Chapter 2

The Meiofauna of the Galápagos

A Review

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1. Introduction

About three hundred and ninety species of the marine meiofauna of the Galápagos Islands in fourteen higher invertebrate taxa are known. These animals are usually found living between sand grains on sandy beaches throughout the archipelago. The number of endemic genera and species is difficult to estimate due to inadequate comparative work in the eastern Pacific. It is supposed that only a smaller part of those approximately 300 taxa described from the Galápagos as new to

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science are endemic to the islands. Almost 90% of the Galápagos meiofauna species were reported by the Göttingen Galapagos Meiofauna Expedition.

From February 1972 to March 1973 a group of zoologists from the University of Göttingen visited the Galápagos Islands and intensively investigated the meiofauna of their beaches. Inspiration for this project was provided by the comprehensive long-term investigations of Peter Ax and his students on the psammobiontic fauna of the beaches of the North Sea Island Sylt. Here, since 1962 the entire spectrum of species, their abundances, and the dynamics of total fauna and individual species populations were recorded, as well as abiotic and biotic environmental factors and their influences on species distribution pattern in time and space within intertidal habitats (e.g., Schmidt, 1968, 1969; Westheide, 1968; Hartwig, 1973; Ehlers, 1973; Sopott, 1973; Hoxhold, 1974). Studies in systematics and morphology were carried out as well as investigations in reproduction, development, and ecology of abundant and characteristic species from a large series of taxa (e.g., Westheide, 1967; Ax, 1969; Teuchert, 1968; Meineke and Westheide, 1979). Early in the 1970s the meiofauna community of Sylt's sandy beaches was considered to be the best known in the world with more than 400 species of ciliates and metazoans having been reported, many of them previously undescribed.

The work on Sylt allowed for a comprehensive comparison with meiofauna communities of warmer seas. In contrast to the temperate area of the North Sea with its considerable seasonal climatic changes, tropical seas exhibit higher water temperatures throughout the year. A comparison of this kind appeared to be a promising way to arrive at general statements about seasonal dynamics, reproductive periods, dominance of taxa, and zonation patterns of the meiofauna inhabiting tidal sand beaches.

The Galápagos Islands seemed to be an appropriate geographic locality for such comparative work—with their differently exposed sandy beaches and water temperatures around 25°C with seasonal variations of only 5 to 6°C. However, the islands were chosen for other reasons, too: like any zoologist who goes to the Galápagos, the members of the expedition especially wanted to learn more about evolution. All of us who participated hoped that meiofaunal organisms, which usually do not possess pelagic larval stages and are not suited for active dispersal within the water column, would have undergone a similarly independent evolution in the island beaches as had been found for the terrestrial vertebrates and plants on the islands. We expected to find examples of radiation and speciation between meiofauna populations of various islands, which might give some indications to the general pattern and rate of speciation in meiofaunal taxa. Because the islands are only 2–3 million years old, we were apprehensive that we might find Galápagos beaches low in diversity. It was thought that the young age of the islands would not have been sufficient for dispersal and diversification of meiofaunal taxa.

Concerns of this sort were not substantiated, but the far-reaching expectations of the project were not totally fulfilled, either. What we found was a species-rich and individual-rich fauna. Many of the species turned out to be familiar "old friend" taxa known from other meiofaunal communities. On first examination, these taxa did not reveal anything spectacular. There were no meiofaunal equivalents of giant tortoises or lava lizards. Nevertheless, careful sampling activities on the islands and subtle evaluation of the material in the following years allowed us to elucidate the entire taxonomic pattern of the meiofauna biocenosis in this group of isolated tropical oceanic islands. These organisms afforded a glimpse of the rate

of speciation within individual meiofauna taxa, and they generally furthered our understanding of differences in island colonization between marine littoral and terrestrial faunas.

Peter Schmidt (now a Professor of Zoology at the Technical University of Aachen) and his wife Adelheid Schmidt stayed in the islands for one year (February 1972 to March 1973). They carried out by far the largest part of the investigations and collected most of the material. Their tremendous sampling program comprised the entire quantitative analysis (more than 1,000 samples with ca. 230,000 individuals), recording of abiotic factors in the beaches and careful sorting of specimens for most of the systematic investigations. Various groups were worked up by Schmidt himself or were coauthored with various colleagues (Macrostomida, Polycladida, Nemertini, Gastrotricha, Kinorhyncha, Aeolosomatidae, so-called archiannelid Polychaeta, Tardigrada, Halacarida, Isopoda). Unfortunately, he left unpublished or without discussion many of his valuable quantitative ecological investigations, leaving unresolved certain questions regarding the general objectives of the expedition.

Peter Ax and Renate Ax (Proseriata, Typhloplanoida), Ulrich Ehlers (Gnathostomulida, Typhloplanoida, Acoela), Siegmar Hoxhold (Kalyptorhyncha), and myself (Polychaeta), each stayed for two months in the islands in 1972, concentrating on sampling and processing of the respective taxa. A number of other specialists from the Göttingen Zoological Institute and from various other institutions, including taxonomists from France, Sweden, the United States, and Chile (see Section 3) subsequently participated in the investigation of the preserved material. In total about 390 species have been identified, the majority of which are new to science. A number of specimens remain to be examined and described in the literature.

The expedition was organized by the Akademie der Wissenschaften und der Literatur, Mainz, under supervision of Peter Ax. Funding was provided by the Volkswagenwerk Foundation, which also funded the salaries of some of the scientists who investigated preserved material in subsequent years.

From 1973 to the present, the Mainz Academy continuously published the results, first in the form of separate issues in the series *Mikrofauna des Meeresbodens* (Editor Peter Ax); and from 1984 on, the descriptions appeared as articles in the volumes of the journal *Microfauna Marina* (Akademie der Wissenschaften und der Literatur, Mainz, and Gustav Fischer Verlag, Stuttgart, New York). Altogether, about 40 articles with more than 1500 pages have been published on the results of the project. This makes the Göttingen Galápagos Meiofauna Expedition the best documented project dedicated to the study of marine meiofauna.

2. Sampling and Extraction

Fig. 1 shows the entire group of islands and the beaches investigated by the Schmidts (Ax and Schmidt, 1973; Schmidt, 1978). Most of these collecting stations were visited with difficulty by small Galapagonian fishing boats. For qualitative sampling, various volumes of sediment from different levels of intertidal and shallow subtidal areas were brought into the laboratory of the Charles Darwin Research Station. Qualitative sampling was done by full transects of the beaches' intertidal regions along a line perpendicular to the low water line at intervals of 1 or

Figure 1.   Schmidt's collection sites of sand beaches during the Göttingen Meiofauna Expedition. Large solid points on Santa Cruz indicate the two beaches (2 = Playa Borrero, 6 = Bahia Academy) where quantitative samples were taken regularly. Small solid points = one quantitative transect. Open circles = qualitative samples only. For more details see Ax and Schmidt (1973), Schmidt (1978).

2 m (tidal amplitudes between 1.2 to 1.9 m, see Houvenaghel and Houvenaghel, 1974). Here the Schmidts used small hand-held tubes for corers (inner diameter 3.5 cm, length about 11 cm) collecting a volume of 100 cm³ of sediment and a surface area of 10 cm². In the upper region of the beach slope, pits of decreasing depths were dug till the groundwater level was reached, and core samples were taken from the vertical face. Time limitations did not allow investigation of the meiofauna below the ground-water level during low tide. This area is, however, generally known to be extremely poor in individuals and species.

Extraction of specimens occurred in the laboratory rooms of the Charles Darwin Research Station near Puerto Ayora on Santa Cruz, within one week after sampling. The seawater–ice technique was used, followed by one intensive washing of the remaining sediment. This resulted in an average extraction efficiency of 84% of the total fauna with minimal efficiency of 51% for Tardigrada and a maximum of 96.5% for Platyhelminthes (Schmidt, 1978). Soft-bodied meiofaunal elements were usually examined with a high quality compound microscope while still alive immediately after extraction from the sediment. This included taking

photographs with a flash system, and taking measurements and drawings of the animals with a camera lucida. The "hard" fauna (e.g., nematodes, halacarids, copepods) were fixed in formalin after counting and transported to Göttingen and to other places for further investigation.

Sampling by the Schmidts was mainly concentrated on sand beaches. The other participants during their stay on the islands usually joined them when taking samples, but also tried to find as many species of their special groups in other habitats, such as mangrove sediments, rock pool sediments, stones and old corals of shallow sublitoral areas. Nevertheless by far the largest part of all animals investigated belong to the meiofauna, especially true interstitial species, with the exception of some polyclad Platyhelminthes and several polychaetes, which comprise a series of smaller non-interstitial and several macrofaunal species.

Special methods of extraction were used for non-sand inhabiting animals, e.g., endofaunal polychaetes living in stones and corals; they were forced to come to the surface within a day or so in water-filled buckets by depletion of oxygen.

Physicomorphological characters considered in Schmidt's investigations included grain size (Md-values between 743–1540 μm on Fernandina and 191–830 μm in Playa Borrero on Santa Cruz), nature of substratum (volcanic sand or fragments of corals, molluscs, echinoderms, etcetera, or a mixture of both), and amount of organic matter by the combustion method at high temperatures (between 0.2 and 0.4% in general), thus revealing all of the beaches to be relatively clean and exposed (Schmidt, 1978).

Water temperature fluctuated only slightly between 23°C and 29°C (1972 was an El Niño year) and probably did not influence the abundance dynamics observed (see below). During low tide, surface temperatures of the beaches reached values of 40°C and above on sunny days. Salinity values of about 40% were measured under such conditions.

3. Composition of Taxa

The following compilation comprises the meiofauna from the Galapagos Islands that was collected during the Göttingen expedition 1972/73, including a few scattered references to earlier collections.

3.1. Platyhelminthes (Fig. 2, 3, 9)

Intensive studies have been carried out on the free-living Platyhelminthes ("Turbellaria"), revealing a high number of different suprageneric taxa, the individuals of which locally may represent more than 50% of the total fauna in individual samples of sandy beaches, e.g., in one sample 339 out of a total of 399 animals were turbellarians. Almost all of the species found were undescribed, several of them belonging to new genera (Ax and Ehlers, 1973; Ax and Ax, 1974; Ehlers and Ax, 1974; Sopott-Ehlers and Schmidt, 1974a; Sopott-Ehlers and Schmidt, 1974b; Sopott-Ehlers and Schmidt, 1975; Schmidt and Sopott-Ehlers, 1976; Ax and Ax, 1977; Ehlers and Dörjes, 1979; Ehlers and Ehlers, 1981; Noldt and Hoxhold, 1984; Ehlers and Sopott-Ehlers, 1989).
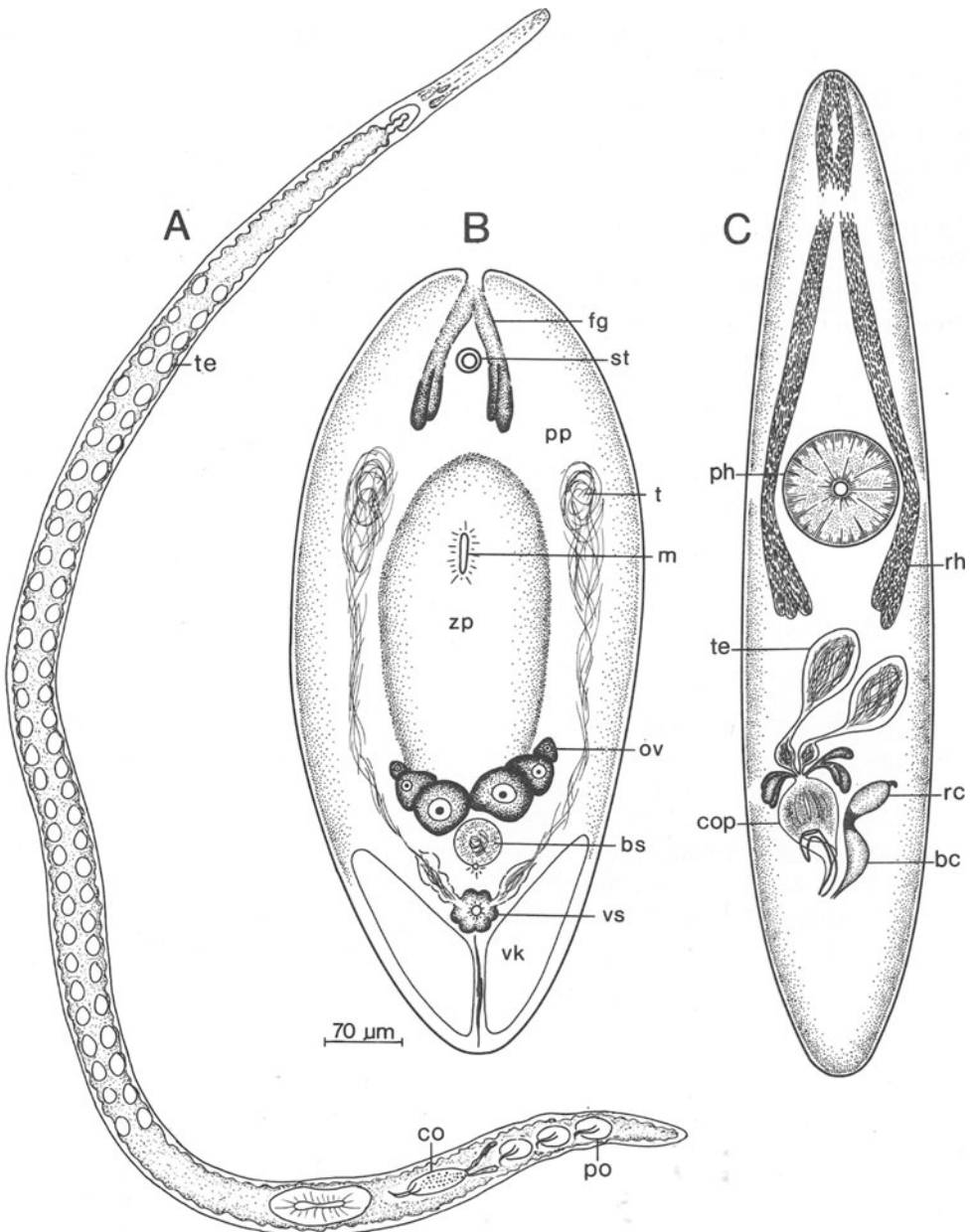
Figure 2. Platyhelminthes. (A) *Polystyliphora darwini* Ax & Ax, 1974 (Proseriata). Length about 3.5 mm. (B) *Pseudmecynostomum tardum* Ehlers & Dörjes, 1974 (Acoela). Length about 600 μm. (C) *Cryptostiopera cornuta* Ehlers & Ax, 1974 (Typhloplanoida). Length about 400 μm. (A) From Ax and Ax (1974), (B) from Ehlers and Dörjes (1974), (C) from Ehlers and Ax (1974).

3.1.1. Acoela

Sixteen species were found from five families:

Convolutidae: *Conaperta colorata* Ehlers & Dörjes, 1979; *Avagina polyvacuola* Ehlers & Dörjes, 1979; *Amphiscolops* sp.; *Praeaphanostoma thalassophilum* Ehlers & Dörjes, 1979; *Praeaphanostoma musculosum* Ehlers & Dörjes, 1979; *Praeaphanostoma vitreum* Ehlers & Dörjes, 1979.
Haploposthiidae: *Pseudohaplogonaria minima* Ehlers & Dörjes, 1979.
Otocelididae: *Otocelis phycophilus* Ehlers & Dörjes, 1979; *Philocelis karlingi pacifica* Ehlers & Dörjes, 1979; *Parotocelis luteopunctata* Ehlers & Dörjes, 1979; *Exocelis exopenis* Ehlers & Dörjes, 1979.
Childiidae: *Philactinoposthia tenebrosa* Ehlers & Dörjes, 1979; *Pseudactinoposthia parva* Ehlers & Dörjes, 1979*; *Paractinoposthia pseudovesicula* (Ehlers & Dörjes, 1979).
Mecynostomidae: *Pseudmecynostomum pellucidum* Ehlers & Dörjes, 1979; *Pseudmecynostomum tardum* Ehlers & Dörjes, 1979 (Fig. 2B).

New genera: *Parotocelis* Ehlers & Dörjes, 1979; *Exocelis* Ehlers & Dörjes, 1979; *Paractinoposthia* Ehlers & Dörjes, 1979 (see *Monoposthia* in Ehlers and Dörjes, 1979).

3.1.2. Macrostomida

Fourteen species were found from two families:

Macrostomidae: *Myozona psila* Sopott-Ehlers & Schmidt, 1974; *Myozona aerumnosa* Sopott-Ehlers & Schmidt, 1974; *Macrostomum astericis* Schmidt & Sopott-Ehlers, 1976; *Macrostomum obelicis* Schmidt & Sopott-Ehlers, 1976; *Macrostomum majesticis* Schmidt & Sopott-Ehlers, 1976; *Macrostomum troubadicis* Schmidt & Sopott-Ehlers, 1976; *Macrostomum prognosticis* Schmidt & Sopott-Ehlers, 1976; *Macrostomum miraculicis* Schmidt & Sopott-Ehlers, 1976; *Macrostomum galloprovinciale* Schmidt & Sopott-Ehlers, 1976; *Macrostomum ideficis* Schmidt & Sopott-Ehlers, 1976; *Siccomacrostomum triviale* Schmidt & Sopott-Ehlers, 1976.
Dolichomacrostomidae: *Myozonaria ascia* Sopott-Ehlers &' Schmidt, 1974; *Paramyozonaria riegeri* Sopott-Ehlers & Schmidt, 1974; *Paromalostomum subflavum* Sopott-Ehlers & Schmidt, 1974 (Fig. 3C).

New genus: *Siccomacrostomum* Schmidt & Sopott-Ehlers, 1976.

3.1.3. Polycladida

The species listed below are interstitial forms of coarse intertidal sediments. Four other species could not be identified due to juvenile specimens or life observations without histological investigations. Altogether 19 polyclad species

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*To distinguish between species authors and references, the symbol "&" is used for the former and the word "and" for the latter.

from five families were found during the investigations, several of them true macrofaunal organisms from non-interstitial habitats as those reported from earlier studies conducted on the Galápagos Islands (Woodworth, 1894; Bock, 1923; Plehn *in* Stummer-Traunfels, 1933; Hyman, 1939, 1953):

Planoceridae: *Amyris favis* Sopott-Ehlers & Schmidt, 1975.
Theamidae: *Theama occidua* Sopott-Ehlers & Schmidt, 1975.
Leptoplanidae: *Copidoplana virgae* Sopott-Ehlers & Schmidt, 1975; *Euplanina horrida* Sopott-Ehlers & Schmidt, 1975; *Mucroplana caelata* Sopott-Ehlers & Schmidt, 1975.
Cestoplanidae: *Cestoplana cuneata* Sopott-Ehlers & Schmidt, 1975; *Cestoplana nexa* Sopott-Ehlers & Schmidt, 1975.
Boniniidae: cf. *Traunfelsia* sp.

New genera: *Euplanina* Sopott-Ehlers & Schmidt, 1975; *Mucroplana* Sopott-Ehlers & Schmidt, 1975.

3.1.4. Proseriata

Seventeen species of this taxon were found belonging to five different families:

Otoplanidae: *Kata galapagoensis* Ax & Ax, 1974a (Fig. 3B); *Parotoplana turgida* Ax & Ax, 1974; *Philosyrtis santacruzensis* Ax & Ax, 1974; *Galapagoplana bituba* Ax & Ax, 1974.
Nematoplanidae: *Nematoplana* (?) *nigrocapitula* Ax, 1966.
Polystyliphoridae: *Polystyliphora darwini* Ax & Ax, 1974 (Fig. 2A).
Coelogynoporidae: *Vannuccia hastata* Ax & Ax, 1974; *Carenscoilia monostyla* Ax & Ax, 1974.
Monocelididae: *Monocelis galapagoensis* Ax & Ax, 1977; *Monocelis oculifera* Ax & Ax, 1977; *Archiloa papillosa* Ax & Ax, 1977; *Minona fernandinensis* Ax & Ax, 1977; *Minona stimula* Ax & Ax, 1977; *Duplominona galapagoensis* Ax & Ax, 1977; *Duplominona karlingi* Ax & Ax, 1977 (Fig. 9A); *Duplominona krameri* Ax & Ax, 1977; *Duplominona sieversi* Ax & Ax, 1977.

New genus: *Galapagoplana* Ax & Ax, 1974.

3.1.5. Typhloplanoida

Typhloplanoids comprise 19 species from five families:

Promesostomidae: *Promesostoma sartagine* Ax & Ehlers, 1973; *Promesostoma tenebrosum* Ax & Ehlers, 1973. *Wydula* (?) *simplex* Ehlers & Ehlers, 1981; *Pararhynchella fusca* Ehlers & Ehlers, 1981; *Kymocarens tibialis* Ehlers & Ehlers, 1981; *Kymocarens proxenetoides* Ehlers & Ehlers, 1981.
Trigonostomidae: *Ptychopera scutulifer* Ehlers & Ax, 1974; *Cryptostiopera cornuta* Ehlers & Ax, 1974 (Fig. 2C); *Ceratopera paragracilis* Ehlers & Ax, 1974; *Ceratopera bifida* Ehlers & Ax, 1974; *Messoplana falcata valida* Ehlers & Ax, 1974; *Trigonostomum setigerum* O. Schmidt, 1852.
Byrsophlebidae: *Maehrenthalia caligulachaena* Ehlers & Ehlers, 1981.
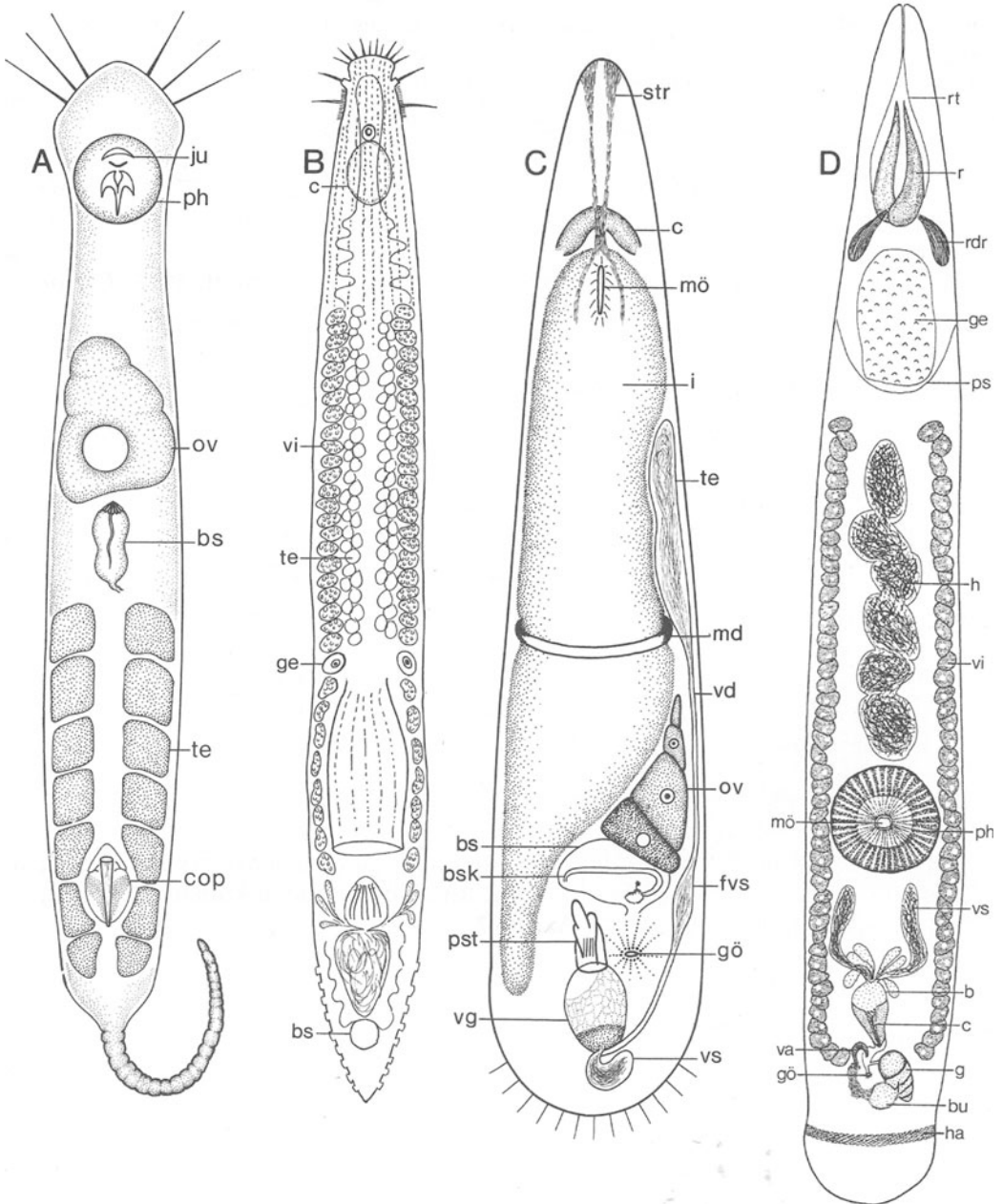Kytorhynchidae: *Neokytorhynchus pacificus* Ehlers & Ehlers, 1981.

Figure 3. (A) *Corculognathia apennata* Ehlers & Ehlers, 1973 (Gnathostomulida). Length about 600 μm. (B) *Kata galapagoensis* Ax & Ax, 1974 (Platyhelminthes, Proseriata). Length 3 mm. (C) *Paramyozonaria riegeri* Sopott-Ehlers & Schmidt, 1974 (Platyhelminthes, Macrostomida). Length about 800 μm. (D) *Schizochilus santacruzensis* Noldt & Hoxhold, 1984 (Platyhelminthes, Kalyptorhynchia). Length 1.7 mm. (A) From Ehlers and Ehlers (1973), (B) from Ax and Ax (1974), (C) from Sopott-Ehlers and Schmidt (1974), (D) from Noldt and Hoxhold (1985).

Typhloplanidae: *Haloplanella semicircula semicircula* Ehlers & Sopott-Ehlers, 1989; *Haloplanella semicircula santacruzensis* Ehlers & Sopott-Ehlers, 1989; *Haloplanella semicircula sancristobalensis* Ehlers & Sopott-Ehlers, 1989; *Haloplanella conversa* Ehlers & Sopott-Ehlers, 1989; *Pratoplana ayorae* Ehlers & Sopott-Ehlers, 1989.

New genera: *Cryptostiopera* Ehlers & Ax, 1974; *Pararhynchella* Ehlers & Ehlers, 1981; *Kymocarens* Ehlers & Ehlers, 1981; *Neokytorhynchus* Ehlers & Ehlers, 1981.

3.1.6. Kalyptorhynchia

Ten species from two families were described:

Schizorhynchidae: *Carcharodorhynchus galapagoensis* Noldt & Hoxhold, 1984; *Carcharodorhynchus tabulaeferus* Noldt & Hoxhold, 1984; *Carcharodorhynchus longicirrus* Noldt & Hoxhold, 1984; *Carcharodorhynchus arista* Noldt & Hoxhold, 1984; *Schizochilus bruneti* Noldt & Hoxhold, 1984; *Schizochilus santacruzensis* Noldt & Hoxhold, 1984 (Fig. 3D); *Coagulescorhynchus virguladivina* Noldt & Hoxhold, 1984.

Karkinorhynchidae: *Cheliplana barringtonensis* Noldt & Hoxhold, 1984; *Cheliplana pacifica* Noldt & Hoxhold, 1984; *Archipelagoplana triplocirro* Noldt & Hoxhold, 1984.

New genera: *Coagulescorhynchus* Noldt & Hoxhold, 1984; *Archipelagoplana* Noldt & Hoxhold, 1984.

3.2. Gnathostomulida (Fig. 3A)

The four new Galápagos species from shallow sublittoral mostly sandy–muddy sediments were among the first records of this taxon from the Pacific area.

Onychognathiidae: *Onychognathia bractearotunda* Ehlers & Ehlers, 1973.
Gnathostomulidae: *Gnathostomula costata* Ehlers & Ehlers, 1973; *Corculognathia apennata* Ehlers & Ehlers, 1973 (Fig. 3A).
Austrognathiidae: *Austrognatharia atraclava* Ehlers & Ehlers, 1973.

New genera: *Corculognathia* Ehlers & Ehlers, 1973.

3.3. Nemertini (Fig. 4B)

The cosmopolitan interstitial hoplonemertean genus *Ototyphlonemertes* is represented by 7 species in the Galápagos Islands (Mock and Schmidt, 1975). They mainly occur in the lower intertidal and the shallow subtidal areas of most of the sand beaches, their individual numbers, however, always being very low (maximum number 11 *O. fila* in 100 cm^3, Isla Barrington, low water line): *Ototyphlonemertes fila* Corrêa, 1953; *O. erneba* Corrêa, 1950; *O. americana* Gerner, 1969; *O. cirrula* Mock & Schmidt, 1975 (Fig. 4B); *O. santacruzensis* Mock & Schmidt, 1975.
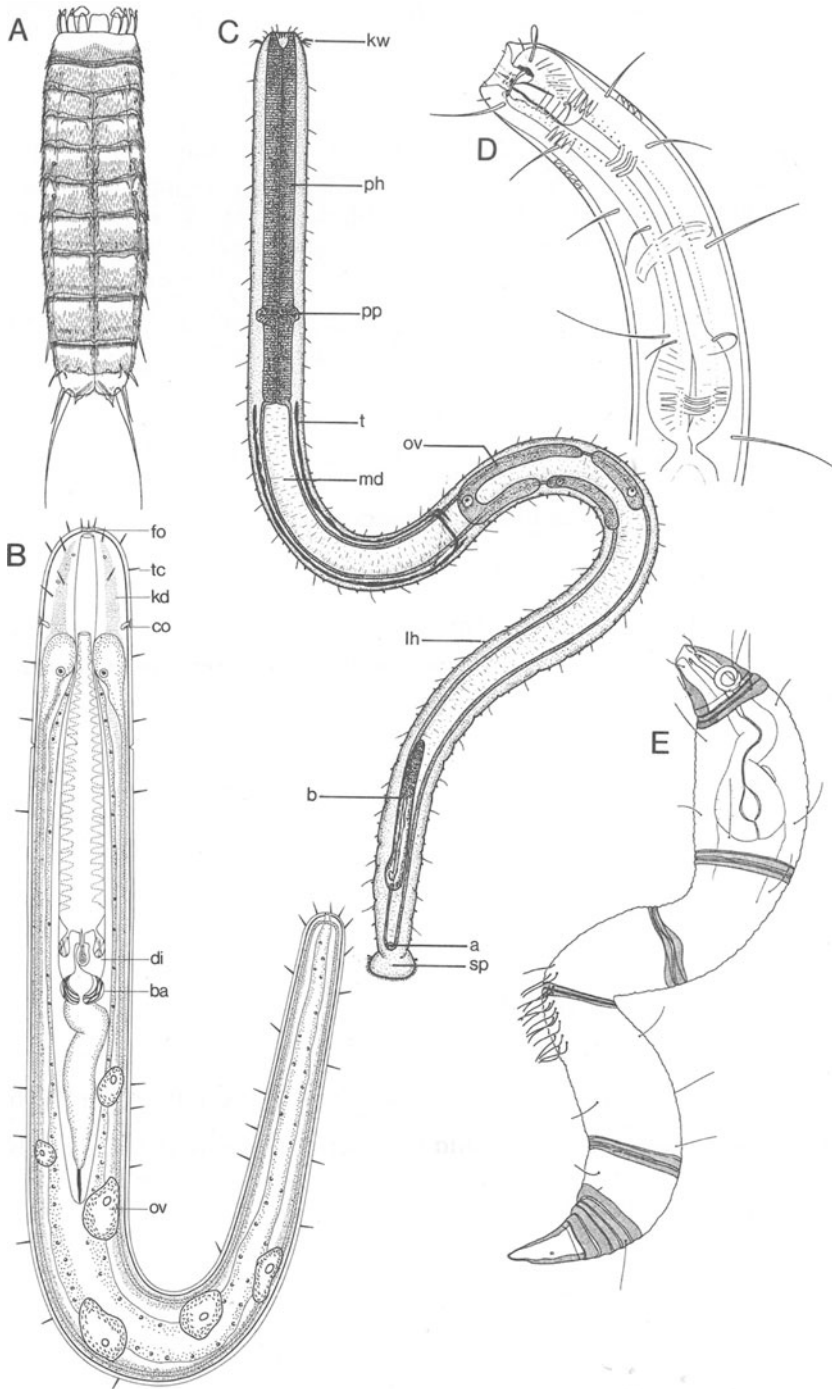
Figure 4. (A) *Echinoderes pacificus* Schmidt, 1974, Female; ventral view (Kinorhyncha, Cyclorhagida). Length 370 μm. (B) *Ototyphlonemertes cirrula* Mock & Schmidt, 1975 (Nemertini, Enopla). Length 3 mm. (C) *Megadasys pacificus* Schmidt, 1974 (Gastrotricha, Macrodasyoidea). Length 3.5 mm. (D) *Hypodontolaimus galapagensis galapagensis* Blome, 1985 (Nematoda, Chromadoridae). Anterior end. Total length about 470 μm. (E) *Bathyepsilonema lissum* Clasing, 1984 (Nematoda, Epsilonematidae). Length about 550 μm. (A) From Schmidt (1974), (B) from Mock and Schmidt (1975), (C) from Schmidt (1974), (D) from Blome (1985), (E) from Clasing (1984).

Two species of this genus possessing stylets composed of two single strands wounded round each other could not be identified because of lack of material.

Individuals of other genera, e.g., *Cephalothrix*, were rarely observed (Mock and Schmidt, 1975).

3.4. Gastrotricha (Fig. 4C)

Schmidt (1974), quite familiar with this typical interstitial group by his studies on the North Sea coast, described 18 species of Macrodasyoidea, including one new genus, *Megadasys* Schmidt, 1974, and 5 species of Chaetonotoidea:

Lepidodasyidae: *Cephalodasys pacificus* Schmidt, 1974; *Paradasys pacificus* Schmidt, 1974.

Macrodasyidae: *Macrodasys pacificus* Schmidt, 1974 (two other *Macrodasys* species were given no distinct specific status); *Megadasys pacificus* Schmidt, 1974 (Fig. 4C).

Dactylopodolidae: *Dendrodasys pacificus* Schmidt, 1974.

Turbanellidae: *Turbanella pacifica* Schmidt, 1974; *Paraturbanella pallida pacifica* Schmidt, 1974.

Planodasyidae: *Crasiella pacifica* Schmidt, 1974.

Thaumastodermatidae: *Tetranchyroderma pacifica* Schmidt, 1974; *Diplodasys ankeli pacificus* Schmidt, 1974; *Platydasys pacificus* Schmidt, 1974.

The chaetonotoids were not identified to species level. The 5 species belong to *Aspidiophus*, *Chaetonotus* (s.l.), and *Xenotrichula*.

3.5. Nematoda (Fig. 4D,E)

From the extremely high number of nematods sorted by the Schmidts on the Galápagos Islands, only the most species-rich taxon Chromadoridae and the morphologically aberrant Epsilonematidae have been published so far (Blome, 1985; Clasing, 1984). Only the cyatholaimid genus *Paracanthonchus* was found to be more abundant.

3.5.1. Chromadoridae

Chromadorinae: *Spiliphera dolichura* De Man, 1893; *Atrochromadora denticulata* Wieser & Hopper, 1967; *Chromadora macrolaimoides* Steiner, 1915; *Chromadora nudicapitata* Bastian, 1865; *Prochromadorella hexapapillata* Blome, 1985; *Prochromadorella paramucrodonta* (Allgen, 1929); *Prochromadorella salpingifera* Blome, 1985; *Prochromadorella zygophora* Blome, 1985.

Euchromadorinae: *Actinonema longicaudatum* (Steiner, 1918); *Endeolophos minutus* (Gerlach, 1967); *Endeolophos spinosus galapagensis* Blome, 1985; *Euchromadora atypica* Blome, 1985; *Rhips galapagensis* Blome, 1985; *Rhips gracilicauda* Blome, 1985; *Trochamus prosoporus* Blome, 1985.

Hypodontolaiminae: *Chromadorita nephramphida* Blome, 1985; *Chromadorita pallida* Blome, 1985; *Dichromadora* sp.; *Hypodontolaimus galapagensis*

galapagensis Blome, 1985 (Fig. 4D); *Hypodontolaimus galapagensis sanctaecrucis* Blome, 1985; *Innocuonema asymmetricum* Blome, 1985; *Spilophorella euxina* Filipjew, 1918 sensu Stekhoven, 1950; *Spilophorella paradoxa* (De Man, 1888).

3.5.2. Epsilonematidae

Bathyepsilonema compactum Clasing, 1984; *Bathyepsilonema lissum* Clasing, 1984 (Fig. 4E); *Epsilonema fernandinense* Clasing, 1984; *Epsilonema lasium* Lorenzen, 1973; *Epsilonema mangrovense* Clasing, 1984; *Leptepsilonema filiforme* Clasing, 1984; *Metepsilonema acanthum* Clasing, 1984; *Metepsilonema bermudae* Lorenzen, 1973; *Metepsilonema callosum* Lorenzen, 1973; *Perepsilonema papulosum* Lorenzen, 1973.

3.6. Kinorhyncha (Fig. 4A)

In upper sublittoral sands of beaches on Santa Cruz and Marchena, Schmidt (1974) found *Echinoderes pacificus* Schmidt, 1974 (Cyclorhagida, Echinoderidae). This is the kinorhynch genus with the highest number of species. A species of the family Semnoderidae could not be described due to inadequate material.

Typical interstitial species of **Rotifera** and opisthobranch **Gastropoda**, also collected by Schmidt (1978), were not investigated taxonomically.

3.7. Annelida—Polychaeta (Fig. 5)

Polychaete collections were repeatedly carried out on the Galápagos, but mainly comprised randomly sampled specimens of macrofaunal species (Kinberg, 1865; Chamberlin, 1919; Augener, 1933; Monro, 1933a,b; Hartman, 1939), with the exception of a more comprehensive collection of Spirorbidae by Bailey and Harris (1968).

More than 100 species (including the so-called archiannelids) were found during the Göttingen Galápagos Meiofauna Expedition, only 69 species of which have been reported in the literature (Westheide, 1974; Schmidt and Westheide, 1977; Westheide, 1977a; Westheide, 1982). Twenty-seven of these were described as new; no new genera were erected. Most species were found in shallow sublitoral areas, including species that inhabited old corals and crevices of stones. Only true macrofaunal representatives (body width 1 mm and wider) are not listed below.

Pisionidae: *Pisione oerstedi pulla* Westheide, 1974; *Pisione galapagoensis* Westheide, 1974 (Fig. 5C).

Phyllodocidae: *Hesionura* spp. (W. Westheide, unpublished results).

Nereidae: *Ceratonereis monronis* Westheide, 1977 (Fig. 5F).

Hesionidae: *Podarke* (?) sp.; *Microphthalmus indefatigatus* Westheide, 1974 (Fig. 5B); *Hesionides arenaria pacifica* Westheide, 1974; *Hesionides unilamellata* Westheide, 1974.

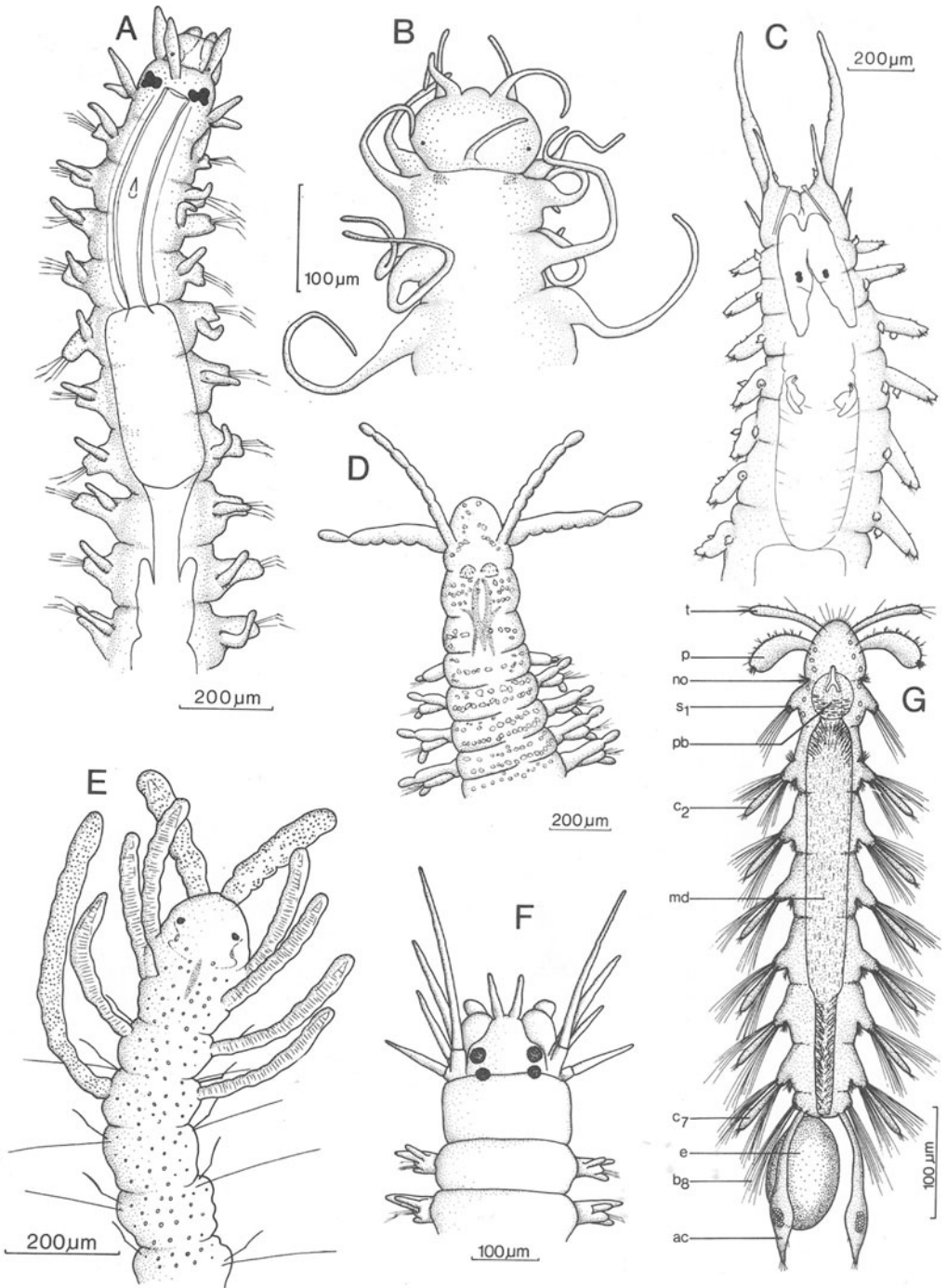Pilargidae: *Synelmis albini* (Langerhans, 1881).

Figure 5. Polychaeta (Annelida). (A) *Brania mediodentata* Westheide, 1974 (Syllidae). (B) *Microphthalmus indefatigatus* Westheide, 1974 (Hesionidae). (C) *Pisione galapagoensis* Westheide, 1974. (D) *Dorvillea pacifica* (Westheide, 1977) (Dorvilleidae). (E) *Macrochaeta multipapillata* Westheide, 1981 (Acrocirridae). (F) *Ceratonereis monronis* Westheide, 1977 (Nereidae). (G) *Nerillidium lothari* Schmidt & Westheide, 1977 (Nerillidae). (A–C) From Westheide (1974), (D), (F), from Westheide (1977), (E) from Westheide (1981), (G) from Schmidt and Westheide (1977).

Eunicidae: *Nematonereis unicornis* (Grube, 1840).

Dorvilleidae: *Dorvillea pacifica* (Westheide, 1977) (Fig. 5D); *Protodorvillea* sp.; *Ophryotrocha* sp.

Dinophilidae: *Dinophilus* sp.

Syllidae: *Haplosyllis spongicola* (Grube, 1855); *Opisthosyllis corallicola* Hartmann-Schröder, 1965; *Trypanosyllis taeniaeformis* (Haswell, 1865); *Ehlersia rosea magna* Westheide, 1974; *Ehlersia* spec.; *Typosyllis hyalina* (Grube, 1863); *Typosyllis variegata* (Grube, 1860); *Typosyllis glarearia* Westheide, 1974; *Typosyllis* spec., *Branchiosyllis exilis* (Gravier, 1900); *Parasphaerosyllis indica* Monro, 1937; *Amblyosyllis granosa* Ehlers, 1897; *Eusyllis homocirrata* Hartmann-Schröder, 1958; *Odontosyllis fulgurans dolerens* Westheide, 1974; *Syllides edentula* (Claparède, 1868); *Syllides japonica edentata* Westheide, 1974; *Brania heterocirra* Rioja, 1941; *Brania subterranea* (Hartmann-Schröder, 1956); *Brania oculata* (Hartmann-Schröder, 1960); *Brania concinna* Westheide, 1974; *Brania mediodentata* Westheide, 1974 (Fig. 5A); *Sphaerosyllis hystrix* Claparède, 1863; *Sphaerosyllis centroamericana* Hartmann-Schröder, 1959; *Sphaerosyllis pumila* Westheide, 1974; *Exogone dispar* (Webster, 1979); *Exogone naidinoides* Westheide, 1974; *Exogone occidentalis* Westheide, 1974; *Exogone longicornis* Westheide, 1974; *Exogone microtentaculata* Westheide, 1974; *Autolytus multidenticulatus* Westheide, 1974; *Autolytus arboreus* Westheide, 1974; *Autolytus* sp.; *Procerea fasciata* Langerhans, 1879; *Procerea* sp.

Nerillidae: *Nerilla parva* Schmidt & Westheide, 1977; *Nerillidium lothari* Schmidt & Westheide, 1977 (Fig. 5G); *Mesonerilla ecuadoriensis* Schmidt & Westheide, 1977.

Protodrilidae: *Protodrilus pierantonii* Aiyar & Alikunhi, 1944; *Protodrilus infundibuliformis* Schmidt & Westheide, 1977; *Protodrilus* spp.

Saccocirridae: *Saccocirrus sonomacus* Martin, 1977; *Saccocirrus* sp.

Polygordiidae: *Polygordius pacificus floreanensis* Schmidt & Westheide, 1977.

Diurodrilidae: *Diurodrilus* sp.

Cirratulidae: *Caulleriella alata* (Southern, 1914); *Cirriformia violacea* Westheide, 1982; *Cirriformia* spec.; *Tharyx* spec.

Ctenodrilidae: *Ctenodrilus serratus* (O. Schmidt, 1857).

Questidae: *Questa media* Westheide, 1982.

Acrocirridae: *Macrochaeta multipapillata* Westheide, 1982 (Fig. 5E).

3.8. Annelida—Aeolosomatidae

From the aeolosomatids, not regarded anymore to be true clitellate annelids, a new subspecies of the only true marine species was described from the sandy intertidal of six islands: *Aeolosoma maritimum dubiosum* Westheide & Schmidt, 1974 (Westheide and Schmidt, 1974).

3.9. Annelida—Oligochaeta

Schmidt's rich collection of oligochaetes contained both Enchytraeidae and Tubificidae; unfortunately, most of these were lost. Of the remaining, mostly

immature specimens, Erséus (1984) identified the tubificid species *Aktedrilus locyi* Erséus, 1984, *Aktedrilus cuneus* Erséus, 1980, and *Heterodrilus pentcheffi* Erséus, 1981; *Bacescuella parvithecata* Erséus, 1978, was found in another collection from the Galápagos Islands. Erséus (1984) also indicated that three species of the enchytraeid genus *Marionina* from Galápagos would be described by K. Coates in a future publication.

3.10. Tardigrada (Fig. 6)

Material for the description of marine Galápagos tardigrades from four families came from collections carried out by M. McGinty-Bayly in 1968, A. DeGauge in 1973, and P. Schmidt in 1972 and was published in a joint paper (McKirdy, Schmidt, and McGinty-Bayly, 1976). Besides a number of terrestrial tardigrades, Schuster and Grigarick (1966) reported two marine species, *Echiniscoides sigismundi* (Schultze, 1865) and *Archechiniscus marci* Schulz, 1953.

Halechiniscidae: *Tanarctus velatus* McKirdy, Schmidt, & McGinty-Bayly, 1976.

Batillipedidae: *Orzeliscus* cf. *belopus* Du Bois-Reymond Marcus, 1952.

Stygarctidae: *Stygarctus abornatus* McKirdy, Schmidt, & McGinty-Bayly, 1976; *Parastygarctus sterreri* Renaud-Mornant, 1970; *Pseudostygarctus triungulatus* McKirdy, Schmidt, & McGinty-Bayly, 1976 (Fig. 6B); *Megastygarctides orbiculatus* McKirdy, Schmidt, & McGinty-Bayly, 1976 (Fig. 6A).

Orcellidae: *Echiniscoides sigismundi* (M. Schultze, 1965); *Anisonyches diakidius* Pollock, 1975. Two specimens of halechiniscids were not identified due to inadequate material.

New genera: *Pseudostygarctus* McKirdy, Schmidt, & McGinty-Bayly, 1976; *Megastygarctides* McKirdy, Schmidt, & McGinty-Bayly, 1976.

3.11. Chelicerata—Acari (Fig. 7C)

Investigations of Schmidt's material by Bartsch (1977) revealed 42 halacarid species in 12 genera, the ecology of which was characterized by Bartsch and Schmidt (1978). Only four species were previously described, and no new genera were erected. Habitats of the species are subtidal and intertidal sandy areas. Several eurytopic species were found not to be restricted to the interstitial habitat.

Rhombognathinae: *Rhombognathus robustus* Bartsch, 1977; *Rhombognathus longiscutatus* Bartsch, 1977; *Rhombognathus semireticulatus* Bartsch, 1977; *Rhombognathus ellipticus* Bartsch, 1977; *Rhombognathus similis* Bartsch, 1977; *Rhombognathus heterosetosus* Bartsch, 1977; *Rhombognathus* spec.; *Isobactrus asper* Bartsch, 1977.

Actacarinae: *Actacarus mollis* Bartsch, 1977; *Actacarus uniscutatus* Bartsch, 1977; *Actacarus hastatus* Bartsch, 1977.

Halacarinae: *Copidognathus lineatus* Bartsch, 1977; *Copidognathus gibboides* Bartsch, 1977; *Copidognathus pauciporus* Bartsch, 1977; *Copidognathus lepidus*
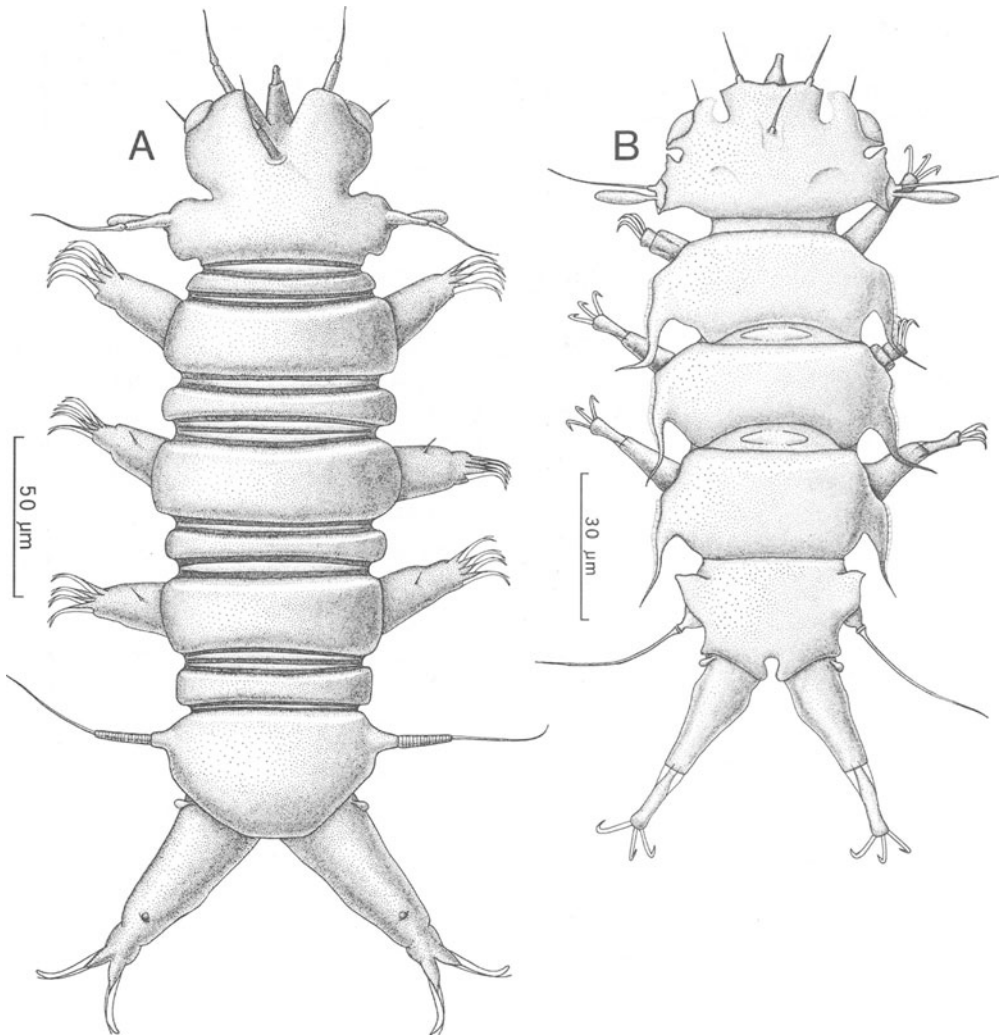
Figure 6. Tardigrada (Heterotardigrada). (A) *Megastygarctides orbiculatus* McKirdy, Schmidt & McGinty-Bayly, 1976. (B) *Pseudostygarctus triungulatus* McKirdy, Schmidt, & McGinty-Bayly, 1976. From McKirdy *et al.*, 1976.

Bartsch, 1977; *Copidognathus scitus* Bartsch, 1977; *Copidognathus bairdi bairdi* Newell, 1947; *Copidognathus grandiculus* Bartsch, 1977; *Copidognathus tuberipes* Bartsch, 1977; *Copidognathus peregrinus* Bartsch, 1977; *Copidognathus gracilis* (Viets, 1936); *Copidognathus guttatus* Bartsch, 1977; *Copidognathus tenuirostris* Bartsch, 1977; *Copidognathus* spec.; *Arhodeoporus bonairensis* (Viets, 1936); *Arhodeoporus bucculentus* Bartsch, 1977; *Agauopsis ornata* (Lohmann, 1893); *Agauopsis denticulatus* Bartsch, 1977; *Agauopsis* spec., *Atelopsalis aliger* Bartsch, 1977.

     <u>Acarochelopodinae</u>: *Acarochelopodia aduncispina* Bartsch, 1977; *Acarochelopodia cuneifera* Bartsch, 1977 (Fig. 7C).

Lohmannelinae: *Scaptognathus pauciporus* Bartsch, 1977; *Scaptognathus gibbosus* (Bartsch, 1977; *Scaptognathides bicornis* Bartsch, 1977.

Simognathinae: *Simognathus similis* Bartsch, 1977; *Simognathus disparilis* Bartsch, 1977; *Acaromantis subasper* Bartsch, 1977; *Acaromantis fastigatus* Bartsch, 1977; *Acaromantis armatus* Bartsch, 1977; *Acaromantis punctulus* Bartsch, 1977; *Acaromantis grandiculus* Bartsch, 1977.

3.12. Crustacea—Copepoda (Fig. 7A)

The harpacticoid copepods probably are the most species-rich taxon in the Galápagos meiofauna. Many were described in a series of voluminous contributions by Mielke (1979, 1981, 1982b, 1984, 1989a, 1989b). Besides the species listed below, the material contained several forms that are poorly understood taxonomically.

Longipediidae: *Longipedia helgolandica santacruzensis* Mielke, 1979.
Canuellidae: *Galapacanuella beckeri* Mielke, 1979.
Ectinosomatidae: *Ectinosoma pectinatum* Mielke, 1979; *Ectinosoma nonpectinatum* Mielke, 1979; *Arenosetella germanica galapagoensis* Mielke, 1979; *Hastigerella abbotti santacruzensis* Mielke, 1979; *Sigmatidium triarticulatum* Mielke, 1979; *Sigmatidium kunzi* Mielke, 1979; *Sigmatidium* spec.; *Noodtiella frequentior* Mielke, 1979; *Noodtiella hoodensis* Mielke, 1979.
Darcythompsoniidae: *Darcythompsonia fairliensis* (T. Scott, 1899).
Metidae: *Metis galapagoensis* Mielke, 1989; *Metis* spec.
Paramesochridae: *Apodopsyllus arcuatus* Mielke, 1984; *Diarthrodella parorbiculata pacifica* Mielke, 1984; *Diarthrodella neotropica* Mielke, 1984; *Diarthrodella galapagoensis* Mielke, 1984; *Leptopsyllus punctatus* Mielke, 1984; *Leptopsyllus platyspinosus* Mielke, 1984; *Paramesochra helgolandica galapagoensis* Mielke, 1984; *Paramesochra unaspina* Mielke, 1984; *Scottopsyllus langi* Mielke, 1984; *Kliopsyllus spiniger spiniger* Wells, Kunz, & Rao, 1975; *Kliopsyllus regulextans* Mielke, 1984; *Kliopsyllus similis* Mielke, 1984; *Kliopsyllus unguiseta* Mielke, 1984.
Tetragonicipitidae: *Tetragoniceps galapagoensis* Mielke, 1989; *Pteropsyllus trisetosus* Mielke, 1989; *Oniscopsis robinsoni* Chappuis & Delamare Deboutteville, 1956; *Phyllopodopsyllus angolensis* Kunz, 1984; *Phyllopodopsyllus thiebaudi santacruzensis* Mielke, 1989; *Phyllopodopsyllus furciger* Sars, 1907; *Phyllopodopsyllus galapagoensis* Mielke, 1989; *Phyllopodopsyllus kunzi* Mielke, 1989.
Cylindropsyllidae: *Leptastacus ctenatus* Mielke, 1982; *Leptastacus dispinosus* Mielke, 1982; *Leptastacus spatuliseta* Mielke, 1982; *Notopontia galapagoensis* Mielke, 1982; *Arenopontia peteraxi* Mielke, 1982; *Arenopontia trisetosa* Mielke, 1982.
Laophontidae: *Laophonte galapagoensis* Mielke, 1981; *Loureirophonte isabelensis* Mielke, 1981; *Heterolaophonte serratula* Mielke, 1981; *Paralaophonte pacifica galapagoensis* Mielke, 1981; *Paralaophonte problematica* Mielke, 1981; *Esola longicauda galapagoensis* Mielke, 1981; *Onychocamptus* spec.; *Echinolaophonte tetracheir* Mielke, 1981; *Afrolaophonte schmidti* Mielke, 1981; *Klieonychocamptoides itoi* Mielke, 1981; *Laophontina triarticulata* Coull & Zo, 1980.
Ancorabolidae: *Paralaophontodes exopoditus* Mielke, 1981.

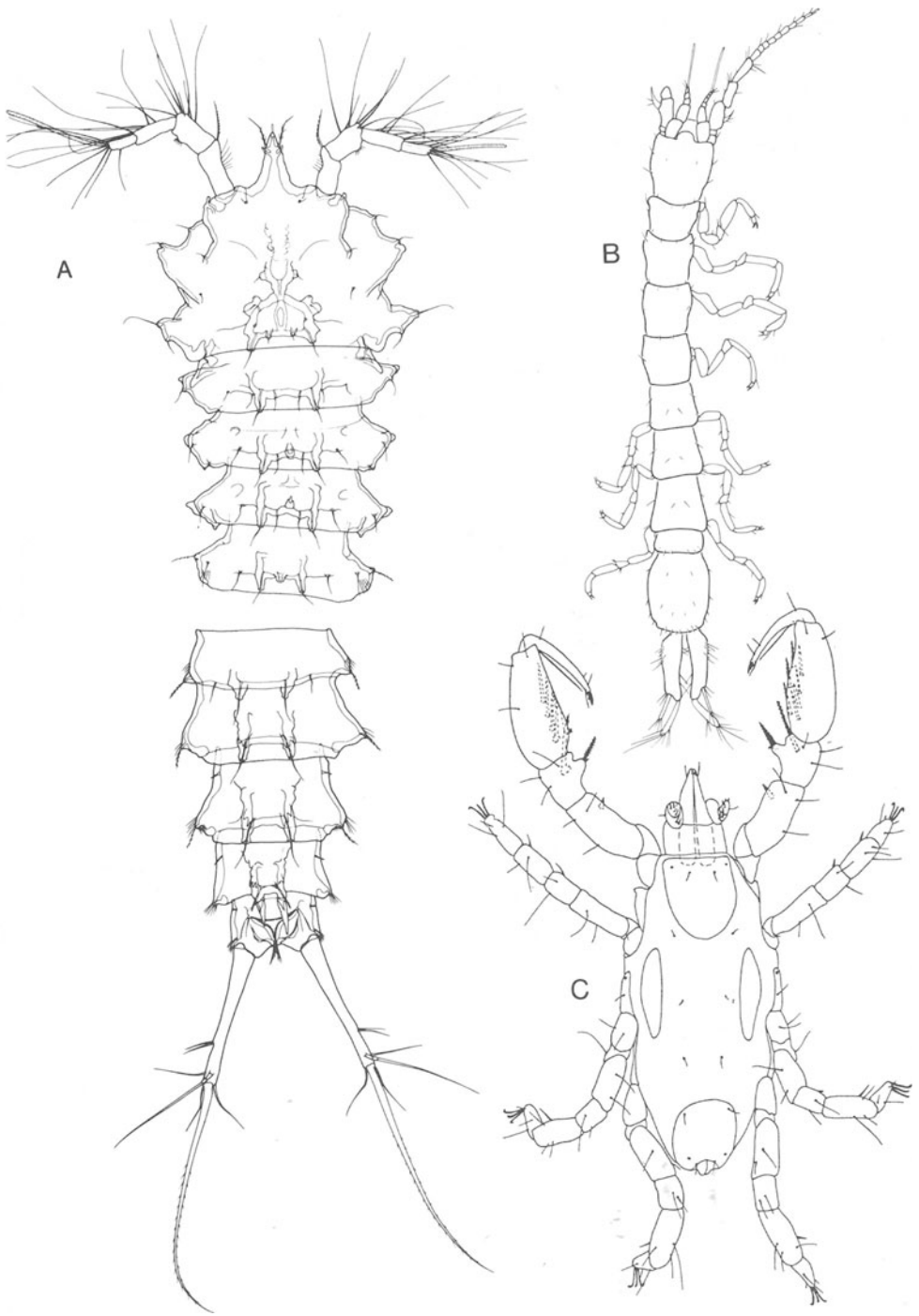New genus: *Galapacanŭella* Mielke, 1979.

Figure 7. (A), (B): *Paralaophontodes exopoditus* Mielke, 1981 (Copepoda, Harpacticoida, Anco-
rabolidae). Female, dorsal view of cephalothorax and pereion (A) and abdomen (B). Length 600 μm. (B)
Microcharon galapagoensis Coineau & Schmidt, 1979 (Isopoda, Asellota, Microparasellidae). Length
about 1.2 mm. (C) *Acarochelopodia cuneifera* Bartsch, 1977 (Acari, Halacaridae). Length about 250 μm.
(A) From Mielke (1981); (B) from Coineau and Schmidt (1979); (C) Courtesy Dr. I. Bartsch, Hamburg.

3.13. Crustacea—Ostracoda (Fig. 11)

Gottwald (1983) stated that he identified at least 60 different species of ostracods in Schmidt's material from sandy beaches of which he described 22 new species in the order Podocopida. Earlier collections from the Galápagos Islands considered species from brackish-water (Triebel, 1956), sublittoral (Pokorny, 1970, 1972), and rockpool habitats (Bate *et al.*, 1981), which, however, are not listed below.

Psammocytheridae: *Psammocythere santacruzensis* Gottwald, 1983.

Cytheromatidae: *Microloxoconcha santacruzensis* Gottwald, 1983; *Fernandinacythere arenicola* Gottwald, 1983.

Cobanocytheridae: *Cobanocythere subterranea* Hartmann, 1959; *Cobanocythere arenicola* Gottwald, 1983; *Cobanocythere lanceolata* Gottwald, 1983; *Cobanocythere psammophila* Gottwald, 1983; *Cobanocythere pacifica* Gottwald, 1983; *Cobanocythere fernandinensis* Gottwald, 1983; *Cobanocythere hoodensis* Gottwald, 1983; *Cobanocythere sublitoralis* Gottwald, 1983; *Cobanocythere santacruzensis* Gottwald, 1983; *Cobanocythere labiata* Hartmann, 1959; *Cobanocythere guttaeformis* Gottwald, 1983; *Cobanocythere elongata* Gottwald, 1983.

Xestoleberididae: *Xestoleberis arcturi darwini* Gottwald, 1983; *Xestoleberis galapagoensis* Gottwald, 1983.

Parvocytheridae (Fig. 11): *Parvocythere fernandinensis* Gottwald, 1983; *Parvocythere galapagoensis* Gottwald, 1983; *Parvocythere schmidti* Gottwald, 1983; *Parvocythere subterranea* Gottwald, 1983; *Parvocythere supralitoralis* Gottwald, 1983.

New genus: *Fernandinacythere* Gottwald, 1983.

3.14. Crustacea—Isopoda (Fig. 7B)

One typical interstitial isopod species, *Microcharon galapagoensis* Coineau & Schmidt, 1979 (Microparasellidae), was described from coarse sands in lower regions of intertidal areas on Santa Cruz, Isabela, Tower, and San Cristobal (Coineau and Schmidt, 1979).

4. Abundance and Dynamics (Fig. 8)

The immense quantitative data collected by Schmidt (1978) allowed him to give convincing abundance values for various beaches in the islands. The values range from an average of 118 ind/100 cm³ (Fernandina) to 667 ind/100 cm³ (Santa Cruz, Playa Borrero), with the highest number in an individual sample of more than 3000 individuals. The maximum number of metazoans under a surface of 10 cm² was 7640 (down to a depth of 1 m). These values are higher than in any other collection site with the exception of Sylt (North Sea), where Schmidt (1968) found a maximum of 10,972 metazoans under a surface of 10 cm². Population dynamics and reproductive periods are strongly correlated with water temperature in temperate sandy beaches, the maximum densities occurring after periods of increasing temperatures in spring and summer (Schmidt, 1968; 1972a; 1972b). Expectations of reduced seasonal fluctuations on the Galápagos archipelago with its relatively
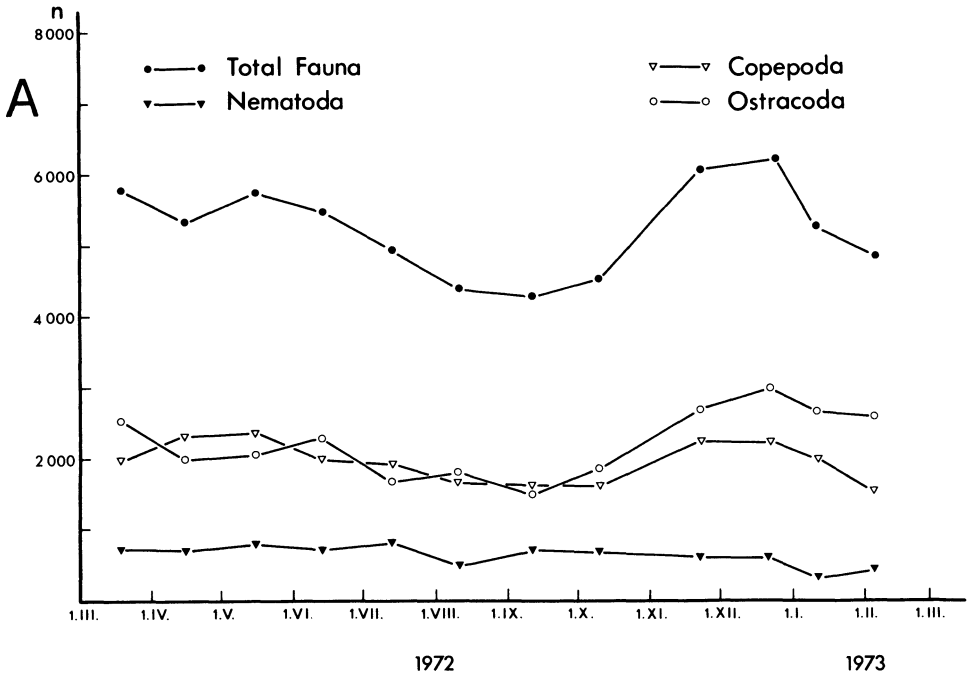
Figure 8. Abundance dynamics of total fauna and dominant taxa. (A) Santa Cruz, Bahia Academy.

constant water temperatures, however, were not supported. In the beach of Bahia Academy (Santa Cruz, southern coast) abundance values of the total fauna in a transect fluctuated between 4267 and 6198 in 50 cm³ sand, with a minimum abundance occurring in August to October (Schmidt, 1978). The fauna from the Playa Borrero collection site on the north coast of Santa Cruz showed considerably higher seasonal variation, with 14,126 individuals in November and 5707 individuals per 50 cm³ in February. Fluctuations especially were dependent upon differences in the dominant taxa Nematoda, Copepoda, and Ostracoda.

As Schmidt (1978) pointed out, these seasonal variations are as large or even larger than those found in the North Sea and the Baltic. The most remarkable result of these two density series is the fact that their minimum and maximum values do not coincide. Schmidt (1978) concluded that these fluctuations were not due to differences in water temperatures but could be explained by specific local events, such as heavy rainfall just before sampling or input of órganic matter by dead macrofauna. Unfortunately, results on population dynamics and reproductive seasonality of smaller taxa or individual Galápagos species have been only sparsely published. The most common halacarids (*Actacarus mollis, Scaptognathides bicornis*) reproduce throughout the year (Bartsch and Schmidt, 1978). Clasing (1984) found conspicuous seasonal variation in the numbers of the nematode *Metepsilonema bermudae* but no marked differences in the ratio of juvenile and adult individuals throughout the year. She also assumed that reproduction is not seasonally restricted in these species. Mielke (1989a), however, presented evidence for a seasonality of reproduction in the copepod *Oniscopsis robinsoni*, based on a higher number of copepodites in May, June, and July.
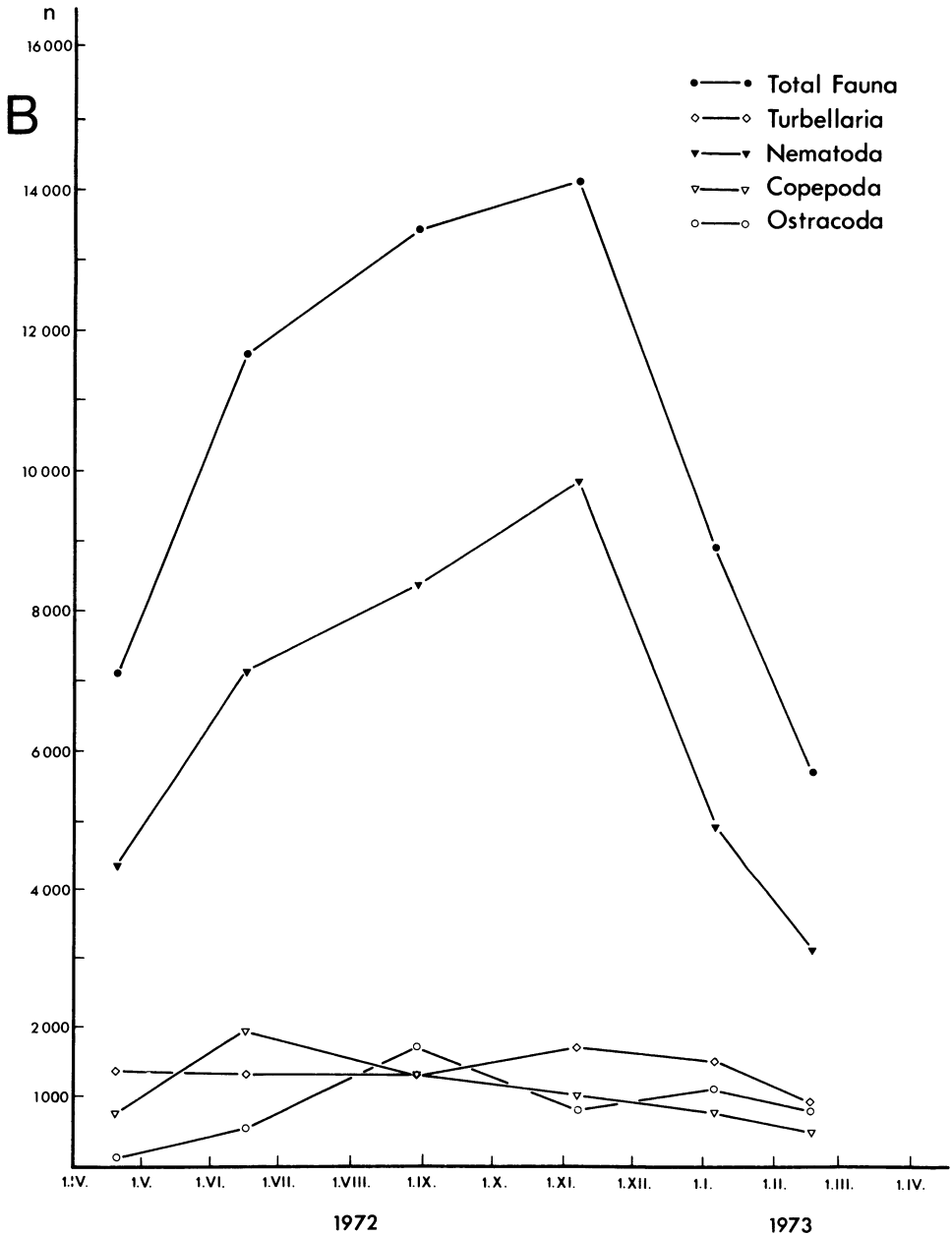
Figure 8. (B) Santa Cruz, Playa Borrero. After Schmidt, 1978.

5. Dominating Groups

Nematoda, Copepoda, and Ostracoda are the groups with the highest mean values of animals in individual island beaches. Platyhelminthes ("Turbellaria") and Polychaeta are present in all beaches. Each taxon comprises at least 2.6% of the total fauna of a given beach transect; in certain individual samples, more than 80% platyhelminths and more than 74% polychaetes were found. Gastrotricha (up to

4.8% on Tower; more than 31% in individual samples on Tower) and Acari (up to 2.6% on Marchena; up to 26% in individual samples from Barrington and Hood) comprise only about 1% in a few beaches. Mean values for the dominant taxa of all beaches investigated are: Nematoda 33.2%, Ostracoda 26.3%, Copepoda 21.2%, Turbellaria 8.9%, and Polychaeta 5.9% (Schmidt, 1978). Whereas nematodes and copepods are the dominant groups of marine sand beaches worldwide, the Galápagos pattern of dominance is surprising because of the high percentage of ostracods. These high numbers of individuals and species cannot be satisfactorily correlated with special environmental conditions within Galápagos beaches. Although sediments and exposition of sandy tidal areas from, for example, Fernandina, Hood, James, Marchena, Barrington, Tower, and Santa Cruz islands are rather different, the share of ostracods in all of the lotic beaches is never below 22.5%. On Hood, ostracods in the large and relatively long beach of Bahia Gardner present more than half of all metazoans (55.9%); in one sample of this beach Schmidt counted 2856 ostracod individuals in 100 cm³, that is 95.6% of the total metazoan fauna. Only in the three moderately lotic beaches on Bartholomé, Floreana, and Santa Cruz (Playa Borrero) was the percent of ostracods comparatively low with values of 1.6, 5.5, and 12.5%, respectively.

But also these values are higher than those found in similarly investigated continental beaches. Neither in temperate—e.g., North Sea, Baltic, Norway (Schmidt, 1968; 1969; 1972a; 1972b)—nor in warm oceanic littoral areas have ostracods normally been found to be one of the dominating groups. One exception is a Delaware beach (Atlantic coast of North America), where Hummon et al. (1976) reported ostracods to be the second most abundant taxon.

It is therefore not unlikely that the dominance of ostracods has to do with the pattern of colonization of the sand beaches in the Archipelago. There is a general worldwide similarity in the interstitial fauna dominance pattern, with nematodes and copepods being almost always the dominant taxa. Let us assume this pattern of dominance represents the stable climax situation of sandy meiofaunal biocoenoses. One may expect that colonization of newly formed isolated islands by different taxa will not take place in the same abundance ratio as individuals found in continental beaches. Individual taxa just might reach the islands earlier than others by chance; some taxa might be better suited for drifting and rafting, or may survive different means of dispersal better than others. This certainly will lead to a gradually timed pattern of colonization by the individual taxon and will influence the dominance pattern of both the founder generations and the subsequent generations.

It appears, therefore, to be a completely open question, if the Galápagos situation should be considered a unique but stable community structure or a successional stage that will lead somehow to the normal nematode–copepod dominance. The considerable variation in the percentages of the three dominant groups within the different beaches (e.g., ostracods between 1.6%–55.9%) may support the latter possibility. In this case the Galápagos faunal structure would allow us to gain insight into the succession of meiofauna beach communities. We would then have to conclude that a period of 1 to 3 million years is not sufficient to establish the climax community structure of these biocoenoses on oceanic islands.

Schmidt (1978) found another peculiarity in the composition of the Galápagos meiofauna: Tardigrada never composed more than 1% of the total fauna in a beach transect; the highest value in an individual sample was 17% (Santa Cruz, Playa

Borrero). Especially in comparison with Schmidt's (1968, 1969) investigations on Sylt and Renaud-Debyser's (1963) analysis of the Arcachon beaches the low percent of tardigrades in Galápagos beaches is striking. Presence and abundance of tardigrade species, however, generally appears to be more irregular over time than that of other groups. Thus Schmidt's tardigrade values from Sylt have not been observed in recent years. My personal observations in continental warm water tropical beaches did not reveal high numbers of this taxon either. On the other hand one of the highest number of individuals of a single taxon ever observed in a littoral sand sample by the author were tardigrades in a Bermuda beach.

Different, however, from the overall dominance pattern is that the total number of individuals in animal groups may be surprisingly similar to other collection sites of the world. An example of this is the Polychaeta (Westheide 1977b), for which Schmidt (1978) found values between 2.2% (Santa Cruz, Playa Borrero) and 15.8% (Floreana), the mean value of all beaches being 6.1%. For comparison, in Sylt beaches (southern North Sea) the share of polychaetes nearly reaches 5%, in Mediterranean beaches near Tunis it is between 1.5 to 4.4%; a percentage of about 1% is known from Southeast India.

6. Zonation

Vertical and horizontal zonation of total meiofauna and individual taxa is typical for tidal beaches throughout the world. The Galápagos beaches are no exception (Ax and Schmidt, 1973; Bartsch and Schmidt, 1976; Schmidt, 1978; Gottwald, 1983; Clasing, 1984). As expected, the majority of individuals inhabited the lower and middle parts of the beach slopes, highest values being found in the upper 10–20 cm of sediment. High air temperatures during low tide, however, may force animals to migrate into deeper layers; heavy rainfalls may kill nearly the entire meiofauna down to a depth of 50 cm.

Three examples may demonstrate single species zonation pattern in the Playa Borrero beach on Santa Cruz. The epsilonematid *Perepsilonema papulosum* lives around the low water line (Clasing, 1984). The macrostomid *Siccomacrostomum triviale* was exclusively found in the middle part of the tidal area, and *Macrostomum ideficis* inhabits the uppermost part just below the high water line (Schmidt and Sopott-Ehlers, 1976). Distribution patterns of congeneric species occurring together in a beach are interesting: they partition the beach environment, with very little overlap (Fig. 10).

7. Number of Species

Extremely low species numbers is a well known characteristic of the terrestrial fauna of small islands. This phenomenon, so easily recognized in Galápagos terrestrial arthropods, is not, however, found in the marine intertidal meiofauna. Surprisingly, Galápagos beaches are not generally species-poor, nor do individual species occur in conspicuously high number [although in several groups, the number of species appear to be distinctly smaller than in the beaches of the North Sea islands of Sylt (e.g., Plathyhelminthes: Ax, 1977)]. It should be kept in mind

that sampling in the Galápagos by the Göttingen group was restricted to a selection of small-scale habitats only, in a relatively short period of time. Thus additional species are to be expected with additional collecting. We also cannot exclude the possibility that the number of species in individual taxa is different in tropical areas, so that the Galápagos situation may simply reflect the normal subtropical and tropical situation (see also discussion in Ehlers and Dörjes, 1979, for Acoela).

It should be emphasized, however, that there are several taxa whose number of species obviously do not differ markedly from other tropical and temperate shore-lines of the world. For instance, this seems to be true for the meiofaunal Polychaeta (Westheide, 1974; 1977a; 1982; Schmidt and Westheide, 1977). Bailey and Harris (1968) came to similar conclusions for the Galápagos spirorbid polychaetes. Blome (1985) found the nematode family Chromadoridae as rich in genera and species as in continental beaches. There is even one example of the number of species in a taxon being considerably higher than elsewhere. The nematode family Epsilonematidae is present on the Galápagos islands with 10 species in 5 genera, a number which according to Clasing (1984) has not yet been found in any other area.

Even more interesting is a comparison of the spectrum of supra-specific taxa. In several groups the identified species generally represent most of the taxa that normally can be found in comparable habitats. This holds true, for example in chromadorid Nematoda (Blome, 1985), Gastrotricha, and Polychaeta. The 13 macro-dasyoid species from the Galápagos represent all 6 families within this gastrotrich order, and the 5 chaetonotoid gastrotrichs belong at least to 3 different genera (Schmidt, 1974). The spectrum of polychaete genera is almost the same as that revealed in the majority of sandy beaches throughout temperate and tropical seas. Even the distribution pattern of polychaete genera within beaches is widely consistent, although species may not be identical. For instance, the shallow subtidal and low tidal areas with coarse sediments are characterized by the genera *Pisione* (Pisionidae), *Hesionura* (Phyllodocidae), *Typosyllis, Exogone, Brania* (Syllidae), *Microphthalmus* (Hesionidae), *Dorvillea* (Dorvilleidae), *Macrochaeta* (Acrocirridae), and *Nerillidium* (Nerillidae). Lower wave-swept parts of the beach slope are inhabited by *Saccocirrus* (Saccocirridae) and *Polygordius* (Polygordiidae), the upper parts by *Hesionides* (Hesionidae), *Protodrilus* (Protodrilidae) and *Diurodrilus* (Diurodrilidae), together with one syllid species (it is usually *Eusyllis homocirrata* in the Galápagos beaches). Each of these genera found in the Galápagos Islands is represented by at least one species in an identical transect position within Mediterranean or Indian beaches (Rao, 1972; Westheide, 1972; 1977b; and unpublished data). The majority of these genera also occur in temperate areas, e.g., in beaches of the North Sea.

Nevertheless there are several widely distributed supraspecific taxa which obviously were not able to disperse to the Galápagos Islands. The well known interstitial cnidarian genus *Halammohydra* Remane is lacking as well as the turbellarian taxon Dalyellioidea and the Mystacocarida (Crustacea) (Ax and Schmidt, 1973). Species-rich genera of polyclad platyhelminths like *Stylochus* and *Notoplana* have not yet been recorded from the islands (Sopott-Ehlers and Schmidt, 1975). Within the Polychaeta it was not possible to find the two typical interstitial genera *Protodriloides* (Protodriloidae) and *Trilobodrilus* (Dinophilidae), both occurring on the North American Pacific coast. Blome (1985) mentioned that the common nematode genus *Neochromadora* was not detected within

the tremendous number of nematode specimens collected from the Galápagos Islands. McKirdy *et al.* (1976) found no *Batillipes* species within the tardigrades. It is not possible to speculate whether this is due to taxon-specific problems of dispersal or simply a matter of chance.

8. Origin of Species

Almost 95% of the species identified belong to known genera; no suprageneric category had to be created. Evolutionary distance to animals outside the Galápagos is generally small. All investigators point to the fact that most of the species or their direct ancestors must have reached the islands independently. This leads to the important question how they managed to do this.

Interstitial meiofauna organisms in general are not suited for active migration within the free water column. Migration on the sea bottom is hardly probable because unfavorable non-sandy sediments will act as unbrigdeable barriers. Only very few of the meiofauna taxa concerned possess pelagic larvae, e.g., the polychaete genera *Pisione* and *Polygordius*. The nauplius larvae of harpacticoid copepods normally do not leave the sediment. It was concluded, therefore, that widespread or even cosmopolitan distribution patterns of species and genera, as well as their widely consistent pattern of distribution within beaches, generally go back to an old supercontinent that already possessed these faunal elements before continental drift occurred (Rao, 1972; Sterrer, 1973; Westheide, 1977b).

The Galápagos Islands, however, are completely oceanic; a land bridge to the American continent, though often discussed, never existed. Thus their entire littoral meiofauna must have been transported or drifted across the ocean within less than 3 million years of the present.

Meiofauna organisms are regularly found drifting in the water column (e.g., Hagerman and Rieger, 1981; Gerlach, 1977), recruited by passive erosion from sediments with subsequent colonization of bottom areas, or by active entry into the water with subsequent settlement or even active site selection (Palmer, 1988; Armonies, 1988). Calculations of Hagerman and Rieger (1981) of the sinking velocity, however, showed long-distance dispersal across oceans of suspended meiofauna to be rather unlikely. This may also be true for the shortest distance between the American continent and the Galápagos archipelago of 1000 km. Other potential means of meiofauna dispersal listed by Gerlach (1977), e.g., transport by birds, by floating materials, by ballast sand in sailing vessels and in the water attached to suspended sediment during periods of heavy storms have to be considered. Besides many accidental observations of rafting, considerable advances have been made in documenting the great potential for dispersal of benthic meiofauna on drifting material (e.g., Hicks, 1988). This suggests that raftborne individuals may well have colonized beaches of oceanic islands like the Galápagos. Under the light of these new findings, it has to be asked if arrival of meiofauna species is as infrequent and genetic isolation as complete on oceanic islands as is usually believed.

The rafting hypothesis implies that there should be some degree of consistency between the direction of the sea currents passing the islands and the geographic origin of the faunal elements. According to Abbott (1966) the South Equatorial

current and the Humboldt current come from the South American west coast, the latter sweeping up the coast to the North before it swings out into the Pacific to pass through the islands. From December to May the warm El Niño from the Central American area displaces the Humboldt current. The influence of the California current may be of less importance. From the open Pacific the islands are reached by the North Equatorial current, the South Equatorial current, and the Equatorial counter current. Currents from the American continent may be considered to have served as transportation vehicles for floating and rafting animals. However, in general one can state that faunistic consistency between the Galápagos and the American Pacific coast line is relatively low. This holds true even if relationships to the Caribbean region are included, which are interpreted as a result of the former connection between the Atlantic and Pacific when the land bridge of Panama was broken up. Mielke (1985) presented evidence that the zoogeographic affinities of copepods between the Panama coast and Galápagos are closer than between the South American coastal areas passed by the Humboldt current. This may be true also for other taxa.

The following discussion contains some of the examples of American west coast affinities to Galápagos meiofauna species.

Of the 15 acoelous turbellarians, *Conaperta colorata* has a distinct sister species relationship to a Pacific North American species, *C. actuosa* Kozloff, whereas most of the closest relations of the other species are known from Europe (Ehlers and Dörjes, 1979). Sopott-Ehlers and Schmidt (1975) stated that some of the Galápagos polyclads may have close affinities to species from the Californian coast. The otoplanid *Philosyrtis sanjuanensis* from the North American Pacific coast is considered to be the sister species of *P. santacruzensis* from Galápagos (Ax, 1977). Another turbellarian, *Nematoplana nigrocapitula* Ax, 1966, from the North American Pacific coast, was also reported from the Galápagos (Ax and Ax, 1974).

Two nemerteans, *Ototyphlonemertes fila* Corrêa and *O. erneba* Corrêa are conspecific to populations from the North and South American east coast (Florida, Brazil); only *O. americana* Gerner was described from the North American Pacific coast (Washington) (Mock and Schmidt, 1975).

The nematodes *Metepsilonema callosum* Lorenzen and *Perepsilonema papulosum* Lorenzen are known from southern Chile (Clasing, 1984). The copepod *Afrolaophonte schmidti* described by Mielke (1981) from the Galápagos, and also found on the Pacific coast of Panama (Mielke, 1982a), is closely related to *Afrolaophonte chilensis* Mielke from the Chilean coast (Mielke, 1985). There are two other Galápagos copepods, *Klienychocamptoides itoi* and *Laophontina triarticulata*, which Mielke (1982a) recorded from the Panamanian Pacific and Atlantic coast, respectively.

Within Polychaeta, the nominate subspecies of *Pisione oerstedi pulla* Westheide was reported from Chile (Castro, 1958). The cosmopolitan nominate subspecies of *Hesionides arenaria pacifica* Westheide is a common representative in various American west coast beaches (see figure 1A in Westheide, 1977b). Rioja (1941) described *Brania heterocirra* from the Mexican Pacific coast, where he also reported *Typosyllis hyalina* Grube. A close relative of *Questa media* Westheide from the Galápagos is *Q. caudicirra* Hartman from the southern Californian coast. One of the *Saccocirrus* species was considered to be identical with *S. sonomacus* Martin from northern California. Unpublished material from South American beaches

may well extend this list of Galápagos–American west coast affinities within the Polychaeta. The oligochaete *Aktedrilus locyi* Erséus, 1980, conforms well with the type specimens from California and Oregon (Erséus, 1984).

Populations of the podocopid ostracods *Cobanocythere subterranea, C. labiata*, and *C. elongata* were found to be conspecific to populations on the Pacific coast of Central America (El Salvador, Panama). The sister species of *C. labiata* is the Caribbean *C. mielkei* (Gottwald, 1983). *Tourconcha lapidiscola* (Hartmann, 1959) and *Coxoconcha lenticuloides* (Swain & Gilby, 1974), two ostracod species living on green algae, were detected on the Galápagos as well as on the Central American coast and in the Caribbean (Bate *et al.*, 1981; Gottwald, 1983).

Generally, zoogeographic relations to nearly all faunistic areas can be stated [e.g., see discussion of zoogeographic distribution of polychaetes (Westheide, 1974) and podocopid ostracods (Gottwald, 1983)]. Discussions of this kind, however, suffer from incomplete or total lack of meiofauna taxonomic investigations in the Pacific area and the generally limited knowledge of meiofauna species distribution. Thus, for the time being, one can neither be relatively sure of the endemic character of the species described from the Galápagos, nor is one able to discuss sister species relationships with a high degree of accuracy. This is demonstrated by the fact that within polyclads and polychaeates (taxa whose systematic investigation occurred prior to that of taxa completely restricted to meiofauna dimensions) the number of endemic species is considerably lower than within the other groups. Even this low percentage of endemicity may be reduced in the near future, as can be shown by the following examples: *Hesionides unilamellata* Westheide, 1974, from the Galápagos was also identified in beach sands from Hawaii and must be removed from the list of endemic species. Russell (1991) found *Exogone naidinoides* Westheide, 1974, and *Exogone occidentalis* Westheide, 1974, in Belize (Central American Atlantic coast). The degree of endemism certainly reflects sampling activities in a certain taxon.

Two other problems have to be mentioned in this context. (1) Species descriptions, especially older ones, are often less detailed than is necessary for elucidation of small-scale differences in morphological characters. (2) In small-sized, so-called soft-bodied animals, availability of exact biometric data is problematic because of small structural diversity and inconstant dimensions of many characters; thus identification of species differences is more difficult than in hard-bodied taxa, e.g., tardigrades, crustaceans, halacarids.

This latter fact, in particular, takes on an increased importance under the light that the percentage of morphologically highly similar but truly distinct species (= "sibling species") in the meiofauna obviously is much higher than previously expected [e.g., see the polychaete *Microphthalmus–listensis*-species-group (Westheide and Rieger, 1985; Specht and Westheide, 1988)]. This affects also the subspecies problem. In taxonomic procedure, small-scale differences in one or very few characters between populations will often lead to the erection of a subspecies, or, as Ax (1977) defined more precisely, Galápagos platyhelminth populations were considered to be subspecies if differences between them and populations outside the archipelago were smaller than between sympatric continental species. Theoretically, however, subspecies populations should be recognized by their ability to interbreed, a criterion, however, that is practically impossible to prove in the majority of meiofauna organisms. The subspecies label on a Galápagos taxon may

thus be nothing more than an indication of relatively slight morphological differences compared to a non-Galápagos population or between geographically separated populations within the archipelago.

9. Meiofauna Speciation in the Galápagos Islands

Meiofaunal species found in the Galápagos can be grouped into the following evolutionary categories (see also Ax, 1977): (1) Species showing virtually no differences compared to populations from other parts of the world. (2) Endemic species and subspecies, the closest relatives of which live outside the archipelago. (3) Groups of two or more congeneric endemic species, which, however, are less related to each other than to species outside the archipelago. This means that their ancestors must have reached the islands independently in separate events not going back to a common stem species from the Galápagos. Obviously the majority of congeneric species belong to this category (see Composition of Taxa). (4) In a few cases which are listed below there is evidence for species multiplication within the Galápagos Islands.

Four new highly similar species of the proseriate platyhelminth family Monocelididae, *Duplominona galapagoensis*, *D. karlingi* (Fig. 9), *D. krameri*, and *D. sieversi*, were shown by Ax (1977) to form a monophyletic group of species that evolved within the Galápagos Islands. *Duplominona* contains 8 species, of which the Galápagos forms present the most evolved members (Fig. 9). The sister species of the Galápagos four-species group is *D. kaneohei* from Hawaii. A synapomorphic feature of the Galápagos group is an enclosed cuticular stylet of the male copulatory organ; the common derived character of *D. kaneohei* with the four Galápagos species is the union of the vagina with the male pore (Fig. 9B). Slight but consistent morphological differences in populations of the typhloplanoid *Haloplanella semicircula* caused Ehlers and Sopott-Ehlers (1989) to erect the three subspecies *H. s. semicircula* (from James), *H. s. santacruzensis* (from Santa Cruz) and *H. s. sancristobalensis* (from San Cristobal). Blome (1985) found the same situation within a nematode species, which he separated into *Hypodontolaimus galapagensis galapagensis* and *H. g. sanctaecrucis*. Although their true subspecies character is not yet proven, these morphologically different allopatric taxa undoubtedly evolved within the archipelago.

Mielke (1979) found evidence for intensive processes of speciation within the islands in the harpacticoid genus *Ectinosoma*. Apparently two *Ectinosoma* species reached the islands independently and gave rise to two different evolutionary lines, each consisting of a series of species or subspecies distributed over the entire archipelago, the systematic arrangement of which, however, could not yet be exactly elucidated. Slight morphological differences between populations of *Phyllopodopsyllus galapagoensis* on Fernandina, Isabela, Santa Cruz and San Cristobal suggest incipient speciation within another harpacticoid taxon (Mielke, 1989).

Ostracods appear to indicate the most obvious examples for actual speciation within the archipelago (Gottwald, 1983). A comprehensive biometric analysis revealed the existence of two forms of *Cobanocythere labiata*, which differ in substrate preference and body length on the different islands.
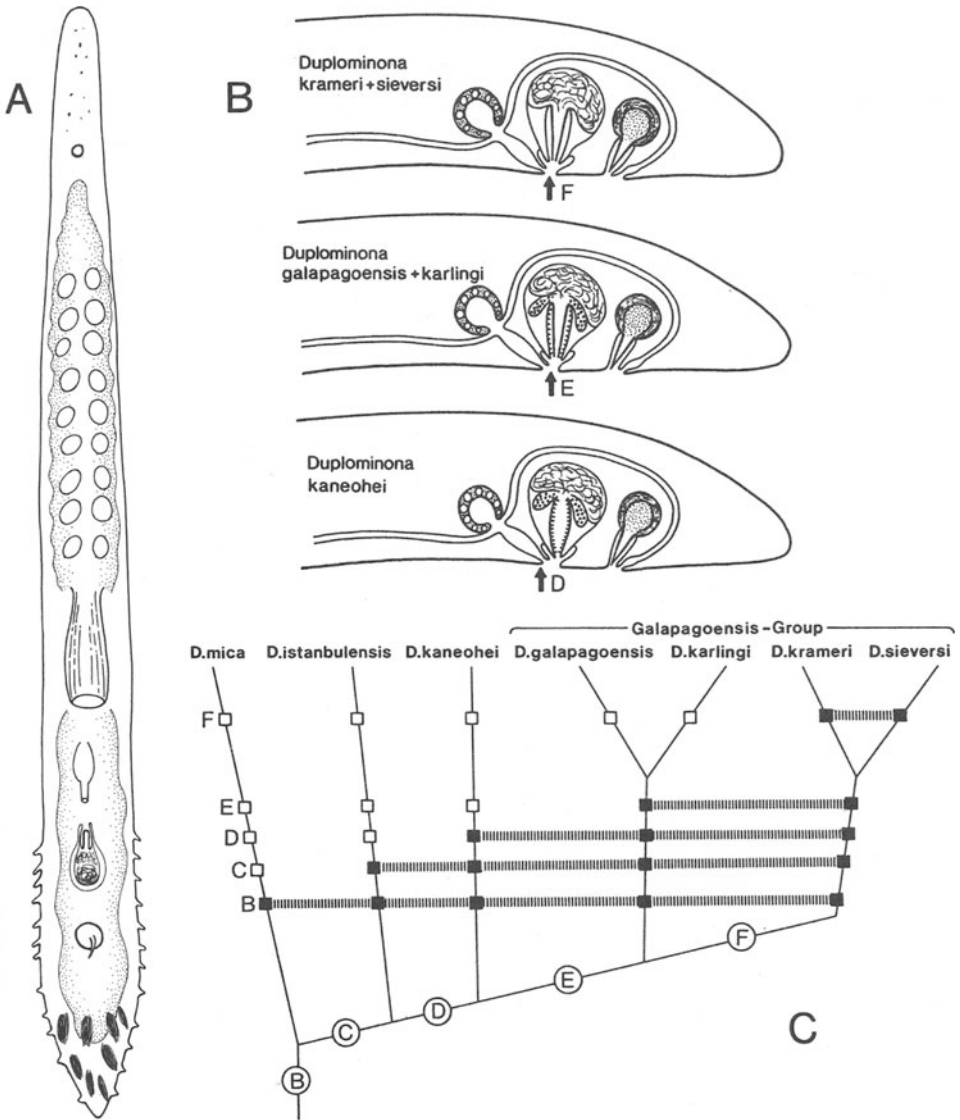
Figure 9. Speciation within *Duplominona* (Platyhelminthes, Proseriata, Monocelididae). (A) *Duplominona karlingi* Ax & Ax, 1977. (B) Position of genital organs within the four Galápagos species of *Duplominona* and the Hawaiian *D. kaneohei*, that forms the sister taxon of the Galápagos group. Apomorphy (= synapomorphy of *D. kaneohei* Karling, Mack-Fira & Dörjes with the Galápagos group): union of the vagina with the male pore. Apomorphy E (= synapomorphy of *D. galapagoensis–D. karlingi* with *D. krameri–D. sieversi*): development of an enclosed cuticucular stylet. Apomorphy F (= synapomorphy of *D. krameri* and *D. sieversi*): reduction of the granule glands and the cirral spines. (C) Cladogram of *Duplominona* Karling, showing the Galápagos species the most evolved group within the genus. (A) From Ax and Ax (1977); (B), (C) from Ax (1977).
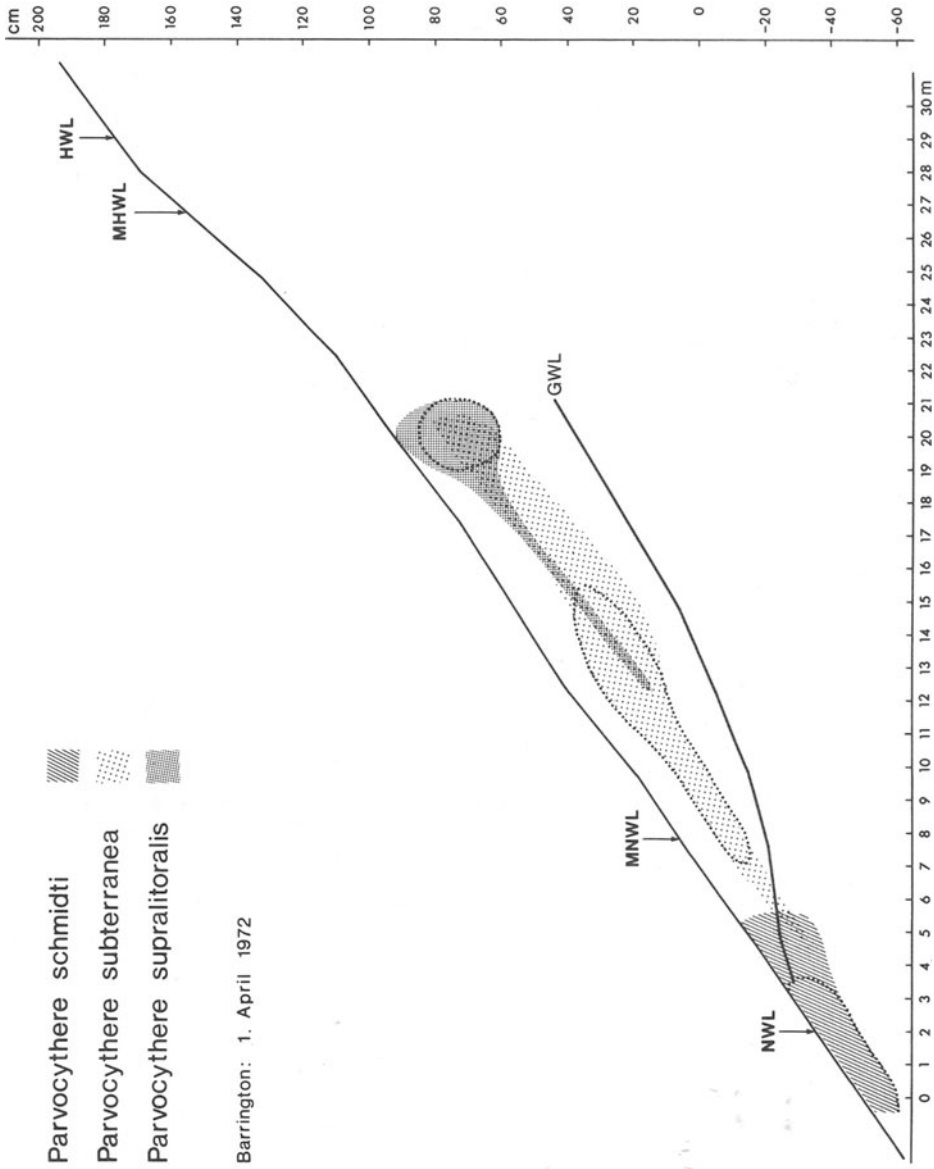
Figure 10. Distribution pattern of 3 species of the ostracod genus Parvocythere within the beach of Barrington (April 1, 1972). The dotted lines surround the area where 90% of the individual species were found. From Gottwald (1983). HWL: high water level. NWL: low water level. GWL: ground water level at low tide.
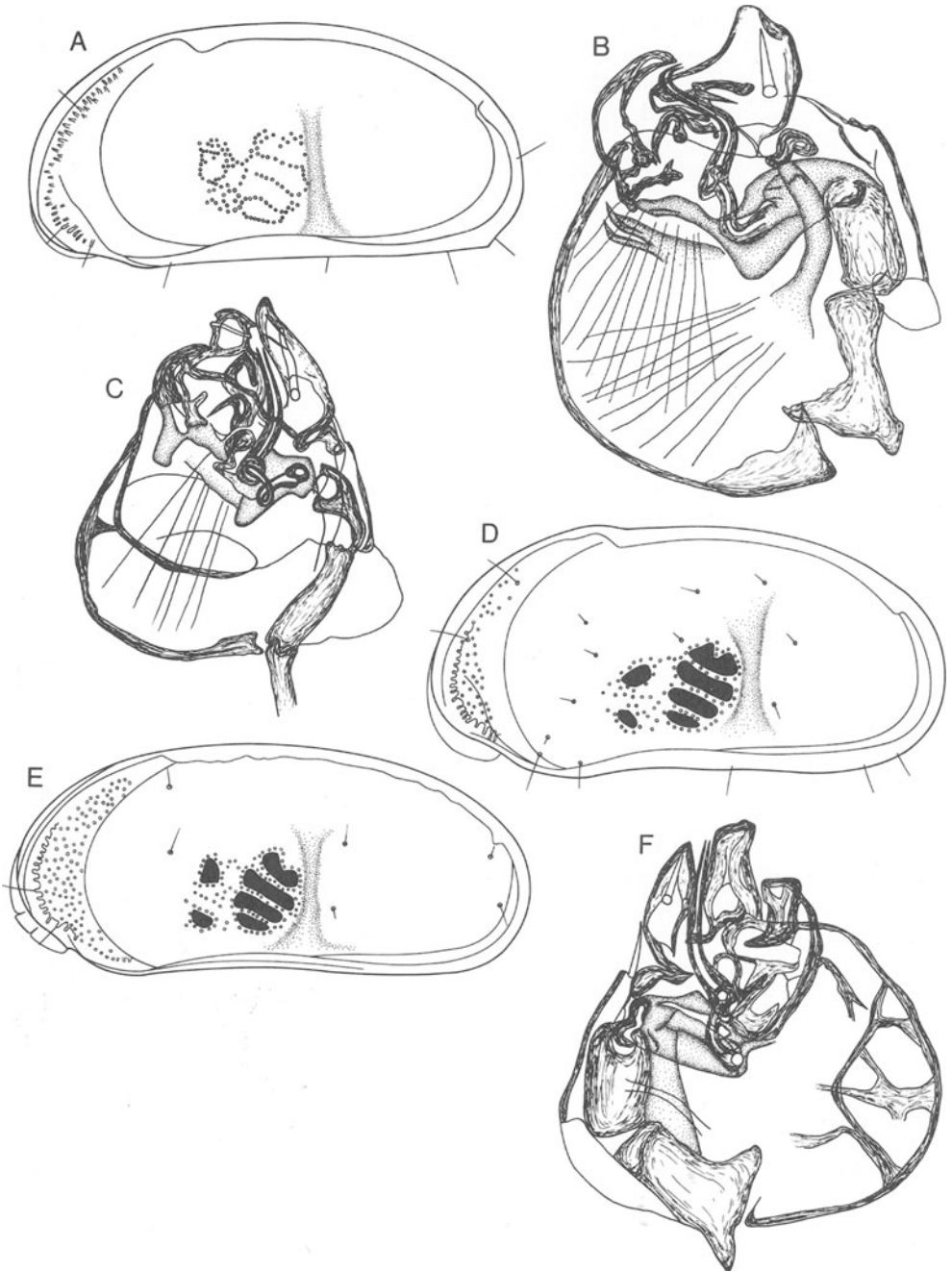
Figure 11. The three most closely related species of the ostracod genus *Parvocythere* in the Galápagos Islands. (A–B) *P. galapagoensis* (A) Left shell, female. (B) Copulatory organ. (C–D) *P. schmidti.* (C). Copulatory organ. (D) Left shell, female, (E–F) *P. subterranea* (E) Left shell, female. (F) Copulatory organ. From Gottwald (1983).

Not less than six species of the *Cobanocythere lanceolata* group are considered to have arisen within the archipelago, their species character being proven by the fact that five of them occur together in one locality without showing any overlap of morphological characters.

There is also much evidence that speciation of *Parvocythere galapagoensis* Gottwald, *P. schmidti* Gottwald, and *P. subterranea* Gottwald occurred within the archipelago, although a synapomorphic character for the three species could not be found. They were sampled on different islands (Fig. 11), but also occur together in two beaches occupying different areas of the beach slope (Fig. 10).

The examples of speciation presented above suggest that a period of about 3 million years (the geological age of the islands), is sufficient for recognizable evolutionary processes in meiofauna organisms. This suggests a relatively rapid rate of speciation on the islands compared to the high degree of meiofaunal species similarity between continents. For instance, the rate of speciation in the many amphiatlantic species and transallopatric meiofauna species pairs on both sides of the Atlantic (Sterrer, 1973; Ruppert, 1977; Westheide and Rieger, 1987; Westheide, 1977b; 1987; Ax and Armonies, 1987) would be comparable only in the case that a supposed "Thule land bridge" broke up not earlier than 2 million years ago— which indeed is believed by a few geologists. Species similarity between other continents, however, generally suggests low rates of speciation within continental beaches considering the long periods of separation from an old supercontinent.

More rapid speciation in Galápagos meiofauna may be due to the fact that the first colonists found empty beaches with nearly the entire spectrum of sand beach niches and resources favoring small-scale evolutionary processes. The crucial difference between potential sand beach colonists and colonists of the terrestrial realm might have been that the latter found only a very small number of suitable habitats allowing survival of only a few forms. Most of the psammobiontic meiofauna species however reaching the islands accidentally, certainly might have found their appropriate habitats. Thus, the beaches were soon filled with a species-rich community resulting in a considerably shorter initial phase of colonization that generally did not allow conspicuous adaptive radiation and speciation. Better "survival during rafting" and better "survival after landing" compared to the terrestrial fauna may be the reason for high species-richness of the Galápagos meiofauna on the one hand and their relatively little evolutionary divergence on the other.

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