

# MEIOBENTHIC COPEPODS OF GALÁPAGOS: SPECIES COMPOSITION, DISTRIBUTION, COLONIZATION, SPECIATION

Wolfgang Mielke

## ABSTRACT

During the Göttingen Galápagos Meiofauna Expedition (February 1972 – March 1973), abundant copepod material was collected in the Galápagos Archipelago for systematic and ecological investigation. Most animals were extracted from sandy beaches, but habitats such as rock-pools, mangroves, and lagoons were also sampled. Thus far, at least 60 species have been identified, as well as representatives of 35 additional genera. As already known from other, primarily boreal regions, the Galápagos species exhibit characteristic distribution patterns in sandy beaches, predominantly above the groundwater level. This is evident in the present study for *Noodtiella hoodensis*, *Diarthrodella neotropica*, and *Klieonychocamptoides itoi*. Despite minor fluctuations in annual water temperature, a distinct seasonality in the life cycles of *Galapalaophonte pacifica* and *Oniscopsis robinsoni* is evident. Preliminary data provide partial evidence that the Galápagos' benthic copepods originated in Central and South America. Comparison among harpacticoid copepods from Galápagos, Panama, Costa Rica, and Chile demonstrate a closer relationship of Galápagos species to those in Central America than to those in Chile. There are some indications of initial steps of speciation processes within the Archipelago. However, all di- or polytypic taxa are composed of species exhibiting independent immigration into the island complex.

The meiobenthic copepod fauna of many regions of the world has been investigated only fragmentarily, or not at all. Therefore, statements on species assemblages, zoogeographical relationships, and distribution patterns would be premature at present. It is reasonable, however, to prepare an interim report if new or supplementary results are gained from a hitherto neglected area.

From February 1972 until March 1973 the Göttingen Galápagos Meiofauna Expedition was carried out by the University of Göttingen, Germany. The aims were, inter alia, (1) recording of the meiofauna; (2) measurement of meiofaunal distributions within the Archipelago; (3) investigation of the species' distribution in the eulittoral zone of sandy beaches; (4) ascertainment of life cycles; (5) identification of possible speciation processes; and (6) search for affinities with species from other geographical regions and presumed origin of the Galápagos meiofauna (Ax and Schmidt, 1973; Schmidt, 1978; Westheide, 1991). Moreover, a comparison with the extensive results on systematics and ecology gained from the well-investigated boreal sandy beach on the east side of the Island of Sylt, Germany, was intended (for copepods see Mielke, 1975, 1976; summary in Armonies and Reise, 2000).

The project resulted in the collection of abundant material from numerous localities of the Archipelago. The treatment of the enormous stock by members of the Göttingen study group led to important contributions to our knowledge of several aspects of the Galápagos meiofauna. Additional samples from diverse sites on the Pacific coasts of Panama, Costa Rica, and Chile yielded further harpacticoid copepod material for comparative studies, thus extending the depth of copepod investigation in the neotropical region (e.g., Mielke, 1981a, 1985, 1987a, 1992).

## MATERIAL AND METHODS

The majority of the samples were taken from selected sandy beaches of different islands of the Archipelago (Fig. 1, circles). The fauna was obtained from quantitative, 100 cm<sup>3</sup> sediment samples, which were taken along transects from the low water line as the starting point (0 mark) to the high tide line. Furthermore, a number of qualitative samples were obtained from other habitats such as rock-pools, lagoons, algae, and mangrove forests. The animals were extracted using the seawater-ice technique, combined with intensive washing of the sediment. The specimens were fixed in a 4% formalin/seawater solution, kept in vials, and transported to the Zoological Institute of Göttingen for further processing. More detailed information on the sampling procedures is available in Ax and Schmidt (1973) and Schmidt (1978). The copepods were dissected and embedded either in W 15<sup>®</sup> medium (Zeiss) or a version of Hoyer's medium. The cover glass was sealed with Eukitt<sup>®</sup> and DePeX<sup>®</sup>.

**STUDY SITE.**—The Galápagos Archipelago extends from 89°14' to 92°01' W, and from 1°25' S to 1°40' N. It is situated about 1000 km west of the continent, off the Ecuadorian coast. The Archipelago consists of about 50 islets and islands, 13 of which have an area of at least 10 km<sup>2</sup> (Fig. 1). The islands are of a volcanic 'hot spot' origin, with continuing volcanic activity in the younger, western region. The oldest exposed parts have been estimated to be 3–4 million years old by potassium-argon dating (e.g., Cox and Dalrymple, 1966; Holden and Dietz, 1972; Bailey 1976; Chavez and Brusca, 1991).

The various Galápagos islands considered herein were each numbered using a Roman-Arabic combination of numerals (Ax and Schmidt, 1973; see Fig. 1, Tables 1 and 2): I = Fernandina, II = Isabela, III = Pinta, IV = Marchena, V = Tower, VI = James, VII = Bartholomé, VIII = Jervis, IX = Santa Cruz, X = Baltra, XI = Barrington, XII = Floreana, XIII = San Cristóbal, XIV = Hood. Extra bold numbers stand for quantitative samples from the eulittoral beach zone (**qn**), normal printed numbers refer to qualitative collections of different habitats (**ql**).

**THE COLONIZATION PROBLEM.**—The Galápagos Islands have never been, in all probability, connected with the American continent (Ax and Schmidt, 1973; Westheide, 1991). Despite their 'geologic youthfulness' (Bailey, 1976), a species-rich copepod assemblage exists in the diversely structured coastal zones. A crucial question concerns the origin and means of transport for fauna and flora in general, and meiofauna in particular. Several paths of invasion have been discussed (Gerlach, 1977): (1) waterfowl; (2) organisms whirled up by heavy storms, enter the water column and are dispersed by currents; (3) transport by floating debris such as driftwood, algae, and coconuts; and (4) transfer in ballast water or sand of ships.

The ability of benthic copepods to disperse on a large scale is generally questioned because pelagic larvae are lacking in most cases, i.e., they are bound to the substratum as copepodids and adults. However, Armonies (1988, 1989) observed a 'semi-planktonic life-style' in several harpacticoid species which leave the sediment during the high tide and swim into the water column. It is probable that in addition to these active movements, passive transport may also occur. By clinging to drifting objects, transport for several days or weeks in open ocean currents seems plausible (Yeatman, 1962). An additional aspect was provided by Hicks (1988), who investigated the mucoid films produced by diatoms. These films can be detached from the substrate and serve as rafts for many meiofaunal organisms. The transfer of copepods, including harpacticoids, by ballast water has been demonstrated repeatedly (Carlton and Geller, 1993; Chu et al., 1997; Lavoie et al., 1999). On the whole, several factors and combinations of copepod transportation means must be taken into consideration.

## RESULTS AND DISCUSSION

The material of the Göttingen Galápagos Meiofauna Expedition contained about 36,000 copepods, 87% belonging to the Harpacticoida, and 13% to the Cyclopoida (not treated). In total, 1260 harpacticoid specimens were dissected and identified to species level. Thus

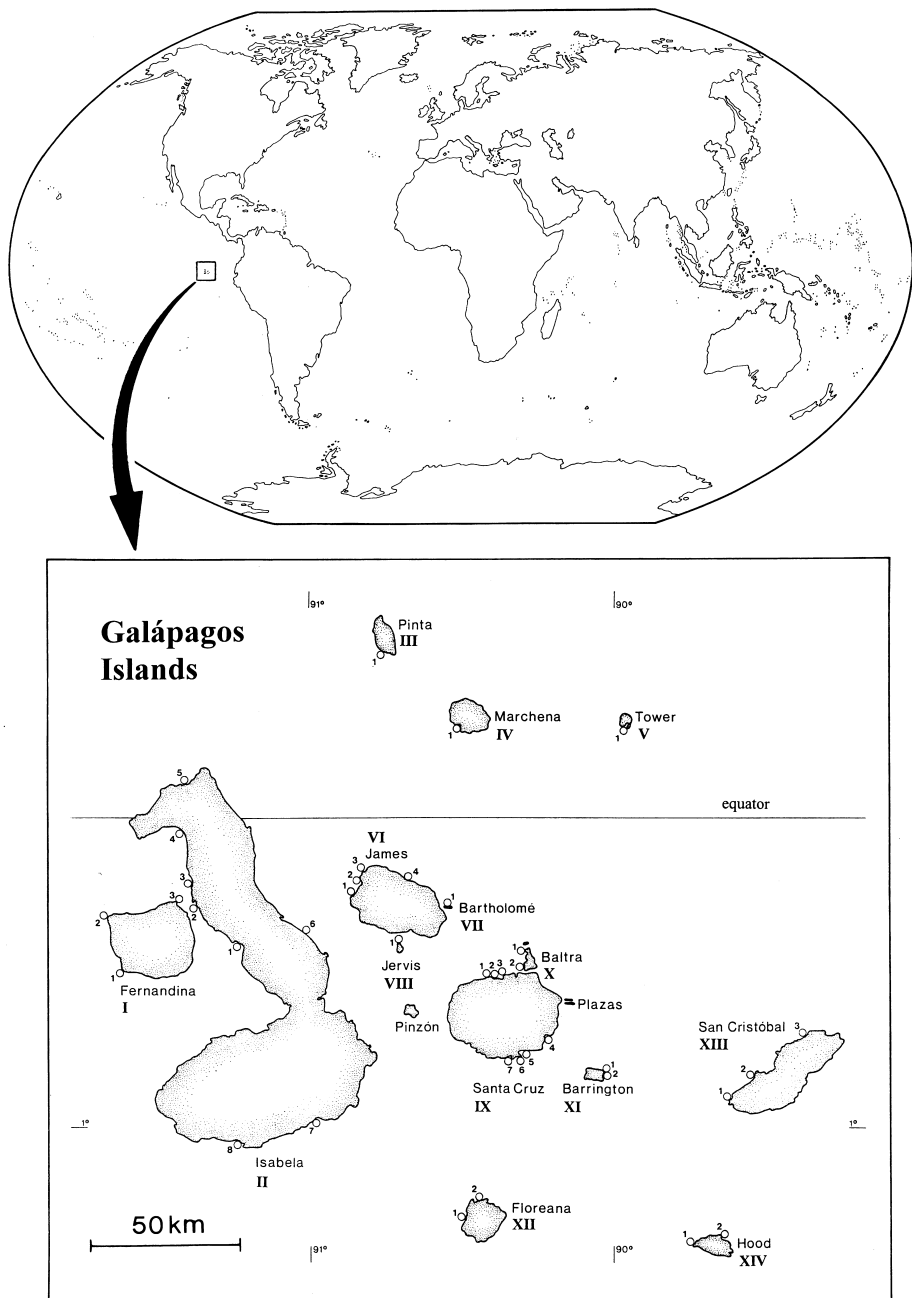


Figure 1. Geographical site (above) and islands of the Galápagos Archipelago (below). Circles indicate the sampling stations.

Table 1. Described species.

Longipediidae Brady, 1880
<i>Longipedia helgolandica santacruzensis</i> Mielke, 1979 (IX,5)
Canuellidae Lang, 1944
<i>Galapacanuella beckeri</i> Mielke, 1979 (IX,6)
Ectinosomatidae Sars, 1903
<i>Ectinosoma pectinatum</i> Mielke, 1979 (V,1 / IX,6 – II,5 / IX,5 / IX,5b / IX,5d / IX,6a)
<i>Ectinosoma nonpectinatum</i> Mielke, 1979 (V,1 / VI,1 / IX,6 / XII,2 / XIV,2 – I,1a / II,3 / XIII,2)
<i>Ectinosoma</i> spec. I–V (briefly characterized sub (species) of uncertain status)
<i>Arenosetella germanica galapagoensis</i> Mielke, 1979 (IV,1 / VI,1 / VII,1 / IX,2 / IX,6 / XII,2 – VI,4 / IX,1 / IX,6a / X,2a / XII,1 / XIII,1)
<i>Hastigerella abbotti santacruzensis</i> Mielke, 1979 (IX,6)
<i>Sigmatidium triarticulatum</i> Mielke, 1979 (IX,6 / XI,1 – IX,5d / XI,1)
<i>Sigmatidium kunzi</i> Mielke, 1979 (IX,6 / XII,2)
<i>Sigmatidium</i> sp. 1 (IX,4a)
<i>Noodtiella frequentior</i> Mielke, 1979 (IV,1 / V,1 / VI,1 / VII,1 / IX,2 / XI,1 / XII,2 – I,2 / IV,1 / V,1a / VI,2 / VI,3 / VIII,1 / IX,1 / IX,2 / X,2a / XI,1 / XI,2 / XII,1)
<i>Noodtiella hoodensis</i> Mielke, 1979 (XIV,2 – XIII,1 / XIV,1 / XIV,2)
Darcythompsoniidae Lang, 1936
<i>Darcythompsonia fairliensis</i> (T. Scott, 1899) (IX,7b)
Paranannopidae Por, 1986
<i>Micropsammis galapagoensis</i> Mielke, 1997 (IX,6)
? Paranannopidae Por, 1986; ? Canthocamptidae Sars, 1906, emend. Monard, 1927, Lang, 1948
<i>Carolinicola galapagoensis</i> Mielke, 1997 (IX,6)
Diosaccidae Sars, 1906
<i>Balucopsylla ? triarticulata</i> Wells and Rao, 1987 (V,1 / IX,2 / IX,6 / XI,1 / XIV,2 – I,3 / II,2 / II,5 / V,1b / IX,4a / IX,5d / X,2a / XI,1 / XIII,1 / XIII,2)
Ameiridae Monard, 1927, emend. Lang, 1936
<i>Nitocra bisetosa</i> Mielke, 1993 (I,2 / IV,1 / V,1 / VII,1 / IX,6 / XI,1 / XII,2 / XIV,2 – I,1b / I,2b / I,3 / II,1 / II,3 / III,1 / VIII,1 / IX,5d / XII,1 / XII,2 / XIII,1 / XIII,2 / XIII,3 / XIV,1)
<i>Nitocra galapagoensis</i> Mielke, 1997 (I,2 / V,1 / IX,6 / XI,1 – I,2b / I,3 / II,1 / II,2 / II,3 / II,4 / III,1 / V,1a / IX,1 / IX,6a / X,2b / XII,1 / XIII,2)
<i>Stenocopia sarsi</i> Mielke, 1997 (V,1 / IX,6)
<i>Stenocopia limicola</i> Willey, 1935 (IX,6 – I,3 / IX,5b / IX,5d)
<i>Praeiptomesochra africana</i> (Kunz, 1951) (IX,2 / XI,1 – IX,4a); unpublished
<i>Pseudoleptomesochrella venezolana</i> Mielke, 1995 (IV,1 / V,1 / VI,1 / VII,1 / IX,2 / IX,6 / XI,1 / XII,2 / XIV,2 – IX,2 / IX,4c / XIII,1); unpublished
Metidae Sars, 1910
<i>Metis galapagoensis</i> Mielke, 1989 (IX,6 – IX,5e / IX,6b)
<i>Metis</i> sp. (IX,5)

Table 1. Continued.

Tetragonicipitidae Lang, 1944	
<i>Tetragoniceps galapagoensis</i> Mielke, 1989	( <b>I,2</b> / <b>VI,1</b> / <b>IX,2</b> / <b>XI,1</b> / <b>XII,2</b> / <b>XIV,2</b> – I,2b / I,3 / II,3 / II,5 / IX,1 / IX,5d / XIII,1 / XIII,2 / XIII,3 / XIV,1 / XIV,2)
<i>Tetragoniceps santacruzensis</i> Mielke, 1997	( <b>IX,6</b> )
<i>Pteropsyllus trisetosus</i> Mielke, 1989	( <b>I,2</b> / <b>IV,1</b> / <b>VI,1</b> / <b>VII,1</b> / <b>IX,2</b> / <b>IX,6</b> – IX,4a)
<i>Oniscopsis robinsoni</i> Chappuis and Delamare Deboutteville, 1956	( <b>I,2</b> / <b>V,1</b> / <b>IX,6</b> / <b>XI,1</b> / <b>XII,2</b> / <b>XIV,2</b> – I,3 / II,2 / II,3 / IX,4a / IX,6a / XIII,2 / XIII,3)
<i>Phyllopodopsyllus angolensis</i> Kunz, 1984	( <b>IX,6</b> – IX,6b)
<i>Phyllopodopsyllus thiebaudi santacruzensis</i> Mielke, 1989	(IX,6b)
<i>Phyllopodopsyllus furciger</i> Sars, 1907	( <b>VI,1</b> / <b>IX,6</b> / <b>XIV,2</b> – I,3 / IX,5b / IX,5c / IX,5d)
<i>Phyllopodopsyllus galapagoensis</i> Mielke, 1989	( <b>IX,6</b> – I,3 / IX,5 / IX,5d / IX,6a / IX,6b)
<i>Phyllopodopsyllus kunzi</i> Mielke, 1989	( <b>V,1</b> / <b>IX,2</b> – I,3 / V,1b / IX,5b)
Paramesochridae Lang, 1944	
<i>Apodopsyllus arcuatus</i> Mielke, 1984	( <b>IX,2</b> – IX,2 / XI,1)
<i>Diarthrodella parorbiculata pacifica</i> Mielke, 1984	( <b>V,1</b> / <b>IX,6</b> – IX,5d)
<i>Diarthrodella neotropica</i> Mielke, 1984	( <b>IX,2</b> / <b>XIV,2</b> )
<i>Diarthrodella galapagoensis</i> Mielke, 1984	( <b>I,2</b> / <b>VI,1</b> / <b>IX,6</b> / <b>XI,1</b> / <b>XII,2</b> – IX,4a / XIII,1 / XIII,2)
<i>Leptopsyllus punctatus</i> Mielke, 1984	( <b>IV,1</b> / <b>VII,1</b> / <b>IX,2</b> / <b>IX,6</b> / <b>XII,2</b> – IX,4a / XI,2)
<i>Leptopsyllus platyspinosus</i> Mielke, 1984	(V,1b / IX,4a)
<i>Paramesochra helgolandica galapagoensis</i> Mielke, 1984	( <b>IX,2</b> )
<i>Paramesochra unaspina</i> Mielke, 1984	(II,3)
<i>Scottopsyllus langi</i> Mielke, 1984	(V,1b / IX,4a / IX,5c)
<i>Kliopsyllus spiniger spiniger</i> Wells, Kunz and Rao, 1975	( <b>I,2</b> / <b>IV,1</b> / <b>VI,1</b> / <b>XII,2</b> / <b>XIV,2</b> – I,3 / II,3 / II,5 / IX,5d / XIII,2)
<i>Kliopsyllus regulexstans</i> Mielke, 1984	( <b>I,2</b> / <b>IX,6</b> / <b>XI,1</b> / <b>XIV,2</b> – IX,1 / IX,4c / XII,1 / XIII,1 / XIII,2)
<i>Kliopsyllus similis</i> Mielke, 1984	( <b>VII,1</b> / <b>IX,2</b> – V,1b / IX,5d)
<i>Kliopsyllus unguiseta</i> Mielke, 1984	(IX,4a / XI,1)
Canthocamptidae Sars, 1906, emend. Monard, 1927, Lang, 1948	
<i>Psammocamptus galapagoensis</i> Mielke, 1997	( <b>IX,6</b> – I,3)
Canthocamptidae incertae sedis	
<i>Cletocamptus axi</i> Mielke, 2000	(IX,4 / XII,1)
<i>Cletocamptus schmidtii</i> Mielke, 2000	(IX,1 / IX,4)
Leptastacidae Huys, 1992	
<i>Schizothrix ctenata</i> (Mielke, 1982)	( <b>XIV,2</b> – IX,5d / XIII,2)
<i>Belemnopontia dispinosa</i> (Mielke, 1982)	(V,1b / IX,5 / IX,5d / XI,1)
<i>Leptastacus spatuliseta</i> Mielke, 1982	(IX,4a)
Cylindropsyllidae Sars, 1909, respectively Leptopontiidae sensu Martínez Arbizu and Moura, 1994	
<i>Leptopontia breviarticulata</i> Huys and Conroy-Dalton, 1996	( <b>IX,2</b> ) (= <i>Leptopontia</i> sp. in Mielke, 1982)
<i>Syrtricola galapagoensis</i> (Mielke, 1982)	( <b>IX,2</b> )
<i>Arenopontia peteraxi</i> Mielke, 1982	(II,6 / IV,1 / VI,2 / VI,3 / VI,4 / VIII,1)
<i>Arenopontia trisetosa</i> Mielke, 1982	( <b>XI,1</b> – IX,4a / IX,4c / XI,2)

Table 1. Continued.

Laophontidae T. Scott, 1904	
<i>Laophonte galapagoensis</i> Mielke, 1981 (IX,6 – III,1 / IX,5 / IX,5d)	
<i>Loureiophonte isabelensis</i> Mielke, 1981 (II,5)	
<i>Heterolaophonte serratula</i> Mielke, 1981 (IX,6 – IX,7a / IX,7b)	
<i>Paralaophonte pacifica galapagoensis</i> Mielke, 1981 (IX,6 / XII,2 – IX,4a / IX,5 / IX,5b / IX,5e / IX,6b / IX,7b)	
<i>Paralaophonte problematica</i> Mielke, 1981 (II,2 / II,5 / IX,5 / IX,5d)	
<i>Esola longicauda galapagoensis</i> Mielke, 1981 (I,2 – IX,5 / IX,5d)	
<i>Onychocamptus</i> spec. (IX,6) (= <i>Folioquinpes chathamensis</i> (Sars, 1904) after Fiers and Rutledge, 1990; see Bodin, 1997)	
<i>Echinolaophonte tetracheir</i> Mielke, 1981 (II,5 / IX,5)	
<i>Afroloophonte schmidtii</i> Mielke, 1981 (I,2 / IV,1 / VII,1 / XII,2 – I,1b / II,3 / IX,1 / IX,5 / XIII,2 / XIV,1)	
<i>Klieonychocamptoides itoi</i> Mielke, 1981 (I,2 / IV,1 / V,1 / VI,1 / IX,6 / XI,1 / XIV,2 – I,2b / I,3 / II,1 / II,3 / II,6 / III,1 / IV,1 / IX,1 / IX,4c / IX,6a / X,1 / XIII,1 / XIII,2 / XIII,3 / XIV,1 / XIV,2)	
<i>Galapalaophonte pacifica</i> Mielke, 1981 (I,2 / IV,1 / V,1 / VI,1 / IX,2 / IX,6 / XI,1 / XII,2 / XIV,2 – I,2b / I,3 / II,1 / II,2 / II,5 / III,1 / IX,1 / IX,5 / IX,5d / IX,6a / X,1 / XI,1 / XII,1 / XIII,1 / XIII,2 / XIV,1 / XIV,2)	
Ancorabolidae Sars, 1909	
<i>Paralaophontodes exopoditus</i> Mielke, 1981 (IX,6 – IX,5 / IX,5d)	

far, more than 60 species and subspecies have been identified (see Table 1). Table 2 enumerates 35 additional genera and is a continuation of that systematic work. This preliminary compilation results from the dissection of about 350 specimens, which were selected from the remaining material. During this study, the majority of the copepods that were collected in the course of the Göttingen project, have been processed to at least the genus level.

**DISTRIBUTION PATTERNS.**—In accordance with results from other regions (e.g., Island of Sylt, North Sea coast of Germany; see Mielke, 1976), the benthic copepods of Galápagos colonize species-specific areas in the beaches (exemplarily illustrated for three species in Fig. 2). Temporary as well as seasonal migrations in horizontal or vertical directions occur in response to changing environmental conditions (Ax and Schmidt, 1973; Schmidt, 1978; for general reference see Hicks and Coull, 1983; Giere 1993). Usually the damp sand zone above the groundwater is preferred, probably because of a slight decrease of the oxygen content in the deeper sector (Jansson, 1966). As an example, the distribution structures of *Noodtiella hoodensis* Mielke, 1979, *Diarthrodella neotropica* Mielke, 1984, and *Klieonychocamptoides itoi* Mielke, 1981 are presented (see Fig. 2) for the beach of Bahía Gardner, Hood (XIV, 2; 30 June 1972). The results are based on 154, 575, and 365 animals (copepodids, ovigerous females, other females, and males). *Klieonychocamptoides itoi* predominantly inhabits the surface layers. *Diarthrodella neotropica*, on the contrary, has its center of colonization around the groundwater level. *Noodtiella hoodensis* occupies an intermediate zone. This phenomenon is clearly illustrated if all samples containing more than 5% of the respective species are considered.

**LIFE CYCLES.**—Preliminary data on the life cycles are available for the species *Galapalaophonte pacifica* Mielke, 1981 and *Oniscopsis robinsoni* Chappuis and Delamare Deboutteville, 1956 (Fig. 3). The results are based on 4209 and 4729 animals, respectively. During a one-year period, from February 1972–March 1973, both sexes and all

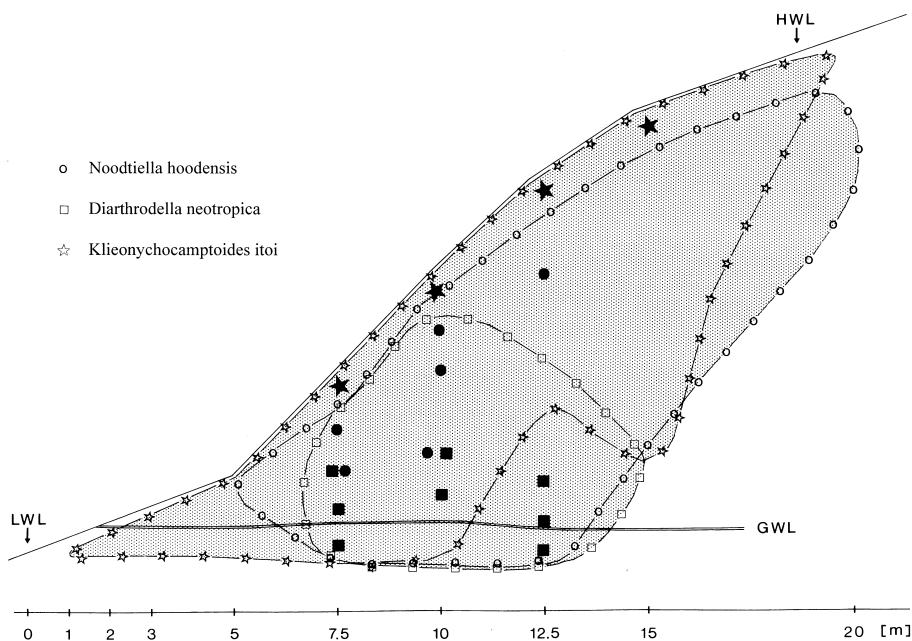


Figure 2. Spatial distribution of *Noodtiella hoodensis* (circles), *Diarthrodella neotropica* (squares), and *Klieonchocamptoides itoi* (stars) in the beach of Bahía Gardner/Hood on 30 June 1972. Solid circles, squares, and stars represent samples containing at least 5% of each population. LWL = low water line, HWL = high water line, GWL = ground water line, m = meters.

developmental stages were constantly present. In all probability this also holds true for the naupliar stages, but because of difficulties in their identification, nauplii were neglected. In any case, the developmental phases appearing prior to and after the nauplius larvae, i.e., ovigerous females and copepodids, existed throughout the year.

Despite the limited 5–6°C fluctuation of surface water temperature close to the beaches in the tropical Galápagos Archipelago (Ax and Schmidt, 1973), a clear but non-uniform seasonality in reproduction was ascertained for both species. These minor differences in temperature, combined with other environmental factors, probably serve as the trigger for increasing or decreasing reproductive activity. In boreal regions the scenario may be comparable for a minority of species, but mostly the distinct decline of temperature in winter suppresses egg production temporarily, thus significantly changing the ratio of larvae, juveniles, and adults (compare Mielke, 1976).

**RELATIONSHIPS GALÁPAGOS—AMERICAN PACIFIC COAST.**—The American Pacific coast can be interpreted as the main source from which all or most of the Galápagos copepods originated. A number of currents reach and influence the Archipelago, e.g., the Panama Current from the north and the Humboldt Current from the south (Ax and Schmidt, 1973; Chavez and Brusca, 1991; Westheide, 1991). Unfortunately, the benthic copepod fauna of large sections of the Pacific coast of Central and South America is still unknown. Preliminary data are available for a number of sites on the Pacific coasts of Panama, Costa Rica, and Chile (Mielke, 1981a, 1985, 1987a, 1992). It must be emphasized that individuals of most species identified from various localities often reveal minor morphological differences. Based solely on light microscopic evidence (morphospecies level), it

Table 2. Undescribed species, identified to genus level. (Several genera stand for two or more species. For example, *Schizopera*, *Ameira*, or *Amphiascus* each comprises at least four species. The total species number referenced in this genus list is probably higher than 60. Except for the species that clearly belong to the genera presented in Table 2, some additional forms of questionable systematic position were found)

Harpacticidae Sars, 1904
<i>Harpacticus</i> sp. (IX,2 / IX,6 / XIV,2–IX,5b)
<i>Perissocope</i> sp. (VII,1)
<i>Zausodes</i> sp. (VI,1 / IX,2 / XIV,2–V,1b / IX,5 / IX,5b / IX,5c / IX,5d / X,2b)
Tisbidae Stebbing, 1910
<i>Scutellidium</i> sp. (IX,6)
<i>Zosime</i> sp. (IX,6)
Superornatiremidae Huys, 1996
? <i>Neoechinophora</i> sp. (IX,6)
Tegastidae Sars, 1904
Undissected specimens (IV,1 / IX,6 / XIV,2–X,2a)
Thalestridae Sars, 1905
<i>Dactylopusia</i> sp. (V,1 / IX,2 / IX,6 / XIV,2–V,1b / IX,4a / IX,5d / IX,7a)
<i>Diarthrodes</i> sp. (IV,1 / IX,6–I,3 / IX,5d / IX,6a)
<i>Idomene</i> sp. (XII,2)
Parastenheliidae Lang, 1944
<i>Parastenhelia</i> sp. (VI,4 / IX,5b)
Diosaccidae Sars, 1906
<i>Amphiascoides</i> sp. (VI,1 / IX,2 / IX,6 / XI,1–IX,6b / XI,1)
<i>Amphiascopsis</i> sp. (IX,5b / IX,7b)
<i>Amphiascus</i> sp. (I,2 / V,1 / VI,1 / VII,1 / IX,2 / IX,6 / XII,2 / XIV,2–I,3 / II,5 / IX,5c / IX,5d / XIII,2)
<i>Diosaccus</i> sp. (IX,2 / X,1–IX,5)
<i>Haloschizopera</i> sp. (IX,6–I,3 / IX,7b)
<i>Paramphiascella</i> sp. (IX,6–I,3 / IX,5 / IX,5c / IX,6a)
<i>Robertgurneya</i> sp. (IV,1 / IX,2 / IX,6 / XIV,2–IX,4a / IX,5b / IX,5c / XI,2)
<i>Robertsonia</i> sp. (IX,6 / XIV,2–IX,4a / IX,7b)
<i>Schizopera</i> sp. (I,2 / IV,1 / V,1 / VI,1 / VII,1 / IX,2 / IX,6 / XI,1 / XII,2 / XIV,2–II,3 / III,1 / IX,4c / XIII,3 / XIV,2)
<i>Stenhelia</i> sp. (IX,6 / XIV,2)
<i>Typhlamphiascus</i> sp. (IX,7b)

is impossible to determine whether these are variable species, subspecies, or unable to interbreed, sibling species. On this basis, comparisons between harpacticoid copepods from Galápagos, Central America, and Chile have clearly demonstrated a closer morphological similarity between populations from Galápagos and Panama/Costa Rica than from Galápagos and Chile. Several examples may be given:

*Noodtiella hoodensis* and *Arenopontia peteraxi* were first described from Galápagos by Mielke (1979, 1982a) and were found again in Panama (Mielke, 1981a, 1982b) and Chile (Mielke 1987a, 1987b). *Afrolophonte schmidtii* and *K. itoi* were discovered in Galápagos (Mielke, 1981b) and identified again in Panama (Mielke, 1982c) and Costa



Table 2. Continued.

Ameiridae Monard, 1927	
<i>Ameira</i> sp. (IV,1 / V,1 / VI,1 / IX,2 / IX,6 / XII,2 / XIV,2–II,5 / IX,5b / IX,5c)	
<i>Ameiropsis</i> sp. (V,1 / IX,6 / XIV,2–IX,5c / IX,5d / XIII,2)	
<i>Ameiropsyllus</i> sp. (IX,4a)	
<i>Karllangia</i> sp. (I,2 / IX,2 / IX,6 / XIV,2–I,3 / IX,5 / IX,6a / XIII,1 / XIII,2 / XIV,2)	
<i>Nitocra</i> sp. (IV,1 / IX,6–I,3 / V,1b / IX,1 / IX,4 / IX,6)	
<i>Parevansula</i> sp. (VII,1 / IX,2 / IX,6 / XI,1)	
<i>Psyllocamptus</i> sp. (V,1 / IX,2 / XIV,2–IX,5c / IX,5d)	
Canthocamptidae Sars, 1906, emend. Monard, 1927, Lang, 1948	
<i>Mesochra</i> sp. (I,2 / V,1 / IX,2 / IX,6 / XII,2–V,1a / IX,5d / IX,5e / IX,7a / IX,7b)	
<i>Nannomesochra</i> sp. (V,1)	
Canthocamptidae (Orthopsyllidae Huys, 1990)	
<i>Orthopsyllus</i> sp. (IV,1 / VI,1 / IX,6 / XII,2–I,3 / IX,5 / IX,5b / IX,5c / IX,5d / IX,6a / IX,7a / IX,7b / XI,2)	
Cletodidae T. Scott, 1904	
<i>Cletodes</i> sp. (I,3 / IX,4a)	
<i>Enhydrosoma</i> sp. (IX,6 – IX,7b)	
<i>Enhydrosomella</i> sp. (IX,7b)	
Normanellidae Lang, 1944 sensu Huys and Willems, 1989	
<i>Cletopsyllus</i> sp. (I,3)	

Rica (Mielke, 1997), but not yet from Chile. Species belonging to the genera *Diarthrodella*, *Kliopsyllus*, *Leptastacus* s.l., and *Afroloaophonte* occur in Galápagos as well as in Chile. However, subspecies or sibling species relationships could not be detected. *Galapalaophonte pacifica*, in all probability distributed both in Galápagos (Mielke, 1981b) and in Panama (Mielke, 1982c), was identified with reservation in Chile (as *Laophontina triarticulata* Coull and Zo, 1980; see Mielke, 1985), but declared a new species by Fiers (1991). In any case, the forms from Galápagos and Panama are morphologically much closer to one another than to the Chilean population.

The immigration of copepods into the Archipelago was a first step to spreading and developing in an area with insignificant or no competition during the early settlement phase. The species took different courses in the subsequent period. The following questions must be considered (compare Ax, 1974): (1) Are there any diverging trends concerning morphology and ecology of Galápagos species compared to representatives of the continent or other regions? (2) Are there any indications of microevolution and species splitting? (3) How can the existence of two or more species of one genus be explained?

For some widespread Galápagos species, slight morphological differences could be established in their partial populations, above all in the *Ectinosoma* complex (Mielke, 1979) or in *Phyllopodopsyllus galapagoensis* Mielke, 1989. In *Scottopsyllus langi* Mielke, 1984 the basal and middle segment of exopodite of pereopod 4 are fused to a large extent. The closely related *S. pararobertsoni*, described by Lang (1965) from the Californian Pacific coast, still has the plesiomorphic 3-segmented exopodite of pereopod 4. The tendency to fuse probably developed in the Archipelago.

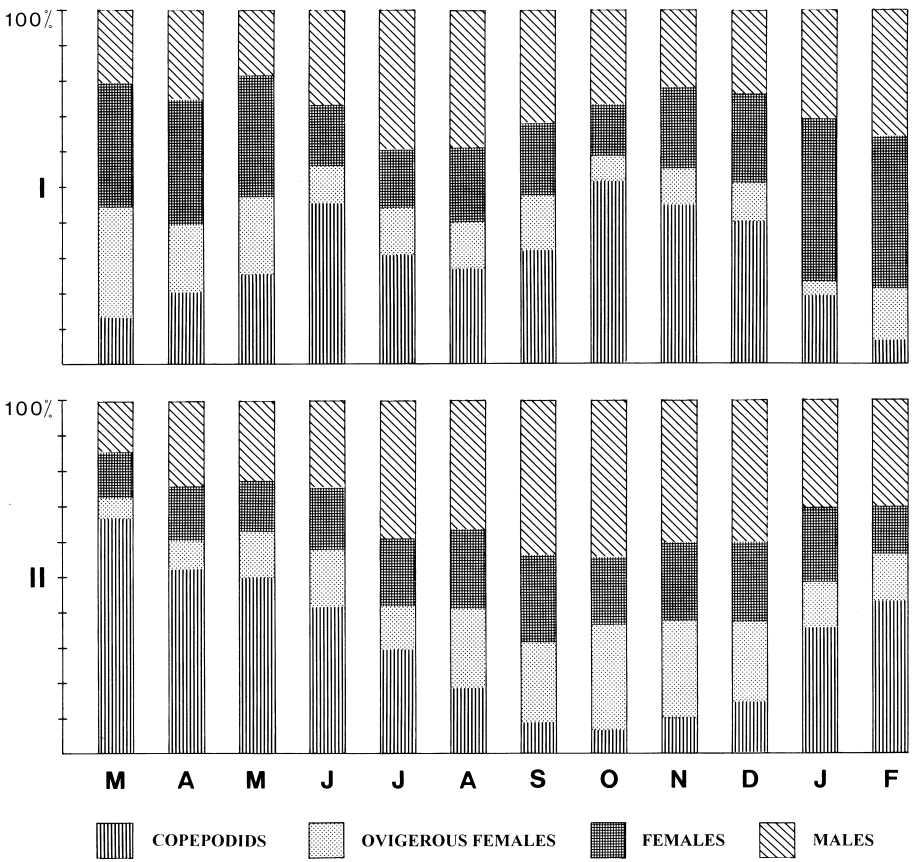


Figure 3. Life cycles of (I) *Galapalaophonte pacifica* and (II) *Oniscopsis robinsoni* in the beach of Bahía Academy/Santa Cruz from March 1972 through February 1973. Columns indicate the monthly percentage of copepodids, ovigerous females, other females, and males.

On the basis of the results of the Copepoda Harpacticoida treated thus far, the occurrence of a definitive case of species splitting within the Galápagos Islands could not be established. In contrast to other meiofaunal groups, e.g., Platyhelminthes (*Duplominona*; see Ax, 1977) or Ostracoda (*Cobanocythere*; see Gottwald, 1983), it must be stressed that all Galápagos copepod taxa with two or more species, cannot be attributed to one stem species that underwent speciation in the Archipelago. For all these species, independent immigration into the Galápagos Islands must be postulated. They are not more closely related to each other than to species of other geographic regions.

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## LITERATURE CITED

- Armonies, W. 1988. Active emergence of meiofauna from intertidal sediment. Mar. Ecol. Prog. Ser. 43: 151–159.
- \_\_\_\_\_. 1989. Meiofaunal emergence from intertidal sediment measured in the field: significant contribution to nocturnal planktonic biomass in shallow waters. Helgoländer Meeresunters. 43: 29–43.
- \_\_\_\_\_. and K. Reise. 2000. Faunal diversity across a sandy shore. Mar. Ecol. Prog. Ser. 196: 49–57.
- Ax, P. 1974. Zur Evolution der marinen Mikrofauna von Galapagos. Akad. Wiss. Lit. Mainz 1949–1974. Pages 90–105.
- \_\_\_\_\_. and P. Schmidt. 1973. Interstitielle Fauna von Galapagos. I. Einführung. Mikrofauna Meeresboden 20: 1–38.
- Bailey, K. 1976. Potassium-argon ages from the Galápagos Islands. Science 192: 465–467.
- Bodin, P. 1997. Catalogue of the new marine harpacticoid copepods (1997 ed.). Doc. trav. Inst. r. Sci. nat. Belg. 89: 1–304.
- Carlton, J. T. and J. B. Geller. 1993. Ecological roulette: The global transport of nonindigenous marine organisms. Science 261: 78–82.
- Chavez, F. P. and R. C. Brusca. 1991. The Galápagos Islands and their relation to oceanographic processes in the tropical Pacific. Pages 9–33 in M.J. James, ed. Galápagos marine invertebrates. Taxonomy, biogeography, and evolution in Darwin's islands, vol 8. Topics in geobiology. Plenum Press, New York.
- Chu, K. H., P. F. Tam, C. H. Fung and Q. C. Chen. 1997. A biological survey of ballast water in container ships entering Hong Kong. Hydrobiologia 352: 201–206.
- Cox, A. and G. B. Dalrymple. 1966. Palaeomagnetism and potassium-argon ages of some volcanic rocks from the Galápagos Islands. Nature 209: 776–777.
- Fiers, F. 1991. A revision of the genus *Laophontina* Norman & T. Scott (Copepoda, Harpacticoida). Bull. Inst. r. Sci. nat. Belg., Biol., 61: 5–54.
- \_\_\_\_\_. and P. Rutledge. 1990. Harpacticoid copepods associated with *Spartina alterniflora* culms from the marshes of Cocodrie, Louisiana (Crustacea, Copepoda). Bull. Inst. r. Sci. nat. Belg., Biol. 60: 105–125.
- Gerlach, S. A. 1977. Means of meiofauna dispersal. Mikrofauna Meeresboden 61: 89–103.
- Giere, O. 1993. Meiobenthology: the microscopic fauna in aquatic sediments. Springer Verlag Berlin Heidelberg, Germany. 328 p.
- Gottwald, J. 1983. Interstitielle Fauna von Galapagos. XXX. Podocopida 1 (Ostracoda). Mikrofauna Meeresboden 90: 1–187.
- Hicks, G. R. F. 1988. Sediment rafting: a novel mechanism for the small-scale dispersal of intertidal estuarine meiofauna. Mar. Ecol. Prog. Ser. 48: 69–80.
- \_\_\_\_\_. and B. C. Coull. 1983. The ecology of marine meiobenthic harpacticoid copepods. Oceanogr. Mar. Biol. Ann. Rev. 21: 67–175.
- Holden, J. C. and R. S. Dietz. 1972. Galápagos gore, NazCoPac triple junction and Carnegie/Cocos Ridges. Nature 235: 266–269.
- Jansson, B. -O. 1966. On the ecology of *Derocheilocaris remanei* Delamare and Chappuis (Crustacea, Mystacocarida). Vie Milieu 17: 143–186.
- Lang, K. 1965. Copepoda Harpacticoida from the Californian Pacific coast. K. svenska vetensk. Akad. Handl. 10: 1–566.
- Lavoie, D. M., L. D. Smith and G. M. Ruiz. 1999. The potential for intracoastal transfer of non-indigenous species in the ballast water of ships. Estuar. Coast. Shelf Sci. 48: 551–564.
- Mielke, W. 1975. Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna Meeresboden 52: 1–134.
- \_\_\_\_\_. 1976. Ökologie der Copepoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna Meeresboden 59: 1–86.

- \_\_\_\_\_. 1979. Interstitielle Fauna von Galapagos. XXV. Longipediidae, Canuellidae, Ectinosomatidae (Harpacticoida). *Mikrofauna Meeresboden* 77: 1–106.
- \_\_\_\_\_. 1981a. Interstitielle Ectinosomatidae (Copepoda) von Panama. *Mikrofauna Meeresboden* 85: 1–45.
- \_\_\_\_\_. 1981b. Interstitielle Fauna von Galapagos. XXVIII. Laophontinae (Laophontidae), Ancorabolidae (Harpacticoida). *Mikrofauna Meeresboden* 84: 1–104.
- \_\_\_\_\_. 1982a. Interstitielle Fauna von Galapagos. XXIX. Darcythompsoniidae, Cylindropsyllidae (Harpacticoida). *Mikrofauna Meeresboden* 87: 1–50.
- \_\_\_\_\_. 1982b. Three variable *Arenopontia* species (Crustacea, Copepoda) from Panama. *Zool. Scr.* 11: 199–207.
- \_\_\_\_\_. 1982c. Einige Laophontidae (Copepoda, Harpacticoida) von Panama. *Crustaceana* 42: 1–11.
- \_\_\_\_\_. 1985. Interstitielle Copepoda aus dem zentralen Landesteil von Chile: Cylindropsyllidae, Laophontidae, Ancorabolidae. *Microfauna Marina* 2: 181–270.
- \_\_\_\_\_. 1987a. Interstitielle Copepoda von Nord- und Süd-Chile. *Microfauna Marina* 3: 309–361.
- \_\_\_\_\_. 1987b. Zwei Spezies der Gattungen *Noodtiella* und *Lineosoma* (Copepoda) von Chile. *Crustaceana* 53: 152–159.
- \_\_\_\_\_. 1992. Six representatives of the Tetragonicipitidae (Copepoda) from Costa Rica. *Microfauna Marina* 7: 101–146.
- \_\_\_\_\_. 1997. New findings of interstitial Copepoda from Punta Morales, Pacific coast of Costa Rica. *Microfauna Marina* 11: 271–280.
- Schmidt, P. 1978. Interstitielle Fauna von Galapagos. XXI. Lebensraum, Umweltfaktoren, Gesamtfaua. *Mikrofauna Meeresboden* 68: 1–51.
- Westheide, W. 1991. The Meiofauna of the Galápagos. A review. Pages 37–73 in M. J. James, ed. *Galápagos marine invertebrates. Taxonomy, biogeography, and evolution in Darwin's islands*, Vol 8, Topics in geobiology. Plenum Press, New York.
- Yeatman, H. C. 1962. The problem of dispersal of marine littoral copepods in the Atlantic Ocean, including some redescrptions of species. *Crustaceana* 4: 253–272.

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ADDRESS: *Institute for Zoology and Anthropology, University of Göttingen, Berliner Str. 28, D-37073 Göttingen, Germany.*