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A human challenge: discovering and understanding continental copepod habitats

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Abstract

Copepods have invaded an astonishing variety of aquatic and humid continental environments and microhabitats. The historical process of discovery and investigation of copepods in ephemeral, acid and thermal waters, subterranean waters and sediments, phytotelmata, humid soils, leaf litter, human-modified and artificial habitats, and other situations extends over about 130 years. The methods developed to collect in and study these habitats range from simple nets to elaborate pumping systems and diving techniques. Investigations of non-lacustrine continental environments have contributed greatly to the understanding of aspects of copepod biology such as reproduction, diapause and population dynamics. Questions regarding faunistics and biological diversity, biogeography, evolution, transport and introductions of alien species have also been informed by such studies. This article briefly reviews these topics, and provides detailed lists of records from some of the less well-known kinds of habitats.

Introduction

Free-living copepod crustaceans are customarily treated as aquatic in the general limnological literature; however, some 130 years of imaginative collecting have revealed that they are capable of invading and surviving successfully in nearly every continental habitat and situation where sufficient moisture and organic matter are present, however intermittently. Certain kinds of habitats, such as phytotelmata, have received a good deal of attention from ecologists, but their copepod fauna has not been reviewed recently. Other kinds, particularly habitats modified or constructed by humans, or extreme habitats such as thermal waters, have been barely treated in the literature pertaining to copepods. This article briefly discusses some of the early history of investigations in the better-studied environments such as ephemeral waters, and discusses the kinds of information gained from studies in semi-aquatic natural or artificial habitats, referring to reviews where possible.

The fauna of acidic waters is normally investigated by standard limnological methods, and is not treated in detail here. Species of several genera of cyclopoids (e.g. *Acanthocyclops*, *Diacyclops*, *Paracyclops*), and harpacticoids (*Bryocamptus*, *Moraria*) have been found in waters of pH 4 or below (Rylov, 1948; Lewis, 1974; Fryer, 1980, 1993). The physiological adaptations that enable some species but not others to thrive in acidic waters have been almost entirely uninvestigated.

Historical process and development of methods

Following the first observation of free-living freshwater copepods, apparently by Blankaart (1688), investigations proceeded sporadically until the era of the great naturalists and collector-explorers in the late 19th century. Although most early investigations focused on plankton, Pratz (1866, cited in Schmeil, 1892) described several cyclopoids from wells in Munich, Germany. Brady (1868) provided the first report of copepods from a deep subterranean, human-altered habitat, a coal mine in England. Studies of copepods in caves began with the collections of Vosseler (1886) near Württemberg, Germany. Scourfield (1903) provided the earliest report of copepods in phytotelmata, in bromeliads and a pitcher plant in botanical gardens in London. The potential for copepods not only to invade man-made habitats but also to survive in them successfully was apparently first recognized by Kraepelin (1886), who collected cyclopoids and calanoids from the city water system of Hamburg, Germany.

In the initial investigations of subterranean waters, natural caves and springs, or relatively large permanent artificial deep holes such as dug and driven wells were sampled. The Karaman-Chappuis method (Chappuis, 1942, 1956) of simply digging holes in sand and gravel banks of streams allowed investigators to reach the top several dm of sediment, in any locality desired. The Bou-Rouch pump (Bou & Rouch, 1967), a simplification of an apparatus developed by Delamare Deboutteville (1954) for use in marine sandy beaches, yielded semi-quantitative water samples from permeable sediments 1–2 m or more deep, and became the standard method for sampling interstitial and phreatic fauna. A modification of the Bou-Rouch pump to avoid damaging the specimens, by capturing them in a container rather than passing them through the pump, was advocated by Vigna Taglianti et al. (1969). The double-packer sampler, developed by Danielopol & Niederreiter (1987), provides simultaneous samples of the fauna and the water. Perhaps the most exact quantitative method is the freeze-coring method of Bretschko & Klemens (1986), in which the meiofauna is first paralyzed by an electric field, and then the core is frozen with liquid nitrogen. What may be the largest semi-portable well-drilling system was used by Stanford & Ward (1988), to reach depths of 30 m in alluvial riverine sediments of the Flathead River valley, Montana, U.S.A. Deeper sediments are more customarily reached by sampling from permanent driven wells.

Habitats

Ephemeral waterbodies

The faunas of vernal pools were reviewed by Wiggins et al. (1980), and those of temporary lentic waters, particularly in semi-arid lands, by W. D. Williams (1985). Adaptive strategies, particularly diapause, of crustaceans for surviving dry periods have been the subject of many studies, and especially the literature on diapause in copepods has been reviewed recently by Dahms (1996), Hairston & Cáceres (1996) and Williams-Howze (1997), among others.

The faunas of ephemeral streams have received much less attention. D. D. Williams & Hynes (1976) found that *Attheyella nordenskioldii* and *Acanthocyclops vernalis* were abundant in the hyporheic zone of a temporary stream in southern Canada, and both species showed habitat-specific adaptations, such as timed reproduction and summer resting stages. Otherwise, copepods (and the meiofaunal community in general) of ephemeral streams seem to have been almost unstudied. Rouch (1992) described two species of harpacticoids of a previously unknown genus, *Psammonitocrella*, from an ephemeral desert stream in Arizona, U.S.A.

Rock hollows and rock or cliff faces

Water collected in natural hollows such as solution holes on bare rocks may come to hold copepods. These are usually common species such as *A. vernalis* and *Eucyclops agilis* in England (Scourfield, 1939), and *Cryptocyclops bicolor linjanticus* (Kiefer, 1928) and *Mesocyclops leuckarti* (probably = *M. aspericornis*) in Fiji (Laird, 1956). However, in Western Australia, the calanoid *Boeckella opaqua* Fairbridge, 1945, is found only in water-filled holes (‘gnammas’) on granite outcrops (Bayly, 1979, 1992). *Allocyclops ritae* is known only from a small pool on granitic rock in the Ivory Coast (Dumont & Lamoot, 1978).

Subterranean habitats

The copepod fauna of groundwater-related and cave habitats has been extensively reviewed (e.g. Graeter, 1910; Chappuis, 1927; Bowman, 1986; Lescher-Moutoué, 1986; Rouch, 1986, 1994). Galassi (2000) traced the changing concepts of subterranean habitats, from the early idea that they are unusual or challenging situations, to the growing realization that subterranean habitats can support a diverse and successful copepod fauna. Indeed, certain groups such as members of the cyclopoid genus *Diacyclops* have been more successful in subterranean than in epigean situations (Stoch, 1995, 2000), although the reasons for their success remain mysterious. Two less-investigated subterranean habitats are discussed here: the interstitial, including the stream-hyporheos; and the ‘pholeteros’ or assemblage in crayfish and crab burrows.

The diverse copepod community inhabiting the interstices among the sand grains of marine beaches, as well as in loose flocculent mud, was discovered by Wilson (1935). He pointed out the particular morphological adaptations, including reduction and uniformity in body size, vermiform shape, increased body flexibility, development of sense organs, shortening and strengthening of swimming legs, shape and carriage of the egg sacs, reduction in egg number with increase in egg size, and behavior, seen in interstitial copepods.

Following the pioneering studies of the microscopic fauna of sandy beaches in European lakes by Sassuchin et al. (1927) and others, copepods in the psammon of freshwater lake beaches were intensively investigated by Pennak (1939a,b, 1940), who also reviewed the early history of investigations of the psammon (Pennak, 1968). Chappuis (1946) called attention to the special groundwater habitat associated with the alluvial sand, gravel and 'cailleurs' sediments below and beside watercourses. This habitat, now known as the hyporheic zone, was apparently first investigated by Leruth (1938), in the groundwater of gravel deposits associated with the Meuse River in Belgium. The development of the Bou-Rouch pump allowed investigators to reach the deeper strata of streambeds and other permeable phreatic sediments.

The concept of the hyporheic zone as an ecotonal habitat was discussed by Rouch et al. (1997). Rouch & Danielopol (1997) argued that hypogean habitats including the sand-interstitial, hyporheic, phreatic, karstic and hole and cave faunas are much richer in species than is commonly estimated, although long-term studies are necessary to estimate faunal diversity adequately. Certainly, in the past six decades, rich hypogean-interstitial copepod faunas have been discovered wherever these habitats have been investigated (e.g. Lescher-Moutoué, 1986; Rouch, 1986).

Crayfish tunnels may serve as refuges for many species of benthic copepods, including rather eurytopic, widely distributed ones such as *Attheyella dentata* (Poggenpol, 1874), *Attheyella trispinosa* (Brady, 1880), *Halectinosoma abrau* (Krichagin, 1877) and *Paracyclops affinis* in burrows of *Astacus fluviatilis* in Europe (Chappuis, 1926; Kiefer, 1927b; Jakubisiak, 1939). In Ontario, Canada, burrows of *Cambarus fodiens* along a temporary stream harbored large populations of *A. vernalis* and *A. nordenskioldii* (D. D. Williams et al., 1974; D. D. Williams & Hynes, 1976). In Victoria, Australia, *Diacyclops cryonastes* Morton, 1985, was found in burrow water of *Engaeus* sp., and in Tasmania, *Acanthocyclops* sp. occurred in burrows of *Parastacoides tasmanicus* (Lake & Newcombe, 1975; Lake, 1977). Even normally planktonic species such as the large calanoid *Osphranticum labronectum* Forbes, 1882, have been found in water in the burrows of *Cambarus diogenes* in Missouri, U.S.A., during a dry spell (Creaser, 1931). The assemblage of animals living in the water in burrows of land crayfish was termed the 'pholeteros' by Lake (1977).

Several species of harpacticoids (*Attheyella crassa, Attheyella northumbrica* (Brady, 1880) (= *dentata*), *Attheyella trispinosa*, *Bryocamptus minutus*, *Canthocamptus staphylinus* (Jurine, 1820) and *Nitocrella hibernica* (Brady, 1880)) have been found on crayfish gills, but may be only accidentals (Chappuis, 1926; Gurney, 1930), and may also use the burrows as refuges.

This possible use of refuges may have led to the development of various degrees of commensalism between certain harpacticoid species and crayfish. *Nitocrella divaricata* (Chappuis, 1923) is found only on the carapace or in the gills of *A. fluviatilis*, *Astacus astacus*, *Astacus leptodactylus* and *Austropotamobius torrentium* in Europe, and is either a commensal or an obligate associate (Chappuis, 1923, 1926; Kiefer, 1937; Jakubisiak, 1939; Straskraba, 1956; Sterba, 1964; Boshko, 1976; Defaye, 1996; Subchev & Stanimirova, 1998). Two North American harpacticoids, *Attheyella pilosa* Chappuis, 1929, and *Attheyella carolinensis* Chappuis, 1932, have an intermediate habit: they occur free-living, but are more frequently found on the bodies of several species of *Cambarus* and *Orconectes rusticus* (Prins, 1964; Bowman et al., 1968).

In the tropics, burrows of land crabs (*Cardisoma carnifex*) containing fresh or slightly brackish water regularly harbor *Mesocyclops aspericornis* and *Paracyclops fimbriatus* on the volcanic islands of French Polynesia (Rivière & Thirel, 1981; Rivière et al., 1987; Rivière, Klein, Duval et al., 1998). Laird (1956) collected *Thermocyclops operculifer* Kiefer, 1930, in crab holes on Tarawa (Gilbert Islands). Yeatman (1983) reported several copepod species from crab holes:*Darcythompsonia inopinata* Smirnov, 1934 (Western Samoa, Fiji), *Ectocyclops phaleratus* (Fiji), *Halicyclops septentrionalis* Kiefer, 1935 (Fiji), *Halicyclops thermophilus* Kiefer, 1929, s. str. (Tonga, Western Samoa, Fiji), *H. thermophilus spinifer* Kiefer, 1935 (Tonga), *Mesocyclops leuckarti* (possibly = *M. aspericornis*) (Tonga, Fiji), *Microcyclops microsetosus* Yeatman, 1983 (Fiji), *Nitokra lacustris pacifica* Yeatman, 1983 (Western Samoa, Tonga), *Nitokra pseudospinipes* Yeatman, 1983 (Tonga, Fiji), *Schizopera tobae* Chappuis, 1931 (Fiji), and *Tisbella pulchella* (Wilson, 1932) (Fiji). Mogi et al. (1984) reported that *Thermocyclops* sp. and *Mesocyclops leuck-*

arti (the latter possibly misidentified) were common in crab holes in the Ryukyus. Laird (1988) collected *Eucyclops serrulatus* and *M. aspericornis* from freshwater, and *H. thermophilus* s. str. from brackish-water crab holes in Western Samoa. Hobbs & Villalobos (1958) reported the presence of harpacticoid copepods on the exoskeleton of the freshwater crab *Pseudothelphusa lamellifrons* in Mexico. The possibility that use of crab holes as refuges may have facilitated the development of copepod commensals remains a subject for future investigations.

Phytotelmata

In humid climates, the recesses of plant structures often contain enough water to support small aquatic invertebrates, of which some species seem to have a predilection for, and others may be specifically adapted for this habitat. The observed behavior of certain species implies that they may climb actively into the plants. These copepods can live in a film of water and tend to climb the walls of glass containers, out of the water, such as *Bryocamptus pygmaeus* (observed by Gurney, 1932) and *P. fimbriatus, P. affinis* and *E. phaleratus* (Schmeil, 1892; Scourfield, 1894).

In the tropics, the water pools in bromeliads have been much investigated, following the discovery and characterization of this habitat by the celebrated naturalist Fritz Müller, working in Brazil (Müller, 1879). Frank (1980) and Janetzky (1997) listed a number of copepod species known from bromeliads; Table 1A extends their lists.

Pitcher plants in temperate acid bogs are also convenient collecting sites for copepods (Table 1B). The tendency of certain species such as *Bryocamptus minutus*, *E. phaleratus* and *P. affinis* to climb out of water onto vertical, though still moist surfaces (Scourfield, 1894; Graham, 1907) may account for the fact that some of these are common in pitcher plants (Hamilton et al., 2000). Unidentified cyclopids occurred in about 40% of the pitcher plants at a site in northern Florida, U.S.A. (Harvey & Miller, 1996). Also in Florida, cyclopoid copepods showed an aggregated distribution in plants, and their occurrence was strongly correlated with biotic factors (Harvey & Miller, 1993).

Treeholes (Table 1C) are probably the best studied type of phytotelm in temperate climates. The European beech (*Fagus silvatica*) is especially prone to develop holes at the junction of the trunk and its elevated limbs. The practice of pollarding trees in Europe has also led to the creation of a large number of treeholes (Scourfield, 1915). Apparently the first person to investigate treeholes was Scourfield (1915), who described a new species of *Moraria.* However, it is unusual for investigations of treeholes to include quantitative estimates of non-insect invertebrates. In an extensive study in Germany, Rohnert (1951) reported only one species of copepod, *Moraria* sp., and considered that copepods were accidental arrivals.

Nearly any plant recess may form a receptacle for water and come to harbor copepods (Table 1D). However, it is clear from the list of recorded species that certain groups favor phytotelmata: *Attheyella* (subgenus *Canthosella*) and some *Elaphoidella* in neotropical bromeliads, and certain *Ectocyclops*, *Paracyclops* and *Tropocyclops*, plus the ubiquitous soil-dwellers *Epactophanes richardi* and *Phyllognathopus viguieri* in both the tropics and temperate zones. Species of *Canthosella* are predominantly found in bromeliads, and *Tropocyclops jamaicensis* invades terrestrial bromeliads quickly and may be an obligate phytotelm dweller (Reid & Janetzky, 1996).

Mosses

The records of harpacticoids and small cyclopoids from aquatic and terrestrial mosses in humid climates are so numerous as to be almost impossible to review. Both aquatic mosses (*Sphagnum, Hypnum*) and terrestrial mosses and liverworts in more humid situations harbor their own, sometimes distinctive, copepod faunas. Masses of aquatic mosses when squeezed yield small species of *Acanthocyclops*, *Diacyclops* and other cyclopid genera. Many species of *Bryocyclops* and *Muscocyclops* live in moss (e.g. Scourfield, 1939). Some 12 species of harpacticoids, mostly canthocamptids, were collected from terrestrial moss in open or forested locations in New Zealand (Lewis, 1984). Seeps on rock outcrops where moss and algae grow may also hold copepods, usually common species such as *B. pygmaeus*, but sometimes rarer ones such as *Speocyclops demetiensis* (Scourfield, 1932) (Gurney, 1932; Scourfield, 1932, 1939) and *Stolonicyclops heggiensis* Reid & Spooner, 1998. Wet moss on rock faces was the home of several canthocamptids in Tasmania (Hamond, 1988).

Leaf litter

The slowly decaying mats of leaf litter in humid temperate forests create a moist habitat favourable to several species of cyclopoids and harpacticoids, mainly canthocamptids (Table 2). Among the earliest reports were those by Gurney (1932) and Remy (1932). The

Table 1. Species of copepods reported from phytotelmata. Species are listed under the current name of the taxon, as far as possible; synonymies of most species were listed by Dussart & Defaye (1985, 1990) for Cyclopoida and Harpacticoida, respectively

Kind of phytotelmata/ Species	Location	Reference
A. Bromeliads		
Harpacticoida		
Attheyella aliena Noodt, 1956	Germany (greenhouse)	Noodt (1956)
Attheyella jureiae Por & Hadel, 1986	Brazil	Por & Hadel (1986)
Attheyella mervini Janetzky, Martínez Arbizu & Reid, 1996	Jamaica	Janetzky et al. (1996), Janetzky (1997)
Attheyella striblingi (Reid, 1990)	Costa Rica	Reid (1990)
Attheyella vera Por & Hadel, 1986	Brazil	Por & Hadel (1986)
Canthocamptus sp.[1]	Java	Menzel (1922, 1924, 1925b)
Elaphoidella bidens (Schmeil, 1894)	Puerto Rico	Reid (1993b)
Elaphoidella bromeliaecola (Chappuis, 1928)	Java	Chappuis (1928, 1931), Thienemann (1934)
Elaphoidella malayica (Chappuis, 1928)	Java	Chappuis (1931), Thienemann (1934)
Elaphoidella sewelli (Chappuis, 1928)	Jamaica	Laessle (1961)
E. sewelli	Puerto Rico	Maguire (1970)
Elaphoidella sp.	Puerto Rico	Reid (1993b)
Epactophanes richardi Mrázek, 1893	England (botanical garden)	Gurney (1932)
E. richardi	Jamaica	Janetzky et al. (1996)
Phyllognathopus viguieri (Maupas, 1892)	Java	Menzel (1922, 1924, 1925b, 1926b)
P. viguieri	England (botanical gardens, purchased pineapples)	Gurney (1932), Lowndes 1931), Scourfield (1903, 1906, 1939)
P. viguieri	Brazil	Chappuis (1936)
P. viguieri	Poland	Jakubisiak (1929)
P. viguieri	Puerto Rico	Maguire (1970)
P. viguieri	Jamaica	Janetzky et al. (1996)
P. viguieri menzeli (Chappuis, 1928)	Java	Chappuis (1928, 1931), Thienemann (1934)
canthocamptids	Australia (botanical gardens)	Hamond (1988)
harpacticoids	Brazil	Lopez et al. (1998)
Cyclopoida		
Bryocyclops anninae (Menzel, 1926)	Java	Menzel (1926a), Thienemann (1934)
Bryocyclops bogoriensis (Menzel, 1926)	Java	Menzel (1926a), Thienemann (1934)
Bryocyclops caroli Bjornberg, 1985	Puerto Rico	Maguire (1970), Reid (1999)
Cyclops sp.[2]	Argentina	Torales et al. (1972)
Diacyclops bisetosus (Rehberg, 1880)	England	Gurney (1933)
Ectocyclops bromelicola Kiefer, 1935	Brazil	Kiefer (1935)
Ectocyclops phaleratus (Koch, 1838)	Costa Rica	Picado (1913)
E. phaleratus	Jamaica	Laessle (1961), Reid & Janetzky (1996)
Ectocyclops strenzkei Herbst, 1959	Brazil	Herbst (1959)
E. strenzkei	Germany (greenhouse)	Herbst (1959)
Ectocyclops sp.	Brazil	Hadel & Carvalho (1988)
Fimbricyclops jimhensoni Reid, 1993b	Puerto Rico	Reid (1993b)
Fimbricyclops sp.	Puerto Rico	Reid (1999)
Muscocyclops operculatus (Chappuis, 1917)	Brazil	Kiefer (1935), Rocha & Bjornberg (1987)

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Table 1. contd.

Kind of phytotelmata/ Species	Location	Reference
Paracyclops bromeliacola Karaytug & Boxshall, 1998	Brazil	Karaytug & Boxshall (1998a)
Paracyclops fimbriatus (Fischer, 1853)	Brazil	Ferreira (1985)
P. fimbriatus f. *bromeliarum* Herbst, 1959	Brazil	Herbst (1959)
Paracyclops punctatus Karaytug & Boxshall, 1998	Brazil	Karaytug & Boxshall (1998a)
Paracyclops reidae Karaytug & Boxshall, 1998	Trinidad	Karaytug & Boxshall (1998a)
Paracyclops sp.	Brazil	Hadel & Carvalho (1988)
Tropocyclop jamaicensis Reid & Janetzky, 1996	Jamaica	Reid & Janetzky (1996), Janetzky (1997), Laessle (1961)
Tropocyclops prasinus (Fischer, 1860)	Puerto Rico	Reid (1993b)
Tropocyclops schubarti Kiefer, 1935	Brazil	Kiefer (1935), Herbst (1959)
Tropocyclops sp.	Brazil	Hadel & Carvalho (1988)
Cyclopoids	Brazil	Lopez et al. (1998)
copepods	Belgium?	Oye (1923); cited by Frank (1980)
B. Pitcher plants (*Sarracenia* spp.)		
Harpacticoida		
Bryocamptus hiatus (Willey, 1925)	Canada	Laird (1988)
Phyllognathopus viguieri	England	Scourfield (1903, 1939)
Cyclopoida		
Acanthocyclops parasensitivus Reid, 1998	U.S.A.	Reid (1998)
Acanthocyclops venustoides pilosus Kiefer, 1934	Canada, U.S.A.	Laird (1988)
Diacyclops harryi Reid, 1992	U.S.A.	Reid (1992)
Diacyclops languidus (G. O. Sars, 1863)	U.S.A.	Ishida (1992)
Paracyclops canadensis (Willey, 1934)	Canada	Willey (1934)
P. canadensis	U.S.A.	Hamilton et al. (2000)
Cyclopidae	U.S.A.	Miller et al. (1994), Harvey & Miller (1996)
'Entomostraca'	U.S.A.	Hegner (1926)
C. Tree holes or stump holes		
Harpacticoida		
Bryocamptus minutus (Claus, 1863)	England, Ireland	Gurney (1932)
Bryocamptus pygmaeus (Sars, 1863)	England	Gurney (1920, 1932)
Epactophanes richardi	Germany	Kiefer (1924)
Moraria arboricola Scourfield, 1915	England	Gurney (1920, 1932), Scourfield (1915, 1939)
Moraria varica (Graeter, 1911)	England	Gurney (1920, 1932), Scourfield (1939)
Moraria sp.	Germany	Rohnert (1951)
Elaphoidella taroi Chappuis, 1955	Fiji	Yeatman (1983)
Phyllognathopus viguieri	Tonga, Western Samoa, Fiji	Yeatman (1983)
Tachidius discipes Giesbrecht, 1882	England	Gurney (1920)
Cyclopoida		
Apocyclops sp.	Fiji	Yeatman (1983)
Australocyclops australis Morton, 1985	New South Wales, Australia	Morton (1985)
Bryocyclops bogoriensis	Fiji (Ivi, *Inocarpus edulis*)	Yeatman (1983)
Bryocyclops fidjiensis Lindberg, 1954	Tonga, Western Samoa, Fiji	Yeatman (1983)
Cryptocyclops linjanticus (Kiefer, 1928)	Fiji	Yeatman (1983)
Diacyclops bisetosus	England	Gurney (1933), Hollowday (1949)

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Table 1. contd.

Kind of phytotelmata/ Species	Location	Reference
Diacyclops spp.	Italy	Stoch (2000)
Halicyclops thermophilus Kiefer, 1929	Tonga, Western Samoa, Fiji	Yeatman (1983)
Mesocyclops aspericornis (Daday, 1906)	French Polynesia: holes in buttresses of *Inocarpus fagifer*	Rivière & Thirel (1981); Rivière et al. (1987)
Paracyclops fimbriatus	Fiji	Yeatman (1983)
Paracyclops poppei (Rehberg, 1880)	U.S.A.	Reid & Marten (1994), Karaytug & Boxshall (1998a)
Cyclopidae	Nukunono, Tokelau Islands	Laird (1956)
copepods	Brunei (dipterocarp forest)	Kitching & Orr (1996)
D. Other phytotelmata		
Harpacticoida		
Attheyella gessneri Chappuis, 1956	Venezuela: leaf axils of *Heliconia bihai* (Musaceae)	Chappuis (1956)
Attheyella inopinata Chappuis, 1931	Sumatra: leaf axils of *Cyrtandra glabra* (Gesneriaceae)	Chappuis (1931), Thienemann (1934)
Attheyella ruttneri Chappuis, 1931	Bali, Java: wet leaves of *Elatostema macrophyllum* (Urticaceae) and leaf axils of *Colocasia indica* (Araceae)	Chappuis (1931), Thienemann (1934)
Bryocamptus pygmaeus	Germany: leaf axils of *Scirpus silvaticus* (Cyperaceae)	Strenzke (1951)
Canthocamptus sp.	Java: leaf axils of *C. glabra*	Menzel (1924)
Elaphoidella bromeliaecola	Java, Sumatra: leaf axils of *Colocasia* sp., *C. glabra* and *Pandanus* sp. (Pandanaceae)	Chappuis (1931), Thienemann (1934)
Elaphoidella cornuta Chappuis, 1931	Sumatra: leaf axils of *C. glabra*	Chappuis (1931), Thienemann (1934)
Elaphoidella elegans Chappuis, 1931	Java: leaf axils of *C. indica*	Chappuis (1931), Thienemann (1934)
Elaphoidella taroi	Fiji: leaf axils of taro (*Colocasia esculenta)* and *Cordyline terminalis* (Agavaceae)	Chappuis (1955)
E. taroi	Fiji, Western Samoa: fallen coconut shells, leaf axils of taro	Yeatman (1983)
E. taroi	Tahiti: fallen coconut shells	Rivière, Klein, Thirel & Chebret (1998)
Elaphoidella thienemanni Chappuis, 1931	Sumatra: leaf axils of *C. glabra*	Chappuis (1931), Thienemann (1934)
Elaphoidella sp.	Fiji: leaf axils of *Colocasia* sp.and *C. terminalis*	Laird (1956)
Epactophanes richardi	Java: leaf-cups of *Nepenthes* sp. (Nepenthaceae)	Menzel (1921)
E. richardi	Sumatra: leaf axils of *C. glabra*	Chappuis (1931), Thienemann (1934), Lang (1935)
E. richardi	Java, Sumatra: inflorescences of *Zingiber macradenia* (Zingiberaceae), leaf axils of *Colocasia* sp. and *C. glabra*	Chappuis (1931)
E. richardi menzeli Chappuis, 1931	Sumatra: leaf-cups of	Thienemann (1932, 1934)

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Table 1. contd.

Kind of phytotelmata/ Species	Location	Reference
	Nepenthes ampullaria; also *C. glabra*, *Zingiber* sp.	
Parastenocaris incerta Chappious, 1931	Sumatra: leaf-cups of *N. ampullaria* in moss	Chappuis (1931); Thienemann Chappuis (1932)
Parastenocaris staheli	Surinam: moss in old leaf axils of *Livistona* (Palmae)	Menzel, 1916
Phyllognathopus viguieri	Algeria: debris of a decaying banana tree	Chappuis (1916)
P. viguieri	Java: leaf axils of *C. glabra*	Menzel (1924, 1925b, 1926b)
P. viguieri	Poland: leaf axils of *Musa encete* (Musaceae)	Jakubisiak (1929)
P. viguieri	Sumatra: leaf axils of *Colocasia* sp.	Chappuis (1931)
P. viguieri	Sumatra: leaf-cups of *N. ampullaria*	Thienemann (1932)
P. viguieri	Java, Sumatra: *Colocasia indica, Cyrtandra* sp., *Zingiber* sp.	Thienemann (1934)
P. viguieri	England: leaf-cups of *Crinum* sp. (Amaryllidaceae)	Scourfield (1939)
P. viguieri	Fiji: leaf axils of *C. terminalis* and *Colocasia* sp.	Laird (1956)
P. viguieri	Madagascar: leaf axils of *Typhonodorum* sp. (Araceae)	Dussart (1982)
P. viguieri	Tonga, Western Samoa, Fiji: taro leaf axils, bamboo	Yeatman (1983)
P. viguieri menzeli	Java, Sumatra: leaf axils of *Colocasia* spp., *C. glabra*, cups of *Nepenthes* sp., and inflorescences of *Z. macradenia*	Chappuis (1931), Thienemann (1934)
P. viguieri menzeli	Guam: leaf axils of *Pandanus*	Watkins & Belk (1975)
Harpacticoida	Sulawesi: leaf axils of taro	Mogi & Sembel (1996)
harpacticoid	Costa Rica: bracts of *Heliconia imbricata* (Musaceae)	Naeem (1988)
Cyclopoida		
Bryocyclops anninae	New Hebrides: empty coconut husks	Lowndes (1928a)
B. anninae	Guam: leaf axils of *Pandanus* sp.	Watkins & Belk (1975)
Bryocyclops bogoriensis	Sumatra: leaf axils of *Colocasia* sp.; Java: leaf axils of *Pandanus* sp.	Kiefer (1933), Thienemann (1934)
Bryocyclops chappuisi Kiefer, 1928	Java: leaf axils of *Crinum hybridum*	Kiefer (1933), Thienemann (1934)
Bryocyclops fidjensis	Fiji: leaf axils of *C. terminalis, Freycinetia milnei* (Pandanaceae), taro (*Colocasia antiquorum*)	Lindberg (1955)
B. fidjiensis	Fiji, Tonga, Western Samoa,	Yeatman (1983)

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Table 1. contd.

Kind of phytotelmata/ Species	Location	Reference
	Hawaii: bamboo, leaf axils of taro and *Pandanus* sp.	
Bryocyclops muscicola (Menzel, 1926)	Sumatra: leaf axils of *Pandanus* sp.	Kiefer (1933), Thienemann (1934)
Bryocyclops sp.	Fiji, Tonga: leaf axils of *Colocasia* sp., *C. terminalis*, and *Freycinetia milnei*; and *Pandanus* sp., respectively	Laird (1956)
Ectocyclops rubescens (as *E. medius*)	Java: leaf axils of *C. indica*, leaves of nettles	Kiefer (1933), Thienemann (1934)
Tropocyclops schubarti dispar Herbst, 1962	Brazil: shells of fallen Brazil nuts, *Bertholletia excelsa* (Lecythidaceae)	Herbst (1962)
Cyclopidae	Tarawa, Gilbert Islands: coconut shell	Laird (1956)
cyclopoids	Singapore: tree roots	Laird (1988)
Cyclopoida	Sulawesi: leaf axils of taro	Mogi & Sembel (1996)
copepods	Puerto Rico: water in fallen leaves	Maguire (1971)
copepods	Singapore: cups of *N. ampullaria*	Ghosh (1928)

[1] Should be considered an unidentified canthocamptid.

[2] Since *Cyclops* is not a tropical genus, this record should be considered an unidentified cyclopoid.

scanty literature on copepods in leaf litter was last reviewed for harpacticoids by Menzel (1946), and more generally discussed by Fiers & Ghenne (2000). Most studies have been done in Europe, where extensive areas are covered by beech (*Fagus sylvatica*) forests, and leaf litter from that and other trees now forms, or historically has formed vast carpets. Beech leaves tend to pack tightly together in a dense layer that retains water, and the animals live mainly in the deeper, more humid layers, directly on top of the forest floor (Nielsen, 1966; Schaeffer, 1991). In Denmark, populations of the harpacticoids *E. richardi* and *Maraenobiotus vejdovskyi tenuispina* reached substantial densities (40 and 1.5 ind/g of leaves respectively) (Nielsen, 1966). Fiers & Ghenne (2000), treating a modest number of litter samples which were sampled and extracted using techniques more suitable for nematodes, listed 9 cyclopoid and 13 harpacticoid species, 9 of these new records for Belgium, and a significant addition to the list of 71 species previously known from that country. The leaf-carpet may be the primary habitat for certain harpacticoid species, such as *Maraenobiotus vejdovskyi* var. *truncatus* (Scourfield, 1939) and some members of *Moraria*, as implied by the Yorkshire records of Fryer (1993). Michailova-Neikova (1973) found that 8 of 9 harpacticoid species living in wet moss beside waterbodies on a mountain in Bulgaria also appeared in the leaf litter.

Outside Europe, leaf litter has been much less investigated (Table 2). Dumont & Maas (1988) described five new species of harpacticoids from leaf litter in Nepal, at altitudes from 1900 to 3900 m.

Moist rotting wood may also harbor copepods. *Elaphoidella cuspidata* Chappuis, 1941, was found by Chappuis (1954) in rotted wood in India. *Phyllognathopus camptoides* was described by Božić (1965) from moist dead wood collected from a forest in Gabon.

Moist soils

Reid (1986) reviewed qualitative and quantitative studies reporting copepods from moist soils. In their study in Belgium, Fiers & Ghenne (2000) also discovered a surprising number of species in soil samples, particularly in fallow soils.

The ecological role of soil copepods is not understood. Birch & Clark (1953) classified *Epactophanes* sp. among the bacterial feeding organisms in a study of

Table 2. Copepods recorded from leaf litter. Species are listed under the current name of the taxon, as far as possible; synonymies of most species were listed by Dussart & Defaye (1985, 1990) for Cyclopoida and Harpacticoida, respectively

Species	Location	Source
Harpacticoida		
Attheyella crassa (Sars, 1863)	Bulgaria	Michailova-Neikova (1973)
Attheyella ilami Dumont & Maas, 1988	Nepal	Dumont & Maas (1988)
Attheyella wierzejskii (Mrázek, 1893)	Bulgaria	Michailova-Neikova (1973)
Bryocamptus hoferi (Douwe, 1907)	Bulgaria	Michailova-Neikova (1973)
Bryocamptus minutus	Bulgaria	Michailova-Neikova (1973)
Bryocamptus pygmaeus	England	Scourfield (1940), Fryer (1993)
B. pygmaeus	France	Klie (1943)
B. pygmaeus	Bulgaria	Michailova-Neikova (1973)
Bryocamptus stouti Harding, 1958	New Zealand	Harding (1958)
Bryocamptus weberi (Kessler, 1914)	England	Scourfield (1940)
Bryocamptus zschokkei (Schmeil, 1893)	Corsica	Klie (1943)
B. zschokkei tatrensis Minkiewicz, 1916	Bulgaria	Michailova-Neikova (1973)
Cantocamptus clavifurcatus Hamond, 1988	Tasmania	Hamond (1988)
Canthocamptus dedeckkeri Hamond,1988	Victoria, Australia	Hamond (1988)
Canthocamptus dumonti Hamond, 1988	Victoria, Australia	Hamond (1988)
Canthocamptus globulisetosus Hamond, 1988	Victoria, Australia	Hamond (1988)
Canthocamptus howardorum Hamond, 1988	Tasmania	Hamond (1988)
Canthocamptus lacinulatus Hamond, 1988	Victoria, Australia	Hamond (1988)
Canthocamptus longifurca Hamond, 1988	Victoria, Australia	Hamond (1988)
Canthocamptus mammillifurca Hamond, 1988	Victoria, Australia	Hamond (1988)
Canthocamptus mortoni Hamond, 1988	Tasmania	Hamond (1988)
Canthocamptus tasmaniae Hamond, 1988	Tasmania	Hamond (1988)
Canthocamptus timmsi Hamond, 1988	Tasmania	Hamond (1988)
Echinocamptus hypophyllus Defaye & Heymer, 1996	Congo (Zaire)	Defaye & Heymer (1996)
Elaphoidella jochenmartensi Dumont & Maas, 1988	Nepal	Dumont & Maas (1988)
Elaphoidella propedamasi Defaye & Heymer, 1996	Congo (Zaire)	Defaye & Heymer (1996)
Elaphoidella pseudocornuta Dumont & Maas, 1988	Nepal	Dumont & Maas (1988)
Epactophanes muscicolus (Richters, 1901)	England	Scourfield (1940)
Epactophanes richardi	England, Ireland	Gurney (1932), Scourfield (1940)
E. richardi	Germany	Precht (1936)
E. richardi	Corsica	Klie (1943)
E. richardi	Denmark	Nielsen (1966)
E. richardi	Hawaii	Evenhuis & Preston (1995)
E. richardi	Congo (Zaire)	Defaye & Heymer (1996)
Fibulacamptus gracilior Hamond, 1988	Victoria, Australia	Hamond (1988)
Fibulacamptus tasmanicus Hamond, 1988	Tasmania	Hamond (1988)
Fibulacamptus victorianus Hamond, 1988	Victoria, Australia	Hamond (1988)
Maraenobiotus vejdovskyi anglicus Gurney, 1932	England	Scourfield (1940)
M. vejdovskyi tenuispina Roy, 1924	Denmark	Nielsen (1966)
M. vejdovskyi tenuispina	France	Remy (1932)
M. vejdovskyi truncatus Gurney, 1932	England	Scourfield (1940)
M. vejdovskyi truncatus	France	Klie (1943)
Moraria arboricola Scourfield, 1915	England	Scourfield (1940), Fryer (1993)
Moraria frondicola Klie, 1943	Corsica	Klie (1943)
Moraria ilami Dumont & Maas, 1988	Nepal	Dumont & Maas (1988)
Moraria poppei (Mrázek, 1893)	Bulgaria	Michailova-Neikova (1973)

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Table 2. contd.

Species	Location	Source
Moraria terrula Kikuchi, 1991	Japan	Kikuchi (1984, 1991b)
Moraria tsukubaensis Kikuchi, 1991	Japan	Kikuchi (1984, 1991a)
Moraria valkanovi Michailova-Neikova, 1973	Bulgaria	Michailova-Neikova (1973)
Moraria varica	England, Ireland	Gurney (1932), Scourfield (1940)
M. varica	France	Božić (1966)
M. varica	England	Fryer (1993)
Parbatocamptus jochenmartensi Dumont & Maas, 1988	Nepal	Dumont & Maas (1988)
Phyllognathopus cf. *camptoides* Božić, 1965	Congo (Zaire)	Defaye & Heymer (1996)
Phyllognathopus viguieri	England	Scourfield (1940)
P. viguieri	Agrihan Is., Marianas	Kikuchi (1994b)
P. viguieri	Hawaii	Evenhuis & Preston (1995)
unidentified harpacticoid	England	Stout (1963)
Cyclopoida		
Allocyclops silvaticus Rocha & Bjornberg, 1988	Brazil	Rocha & Bjornberg (1988)
Bryocyclops anninae	Hawaii	Evenhuis & Preston (1995)
Bryocyclops phyllopus Kiefer, 1935	Congo (Zaire)	Defaye & Heymer (1996)
Goniocyclops sylvestris Harding, 1958	New Zealand	Harding (1958)
Metacyclops hirsutus Rocha, 1994	Brazil	Rocha (1994)
Muscocyclops operculatus	Brazil	Rocha & Bjornberg (1987)
Paracyclops bromeliacola Karaytug & Boxshall, 1998	Brazil	Karaytug & Boxshall (1998a)
Paracyclops chiltoni (Thomson, 1882)	Brazil	Karaytug & Boxshall (1998b)

soil fauna in Australia. However, *Epactophanes,* like *P. viguieri*, may be a predator on nematodes. Copepods are inefficiently sampled by the Tullgren funnel and other extraction methods used for soil fauna (Fiers & Ghenne, 2000), and their true numbers in soils are probably underestimated.

Thermal waters

It is difficult to define 'thermal', but 30 °C may be a reasonable limit above which temperate-zone copepods do not easily survive. There are relatively few records of copepods, mostly cyclopoids, from thermal waters. Menzel (1925a) reported a species of *Halicyclops* (subsequently described as *Halicyclops thermophilus* by Kiefer, 1929, 1933) from a hot saline spring on Java (37–45 °C, pH 6.7–7.1, salinity 26.7). Many of the temperatures reported by Kiefer (1933) from waters on Sumatra investigated by the Sunda-Expedition were over 30 °C: a young cyclopoid was found in a warm acid spring (35.5 °C, pH 2.68); other warm springs (29.5–39 °C, pH 7.3–7.6) harbored *Paracyclops eucyclopoides, P. fimbriatus, Mesocyclops aequatorialis, Microcyclops varicans* s. str., *M. varicans subaequalis,* and *Thermocyclops decipiens.* Brehm (1936) mentioned a species of *Eucyclops* from 'heißen Quellen' near Cuzco, Peru; no temperature or water chemistry data were available. *Mesocyclops 'leuckarti'* was reported by Lindberg (1942) from a basin of a soap factory in Iran, water temperature 40 °C. In Iceland, a thermal pool (34 °C) harbored the eurytopic species *E. serrulatus* and *Megacyclops viridis* (Starmühlner, 1969). Dussart (1974) reported *Cletocamptus deitersi, Cryptocyclops linjanticus micrura* and *Mesocyclops aequatorialis* from warm springs in Ethiopia, without further habitat data. Lewis (1974) described *Paracyclops waiariki* from thermal springs in New Zealand, but at a relatively low temperature of 27 °C (and pH 3.0). Reid (1994) found a cyclopoid, *Microcyclops* sp., in a spring-fed thermal (about 40 °C) pond in Brazil.

Other harpacticoids besides *C. deitersi* have been found in thermal waters. Chappuis (1931) reported *Elaphoidella bidens coronata, Schizopera tobae* and *Parastenocaris longicaudis* from a warm spring (29.5 °C) on Sumatra. Por (1964) described *Nitokra balnearia* from hot mineral springs (31 °C) on the Dead Sea shore in Israel, where it reached immense numbers. *Thermomesochra reducta* Itô & Burton, 1980,

Table 3. Copepods reported from thermal waters. Species are listed under the current name of the taxon, as far as possible; synonymies of most species were listed by Dussart & Defaye (1985, 1990) for Cyclopoida and Harpacticoida, respectively

Species	Temp. (°C)	Location: habitat	Reference
Harpacticoida			
Cletocamptus deitersi (Richard, 1897)	-	Ethiopia: thermal springs	Dussart (1974)
Elaphoidella bidens coronata (Sars, 1904)	29.5	Sumatra: thermal spring	Chappuis (1931)
Nitokra balnearia Por, 1964	31	Israel: hot mineral spring	Por (1964)
Parastenocaris longicaudis Chappuis, 1931	29.5	Sumatra: thermal spring	Chappuis (1931)
Schizopera tobae Chappuis, 1931	29.5	Sumatra: thermal spring	Chappuis (1931)
Thermomesochra reducta Itô & Burton, 1980	38–58	Malaysia: hot spring	Itô & Burton (1980)
Cyclopoida			
Cryptocyclops linjanticus	-	Ethiopia: springs	Dussart (1974)
Cyclops sp.[1]	37–46	India: spring	Jana (1978); Jana & Sarkar (1971)
Cyclops sp.[1]	31–34	Nigeria: spring	Egborge & Fagade (1979)
Eucyclops serrulatus (Fischer, 1851)	34	Iceland: spring	Starmühlner (1969)
E. serrulatus	28.6–29.7 (surface)	Hungary: spring-fed lake	Ponyi (1992)
Halicyclops thermophilus	37–45	Java: saline spring	Menzel (1925a); Kiefer (1929, 1933)
Macrocyclops albidus (Jurine, 1820)	28.6–29.7 (surface)	Hungary: spring-fed lake	Ponyi (1992)
Megacyclops viridis (Jurine, 1820)	34	Iceland: spring	Starmühlner (1969)
Mesocyclops aequatorialis Kiefer, 1929	-	Ethiopia: springs	Dussart (1974)
M. aequatorialis	29.5–39	Sumatra: springs	Kiefer (1933)
Mesocyclops leuckarti (Claus, 1857)	40	Iran: basin	Lindberg (1942)
Microcyclops varicans (Sars, 1863)s. str.	29.5–39	Sumatra: springs	Kiefer (1933)
M. varicans	28.6–29.7 (surface)	Hungary: thermal spring-fed lake	Ponyi (1992)
M. varicans subaequalis (Kiefer, 1928)	29.5–39	Sumatra: thermal springs	Kiefer (1933)
Microcyclops sp.	40	Brazil: spring-fed thermal pond	Reid (1994)
Paracyclops eucyclopoides Kiefer, 1929	29.5–39	Sumatra: thermal springs	Kiefer (1933)
Paracyclops fimbriatus	29.5–39	Sumatra: thermal springs	Kiefer (1933)
Paracyclops waiariki Lewis, 1974	27	New Zealand: thermal springs	Lewis (1974)
Thermocyclops decipiens Kiefer, 1929	29.5–39	Sumatra: thermal springs	Kiefer (1933)
unidentified cyclopoid	35.5	Sumatra: thermal acid spring	Kiefer (1933)

[1] These records should be considered as unidentified cyclopoids.

from a hot spring in Malaysia, holds the survival record at temperatures between 38 and 58 °C.

High altitude and high latitude habitats

There has historically been much interest in the aquatic faunas of high-altitude regions, although of course most studies have been carried out in lakes. The non-lacustrine copepod fauna of the Alps is comparatively well known (e.g. Thienemann, 1950; Gaviria, 1998). Several surveys in montane regions outside Europe, mainly by Heinz Löffler, have included samples from non-lacustrine 'minor' habitats. Examples from the Andes include the reports of Harding (1955) and Löffler (1960) from Peru and Bolivia. Löffler (1965, 1968a) reported on *Maraenobiotus* and other copepods from the high mountains of eastern Africa. In Asia, Löffler has reported on *Maraenobi-*

otus and other harpacticoids from Nepal (1968b) and Borneo (Mt. Kinabalu; Löffler, 1973).

Although the plankton of lakes at extremely high altitudes tends to be species-poor (except in the Alps; see Löffler, 1968c), most of these surveys have indicated the existence of a rich semiterrestrial copepod fauna in locations where there is some vegetation and moisture, even in the presence of permafrost. Typical altitudes reached by copepods are up to about 4100 m in Mexico and Central America (Löffler, 1972) and the Colombian páramo region (Gaviria, 1989), 3800 m on Mt. Kinabalu, Borneo (Löffler, 1973), 2140 m in the Great Smoky Mountains, eastern U.S.A. (J. W. Reid & W. Reeves, unpublished data), and to the glacier line (2300–2600 m) in the Austrian Alps (Gaviria, 1998). Dumont & Maas (1988) described five species of harpacticoids living in leaf litter in montane forests of Nepal at moderate to high altitudes (1900–3900 m). Two planktonic species of calanoids and an unidentified cyclopoid live in lakes in Nepal at altitudes from 4600 to 5460 m (Manca et al., 1994). The record for altitude is probably held by *Glaciella yalensis* Kikuchi, 1994a, which inhabits melt (cryconite) pits on the Yala Glacier in Nepal, at altitudes between 5100 and 5700 m (Kikuchi, 1994a).

Copepods living in extreme north and south latitudes confront similar problems of a short growing season and lack of organic matter. For instance, saline lakes in Antarctica support a limited assemblage consisting of three species of harpacticoids and two of calanoids (Wright & Burton, 1981); and freshwater Antarctic lakes harbor two calanoids, *Boeckella poppei* (Mrázek, 1901) and *Gladioferens antarcticus* Bayly, 1994, and one species of cyclopoid, *Acanthocyclops mirnyi* Borutzky & Vinogradov, 1957 (Bayly & Burton, 1993; Bayly, 1994). The known copepod fauna of Iceland is similarly species-poor (Starmühlner, 1969).

Students of biogeography have been much interested in the distribution and relationships of invertebrate montane faunas. The isolation of populations within and between mountain ranges has contributed to the development of a confusingly rich array of morphologically distinct populations of certain species. This phenomenon is well studied in the genus *Maraenobiotus* (Löffler, 1965, 1968a,b, 1973), and in several canthocamptid species in Japan (e.g. Ishida, 1991, 1994). Husmann (1975) argued that the edges of melting glaciers provided large areas of sand and gravel layers, followed by the moss tundra, which may have formed a 'combined system of migration ways' for interstitial organisms to follow from warmer regions. However, Strayer & Reid (1999) found that previously glaciated sites in the U.S.A. contained fewer species of interstitial specialist cyclopoid copepods (although equivalent numbers of generalist species) than historically unglaciated sites. This suggests that it was mainly the eurytopic species that were able to follow these 'migration ways'.

Unclassifiable natural habitats

Some of the odder locations where copepods have been found include a sea shell in Fiji, which contained *Halicydops septentrionalis* Kiefer, 1935 (Yeatman, 1983), and ants' nests (B. H. Dussart, mentioned by Reid, 1986).

Human-modified or artificial habitats

Holes in the ground created by the multiplicity of human actions may easily be colonized by copepods and other aquatic animals. Ditches and borrow pits are common sites to find copepods. For instance, Brady (1907) and Graham (1907) described several species of harpacticoids and cyclopoids from railway borrow pits and gold mine pits in the African Gold Coast. Münchberg (1956) described the limnological conditions and aquatic faunas of ca. 10-year-old bomb craters in Germany, which included mainly common, generalist species such as *Cyclops* cf. *strenuus* Fischer, 1851, and *Macrocyclops albidus.* Some examples of species collected from road ruts include *Canthocamptus australicus* (Sars, 1908) in Australia (Hamond, 1988), *Mesocyclops leuckarti* (probably = *M. aspericornis*) in Guam (Watkins & Belk, 1975), and *Metacyclops minutus* (Claus, 1863) and several other species by Maier (1992, 1998) and Maier et al. (1998). Even footprints may serve as copepod microhabitats: Brehm (mentioned in Gurney, 1933: 221) found *Diacyclops bicuspidatus* (Claus, 1857) in the small pools formed by his own footprints in spongy woodland soil. The ecological role of borrow ditches and pits in providing refuges for the aquatic faunas in arid regions might fruitfully be examined.

Copepods have invaded a variety of man-made habitats (Table 4), for example the roof of a tunnel in a coal mine (Brady, 1868), the filter beds of sewage treatment plants, and deeply buried agricultural drainage tiles (D. D. Williams, 1976). Copepods have been noticed in water systems of various sizes and uses, especially in older municipal systems where much of the water was drawn from subterranean sources, with minimal treatment. It is probably no accident

Table 4. Copepods reported from man-made or altered habitats. Species are listed under the current name of the taxon, as far as possible; synonymies of most species were listed by Dussart & Defaye (1985, 1990) for Cyclopoida and Harpacticoida, respectively

Species	Location: habitat	Reference
Harpacticoida		
Attheyella nordenskioldii (Lilljeborg, 1902)	Canada: agricultural drainage tiles	Williams, D. D. (1976)
Bryocamptus aquaeductus Borutsky, 1934	Ciscaucasia: city water pipe	Borutsky (1934)
Bryocamptus echinatus (Mrázek, 1893)	Germany: city water pipes	Kiefer (1926a, 1927a)
Bryocamptus luenensis (Schmeil, 1894)	Hungary: city water pipes	Török (1961)
Bryocamptus minutus	England: coal mine	Brady (1868)
B. minutus	Germany: city water pipes	Kiefer (1927a)
B. minutus	Romania: city water pipes	Damian (1958, 1959)
Bryocamptus pygmaeus	Romania: city water pipes	Damian & Botosaneanu (1954)
Bryocamptus typhlops (Mrázek, 1893)	Germany: city water pipes	Kiefer (1926a, 1927a)
Canthocamptus sp.	Germany: moist decaying mine timbers	Mrázek (1893)
Chappuisius inopinus Kiefer, 1938	Hungary, Romania: city water pipes	Török (1951), Damian (1958, 1959), respectively
Elaphoidella dubia Kiefer, 1931	Romania: city water pipes	Damian (1958, 1959)
Elaphoidella elaphoides (Chappuis, 1924)	Romania: city water pipes	Damian (1958, 1959)
Elaphoidella gracilis serrulata Damian & Botosaneanu, 1954	Romania: city water pipes	Damian & Botosaneanu (1954)
Elaphoidella grandidieri (Guerne & Richard, 1893)	Western Samoa: old tires	Yeatman (1983)
Elaphoidella juxtaputealis Damian & Botosaneanu, 1954	Romania: city water pipes	Damian & Botosaneanu (1954)
Elaphoidella phreatica (Chappuis, 1925)	Romania: city water pipe	Chappuis (1925)
Elaphoidella putealis (Chappuis, 1925)	Romania: city water pipe	Chappuis (1925)
Elaphoidella taroi	Fiji: tin cans	Yeatman (1983)
Epactophanes richardi	Hawaii: leaf-litter filled cup traps on trees	Evenhuis & Preston (1995)
E. richardi	Germany: trickle filters, activated charcoal filters	Husmann (1966, 1982)
Nitocrella calcaripes Damian & Botosaneanu, 1954	Romania: city water pipes	Damian & Botosaneanu (1954)
Nitocrella chappuisi Kiefer, 1926	Germany: city water pipes	Kiefer (1926b, 1927a)
Nitocrella hibernica s. str.	Germany: activated charcoal filters	Husmann (1982)
N. hibernica hyalina (Jakubisiak, 1929)	Poland: city water pipe	Jakubisiak (1929)
Nitocrella hirta Chappuis, 1924	Romania, Hungary: city water pipes	Chappuis (1925), Török (1951), respectively
N. hirta bucarestiensis Damian & Botosaneanu, 1954	Romania: city water pipes	Damian & Botosaneanu (1954)
Nitocrella kosswigi Noodt, 1954	Romania: city water pipes	Damian (1958, 1959)
Nitocrella omega Hertzog, 1936	France, Hungary: city water pipes	Hertzog (1938), Török (1961), respectively
Nitokra psammophila Noodt, 1952	Germany: activated charcoal filters	Husmann (1982)
Nitokra reducta Schäfer, 1936 s. str.	Germany: activated charcoal filters	Husmann (1982)
Nitokra sewelli husmanni Kunz, 1976	Germany: activated charcoal filters	Husmann (1982)

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Table 4. contd.

Species	Location: habitat	Reference
Nitokra spinipes Boeck, 1864	Germany: activated charcoal filters	Husmann (1982)
Paracamptus schmeili (Mrázek, 1893)	France: city water pipes	Hertzog (1938)
P. schmeili biserialis (Micoletzky, 1912)	Romania: city water pipes	Chappuis (1925)
Parastenocaris aedes Hertzog, 1938	France: city water pipes	Hertzog (1938)
Parastenocaris aquaeductus Chappuis, 1925	Romania: city water pipes	Chappuis (1925)
Parastenocaris budapestinensis Török, 1935	Hungary: city water pipes	Török (1935)
Parastenocaris clujensis Chappuis, 1925	Romania: city water pipes	Chappuis (1925)
Parastenocaris entzii Török, 1935	Hungary: city water pipes	Török (1935)
Parastenocaris germanica Kiefer, 1936	Hungary: city water pipes	Török (1951)
Parastenocaris hippuris Hertzog, 1938	France: city water pipes	Hertzog (1938)
Parastenocaris jeanneli Chappuis, 1924	Romania: city water pipes	Damian (1958, 1959)
Parastenocaris karamani brevicauda Damian, 1958	Romania: city water pipes	Damian (1958, 1959)
Parastenocaris latisetosus Damian & Botosaneanu, 1954	Romania: city water pipes	Damian & Botosaneanu (1954)
Parastenocaris minuta Chappuis, 1925	Romania: city water pipes	Chappuis (1925)
Parastenocaris nana Chappuis, 1925	Romania: city water pipes	Chappuis (1925)
Parastenocaris pannonica Török, 1935	Hungary, Romania: city water pipes	Török (1935, 1961), Damian (1958, 1959), respectively
Parastenocaris similis Török, 1935	Hungary: city water pipes	Török (1935, 1961)
Parastenocaris subterraneus Damian, 1959	Romania: city water pipes	Damian (1958, 1959)
Parastenocaris uncinatus Damian & Botosaneanu, 1954	Romania: city water pipes	Damian & Botosaneanu (1954)
Parastenocaris spp.	Germany: trickle filters	Husmann (1966)
Phyllognathopus viguieri	Germany: aquarium	Kessler (1914)
P. viguieri	Switzerland: aquarium	Chappuis (1916)
P. viguieri	Germany: indoor swimming pool	Klie (1924)
P. viguieri	Germany: water in coal mine	Ziegelmayer (1923)
P. viguieri	England: 'experimental filters'	Gurney (1932), Scourfield (1939)
P. viguieri	Romania, Germany: trickle filters	Damian-Georgescu (1966), Husmann (1966), respectively
P. viguieri	Tonga, Western Samoa, Fiji: old tires, tin cups, plastic containers, old boats	Yeatman (1983)
P. viguieri	Hawaii: leaf-litter–filled cup traps on trees	Evenhuis & Preston (1995)
Spelaeocamptus spelaeus (Chappuis, 1925)	Romania: city water pipes	Chappuis (1925, 1927)
Unidentified Harpacticoida	U.S.A.: old tires	Nasci et al. (1987)
Cyclopoida		
Acanthocyclops exilis (Coker, 1934)	U.S.A.: old tires	Nasci et al. (1987)
Acanthocyclops rhenanus Kiefer, 1936	France: city water pipes	Hertzog (1938)
Acanthocyclops robustus (Sars, 1863)	Romania: city water pipes	Damian (1958, 1959)
Acanthocyclops venustus (Norman & Scott, 1906)	France: city water pipes	Hertzog (1938)
Acanthocyclops vernalis (Fischer, 1853)	Canada: agricultural drainage tiles	Williams, D. D. (1976)
A. vernalis	U.S.A.: old tires	Nasci et al. (1987), Marten (1989), Reid & Marten (1994)
Bryocyclops anninae	Hawaii: leaf-litter–filled cup traps on trees	Evenhuis & Preston (1995)

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Table 4. contd.

Species	Location: habitat	Reference
Bryocyclops fidjiensis	Fiji, Tonga, Western Samoa: tin cans, bottles	Yeatman (1983)
Cryptocyclops linjanticus	Fiji: metal drums	Yeatman (1983)
Cyclops sp.	Germany, Romania: city water pipes	Kraepelin (1886), Damian (1958, 1959), respectively
Diacyclops clandestinus (Kiefer, 1926)	Germany: city water pipes	Kiefer (1926a, c, 1927a)
D. clandestinus	Romania, Hungary: city water pipes	Damian (1958, 1959), Török (1961), respectively
Diacyclops crassicaudis (Sars, 1863)	Romania: city water pipes	Damian (1958, 1959)
Diacyclops languidoides hiberniae (Gurney, 1927)	Wales: cistern	Gurney (1933)
Diacyclops navus (Herrick, 1882)	U.S.A.: old tires	Nasci et al. (1987; as *Thermocyclops dybowskii*), Marten (1989), Reid & Marten (1994)
Diacyclops ? stygius (Chappuis, 1924)	Romania: city water pipes	Damian & Botosaneanu (1954)
Ectocyclops phaleratus	U.S.A.: old tires	Nasci et al. (1987)
Ectocyclops rubescens	U.S.A.: old tires	Marten (1989), Reid & Marten (1994)
Eucyclops agilis (Koch, 1838)	France: city water pipes	Moniez (1889)
E. agilis	U.S.A.: old tires	Nasci et al. (1987), Marten (1989), Reid & Marten (1994)
Eucyclops elegans (Herrick, 1884)	U.S.A.: old tires	Nasci et al. (1987; as *E. speratus*); Reid & Marten (1994)
Eucyclops serrulatus	Germany: city water pipes	Kiefer (1927a)
E. serrulatus	Romania: city water pipes	Damian & Botosaneanu (1954)
Graeteriella unisetigera (Graeter, 1908)	Germany: city water pipes, trickle filters	Kiefer (1926a, 1927a), Husmann (1966), respectively
Halicyclops thermophilus s. str.	Tonga, Western Samoa, Fiji: old tires	Yeatman (1983)
Macrocyclops albidus	U.S.A.: old tires	Marten (1989), Marten et al. (1993), Reid & Marten (1994)
M. albidus	Romania: city water pipes	Damian (1958, 1959)
Megacyclops gigas (Claus, 1857)	Germany: city water pipes	Kiefer (1927a)
Megacyclops viridis	France: city water pipes	Moniez (1889)
M. viridis	England: water tank	Scourfield (1939)
Mesocyclops affinis Van de Velde, 1987	Vietnam: water containers	Vu et al. (2000)
Mesocyclops aspericornis	French Polynesia: barrels in pigpen and old tires	Rivière & Thirel (1981), Rivière et al. (1987)
M. aspericornis	Hawaii: containers	Marten (1984)
M. aspericornis	Colombia: mosquito rearing containers	Suárez et al. (1984)
M. aspericornis	Vietnam: water containers	Vu et al. (2000)
M. leuckarti	Iran: basin of soap factory	Lindberg (1942)
Mesocyclops longisetus (Thiébaud, 1912)	Venezuela: drinking tank	Dussart (1984)
Mesocyclops ogunnus Onabamiro, 1957		
Mesocyclops cf. *pehpeiensis* Hu, 1943	Vietnam: water containers	Vu et al. (2000)
Mesocyclops ruttneri Kiefer, 1981	Vietnam: water containers	Vu et al. (2000)

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Table 4. contd.

Species	Location: habitat	Reference
Mesocyclops thermocyclopoides Harada, 1931	Vietnam: water containers	Vu et al. (2000)
Mesocyclops woutersi Van de Velde, 1987	Vietnam: water containers	Vu et al. (2000)
Mesocyclops yenae Holynska, 1998	Vietnam: water containers	Vu et al. (2000)
Metacyclops planus (Gurney, 1909)	Romania: city water pipes	Damian (1958, 1959)
Metacyclops tredecimus (Lowndes, 1934)	Venezuela: drinking tank	Dussart (1984)
Orthocyclops modestus (Herrick, 1883)	U.S.A.: old tires	Marten (1989), Reid & Marten (1994)
Paracyclops affinis (Sars, 1863)	Senegal: laboratory cultures of nematodes	Reversat et al. (1992)
Paracyclops chiltoni	England: percolating filters of sewage works	Karaytug & Boxshall (1998b)
Paracyclops fimbriatus	France: city water pipes	Moniez (1889)
P. fimbriatus	Germany: city water pipes	Kiefer (1926a, 1927a)
P. fimbriatus	Romania: city water pipes	Damian & Botosaneanu (1954)
P. fimbriatus	Fiji: old tire	Yeatman (1983)
P. fimbriatus	U.S.A.: old tires	Marten (1989), Reid & Marten (1994)
P. fimbriatus s. lat.	Easter Island: stone basins and mouth of stone statue	Dumont & Martens (1996)
Paracyclops poppei	U.S.A.: old tires	Marten (1989), Reid & Marten (1994), Karaytug & Boxshall (1998a)
Tropocyclops prasinus	England: water tank	Scourfield (1939)
T. prasinus	U.S.A.: old tire	Reid & Marten (1994)
Calanoida:		
'Calaniden'	Germany: city water systems	Kraepelin (1886)

that most records predate the use of modern water sanitation procedures. Kraepelin (1886) was apparently the first to report copepods (*Cyclops* sp. and 'Calaniden') in a municipal water system, in Hamburg, Germany. Shortly thereafter, Moniez (1889) found several common species of cyclopoids in the water pipes of Lille, France. Chappuis (1925), Török (1935) and Hertzog (1938) described several new species of parastenocaridid harpacticoids from city water pipes in Europe.

A human-created analogue to the natural psammon is the sand-filter beds (trickle filters) of water treatment plants. Psammic or hypogean cyclopoids and harpacticoids such as *Graeteriella unisetigera*, *E. richardi, P. viguieri*, and species of *Parastenocaris* may colonize trickle filters (e.g. Husmann, 1961, 1966; Duncan, 1989). Even activated charcoal filters may harbor copepods (Husmann, 1982). The literature on copepods in various kinds of filters, much of it in obscure local reports, is difficult to review; but some examples are included in Table 4.

Discussion

Studies in the more cryptic habitats have contributed substantially to fundamental understanding of the biology of copepods. These have provided information on developmental rates, adaptations to low food supply and/or low temperatures, dispersal by natural and human agencies, biogeography, evolution and conservation.

Some of the fastest-developing copepods live in temporary ponds. The most spectacular example is the cyclopoid *Metacyclops minutus*, which in tiny ponds in Germany may pass through 8 or more generations in a single growing season. Under natural conditions they may develop from egg to adult in 4.7–8.6 days, and in the laboratory have matured in as little as 4 days at 30 °C (Maier, 1992). In this species also, males differ little from females in size, females and males mature at about the same rate, and adults and subadults may pass through dry phases in a state of quiescence, and through the winter in diapause (Maier, 1992).

Adaptations to extreme conditions of low food supply and/or low temperatures include reduction in the number (usually with enlarged size) of eggs, as in the harpacticoid *Pseudomoraria triglavensis* (Brancelj, 1994). Some soil harpacticoids may produce only 2 eggs at a time, and drop them or actively lay them in the leaf substrate (Nielsen, 1966); some small cave cyclopoids also produce as few as 2 large eggs, and drop them (Lescher-Moutoué, 1973).

Fiers & Ghenne (2000) found *Graeteriella unisetigera*, previously supposed to be a strict stygobiont, in several beech litter samples, documented the striking coincidence between its known distribution and the historical limits of beech forests, and advanced the hypothesis that the animals are able to travel along the ground, rather than being restricted to particular drainage basins. They pointed out that not only might this be a convenient dispersal route, but would prevent physical and genetic separation of populations in different drainage basins, thus reducing speciation. Fiers & Ghenne (2000) noted that while larger stygobionts tend to be restricted within drainage basins (examples given by Notenboom et al., 1996), the tiny (about 0.5 mm long) copepods are usually more widely distributed. They may be not only less limited by such factors as sediment permeability, but be more eurytopic than previously estimated and able to exploit continuous epigean highways of leaf litter, mosses, and moist soils. Remy (1932) early remarked on the relative uniformity of the leaf-carpet in space and time, and suggested a possible role of humid forest habitats as a refuge for specialists, particularly trogloxenes or troglophiles, as well as for less specialized generalist species.

A similar idea was advanced by Frey (1980), who developed a concept of a worldwide rainforest habitat and predicted that endemic or uniquely adapted species would be found there. Lewis (1986) remarked on the analogous distribution of one harpacticoid genus of the damp forest, *Loefflerella*, which occurs in Patagonia, Chile and New Zealand, to that of the genus of semiterrestrial cladocerans, *Bryospilus,* known from Puerto Rico, Venezuela and New Zealand (Frey, 1980). The canthocamptid harpacticoid genus *Fibulacamptus* is confined to wet temperate southern Australia and Tasmania, mainly in semiterrestrial situations: a river, muddy gravel and dead leaves, and wet moss and leaf litter (Hamond, 1988). *Antipodiella* is endemic to New Zealand (Lewis, 1986). Among cyclopoids, several genera are endemic to humid forests, and the known ranges of some are apparently restricted, e.g. *Cochlacocyclops, Goniocyclops* and *Psammocyclops* in Madagascar (Kiefer, 1955); *Fimbricyclops* in Puerto Rico (Reid, 1993b); *Goniocyclops* in New Zealand (Harding, 1958); *Muscocyclops* mainly in the Atlantic coastal forest of South America, with outliers in continuous wetlands in central Brazil (Reid, 1987; Rocha & Bjornberg, 1987).

Lewis (1984) pointed out that in the harpacticoid fauna of New Zealand, isolated since the Mesozoic, only 2 of 16 genera are endemic but endemism at the species level is high. The general picture of the biogeography of the Canthocamptidae presented by Lewis (1986) has not much changed with the addition of further data. Some exceptions are that a few genera are now known to occur on more than one continent, e.g. *Gulcamptus* in North America as well as eastern Asia (Reid & Ishida, 1996). On the other hand, advances in systematic understanding may alter this picture for some groups; for instance, the New World species of *Attheyella (Canthosella)* form a distinct group from the Asian species, and likely should be considered a separate genus (Janetzky et al., 1996).

Future collections in semiterrestrial habitats outside Europe may reveal that some genera or species are more widely distributed than presently thought. For instance, although the genus *Bryocamptus* s. lat. is widely distributed in the temperate northern hemisphere, in the southern hemisphere species have been found in New Zealand (Lewis, 1986) and a wet campo (hillside flush marsh) in central Brazil (Reid, 1993, 1994). The known distribution of *Itocyclops yezoensis* (Ito, 1953) was extended by recent collections from Japan and Alaska to the Great Smoky Mountains in the eastern U.S.A. (Reid & Ishida, 2000).

Passive transport is usually invoked as an effective distribution mechanism for microcrustaceans. Maguire (1971) described the colonization of phytotelmata as "the result of a series of interlinked events – dispersal, immigration and establishment." Janetzky (1997) suggested the possibility that disseminules might be blown by the wind, since *P. viguieri* appeared in a rain gauge in Jamaica. Obviously protective resting stages have been observed in few species of harpacticoids, although the eggs of at least some leaf litter- and soil-dwelling species resist desiccation to some degree (e.g. *Bryocamptus (Arcticocamptus)* spp., see Borutsky, 1952; *E. richardi*, see Nielsen, 1966), and adults of a few others (e.g. *A. nordenskioldii*, see D. D. Williams & Hynes, 1976) form drought-resistant cysts.

There are few papers that discuss natural transport, even by implication. Rouch (1972) described two harpacticoids, *Phyllognathopus bassoti* and *Nitocrella balli*, which had established good populations on a small sandy island that appeared in Wisdom Lake, a shallow crater lake on Long Island, Papua New Guinea. The copepods were collected 20 months after formation of the small island.

Copepods are apparently easily transported by various human activities. They may be carried in plant parts and moist soil, and exotic tropical copepods have been found in greenhouses or associated with tropical aquatic or terrestrial plants in several parts of the world: the East Asian *Sinodiaptomus sarsi* (Rylov, 1923) in California, U.S.A. (Light, 1939); the Brazilian *Attheyella aliena* in Germany (described by Noodt, 1956); the Asian *Mesocyclops ruttneri* in Austria (reported and described by Kiefer, 1981), Louisiana, Mississippi and Washington, D.C., U.S.A. (Reid, 1993a, 1996); and *Bryocyclops muscicola*, which was first described from Indonesia, in Florida, U.S.A. (Reid, 1999). Harpacticoids of the genus *Phyllognathopus* are frequently found in moist soils, and are probably so easily carried as to make determination of the origin of a particular population nearly impossible. *Phyllognathous viguieri* has been reported from greenhouse soils and the recesses of tropical plants (Lang, 1948; Borutsky, 1952; Lehman & Reid, 1993; Table 1). Hitchhiking with commercially cultured fish and crustaceans is more often invoked as a transport mechanism (reviewed by Reid & Pinto-Coelho, 1994).

The subterranean realm has been a hospitable situation for copepods (Stoch, 1995, 2001; Galassi, 2001). Attempting to account for the relatively high species and genus richness in certain hypogean areas, Stoch (1995) proposed the adaptive zone model, involving steps of colonization, speciation events and radiation, to describe the process of invasion of epigean species and their subsequent evolution in hypogean environments.

Copepods in general are an ancient group (Huys & Boxshall, 1991; Stock, 1991), and they may evolve extremely slowly in stable habitats, that is in habitats that do not themselves change much or allow easy physical access to other kinds of habitats. An example is the allopatric species-pair *Acanthocyclops sensitivus* (Graeter & Chappuis, 1914) in Europe and *A. parasensitivus* Reid, 1998, in eastern North America. These are identical in gross morphological characters such as appendage segmentation and setation, and differ only in certain proportions and finer ornamentation (Pospisil, 1999). Since both are rare and found only in groundwater-related habitats, we can assume that gene flow between the European and North American populations is nil. These two taxa have diverged only slightly since the continents separated.

However, where they have invaded complex habitats such as large lakes, particularly epibenthic and infaunal copepods have radiated to a sometimes surprising degree, sometimes over a relatively short time. The most complex species-flocks exist in Lake Baikal, where cyclopoids (3 flocks of 3, 4 and 13 species) and harpacticoids (6 flocks of 3–21 species) account for a large proportion of the 120 or more copepod taxa in the lake (Boxshall & Evstigneeva, 1994). The Baikal basin complex has existed (as one or several basins) since the Tertiary, and this long period has apparently allowed the development of a high degree of trophic specialization and mouthpart structure among the cyclopoids, and extreme sexual dimorphism in the caudal rami among the harpacticoids (Boxshall & Evstigneeva, 1994). The more recent formation (during the Pleistocene) of large subterranean lakes or cenotes in the Yucatan Peninsula apparently allowed primarily epigean benthic cyclopoids in the genera *Diacyclops* and *Mesocyclops* to radiate into small flocks of 2 and 3 species, respectively, including true planktonic forms (Fiers et al., 1996).

Many rarely collected copepods live preferentially in and are adapted to ephemeral waters. In Germany, where naturally created temporary habitats are disappearing, tiny pools maintained in early stages of succession by vehicular activity or other factors harbor several rare or endangered species of copepods, cladocerans and branchiopods (Herbst, 1982; Maier, 1998; Maier et al., 1998). Herbst (1982) listed 6 species of calanoids, 16 cyclopoids and 37 harpacticoids that are at some degree of risk in Germany because they inhabit special habitats, including small perennial plant-rich waterbodies, oligotrophic to mesotrophic ponds, acid bogs and moorland waters, cave waters, moss, saline waters and lake beaches, in addition to tiny ephemeral pools. Because the highly organic soils of the wet campo, a kind of hillside flush marsh in Brazil which harbors an extremely diverse copepod fauna (Reid, 1994), are valuable for truck farming, wet campos that are not in protected areas are at risk of being drained and destroyed. Bayly (1992, 1997, 1999) reviewed the highly diverse fauna in gnammas (rock pools) and seepage films on rock outcrops in Western Australia, and argued strongly for their protection.

"Sehr zu Unrecht sind die Kleingewässer und ihre Lebewelt bisher von der Wissenschaft etwas vernachlässigt worden" (Kiefer, 1925). Hollowday (1949) also urged that attention to neglected habitats would result in valuable new information: "It is by the investigation of such habitats as these that peculiar and specialized forms are often met with". Further pursuit of imaginative collecting, and ecologically oriented studies of copepods living at the natural extremes permissible to these basically aquatic forms are bound to provide additional insights on many aspects of their fundamental biology.

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