

Making Waves: The Repeated Colonization of Fresh Water by Copepod Crustaceans

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I. SUMMARY

Twenty-two independent colonizations of fresh and inland continental waters are identified within six of the 10 currently recognized orders of copepods. This number is a minimum estimate and is expected to increase as knowledge of the phylogenetic relationships within copepod families improves. It does not include mere incursions into fresh water, defined as invasions without subsequent diversification (= speciation). The timing of colonization events is estimated, where possible, by inference from biogeographical data. This preliminary analysis supports, in general, a direct relationship between lineage diversity and time elapsed since colonization of fresh water. It is hypothesized that the invasion of South America by the Diaptominae, penetrating from the north, resulted in the displacement of the original calanoid inhabitants of that continent, the *Boeckella* group within the family Centropagidae, except at high altitude and higher latitudes. A similar, but more ancient, invasion by the

Diaptominae is envisaged for Africa, with the original calanoid inhabitants, the Paradiaptominae, now being confined to marginal habitats, such as temporary waters. The analysis indicates a succession of at least four major waves of colonization of inland continental waters, although this may well be an artefact reflecting the indirect method of estimating colonization dates. Taxa currently making incursions into fresh waters may represent the next, or fifth, wave.

II. INTRODUCTION

Ancient lakes are qualitatively different from other lakes, particularly in the relatively high proportion of endemic species that they contain. The key element seems to be time, since the only factor common to all ancient lakes is that they are ancient (i.e. more than 100 000 years old: see discussion in Gorthner, 1994). Copepod crustaceans are present in all ancient lakes, but the levels of diversity and endemism vary and, again, no common factor or general rule is apparent. Copepod diversity and the degree of endemism reflect in part, the age of the lake, area effects and its colonization history. It thus seemed interesting to pursue the concept of time as a factor influencing freshwater copepod diversity in general. A preliminary exploration is presented of the hypothesis that the time elapsed since colonization of fresh water by a lineage of copepods is directly correlated with the species richness of that lineage.

To achieve even a preliminary consideration of this question, it is necessary to make some assumptions. First, it is assumed that knowledge of the systematics of freshwater copepods has improved to the extent that comparing lineage diversity by using absolute numbers of described species is meaningful. This assumption is probably acceptable, although the sampling of some specialist groundwater taxa, such as the Parastenocarididae, is probably uneven geographically and introduces a source of error into the analysis. Secondly, it is assumed that the general patterns of distribution of freshwater taxa contain a high signal: noise ratio, i.e. on balance they reflect historical tectonic events rather than subsequent dispersal events. The present authors also regard this assumption as acceptable, although acknowledging that dispersal of freshwater copepods is an important factor, as testified by the presence of *Paracyclops chiltoni* Thomson on the remote volcanic Easter Island and of diaptomids on the volcanic Galapagos Islands.

In this chapter the number of independent colonizations of fresh water by copepods is identified, then an attempt is made to date some of these colonization events by biogeographical analysis. A colonization of fresh water is defined here as the invasion of inland continental and/or fresh water by the ancestor of a lineage followed by the subsequent diversification of that lineage within continental waters. The subsequent diversification within fresh water requires that the lineage must comprise at least two related taxa. This definition is necessary in order to differentiate between a colonization event and a mere

incursion. Several copepod lineages appear to have made incursions into fresh water: such lineages are predominantly coastal marine and estuarine in distribution but their basic euryhalinity allows them to move into fresh water. However, in such cases, no subsequent diversification has occurred within fresh water. The Pseudodiaptomidae is an example of a family that is regarded as having made one or more incursions into fresh water but that has not truly colonized it. Even though any or all of the successful colonization may have been initiated by an original incursion, it is useful to distinguish between them. Each modern incursion into fresh water represents a potential colonization event.

III. COPEPODS OF INLAND CONTINENTAL WATERS

Copepods are abundant and diverse in fresh and inland saline continental waters, occurring as a major component of most planktonic, benthic and groundwater metazoan communities. In addition, they have successfully colonized restricted microhabitats such as phytotelmata, and extreme environments such as hot springs and glacial meltwaters. Copepods of continental waters exhibit an enormous range of lifestyles from small-particle feeders, to predators and parasitic forms, which utilize a wide variety of fishes and a few invertebrates as hosts. In summary, copepods occur in most habitats with sufficient water, including semiterrestrial situations, such as damp moss and leaf litter in humid forests.

Representatives of six of the 10 copepod orders can be found in freshwater habitats (Table 1). The ordinal phylogenetic analysis of Huys and Boxshall (1991) suggested that all orders of copepods originated in marine waters. A minimum of six colonization events is therefore supported; however, in the larger of these orders, it is apparent from available information on phylogenetic relationships that more than one lineage has moved into continental waters independently. The number of independent colonizations is analysed below, order by order.

A. The Order Calanoida

In the order Calanoida, with few exceptions, the fresh and continental water taxa belong to the superfamily Diaptomoidea (= Centropagoidea). This should not be interpreted as evidence that only a single lineage within this superfamily has successfully invaded continental waters. The Centropagidae comprises marine, brackish-water and freshwater species. The type genus *Centropages* Krøyer is marine, comprising 28 species that typically occur in coastal waters, but the family also contains large freshwater genera such as *Boeckella* Guerne and Richard. The phylogenetic relationships between the genera of centropagids are unresolved, but the present authors suggest that the

Table 1
Copepod lineages found in continental waters

Order	Family – lineage	Mar	BrW	FW	Mar/FW
Calanoida	Centropagidae	++	++	++	
	Diaptomidae			+++	
	Pseudodiaptomidae	++	++	+	
	Acartiidae	++	++	+	
	Temoridae	++	++	++	
	<i>Senecella</i>		+	+	
Harpacticoida	Ectinosomatidae	+++	+	+	
	Phyllognathopodidae			++	
	Chappuisiidae			+	
	Harpacticidae	++	+	+	
	Diosaccidae	+++	++	++	
	Ameiridae	++	++	+++	
	“Canthocamptidae”	++	++	+++	
	Parastenocarididae			+++	
	Cletodidae	++	+	+	
	Laophontidae	+++	+	+	
Cyclopoida	Oithonidae	++	+	+	
	Cyclopidae	++	++	+++	
	Ozmanidae			+	
	Lernaeidae			+++	
Siphonostomatoida	Caligidae	+++	+	+	
	Dichelethiidae	+			+
	Lernaeopodidae	+++		+++	+
Poecilostomatoida	Ergasilidae	++	++	+++	+
Gelyelloida	Gelyellidae			+	

+, one to nine species; ++, 10–99 species; +++, 100 or more species. Mar, Marine; BrW, brackish water; FW, fresh water; Mar/FW, parasitic on anadromous fishes migrating between marine and fresh waters.

family invaded fresh water at least twice. The Centropagidae is the most important family of calanoids in continental waters in Australasia and southern South America. The large group of species contained in *Boeckella* and related genera shows a Gondwana distribution, with representatives even on the smaller fragments of Gondwana such as New Caledonia (Defaye, 1998). Centropagids are absent from African inland waters. Three genera, *Limnocalanus* Sars, *Osphranticum* Forbes and *Sinocalanus* Burckhardt, are present in continental waters in the northern hemisphere. *Osphranticum* is monotypic. *Limnocalanus* comprises two species, both of which occur in marine and fresh waters (Holmquist, 1970). These species are here interpreted as representing incursions into fresh water. *Sinocalanus* currently comprises five species found in estuarine and fresh waters. It may have diversified in fresh water and is here treated as a colonization, rather than as an incursion. It is inferred here that the *Boeckella* group and *Sinocalanus* represent independent colonizations of fresh water. It may be estimated that a minimum of at least two independent colonization events has occurred within the family.

The Diaptomidae is the largest family within the order Calanoida, comprising in excess of 515 valid species from inland waters. Members of the family are primarily small particle feeders, but some are predatory. Most inhabit the water column but some are benthic and a few, small-sized species, inhabit subterranean waters. It is assumed here that the ancestral stock of the Diaptomidae inhabited fresh water and that the family, therefore, represents a single colonization event for the purposes of this analysis. It is possible, however, that the Paradiaptominae and Diaptominae (plus Speodiaptominae and Microdiaptominae) colonized fresh waters independently.

The Pseudodiaptomidae comprises about 50 species of primarily coastal and estuarine species. A small number of species may be found in fresh water and continental waters but this may be considered to be the result of numerous separate incursions into fresh water, rather than representing a true, independent colonization. Members of the Acartiidae, like the pseudodiaptomids, are primarily coastal and estuarine in distribution, but a very small number of species occurs in freshwater habitats. In the absence of information on the phylogenetic relationships of freshwater *Acartia* Dana species, this family is also treated here as having made incursions into fresh water rather than having colonized it.

The Temoridae comprises coastal marine (e.g. *Temora* Baird), estuarine (e.g. some species of *Eurytemora* Giesbrecht) and freshwater (e.g. *Epischura* Forbes and some species of *Eurytemora*) taxa. At least in continental waters, the family is restricted to the northern hemisphere. In Lake Baikal, the temorid *Epischura baikalensis* Sars is usually the dominant copepod in the plankton community. It is assumed that the family represents a single colonization event for the purposes of this analysis, although this may be an underestimate.

The phylogenetic relationships, and hence the classification, of the genus *Senecella* Juday are uncertain. It has been placed in the family Clausocalanidae

(see Dussart and Defaye, 1983, as Pseudocalanidae) but was transferred to the Aetideidae by Vyshkvartzeva in 1994. It comprises just two species and, according to its placement in either of these families, appears to represent an independent colonization of fresh water. However, both species can be found in brackish coastal waters and it is possible that this should be treated as two separate incursions into fresh water.

Finally, for completeness, the Fosshageniidae must be mentioned. This monotypic family was established on the basis of material collected from the superficial brackish-water lens overlying the saline water in an anchialine cave in the Caicos Islands (Suárez-Morales and Iliffe, 1996). It was placed in a new superfamily, the Fosshagenioidea, but this taxon is weakly supported and the family probably belongs in the superfamily Diaptoimoidea. It is not included as a freshwater taxon in Table 1.

B. The Order Harpacticoida

Within the order Harpacticoida the situation is similar. One large family of more than 210 species, the Parastenocarididae, is exclusively freshwater in distribution, as are two smaller families, the Chappuisiidae (two species) and the Phyllognathopodidae (about 13 species). Lang (1948) indicated that the Chappuisiidae and Phyllognathopodidae may have shared a common ancestor (and this may already have lived in fresh water), but Huys and Iliffe (1998) regarded the former as a specialized lineage within the superfamily Tisboidea. These three families are, therefore, treated as representing three separate colonization events.

The Ectinosomatidae is a primarily marine family, which contains a few estuarine species and even fewer freshwater species, particularly in the genus *Halectinosoma* Lang. This is treated here as representing a single independent colonization event since there may have been some diversification within fresh water.

The Harpacticidae is similar, a primarily marine family with a few freshwater forms, including *Harpacticella inopinata* Sars, one of the most abundant copepods in Lake Baikal. This is also treated here as an independent colonization event.

The Diosaccidae is another predominantly marine family, but it contains numerous freshwater forms, especially in the genus *Schizopera* Sars. There is, for example, a small species flock of at least 10 species described from the ancient Lake Tanganyika. Other species flocks are known, but for the purposes of this chapter, the diosaccids are treated as a single independent colonization event.

The Ameiridae is one of the larger and more diverse families of harpacticoids that inhabit fresh water. The radiation in freshwater habitats is dominated by the group of genera related to *Nitokra* Boeck and particularly to *Nitocrella*

Chappuis. These genera, such as *Nitocrella*, *Parapseudoleptomesochra* Lang, *Nitocrellopsis* Petkovski and *Stygonitocrella* Petkovski, inhabit karstic systems, inland caves and other subterranean waters (Rouch, 1986). Some ameirids have occupied specialized habitats, such as the hyporheic zone of rivers (e.g. *Psammonitocrella* Rouch), and others have entered into symbiotic relationships with a variety of invertebrate hosts (e.g. species of *Nitokra*). Given the lack of a recent analysis of phylogenetic relationships within the family, the ameirids are treated as a single independent colonization event, but this probably represents an underestimate.

The Canthocamptidae is the largest family of the Harpacticoida, comprising in excess of 600 species, and it is predominantly freshwater in distribution. Determining the evolutionary history, in particular the pattern of colonization of continental waters, of the canthocamptids is grossly obstructed by the lack of a coherent scheme of phylogenetic relationships for the family. The family as currently constituted contains fully marine, even deep-sea forms, such as *Bathycamptus* Huys and Thistle, estuarine forms, such as *Mesochra* Boeck, as well as the mass of true freshwater forms. For this analysis the authors assume only a single colonization event of fresh water, but recognize that this is a minimum estimate for a taxon that is almost certainly polyphyletic.

The Cletodidae and Laophontidae are both predominantly marine families, which contain a small proportion of brackish-water and freshwater taxa. Because the current understanding of phylogenetic relationships is insufficient to allow precise identification of any particular freshwater lineages within these families, in both cases the present discussion is restricted to a minimum assumption of a single colonization event for each family.

C. The Order Cyclopoida

The largest family within the order Cyclopoida is the Cyclopidae. It comprises over 700 species, the great majority of which belongs in the two freshwater subfamilies, Cyclopininae and Eucyclopininae. The small subfamily Euryteinae contains marine and estuarine species only, and the fourth subfamily, the Halicyclopininae, consists predominantly of brackish-water forms belonging to the type genus *Halicyclops* Norman. The Cyclopidae is cosmopolitan in fresh waters and its members exploit a huge variety of habitats from subterranean waters to ancient lakes. Species may be small particle feeders, benthic surface feeders, predators or even specialized symbionts on freshwater sponge hosts. The Cyclopidae is treated as representing a single colonization event.

The Oithonidae contains primarily coastal marine planktonic forms but many species are found in brackish-water habitats and a few occur in fresh water. Some species within the genus *Oithona* Baird are reported exclusively from fresh water. *Limnoithona* Burckhardt species also occur in fresh and brackish waters. Accepting the current taxonomy as valid indicates two

independent colonizations of fresh water, one within each of these genera. The existence of a small cluster of *Oithona* species in east-coast drainages of South America (Ferrari and Bowman, 1980) provides evidence of colonization in this lineage, rather than mere incursion into fresh water.

The monotypic Ozmanidae is known from Amazonia. The only species is an endoparasite of a freshwater gastropod mollusc. According to the latest phylogenetic analysis of the Cyclopoida, the Ozmanidae is the sister group of the Lernaecidae (Ho *et al.*, 1998). The Lernaecidae is the second largest family of Cyclopoida found in freshwater habitats. It comprises just over 110 species, all of them parasites of freshwater fishes. For the purposes of this chapter the Ozmanidae and Lernaecidae are treated together as representing a single independent colonization of fresh water following the phylogenetic scheme of Ho *et al.* (1998).

D. The Order Siphonostomatoida

The only members of the Siphonostomatoida found in fresh water are parasites of fishes. One of the two extant monotypic genera in the family Dichelesthidae parasitizes sturgeons (family Acipenseridae). Since its hosts are anadromous species, migrating between fresh and marine waters, the colonization of fresh water by *Dichelesthium* Abildgaard could probably be classified as passive, with the parasite having been passively carried there on its hosts. The existence of only a single species in fresh water defines this as an incursion into fresh water, rather than a colonization. However, the existence of a Lower Cretaceous fossil copepod, *Kabatarina pattersoni* Cressey and Boxshall, parasitic on the gills of a fossil fish that may have lived in an estuarine habitat (Cressey and Boxshall, 1989), hints at the possibility of colonization by a larger lineage.

One clade only within the large family Lernaepodidae has radiated in fresh water (Kabata, 1979). The *Salmincola* Wilson lineage comprises 38 species in seven genera. These parasites occur on various freshwater fish hosts, including silurids, cyprinids and coregonids, as well as salmonids and anadromous acipenserids. The original colonization of fresh water by this lineage might also have been passive.

The large family Caligidae contains a single freshwater species, *Caligus lacustris* Steenstrup and Lütken, among several hundreds of marine ones. Another fish parasite, its arrival into fresh water may again be attributed to passive transport via fish hosts and subsequent establishment. It also occurs in brackish waters and in the Black Sea. This is treated as an incursion into fresh water rather than a colonization.

E. The Order Poecilostomatoida

Only one of more than 60 families within the order Poecilostomatoida has successfully colonized inland continental waters. This family, the Ergasilidae, has a unique life cycle: its developmental stages, from nauplius up to adult, occur as free-living members of the plankton community; only after mating do the fertilized adult females seek out and infest hosts for the final, parasitic phase of their life cycle. Most ergasilids are known only from their parasitic females, and these typically utilize fishes as hosts, with a few species on bivalve molluscs. Levels of host specificity appear to be relatively low in the family, partly because of the limitation of the parasitic phase to the postfertilization period of the adult female only. Some ergasilids are fully marine, occurring on coastal fishes, many occur in brackish-water estuaries and lagoons, and many are freshwater. This family is here treated as representing a single colonization event, since the phylogenetic relationships within the group are unresolved and since the complex interactions between host utilization patterns and salinity regimes are not yet understood. It is probably a gross underestimate since several tentatively identified lineages (e.g. *Acusicola* Cressey; see El-Rashidy and Boxshall, 1999) include both marine and freshwater representatives.

F. The Order Gelyelloida

Finally, the order Gelyelloida comprises a single family, the Gelyellidae, one genus and two species. These species occur in European subterranean waters. The family is counted here as an independent colonization of fresh water from a marine origin (Huys and Boxshall, 1991).

In summary, there is evidence of a minimum number of five independent colonizations of continental waters by members of the order Calanoida, 10 by members of the Harpacticoida, four by members of the Cyclopoida, and one each by members of the Siphonostomatoida, Poecilostomatoida and Gelyelloida. The grand total is 22 colonization events. This is a minimal estimate, which will undoubtedly increase as the knowledge of phylogenetic relationships within lineages improves.

IV. BIOGEOGRAPHY AND THE TIMING OF COLONIZATION EVENTS

Using the comparative method the aim was to test whether there is a correlation between the timing of these 22 independent colonization events and the diversity of each taxon in fresh water. The extremely fragmentary nature of the fossil record for the Copepoda (see Cressey and Boxshall, 1989) is a hinderance here, removing one potential set of test data. It is necessary, therefore, to arrive at some estimates of the timing of the original colonization

events for each lineage, based on biogeographical data. This method is fraught with difficulties; in particular, the incompleteness of phylogenetic understanding of copepod lineages renders some of the basic data (i.e. the 22 taxonomic lineages enumerated above) doubtful. However, even at this stage it is possible to make a preliminary examination of the correlation between the diversity of a freshwater taxon (estimated as simple species richness) and the time elapsed since initial colonization of fresh water.

A. The Order Calanoida

1. *The Family Centropagidae: The Boeckella Group*

The species of the *Boeckella* group, within the Centropagidae, occur in fresh and athalassic waters in Australia, New Zealand, southern South America and New Caledonia (Dussart and Defaye, 1983; Defaye, 1998). A single species occurs in Mongolia. Their distribution led Bayly and Morton (1978) and Bayly (1992) to suggest that the lineage first invaded continental waters before the break-up of Gondwana. However, this lineage is not represented in African waters, indicating that this invasion occurred after the separation of Africa from the rest of Gondwanaland (except for South America). The present authors support this suggestion and infer that the *Boeckella* group invaded South America before 120 Mya (= Aptian, Lower Cretaceous) when South America became disconnected from the rest of Gondwanaland (except for Africa).

The *Boeckella* group apparently did not spread into Africa. The progressively deeper incision of the Proto-South Atlantic might have constituted a barrier preventing their spread from South America into Africa until these two continents were completely separated by the South Atlantic, about 95 Mya. Given the lack of a scheme of phylogenetic relationships for the family, the *Boeckella* lineage is defined here as comprising at least those approximately 60 species referred *Boeckella*, *Pseudoboeckella* Mrázek, *Meta-boeckella* Ekman, *Hemiboeckella* Sars and *Parabroteas* Mrázek. This lineage may be even larger, including other continental waters genera such as *Gladioferens* Henry and *Calamoecia* Brady (cf. Maly, 1996). It may be speculated that the centropagids were the only calanoid family represented in fresh water in the southern supercontinent of Gondwana, excluding Africa. Africa was probably never colonized by centropagids, although it is possible that their absence is secondary, the result of regional extinction on that continent.

2. *The Family Diaptomidae*

The Diaptomidae is the dominant calanoid family in inland waters in Europe, Asia, North America, Africa and northern South America. It does not occur in New Caledonia and New Zealand, and only two species (of *Eodiaptomus*

Kiefer and of *Tropodiptomus* Kiefer) have been found in Australia. The family comprises about 515 species in four subfamilies, the two largest subfamilies comprising 22 species (the Paradiptominae) and about 490 species (the Diaptominae). The biology, diversity and evolutionary histories of these two subfamilies differ markedly. Members of the Paradiptominae are restricted to Africa, with some dispersal outwards to adjacent areas, including southern Europe and the Middle East. They are largely restricted to marginal habitats, such as temporary or inland saline waters. The members of the Diaptominae are extremely widely distributed throughout the range of the family and occupy prime habitats, such as lakes.

It is speculated here that the original colonization of continental waters by the subfamily Diaptominae of the Diaptomidae occurred in the northern supercontinent of Laurasia some time after the break-up of Pangaea around 160 Mya. It is further speculated that the ancestors of the Paradiptominae were the first calanoids to colonize fresh water on the African plate. The timing of this invasion is difficult to establish. No paradiptomines have been reported from the neotropical region, suggesting that this invasion occurred only after Africa separated from South America (around 95 Mya). However, the colonization may have been considerably more ancient, if the barriers that prevented the spread of the *Boeckella* group from South America into Africa also acted to prevent the spread of the paradiptomines in the opposite direction.

A third possibility is that the ancestors of the paradiptomines may have penetrated into Africa from Laurasia via the Iberian peninsula during the Late Eocene (37 Mya), when Africa was separated from Laurasia by only a narrow passage marking the opening of the Tethys Sea into the Atlantic.

It may be postulated that the presence of diaptomines in northern South America results from a later invasion from North/Central America. After invading from the north, the diaptomines spread rapidly, through the highly interconnected, lowland river systems that make South America unique. They probably replaced the existing calanoid fauna of *Boeckella* group centropagids except at high altitude (i.e. the Andean cordillera) and at high latitude (e.g. Patagonian) areas, where they are still dominant today. The timing of this invasion from the north most probably occurred when North America and South America came back into contact at the closing of the Panama gap in the Pliocene (3 Mya). The remarkable rapidity of the spread through northern South America is attributed here to the exceptional interconnectedness of the major neotropical river systems. Some support for this scenario can be derived from the current state of the systematics of the genus *Notodiptomus* Kiefer, the dominant and most speciose genus of Diaptominae in South America (Santos Silva *et al.*, 1999). The species of *Notodiptomus* are notoriously difficult to distinguish on the basis of morphological characters. This is probably not due to especially poor descriptive taxonomy, but is a reflection of the lack of morphological differentiation between recognized species. This, in

turn, might be related to the relative recency of the diversification of the genus within South America. The presence of the vagile species *Arctodiptomus dorsalis* (Marsh) in lowland habitats on the extreme north-western corner of South America is here interpreted as the result of a recent, independent dispersal onto the continent from Central America.

Surprisingly, a somewhat similar scenario can be envisaged for Africa. As mentioned above, the Paradiptominae can be regarded as the first calanoid group to have colonized African fresh waters. It may be speculated that the diaptomines also invaded the African continental waters, initially from the north, and spread southwards, diversifying and displacing the existing calanoid taxon, the paradiptomines, except those in marginal habitats, such as saline and temporary waters. The authors regard this invasion as considerably more ancient than the corresponding invasion of South America by representatives of the Diaptominae. First, because the degree of interconnectedness of African river systems is much less (the different African drainage basins are clearly demarcated and faunistically distinct) and the climatic history is different, so the spread of the diaptomines across the continent must have been slower. Secondly, the morphological differentiation between species of the dominant and most speciose genus (*Tropodiptomus*) is generally greater than between species of *Notodiptomus*, suggesting an older radiation. A possible date for this colonization is about 17 Mya, when the Arabigo-African and Anatolian plates were connected via the Middle-East landbridge, with great interchange of terrestrial fauna.

The central analysis of this chapter, attempting to identify any correlation between time in fresh water and lineage diversity, treats the Diaptomidae as a single lineage, given that the common ancestor of all subfamilies was almost certainly already an inhabitant of fresh water. However, the postulated displacement of one subfamily lineage within the family by another indicates one of the more obvious possible sources of error in the analysis.

3. *The Family Temoridae*

According to Dussart and Defaye (1983), the Temoridae of continental waters number about 27 species in three genera, *Eurytemora*, *Epischura* and *Heterocope* Sars. Most *Eurytemora* species are essentially brackish-water forms, although *E. velox* (Lilljeborg) and *E. lacustris* (Poppe) are freshwater species, and the true diversity of the temorid freshwater lineage is almost certainly considerably less than this figure of 27 species. All are restricted to the higher latitudes of the northern hemisphere and it seems likely that the distribution of this family in continental waters has been profoundly influenced by the Pleistocene glaciations.

4. *The "Senecella" Lineage*

Senecella calanoides Juday occurs in fresh water in North America, and *S. siberica* Vyshkvarzeva occurs in the brackish waters of the Kara and Laptev

Seas of northern Siberia. The extreme northerly distribution, in areas covered by the ice cap during the Pleistocene glaciation, identifies this as a postglacial colonization.

B. The Order Harpacticoida

1. *The Canthocamptidae Lineage and the Family Parastenocarididae*

The two large harpacticoid families Canthocamptidae (> 600 species) and Parastenocarididae (> 210 species) both have cosmopolitan distributions, except for the latter's absence from New Zealand (Dussart and Defaye, 1985). Both are presumed here to have inhabited a variety of freshwater habitats on Pangaea. The difference in species richness may be an artefact due to incomplete sampling of the groundwater habitats favoured by parastenocaridids (see Ahnert, 1998), or it may reflect a slower rate of speciation in groundwaters compared with surface waters.

2. *The Family Ameiridae*

The Ameiridae contains a large number (100+) of freshwater forms, especially from subterranean waters (Rouch, 1986) and these are distributed widely across Europe, Asia, North America and Africa, especially northern Africa (Dussart and Defaye, 1990), although this may represent sampling bias. Few freshwater ameirids are reported from South America, although typically brackish-water forms, such as some *Nitokra* species, can be found. The Ameiridae have probably colonized continental waters more than once, but the main lineage of subterranean forms probably originated in Laurasia. It seems likely that they colonized Africa early in their radiation.

3. *The Family Diosaccidae*

The freshwater representatives of the Diosaccidae are found primarily in western Eurasia and in Africa, especially in the Great Lakes Tanganyika and Malawi, where an evolutionary radiation seems to have taken place. These lakes are estimated as having been in existence approximately 9–12 My and 2 Mya, respectively (Cohen *et al.*, 1993; Ribbink, 1994).

4. *The Family Harpacticidae*

The Harpacticidae contains genera such as *Tigriopus* Norman, which typically live in splash zone pools and are tolerant of extreme variations in temperature and salinity. There is, however, only one colonization of fresh water within the family, and it consists of *Harpacticella* Sars species, which are restricted to the Palaearctic region.

C. The Order Cyclopoida

1. *The Family Cyclopidae*

The largest family of copepods in fresh water is the Cyclopidae (order Cyclopoida). Members of this family occur on all continents and it is likely that this lineage first invaded and colonized fresh waters prior to the break-up of Pangaea.

2. *The Family Oithonidae*

The main invasion of the genus *Oithona* within the Oithonidae into fresh water has taken place in Amazonia, where a small cluster of species has been recorded (Ferrari and Bowman, 1980). The extensive brackish-water interface between marine and freshwater habitats in the Amazon probably provided the route by which *Oithona* has colonized neotropical fresh waters, but the possibility that *Oithona* arrived during a marine incursion into the Upper Amazon cannot be excluded (see Lovejoy *et al.*, 1998).

3. *The Family Lernaeyidae*

Unravelling the biogeographical history of parasitic families, such as the cyclopoid family Lernaeyidae, is difficult because of the added dimension, the availability of suitable hosts. Ho (1998) demonstrated that the family comprises two monophyletic lineages, the subfamilies Lernaeyinae and Lamproglenninae. The 57 species of the Lamproglenninae are found only in Eurasia (mostly from Asia, since this total includes only two species from Europe) and Africa. The 56 species of the Lernaeyinae are more widely distributed, with 38 old-world species and 15 new-world species. South America harbours only five species and the South Pacific/Australasia region only two species. Ho (1998) noted that 101 of the 113 species of Lernaeyidae are confined to Asia and Africa. This peculiar pattern seems to have resulted from an explosive cladogenesis on the "Indian raft", and this only took place after the ancestral lernaeyids colonized the diverse fish family Cyprinidae as hosts. Ho inferred that the ancestral stock of the family invaded Gondwana before the separation of the Indian subcontinental plate from Africa in the Late Cretaceous (about 80 Mya). This invasion presumably occurred after the separation of Africa/India from the rest of Gondwanaland about 95 Mya.

D. The Order Siphonostomatoida

The only colonization of fresh water by siphonostomatoid copepods was by ancestors of the *Salmincola* lineage within the family Lernaeyopodidae. Members of this lineage exhibit a boreal distribution, mostly restricted to the higher latitudes of the northern hemisphere. The distribution of this family in

continental waters has probably been profoundly influenced both by the Pleistocene glaciations and by the availability of suitable hosts.

E. The Order Poecilostomatoida

The evolutionary history of the Ergasilidae is complex. Ergasilids are found on and around the coastal margins of all continents, with the exception of Antarctica, and they occur in various salinity regimes. It is not possible here to analyse fully the geographical distribution patterns exhibited within the family; however, El-Rashidy (1999) has postulated that most South American ergasilids belong to a single monophyletic lineage. This lineage has invaded and diversified spectacularly in the Amazonian region and has subsequently spread northwards into Central America. The penetration of species of the genus *Acusicola* as far north as Texas indicates that the closure of the Panama gap in the Pliocene may have permitted an intense period of north/south aquatic faunal exchange in both directions. Thatcher (1998) calculated that only a tiny proportion of the possible ergasilid fauna of Amazonia is currently known to science. The biogeographical knowledge of the Ergasilidae is too incomplete to permit its use in the central analysis of this chapter.

F. The Order Gelyelloida

The Gelyelloida are currently reported only from groundwater habitats of north-western Europe, but the authors consider them to be similar to other lineages with a distribution in the northern part of the northern hemisphere.

The estimated colonization dates derived by inference from modern distributions are summarized in Table 2, which also provides approximate estimates of the species richness for each lineage considered.

V. DISCUSSION

This analysis is preliminary. Accurate species richness data are not available for all lineages and there are no fossil data to provide confirmation of colonization dates estimated from modern distribution patterns. Consequently, it is only possible to make a general inference – that the diversity of a lineage appears to be directly proportional to the length of time elapsed since initial colonization of fresh water by that lineage, i.e. the more ancient the colonization, the larger the number of species in the lineage. This inference relies on the assumption, used in the analysis, that tectonic events have shaped modern distributions more than subsequent dispersal events. There is also an obvious link between timing of colonization and the area of habitat available for colonization. The earliest colonists could exploit the whole of Pangaea, but

Table 2

Estimated dates for the colonization of fresh and inland continental waters by copepod lineages and approximate species richness data (number of species in fresh water) for each lineage. The position of the Paradiaptominae is uncertain

Pangaeian	Post-Gondwana/ Laurasia split	Post-isolation of Africa/India	Postglacial
Cyclopidae (700+ species)	[Centropagidae] <i>Boeckella</i> group (60 species)	Lernaeidae (110 species)	[Centropagidae] <i>Sinocalanus</i> group (five species)
Canthocamptidae (600+ species)	Diaptominae (490 species)		[Temoridae] <i>Eurytemora</i> group (27 species)
Parastenocarididae (210+ species)	[Ameiridae] <i>Nitocrella</i> group (100+ species)	[Diosaccidae] <i>Schizopera</i> group (12 species)	<i>Senecella</i> (two species)
	Paradiaptominae? (22 species)	Paradiaptominae? (22 species)	Gelyelloida (two species)
			[Lernaeopodidae] <i>Salmincola</i> group (38 species)
			[Harpacticidae] <i>Harpacticella</i> group (four species)

later colonists had only particular fragments of Pangaea and, therefore, smaller areas available. Unravelling the interplay between time and area effects will be the subject of a future study.

It is surprising that few exceptions have been identified, in the form of ancient but small, relict lineages. One possible candidate must be the family Phyllognathopodidae, which is not included in Table 2. This is a relatively primitive family with a widespread distribution but with few valid species, some of which occur in marginal habitats such as phytotelmata. It apparently contradicts the above general inference; however, its presence in phytotelmata indicates a high dispersal ability. This, in turn, suggests the possibility that the distribution pattern is shaped more by dispersal than by plate tectonics.

The simple estimates of the timing of colonization events generated by interpretation of modern distributions indicate a succession of colonizations. Families such as the Cyclopidae, Parastenocarididae and Canthocamptidae were in the first wave of copepods to colonize and disperse through the varied freshwater habitats of Pangaea. They were followed by a second wave of families, such as the Ameiridae and Diaptomidae (subfamily Diaptominae) invading the northern supercontinent of Laurasia, and the Centropagidae invading the southern supercontinent of Gondwana. Later still came the

invasion of Africa/India by the parasitic family Lernaeidae and one or more clades within the Diosaccidae. The Paradiaptominae may also belong in this third wave, or possibly in the second wave. More recently came a fourth wave, but only in the northern part of the northern hemisphere, comprising the *Sinocalanus* group, the Temoridae, *Senecella* species, the Gelyelloida, the *Harpacticella* group and the parasitic *Salmincola* lineage. The restriction of all of these relatively small lineages to the northern part of the Holarctic region suggests that the Pleistocene glaciations may have had a profound effect on their distributions. All may be postglacial invasions.

The taxa identified here as representing modern incursions into fresh water because they have not diversified, for example the Acartiidae, Laophontidae, Cletodidae and the Pseudodiaptomidae, may each be potential colonizers. These taxa may be in the vanguard of the next great wave of copepods to shift from marine into inland continental waters.

The sequence of waves of colonization identified in this analysis is probably an artefact reflecting the indirect method of estimating colonization dates from gross distribution patterns, but it provides a convenient way of grouping the invasions.

The dynamics of the interactions between colonizers and existing faunas is interesting. The hypothesis presented here, that the neotropical diaptomines represent a recent invasion which has swept southwards, displacing the existing *Boeckella* group calanoids in lowland tropical to warm temperate zones, requires testing. To facilitate the testing process the authors predict that the vast majority of South American diaptomines will belong to a single monophyletic lineage (the only likely exceptions being vagile dispersalist species, such as *Arctodiaptomus dorsalis*). Molecular clock dating of this neotropical lineage should indicate a relatively recent radiation (about 3 Mya) to be consistent with this hypothesis. The sister group of this lineage should be found in Central/North America. Similarly, the great majority of African diaptomines should also belong to one or a small number of monophyletic lineages, but the colonization of, and radiation within Africa of the diaptomines may have taken place about 17 Mya. The colonization scenario presented here should provide a framework within which to investigate the colonization history and species diversification of copepods within ancient lakes.

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