 species of the cytheroid family Entocytheridae were not included in the present list. Entocytheridae are parasitic or commensal on gills and other body parts of other crustaceans, such as Isopoda, Amphipoda and crayfish; they mostly occur in the Holarctic, with highest diversity in the Nearctic, and in the northeastern part of the Neotropical region.
3. Karanovic (2007) described several dozens new species and several new genera from groundwater of the Pilbara (NW Australia). As this document was not available to us during the

present research, these taxa are not included here.

4. Seemingly ad hoc synonyms (e.g. for the candonids of North America) were not included. At a time when increasing numbers of cryptic species are discovered, it seems unwise to lump existing taxa together without checking type specimens, which in many cases are available in public museums.

Diversity and endemicity of non-marine Ostracoda

Species and generic diversity

There are 1,936 subjective aquatic species of extant non-marine Ostracoda species (and 12 limno-terrestrial species—Table 1) and about 189 aquatic genera (and 5 limno-terrestrial—Table 2). Both in species and in genera, the family Cyprididae as it stands today (i.e. including the Cypridopsinae) takes up about half of diversity, with the Candonidae taking about 25% of the total diversity. Of the 11 other families, only the Limnocytheridae with c. 10% of total diversity of genera and less of specific diversity can also be called speciose. All other families are limited to smaller numbers of genera and species.

At a specific level, nearly all families, including the large Cyprididae and Candonidae, have endemicity rates of around 90%, meaning that only about a tenth of all species have intercontinental distributions. Calculated over all known species, close to 94% of all species are thus far known from one zoogeographical region only.

At the generic level, endemicity is of course lower, with about 60% of the genera occurring in one zoogeographical region only. In Cyprididae, c. 60% of all genera are endemic, in Candonidae and in Limnocytheridae almost 75%. Most families occur in all zoogeographical regions, except for Notodromadidae which have thus far not been recorded with certainty from the Neotropical region (Tables 1, 2). The hotspot of diversity of this group is without any doubt in the Oriental region. Darwinulidae have several genera and species with intercontinental

Table 1 Total number of species (endemic species between brackets) of extant non-marine Ostracoda in the zoogeographical provinces

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Cyprididae	206 (163)	154 (101)	169 (137)	317 (292)	154 (132)	106 (99)	3 (0)	2 (2)	998 (926)
Candonidae	333 (306)	101 (74)	40 (36)	52 (52)	17 (14)	35 (35)	0	0	545 (517)
Ilyocyprididae	27 (22)	3 (0)	2 (0)	1 (1)	8 (4)	3 (2)	0	0	33 (29)
Notodromadidae	5 (2)	3 (0)	3 (3)	12 (10)	15 (12)	5 (4)	0	0	36 (31)
Darwinulidae	6 (3)	3 (1)	12 (7)	9 (6)	4 (2)	9 (6)	1 (0)	0	29 (25)
Limnocytheridae	34 (32)	29 (25)	25 (23)	45 (44)	1 (1)	14 (14)	1 (1)	1 (1)	144 (141)
Cytherideidae	60 (58)	8 (4)	10 (8)	19 (18)	0	3 (2)	0	0	93 (90)
Leptocytheridae	19 (19)	1 (1)	0	0	0	1 (1)	0	0	21 (21)
Xestoleberidae	3 (2)	1 (1)	2 (1)	0	0	0	0	0	6 (4)
Cytheruridae	4 (4)	2 (2)	14 (14)	0	0	0	0	0	20 (20)
Loxoconchidae	4 (3)	1 (0)	0	0	0	0	0	0	4 (3)
Hemicytheridae	1 (1)	0	0	0	0	0	0	0	1 (1)
Incertae sedis (*Romeis*)	1 (1)	0	0	0	0	0	0	0	1 (1)
Total	702 (620)	298 (211)	275 (232)	455 (424)	199 (165)	176 (163)	5 (1)	3 (3)	1,936 (1819)
Limno-terrestrial									
Cyprididae	1 (1)	0	2 (2)	4 (4)	0	3 (3)	0	0	10 (10)
Candonidae	1 (1)	0	3 (3)	1 (1)	0	0	0	0	5 (5)
Terrestricytheridae	4 (3)	0	0	0	0	0	2 (0)	0	4 (2)

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian; PAC: Pacific Oceanic Islands, ANT: Antarctic

Table 2 Total number of genera (endemic genera between brackets) of extant non-marine Ostracoda in the zoogeographical provinces

Genera	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Cyprididae	41 (10)	30 (3)	21 (2)	45 (21)	28 (4)	31 (16)	2 (0)	2 (0)	94 (56)
Candonidae	16 (6)	11 (3)	9 (3)	8 (4)	7 (1)	15 (12)	0	0	39 (29)
Ilyocyprididae	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	0	0	1 (0)
Notodromadidae	3 (0)	3 (0)	2 (0)	3 (1)	5 (1)	2 (0)	0	0	8 (2)
Darwinulidae	4 (0)	3 (0)	5 (0)	4 (0)	4 (0)	3 (0)	1 (0)	0	5 (0)
Limnocytheridae	10 (6)	3 (0)	6 (4)	6 (2)	1 (1)	3 (1)	1 (0)	1 (0)	19 (14)
Cytherideidae	2 (0)	2 (0)	1 (0)	6 (5)	0	1 (0)	0	0	7 (5)
Leptocytheridae	1 (0)	1 (0)	0	0	0	1 (0)	0	0	1 (0)
Xestoleberidae	1 (0)	1 (0)	1 (0)	0	0	0	0	0	1 (0)
Cytheruridae	2 (1)	1 (0)	3 (1)	0	0	0	0	0	4 (2)
Loxoconchidae	3 (2)	1 (0)	0	0	0	0	0	0	3 (2)
Hemicytheridae	1 (1)	0	0	0	0	0	0	0	1 (1)
Incertae sedis (*Romeis*)	1 (1)	0	0	0	0	0	0	0	1 (1)
Total	87 (27)	57 (6)	55 (11)	73 (34)	46 (7)	57 (29)	4 (0)	3 (0)	189 (114)
Limno-terrestrial									
Cyprididae	1 (0)	0	1 (0)	1 (1)	0	1 (1)	0	0	3 (2)
Candonidae	1 (0)	0	2 (1)	1 (1)	0	0	0	0	3 (2)
Terrestricytheridae	1 (0)	0	0	0	0	0	1 (0)	0	1 (0)

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian; PAC: Pacific Oceanic Islands, ANT: Antarctic

distribution, which is surprising for a group without drought-resistant eggs, but the age of the group (see below) and the reproductive mode might at least partly explain this.

Genetic diversity

Little information is available on genetic diversity in non-marine Ostracoda. Rossi et al. (1998) found more than 200 allozyme clones for *Eucypris virens* in Europe, while Schön et al. (2000) found 18% divergence in the mitochondrial COI marker for the same species in a similar number of European populations. The same authors found a much lower genetic variability in *Darwinula stevensoni*: only 7 clones and 3.5% divergence, respectively. These and subsequent authors have correlated this discrepancy with reproductive modes: *E. virens* is a species with mixed reproduction (both sexual and parthenogenetic females exist) with high-standing clonal variability and the ability to generate new genetic variability through (mainly intraspecific) hybridization between males and asexual females. There is also a high incidence of polyploidy in *E. virens*. *Darwinula stevensoni*, on the other hand, is a putative ancient asexual which has an almost identical genotype from northern Europe to South Africa. The presence of several reproductive modes makes Ostracoda an excellent model group for the study of one of the main evolutionary questions: the paradox of sex.

Phylogeny and historical processes

Marine ostracods invaded non-marine habitats from different lineages and at various times. According to the summary of Martens & Horne (in press), the Darwinulidae (one of the least diverse groups to date) most likely are the oldest living non-marine group, as they invaded non-marine habitats in the Devonian (c. 400–370 Myr ago). Limnocytheridae and Cytherideidae followed at the end of the Permian (c. 250 Myr). All four Cypridoidean families most likely invaded non-marine habitats sometime in the Mid to Late Jurassic (c. 175–150 Myr), but it is at present not at all clear if this involved one common ancestor, or if the four lineages derived from different invasions from different marine ancestors. It is thought that the other families, which mostly are largely marine and all cytheroidean (e.g. Xestoleberidae, Leptocytheridae, Loxoconchidae, etc.), only recently invaded non-marine habitats, e.g. in the Neogene or even in the Quaternary (Horne, 2003). Finally, the history of the limno-terrestrial species is unclear as no fossil record is available here. So, depending on whether or not cypridoidean colonization was by 1 or 4 ancestors, there have been between 9 and 12 independent incursions from marine to non-marine habitats during the past 400 million years.

Present distribution

The Zoogeographical Region with the highest specific diversity is the Palaearctic (Fig. 3), with more than 700 species, 80% of these are endemic (of which c. 200 are endemic to Lake Baikal). The Nearctic has only about 300 species, of which 71% are endemic, but c. 200 largely endemic species of the Entocytheridae are not included here, as they are all parasitic/commensal. Nearctic and Palaearctic together hold almost half of all described species. There is also a discrepancy between the Afrotropical (with 455 species (93% endemic) and the Neotropical with c. 275 species (84% endemic). The 176 species (92% endemic) of the Australian region and the c. 200 species of the Oriental region (OL—83% endemic) are with certainty a gross underestimation of the actual diversity. Antarctica and the Pacific regions are virtually unknown and will not further be discussed here.

At the generic level (Fig. 3), the picture is largely congruent. Again, the highest levels of endemicity are in Palaearctic (87, 30% endemic), whereas the Nearctic has only 6 endemic out of 57 genera (c. 10%). Both the Neotropical and the Oriental region have few endemic genera, while the Australian region has the highest percentage of endemic genera (29 out of 57 or about 50%). In the Afrotropical region, about half of the 73 genera are endemic and this number is almost certain to increase through further studies because of the high diversity of the Cypridopsinae.

Cyprididae are most common in the Afrotropical region (Fig. 4). Of the 25 subfamilies (including 3 presently unnamed), 5 are monospecific. Of the remaining 20, the 5 most speciose are the Eucypridinae (78 species mostly in Palaearctic), the Cyprinotinae (129 species, mostly in Afrotropical region), the Herpetocypridinae (151 species, mostly in Palaearctic and Neotropical), the Cypricercinae (171 species, mostly in Afrotropical region and Neotropical) and the Cypridopsinae (202 species, almost half of these in the Afrotropical region).

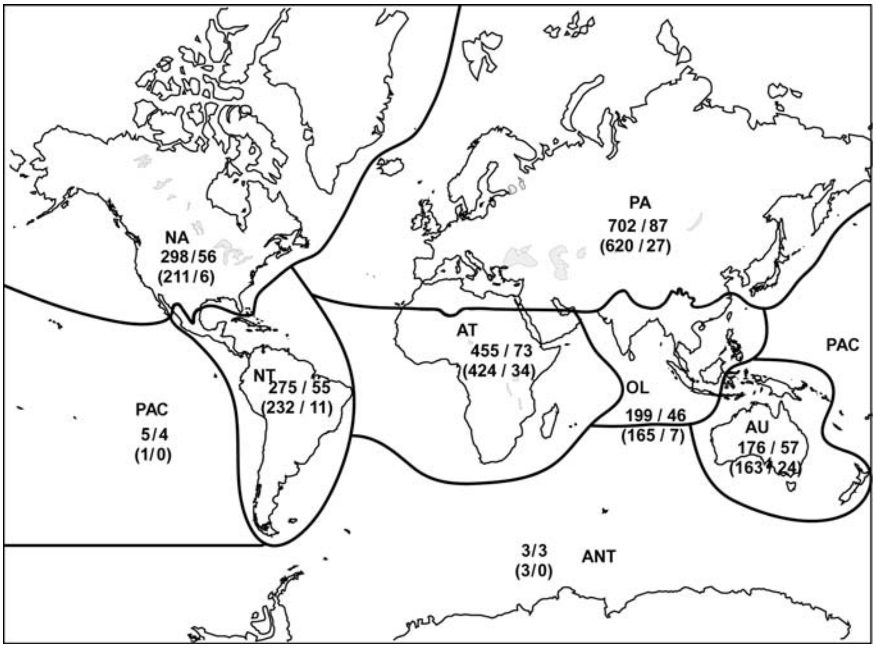

Fig. 3 Diversity and endemicity of ostracods (species/genus numbers and in parentheses endemic species/ endemic genus numbers). PA—Palaearctic, NA—Nearctic, NT—Neotropical, AT—Afrotropical, OL—Oriental, AU—Australasian, PAC—Pacific Oceanic Islands, ANT—Antarctic

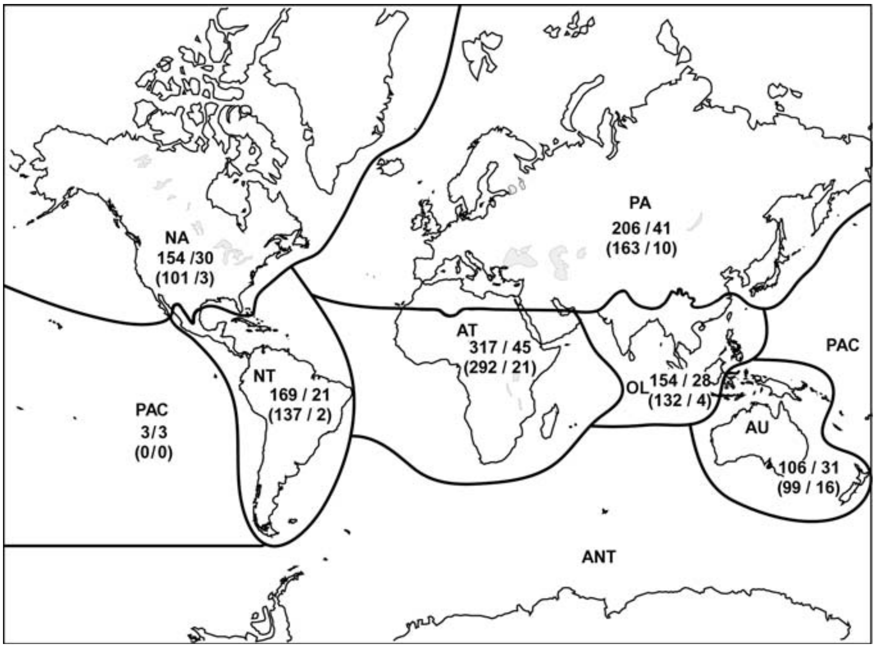

Fig. 4 Diversity and endemicity of Cyprididae (species/genus numbers and in parentheses endemic species/endemic genus numbers). PA—Palaearctic, NA—Nearctic, NT—Neotropical, AT—Afrotropical, OL—Oriental, AU—Australasian, PAC—Pacific Oceanic Islands, and ANT—Antarctic

Most non-marine ostracods either have dry resistant eggs, or are parthenogenetic, or are brooders, or have a mixture of all of these strategies, which are thought to facilitate long-distance dispersal. Indeed, wind, aquatic birds and humans could easily transport such stages (McKenzie, 1986) and in the case of parthenogenetic or gravid brooding females, one specimen is theoretically enough to found a new population. However, global comparison at neither the specific nor the generic levels supports these views. It would thus appear that ostracods are not such good dispersers at all. This is further shown by the existence of habitat-related endemic radiations, like the ones cited below from groundwater, ancient lakes and even temporary pools.

One of the reasons for this is that efficient dispersal does not guarantee the establishment of viable populations. This is, for example, supported by the very low number of species shared between Afrotropical and Neotropical regions (c. 15% shared), even if some taxonomic confusion might introduce some bias in this number. If intercontinental dispersal were indeed important, then the number of shared species would be considerably higher.

Another reason might be that ostracods in general are far less speciation prone than some other groups, and can show morphological stasis over long time spans. Taxa can be quite ancient: the species *Darwinula stevensoni* might be as old as 20–25 Myr (Straub, 1952), the extinct genus *Pattersoncypris* lived 150 Myr ago (Smith, 2000) and closely resembles the present day Cyprinotinae. Horne & Martens (1998) argue that *Cyprois* and *Stenocypris*-like species were already present in the Early Cretaceous (150–100 Myr).

In spite of the preceding arguments, there are some habitat types that hold higher numbers of endemics than others. Ancient lakes, especially Lake Tanganyika and Lake Baikal, hold extensive ostracod radiations, for example, the species flocks in the Cytherideidae and the Candonidae (Mazepova, 1990; Martens, 1994; Wouters & Martens, 2001). Younger ancient lakes such as Lake Titicaca, Lake Ohrid and some further East African lakes have extensive flocks in the Limnocytheridae and the Candonidae (Martens, 1994). With c. 200 species in Lake Baikal, about 100 in Lake Tanganyika and several dozens in other lakes, the ancient lakes are thought to hold 20–25% of the total non-marine ostracod diversity in the world.

Other speciation-prone habitats are those that have no or reduced predation pressure, for example temporary pools. In this case, speciation often coincides with gigantism. In temporary habitats, extensive radiations are known in Megalocypridinae (Afrotropical) and Cypridinae (Afrotropical and

Neotropical). The temporary pool fauna of South West Africa has a generic endemicity equalled only by the East African ancient lakes (Martens, 1998b).

Several ostracod groups in the Australian region are well adapted to lacustrine life in habitats with changing salinities, for example the Mytilocypridinae, the genera *Reticypris* and *Diacypris* and several others.

Subterranean ostracod faunas (Danielopol et al., 1994), finally, are well documented from the West Indies (Broodbakker, 1984). They seem poorly represented in most of Africa, although this could be owing to a lack of study. The recent discovery of dozens of endemic genera and close to 100 endemic species in the Pilbara area of western Australia exemplifies this possibility (Karanovic, 2007).

Finally, limno-terrestrial ostracods were thus far known from a few isolated cases in mainly Afrotropical and Australian regions. Recently, extensive radiations of especially Darwinulidae and Candonidae have been discovered and are being described from South America (Pinto et al., 2005).

Conclusions

With about 2,000 species worldwide, non-marine ostracods are not amongst the most species-rich groups in the freshwaters of the world. Whereas Holarctic faunas are reasonably well documented, southern hemisphere regions remain ill-explored. Especially the ancient lakes of the world (presently accounting for 20–25% of the world's non-marine ostracods) and groundwater faunas in Australia, Africa and South America could comprise significant numbers of presently undescribed taxa. Extant collections hold dozens of undescribed species, but further exploration is vital if non-marine ostracod faunas of the world are to be described with any degree of accuracy. Ostracods are the most common extant arthropod group with the most complete fossil record. Continued documentation of extant distribution patterns will therefore confirm their status as a model group for evolutionary studies.

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References

Balian, E., H. Segers, C. Lévèque & K. Martens, 2008. An Introduction to the freshwater animal diversity assessment (FADA) project. In Balian, E. et al. (eds), Freshwater Animal Diversity Assessment. Hydrobiologia, doi: 10.1007/s10750-007-9235-6

Broodbakker, N. W., 1984. The distribution and zoogeography of freshwater Ostracoda (Crustacea) in the West Indies, with emphasis on species inhabiting wells. Bijdragen tot de Dierkunde 52(2): 25–50.

Danielopol, D. L., P. Marmonier, A. J. Boulton & G. Bonaduce, 1994. World subterranean ostracod biogeography: dispersal or vicariance? Hydrobiologia 287: 119–129.

Holmes, J. A. & A. Chivas (eds), 2002. The Ostracoda: Applications in Quaternary Research. American Geophysical Union, Washington, DC.

Horne, D. J., 2003. Key events in the ecological radiation of the Ostracoda. In Park, L. E. & Smith, A. J. (eds), Bridging the Gap: Trends in the Ostracode Biological And Geological Sciences. The Paleontological Society Papers 9: 181–201.

Horne, D. J. & K. Martens, 1998. An assessment of the importance of resting eggs for the evolutionary success of non-marine Ostracoda (Crustacea). In Brendonck, L., L. De Meester & N. Hairston (eds), Evolutionary and Ecological Aspects of Crustacean Diapause. Advances in Limnology 52: 549–561.

Karanovic, I., 2007. Candoninae Ostracodes from the Pilbara Region in Western Australia. Crustaceana Monographs 7: 432 pp.

Kempf, E., 1980a. Index and Bibliography of non-marine ostracods. 1. Index A. Geologisches Institut, Universität Köln, 35: 188 pp.

Kempf, E., 1980b. Index and Bibliography of non-marine ostracods. 4. Bibliography A. Geologisches Institut, Universität Köln, 38: 186 pp.

Kempf, E., 1991a. Index and Bibliography of non-marine ostracods. 6. Index A, Supplement 1. Geologisches Institut, Universität Köln, working copy 10: 51 pp.

Kempf, E., 1991b. Index and Bibliography of non-marine ostracods. Bibliography C. Geologisches Institut, Universität Köln, working copy, 9: 72 pp.

McKenzie, K. G., 1986: Ostracoda: new aspects of their biogeography. In Gore, R. H. & K. L. Heck (eds), Crustacean Biogeography. A.A. Balkema, Rotterdam, Boston: 257–277.

Martens, K., 1984. Annotated checklist of non-marine ostracods (Ostracoda, Crustacea) from African inland waters. Zoologische dokumentatie van het koninklijk Museum voor Midden Afrika, Tervuren, 20: 51 pp.

Martens, K., 1994. Ostracod speciation in ancient lakes: a review. In Martens, K., Goddeeris, B. & Coulter, G. (eds), Speciation in Ancient Lakes. Advances in Limnology 44: 203–222.

Martens, K. (ed.) 1998a. Sex and Parthenogenesis – Evolutionary Ecology of Reproductive Modes in Non-marine Ostracods. Backhuys Publishers, Leiden, 334 pp.

Martens, K., 1998b. Diversity and endemicity of Recent non-marine ostracods (Crustacea, Ostracoda) from Africa and South America: a faunal comparison. Verhandlungen der Internationalen Vereinigung für Limnologie 26(4): 2093–2097.

Martens, K., 2003. On the evolution of *Gomphocythere* (Crustacea, Ostracoda) in Lake Nyassa/Malawi (East Africa), with the description of five new species. Hydrobiologia 497: 121–144.

Martens, K. & F. Behen, 1994. A checklist of the non-marine ostracods (Crustacea, Ostracoda) from South-American inland waters and adjacent islands. Travaux scientifiques du Musée d'Histoire naturelle de Luxembourg 22: 81 pp.

Martens, K. & D. J. Horne, (in press). Ostracoda. In G. Likkens (ed.), Encyclopedia of Inland Waters. Elsevier Publ.

Mazepova, G., 1990. Rakushkovye ratchki (Ostracoda) Baikala. Nauk. Sib. Otdel. Akad. Nauk. SSSR, Novosibirsk, 470 pp.

Meisch, C., 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag GmbH, Heidelberg, Berlin, 522 p.

Pinto, R. L., C. E. F. Rocha & K. Martens, 2005. On new terrestrial ostracods (Crustacea, Ostracoda) from Brazil, primarily from Sao Paulo State. Zoological Journal of the Linnean Society 145: 145–173.

Rossi, V., I. Schön, R. K. Butlin & P. Menozzi, 1998. Clonal genetic diversity. In Martens, K., (ed.), Sex and Parthenogenesis, Evolutionary Ecology of Reproductive Modes in Non-marine Ostracods. Backhuys Publishers, Leiden: 257–274.

Schön, I., A. Gandolfi, E. Di Masso, V. Rossi, H. I. Griffiths, K. Martens, R. K. Butlin, 2000. Long-term persistence of asexuality through mixed reproduction in *Eucypris virens* (Crustacea, Ostracoda). Heredity 84: 161–169.

Smith, R. J., 2000. Morphology and ontogeny of Cretaceous ostracods with preserved appendages from Brazil. Palaeontology 43: 63–98.

Straub, E. W., 1952. Mikropaläontologische Untersuchungen im Tertiär zwischen Ehingen und Ulm an dem Donau. Geologisches Jahrbuch 66, 433–523.

Wouters, K., K. Martens, 2001. On the *Cyprideis* species flock (Crustacea, Ostracoda) in Lake Tanganyika, with the description of four new species. Hydrobiologia 450: 111–127.