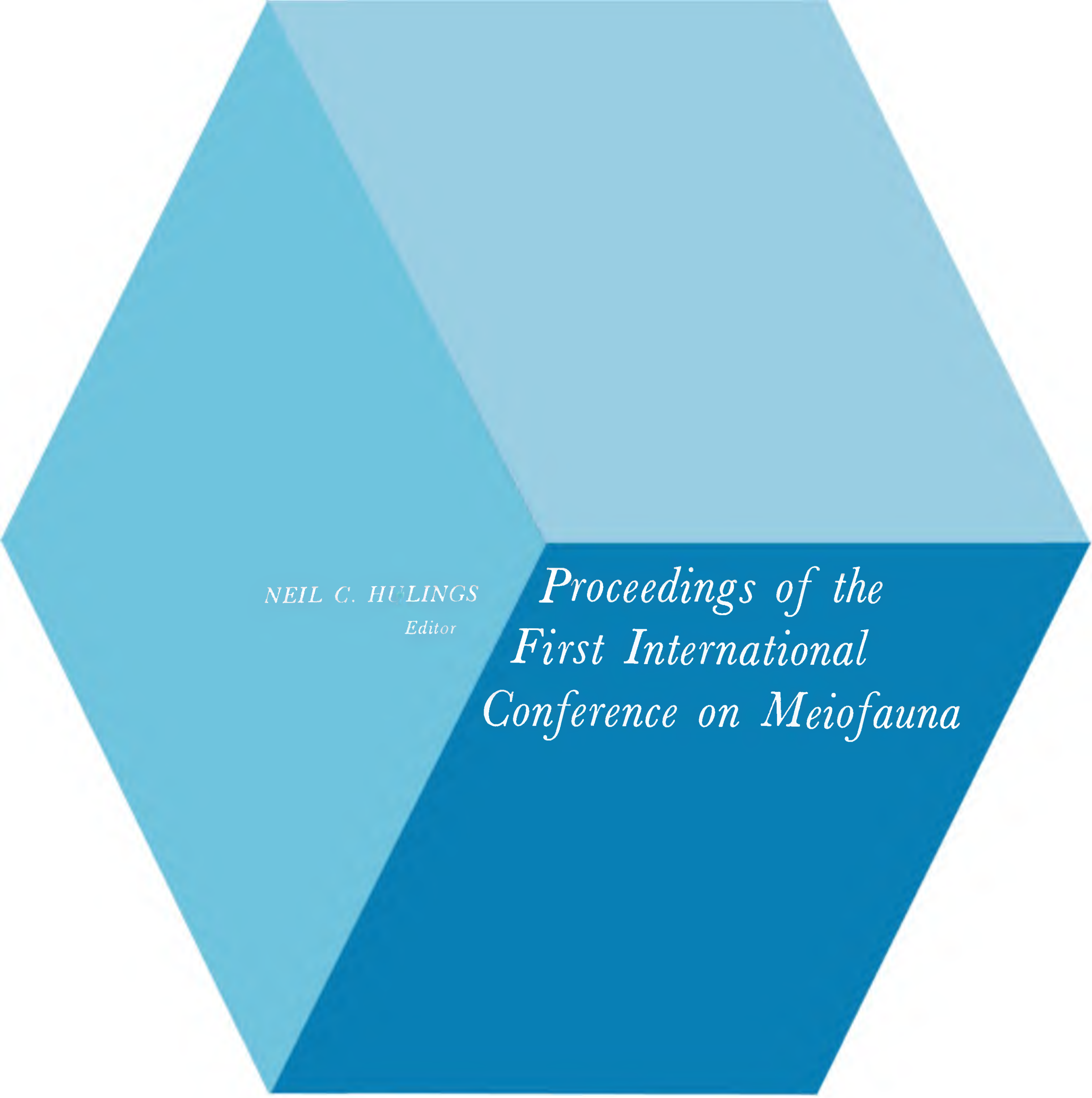

Proceedings of the First International Conference on Meiofauna

NEIL C. HULINGS
Editor

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY NUMBER 76

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SMITHSONIAN CONTRIBUTIONS TO
ZOOLOGY

NUMBER 76

Neil C. Hulings
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International Conference on Meiofauna

1-11 July 1969, Tunis, Tunisia

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Foreword

The First International Conference on Meiofauna was held in Tunis, Tunisia, 1-11 July, 1969. Twenty-eight invited participants from seven countries assembled to review the status of the systematics and ecology of meiofaunal taxa, the ecology of meiobenthic communities, and techniques of faunal and environmental analyses. Of the 30 papers presented at the conference, 27 are included in this volume.

The convening of the conference was stimulated by the increasing emphasis on and need for investigations of the systematics and ecology of meiofauna and for a means to provide an exchange of ideas between systematists and ecologists. Also it was felt that there was a need to standardize techniques of collecting and reporting data so that results from one area of investigation could be compared with those from another area. Toward this end, all participants contributed to "A Manual for the Study of Meiofauna" (Neil C. Hulings and John S. Gray, 1971, *Smithsonian Contributions to Zoology,* Number 78).

There remains much to be done in the sphere of meiofauna investigations. One of the most pressing problems is the need for more attention to the problem of sampling. Statistical evaluation of various techniques of sampling and statistical treatment of the sampling efforts are imperative. Not only must there be concern for individual species but also for the community as a whole. There must be continuous dialogue between systematists and ecologists to advance properly our knowledge of meiofaunal species and communities. Ultimately, the ecologist must consider all specimens to the species level. By the same token, the systematist must take into consideration taxa other than those of his particular interest. In this way he can provide taxa that are properly preserved for study by other systematists. It is through such consideration and cooperation that our knowledge of meiofauna will be increased greatly. These approaches assume an even greater significance when considering the effects of pollution on meiofauna.

Other pressing problems exist in the area of the physiology of meiofauna. In terms of collecting and properly preserving specimens for study, what are the effects of various preservatives and anesthetizing agents now available? In the past, only the traditional agents have been used. New agents need to be evaluated, for it may be that these give better results than the traditional ones. To what degree do taxa, from the polar regions to the tropics, react differently to pre-preservation storage and various extraction techniques? Preliminary evidence indicates the reaction is considerably different, and further evaluation of this aspect may result in greater extraction efficiency. This emphasizes the need for taking the local environmental conditions of the organism into consideration. Investigations in the area of culture of meiofaunal taxa must be accelerated to determine the degree of rsponse to various environmental parameters.

Such needs represent some of the more pressing problems in the study of meiofauna. These and other problems in the study of meiofuna are apparent in this volume and in the "Manual for the Study of Meiofauna." It is hoped that the papers presented in both publications will stimulate research along these and other lines.

I am indebted to many persons for assistance in organizing the conference and in editing the papers of this volume. John S. Gray and Robert P. Higgins were of invaluable assistance in organizing and convening the conference. The personnel of the Mediterranean Marine Sorting Center, Salammbo, Tunisia—especially Dr. Hédia Baccar, Mrs. Genèvieve Dargouth, and Mr. Mohammed Shili—freely provided assistance prior to and during the conference. The Tunisian government—especially the National Scientific and Technical Institute for Oceanography and Fisheries, the Department of Higher Education and Scientific Research, and the Ministry of Foreign Affairs—endorsed the conference and assisted in many ways. The American Embassy, Tunis, was most helpful on numerous occasions. Funding for the conference was made possible through the Office of International Activities of the Smithsonian Institution. The assistance of Dr. Ray Manning and his staff of the Department of Invertebrate Zoology, Smithsonian Institution, is gratefully acknowledged. And lastly, sincere appreciation is expressed to the authors of the papers in this volume for their patience and cooperation.

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SYSTEMATICS AND ECOLOGY OF MEIOFAUNA TAXA

Claus Clausen

Interstitial Cnidaria: Present Status of Their Systematics and Ecology

ABSTRACT

A synopsis is given of the interstitial Cnidaria (Hydrozoa: *Protohydra, Psammohydra, Siphonohydra, Armorhydra, Halammohydra, Otohydra*; Scyphozoa: *Stylocoronella*; Anthozoa: *Sphenotrochus*). Systematics, ecology, adaptive morphological characters, and geographic distribution are discussed.

The number of cnidarian species inhabiting interstitial environments is small, both in proportion to other Cnidaria and when compared with the number of interstitial species of many other invertebrate phyla. Only twelve cnidarians are known from this milieu, There are seven recognized genera, of which five belong to the class Hydrozoa and one to each of the classes Scyphozoa and Anthozoa. Despite this small number, the group shows many interesting features, some of which exhibit remarkable adaptations to the habitat.

Class HYDROZOA

Genus *Protohydra* Greeff

Protohydra leuckarti Greeff is a small (1.5 mm), solitary polyp that is shaped like *Hydra* and lacks tentacles. It was discovered by Greeff in 1868 in an oysterpark near Ostende, Belgium, where it occurred in muddy substrate rich in diatoms. The polyp may fasten itself with a basal disk, or it may move like a caterpillar larva. The sexes are separate. Gonads, however, are only rarely present; reproduction is mostly asexual, the polyp dividing transversely.

Protohydra leuckarti has a very wide distribution. In Europe it has been found in England, near Plymouth, in brackish water (Baker, 1913), at Tvärminne (Luther, 1923), along the coasts of Sweden and Norway (Westblad, 1929, 1954), in the North Sea at Amrum (Schulz, 1950a), in the British Channel at Roscoff (Teissier, 1950), in the Biskaia at Arcachon, in the Mediterranean at Canet and Banyuls (Nyholm, 1951); and in the Black Sea (Valkanov, 1947).

Outside of Europe *Protohydra leuckarti* has been reported from a lake in Kamtschatka (Abonyi, 1929), along the east coast of the United States (Ruebush, 1939), and in Puget Sound (Wieser, 1958). In addition, Remane claims to have found a specimen of *Protohydra leuckarti* or closely related species in samples from South-West Africa (Schulz, 1950a); Omer-Cooper (1957) reported a species of *Protohydra* from South Africa; and Dawydoff (1930) described *Protohydra caullery* from the coast of Indo-China.

Protohydra leuckarti is a shallow-water form occurring from just a few centimeters below the water surface (Westblad, 1929) down to at least 13 m (Schulz, 1950a). The salinity range is wide, from 4 ppt in the Baltic (Schulz, 1950a) to 36 ppt at Canet Plage (Delamare Deboutteville, 1960). This species has a preference for sheltered places, being absent in the zone of *Otoplana* (Schulz, 1950a); otherwise, it appears that the biotopes are quite varied. A frequent bottom type is mud, with a layer of diatoms and detritus; but sand—fine or coarse, pure or mixed with mud—as well as algal vegetation also are frequent biotopes. *Protohydra leuckarti* has been found in coastal subsoil water

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(as noted by Delamare Deboutteville, 1960), and it is the only cnidarian known from that particular habitat. As for food, Schulz (1950a) found nematodes, larvae of mosquitos, copepods, ostracods, and parts of gastrotrichs and oligochaetes. Thiel (1962, after Naumov) maintains the classification of *Protohydra* in a separate family, Protohydridae, within the order Hydrida, that is equivalent to the suborder Hydrina of Werner (1965b).

Genus *Psammohydra* Schulz

Psammohydra is the smallest known polyp, reaching a length of 250 to 400 μ. A little above the middle of the slender, cylindrical body are three to five (usually four) short tentacles. A swollen proboscis terminates in a distensible mouth. At the base of the polyp are small papillae by which the animal adheres to a sand grain. Gonads seem to be absent. Sexual reproduction by binary fission, as in *Protohydra,* has been observed. The locomotion is like that of *Protohydra*; the proboscis adheres to the substrate, and the hind end is loosened from the grain and fastened again near the proboscis. According to Schulz (1950b) *Psammohydra* belongs to the *Turbanella hyalina* coenose. As to nutrition, Schulz (1950b) observed that copepod nauplii were ingested.

Psammohydra nanna Schulz (Figure 1) was described by Schulz (1950b) from the Baltic, north of Kiel, where he found it in fine sand at a depth of 2 m. Currently, there are only two other reports of *Psammohydra nanna.* Swedmark (1956) found it in fine sand at Roscoff together with another interstitial cnidarian, *Halammohydra octopodides.* Another finding was made by Salvini Plawen (1966) in the Adriatic Sea near Rovigne where it was found at depths of 4 to 8 m, mostly in medium-fine to medium-coarse sand, together with six other cnidarians *Halammohydra octopodides, H. schulzei, Otohydra vagans, Armorhydra janowiczi, Siphonohydra adriatica,* and *Styolcoronella riedli.* Like *Protohydra leuckarti, Psammohydra nanna* must be characterized as being euryhaline.

Regarding the taxonomy, Schulz (1950b) left *Psammohydra nanna* incertae sedis, whereas Salvini Plawen (1966) thought it should be placed within the Athecata in the family Tubulariidae.

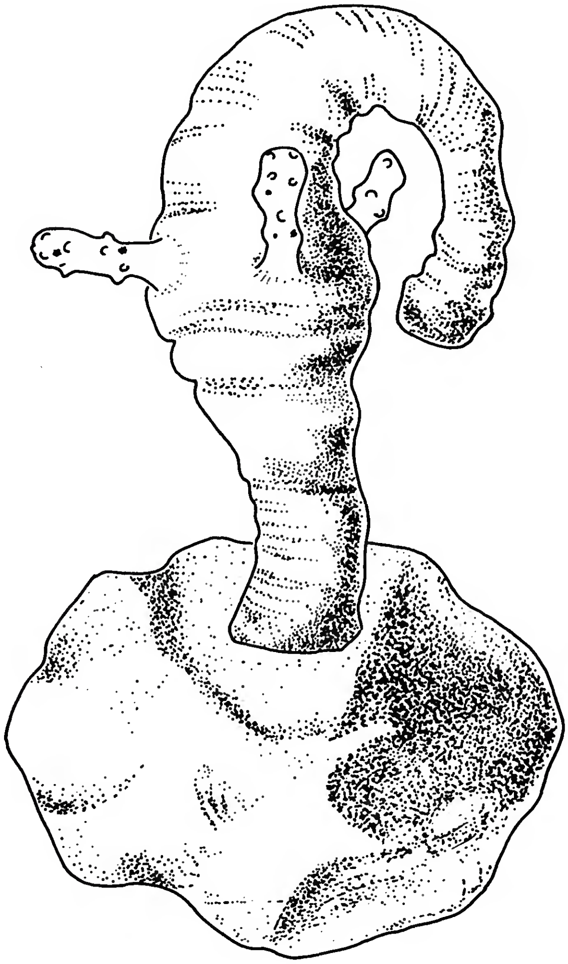

FIGURE 1.—*Psammohydra nanna* from life. (Redrawn from Schulz, 1950b.)

Genus *Siphonohydra* Salvini Plawen

In 1965 Salvini Plawen found a new interstitial polyp, *Siphonohydra adriatica* Salvini Plawen, in coarse sand at a depth of 6 m near Rovigne. He found two specimens whose lengths were 0.75 mm and 1.2 mm. The body is composed of a lengthened, saclike hydranth, emerging from a hydrocaulus, that comprises little more than a third of the total length. The hydranth bears two widely separated whorls of alternating tentacles, four tentacles in each whorl. Four processes, each covering a gonophore, are located at the base of the hydranth, in the axis of the oral tentacles.

The gonophores consist of reduced but elongate medusoids. Asexual reproduction appears predominant, and buds develop on the hydranth and later detach to form new individuals. The buds may possess secondary buds or tentacles before their detachment.

At the type-locality, *Siphonohydra adriatica* was associated with *Psammohydra nanna, Halammohydra schulzei, Armorhydra janowiczi,* and *Stylocoronella riedli.*

Salvini Plawen (1966) placed the new genus within the family Tubulariidae because of the similarities with the already existing genera of the family. Chief similarities include shape and arrangement of the tentacles, absence of rhizoids, and sexual reproduction by medusoids.

Genus *Armorhydra* Swedmark and Teissier

Armorhydra janowiczi Swedmark and Teissier resembles both a craspedote medusa and an ovoid polyp. There is a single whorl of tentacles inserted near the oral end and the tentacles are differentiated into catching and adhesive tentacles. The latter have distal thickenings provided with small mobile papillae (Lacassagne, 1968c). Whereas nematocysts are plentiful in the defensive tentacles, they are wanting in the adhesive tentacles. This high degree of specialization of the tentacles is a noticeable adaptation to the interstitial mode of life.

The sexes are separate and the gonads are arranged in longitudinal fields at the surface of the manubrium. The manubrium is connected with the umbrella through a system of longitudinal, mesogleal septa, radiating across the subumbrellar cavity. There is no form of adhesive structure at the aboral end.

The life cycle of *Armorhydra* is unknown. In 1966, however, F. Monniot discovered, in Morlaix Bay near Roscoff, a new interstitial polyp, only 1 mm long, that had a cnidome quite similar to that of *Armorhydra janowiczi* (Lacassagne, 1968c). The polyp reproduces by podocysts and also by shedding a tentacle which may grow into a new polyp (Lacassagne, 1968c). Lacassagne also noted a close resemblance to the limnomedusa *Ostroumovia horii* (Uchida and Uchida) with respect to the asexual reproduction. Since medusa buds have not been observed in the new polyp, it would be only a hypothesis to regard this polyp as the asexual form of *Armorhydra*; however, if such could be shown, the classification of *Armorhydra* within the Limnohydrina would seem justified.

Apart from the findings at Roscoff, there have been two other findings of *Armorhydra janowiczi* in the Mediterranean, one at Rovigne by Salvini Plawen (1966) and the other at Ischia by the author (unpublished). *Armorhydra janowiczi* is one of the largest of the interstitial cnidarians, reaching a length of 2 mm. At all three localities it was found in coarse sand.

Genus *Halammohydra* Remane

The curious hydrozoan *Halammohydra* (Figure 2) was discovered by Remane in Kiel Bay in 1924 (Remane, 1927) and was the first cnidarian known to inhabit interstitial environments. It reaches a size of 0.3 to 1.3 mm and has the characters of both polyp and medusa.

The body, which is entirely ciliated (or flagellated), consists of two main parts: a lengthened gastric tube and a small, conical-shaped aboral cone. The two parts are joined by a neck-like part.

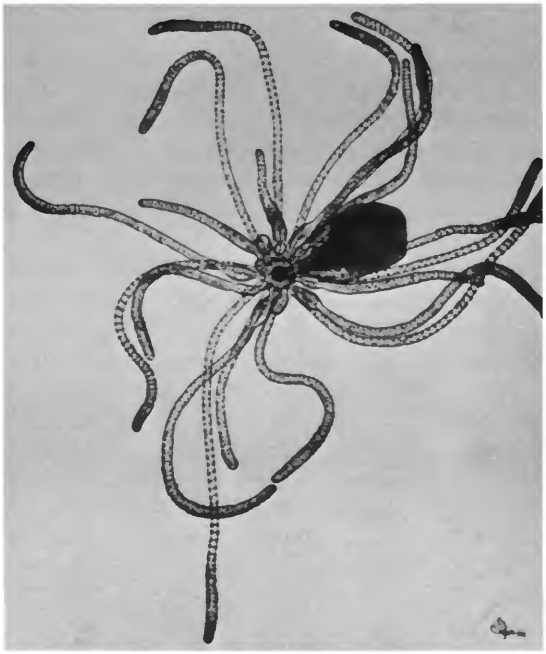

FIGURE 2.—*Halammohydra schulzei.* (From Clausen, 1967.)

Two whorls of long, slender tentacles arise from the aboral cone. Alternating with the oral tentacles are statocysts of the lithostyle type, which are innervated from a nerve ring in the aboral cone. An urn-shaped depression in the point of the aboral cone serves as an adhesvie organ. The sexes are separate, and the gonads lie between the epidermis and the gastrodermis of the gastric tube.

Swedmark and Teissier (1950, 1957a,b) have studied the development of two of the species. The eggs are shed through the mouth before they are fertilized. The fertilized egg develops directly via an actinula-like stage into a young animal basically like the adult but having only four statocysts and four tentacles in each whorl. This is called the halhydrula stage.

Despite its simple structure, *Halammohydra* shows a great variation in character, both quantitatively and qualitatively, and six species have been described: *Halammohydra octopodides* Remane, *H. schulzei* Remane, *H. vermiformis* Swedmark and Teissier, *H. adherens* Swedmark and Teissier, *H. intermedia* Clausen, and *H. coronata* Clausen. Populations of the same species frequently differ, especially with respect to the cnidome; the rhopaloids (penetrants) are present in either of two size categories.

Locomotion is by flagella. Like a medusa, *Halammohydra* swims in the direction of the aboral pole, but the body is kept horizontal. *Halammohydra octopodides* and *H. vermiformis* are very active animals; *H. adherens* is characteristically semisessile. The food seems to consist of nematodes and small crustaceans.

While the group as a whole inhabits different kinds of sediment—from fine sand to coarse shell gravel—a given form, as Swedmark (1957) first noticed, usually is found in the same type of sediment over wide geographic areas. This isolation of the populations obviously promotes the pronounced raciation. *Halammohydra* prefers well-aerated sediments and is more frequent in euhaline than in oligohaline water—in the Baltic, only *Halammohydra octopodides* and *H. schulzei* are observed, and in small numbers (Remane, 1927; Schulz, 1952). It has been found from the tidal zone (*H. vermiformis*) down to 60 m (*H. adherens*).

In Europe the distribution, in addition to the western Baltic, includes Great Britan and from the Barents Sea (Mamkaev, 1962) to the Adriatic Sea (Salvini Plawen, 1966). Outside Europe, *Halammohydra* has been reported from Indian waters (Rao and Ganapati, 1966), and it also occurs on the east coast of North America (W. Sterrer, personal communication).

Genus *Otohydra* Swedmark and Teissier

Otohydra vagans Swedmark and Teissier was discovered in 1957 at Roscoff, where it was found in coarse shell gravel together with *Halammohydra adherens* and *Armorhydra janowiczi.* Salvini Plawen (1966) has reported *Otohydra vagans* from Rovigne.

The structure of *Otohydra* is polypoid. One whorl of 12 to 24 tentacles surrounds a short hypostome which terminates in a very distensible mouth. Between the tentacle bases are up to twelve statocysts of the lithostyle type. The body reaches a length of 350 μ; the tentacles are a little longer. By means of flagellae, which cover the entire surface, the animal swims actively through the interstices with the aboral pole in front.

Otohydra is hermaphroditic. Fertilization is internal, and the development of the larva, which is direct, occurs in an incubatory chamber in the gastral region between the epidermis and gastrodermis. The young have eight tentacles when set free. Two or three embryos of different developmental stages may be present at the same time in the chamber.

When considering the taxonomic position of *Otohydra,* Swedmark and Teissier (1958) pointed to its similarities with *Halammohydra.* Egg cleavage and gastrulation are of the same type in both genera and there is no planula stage. Both genera possess flagella and have statocysts of the same type; and the young animal of either genus, apart from the statocysts, has the organization of an actinula. Yet, there are great differences between the two genera; for example, *Otohydra* lacks an adhesive organ, has only one whorl of tentacle, and is hermaphroditic and viviparous. Despite the differences, Swedmark and Teissier (1958, 1966) saw a clear relationship and denied the interpretation of either genus as a medusa or a polyp. As neither genus could be placed satisfactorily in any of the existing orders—Hydroida, Trachylida, and Siphonophora—they felt justified in creating a new order, which they called Actinulida, to include the families Halammohydridae and Otohydridae. In support of this action, they pointed to the fact that the once-advanced actinula theory (Böhm, 1878; Brooks, 1886) had been defended by Hyman (1940), Rees (1957), and others as the only one that gives a satisfactory explanation of the phylogeny of the Hydrozoa.

While Kramp (1961) and others adopted the order Actinulida, other writers had objections to it. Werner (1965a) could not accept the Actinulida (nor the earlier interpretation of *Halammohydra*) as a narcomedusa and claimed that *Halammohydra* should be placed within the Hydroida. One of Werner's arguments was that he could prove that flagellae are common among adult hydromedusae. Further, in the anthomedusa *Margelopsis haeckeli* Hartlaub and in the limnomedusa *Gonionemus vertens* A. Agassiz a reduction of the umbrella may occur under certain circumstances, giving these species an appearance rather similar to that of *Halammohydra*. A third argument was that the combination of nematocysts in *Halammohydra* differs from that in the Trachylida, while it is found in the Hydroida and Siphonophora.

Recent discoveries regarding the cnidome of *Halammohydra* and *Otohydra* have provided additional information. In an undescribed species of *Otohydra*, Lacassagne (1968a) described a new type of nematocyst, the spirotele euryteloid, which shares the characteristics of both desmonemes and euryteles. The new type can be referred to the group astomocnida. Lacassagne (1968a) also observed euryteloids, the aspiroteles, in a population of *Halammohydra*. The findings are circumstantial evidence of the relationship between the two genera.

Lacassagne (1968b) discovered in *Halammohydra* still another type of nematocyst, the atrichous anisorhizas. The number of categories of nematocysts in *Halammohydra* and *Otohydra*, viewed together, is now up to seven, of which three are known only from these two genera. It is clear that

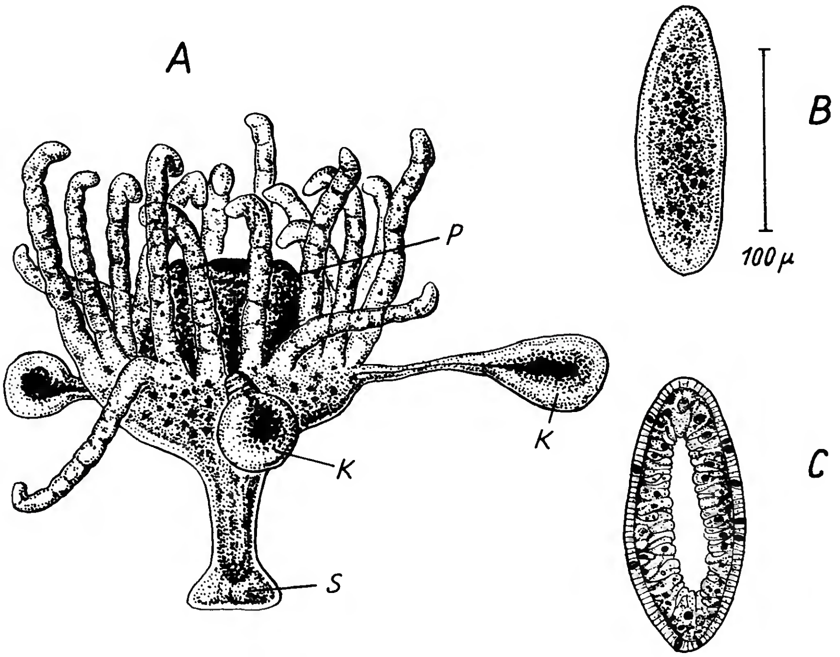

FIGURE 3.—*Stylocoronella riedli: a,* segmentation of buds; *b,* free planuloid; *c,* longitudinal section through the planuloid; *k,* bud; *p,* proboscis; *s,* pedal disk. (From Salvini Plawen, 1966.)

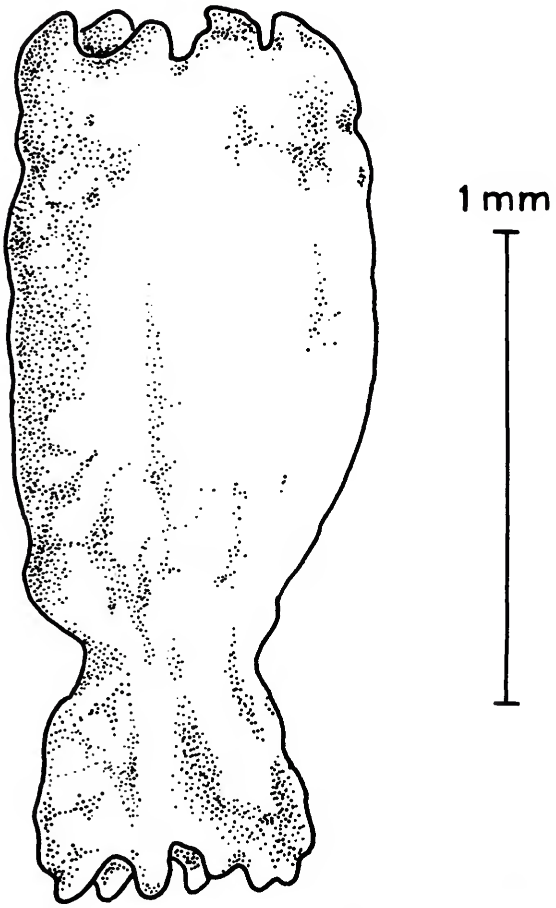

FIGURE 4.—*Sphenotrochus* sp. (Redrawn from Swedmark, 1964.)

the concept of Actinulida has a more substantial foundation because of these findings.

Class SCYPHOZOA

Genus *Stylocoronella* Salvini Plawen

Monniot (1962) reported the occurrence of an interstitial scyphozoan, about 1 mm long, in "*Amphioxus* sand" from Banyuls. The first description of an interstitial scyphozoan, however, was by Salvini Plawen in 1966 when he described *Stylocoronella riedli* from Rovigne. Salvini Plawen found several specimens that were very similar to the form from Banyuls. He stated that the maximum size is 400 μ, of which the stalk makes up 150 μ. There are up to 24 tentacles surrounding a prominent proboscis. Each tentacle has an ocellus at the subumbrellar base (Figure 3). *Stylocoronella riedli* is semisessile. It may creep with the aid of the tentacles, the ends of which are haptic because of a local concentration of sticky isorhizes.

Only asexual reproduction is known. Interradial stolonial buds grow out just basad to the tentacles. The buds are shed as unciliated planuloids which fasten after some days and grow into new polyps. Strobilation was not observed.

Because of the lack of knowledge of sexual reproduction, the grouping of the new genus within the Scyphozoa is difficult; the ocelli and the planuloids are characters shared with the Stauromedusae, while the number of tentacles is more in agreement with the conditions in the Semaestomae.

Class ANTHOZOA

Genus *Sphenotrochus* Milne-Edwards and Haime

The first interstitial anthozoan was recorded from the Mediterranean, near Marseilles, where the madreporarian *Sphenotrochus* sp. (Figure 4) was found at a depth of 15 to 20 m (Rossi, 1961). It belongs to the family Caryophylliidae (subfamily Turbinolinae), and, according to Rossi (1961), is probably conspecific with *Sphenotrochus wrighti* described by Gosse (1859) from the Irish Sea. *Sphenotrochus* sp. later was found also in the shell dunes at Roscoff (Swedmark, 1964).

The organization of this small madreporarian, which attains a length of only 2 mm, is bipolar, with both the upper and lower extremity, in some cases, having a mouth and a tentacle crown. The lower extremity generates a new polyp opposite to the upper extremity. Rossi (1961) stressed the peculiar adaptation to life on sandy bottom as shown by the bipolarity and asexual mode of reproduction.

Summary

Even though the interstitial cnidarians are few, their discovery has raised several ecological and phylogenetic questions. Wide geographic areas still are uninvestigated, however. Discoveries of new forms and a better knowledge of the distribution of known forms may provide answers to some of these questions.

Literature Cited

Abonyi, A.

1929. Über *Protohydra leuckarti* Greeff und ihre geographische Verbreitung. *Proceedings of the 10th International Congress of Zoology, Budapest,* 8:1452–1460.

Baker, R. J.

1913. *Protohydra leuckarti,* Tidal Pools River Tavy. *Transactions of the Plymouth and District Field Club,* 1.

Böhm, R.

1878. Helgoländer Leptomedusen. *Jenaische Zeitschrift für Naturwissenschaft,* 12:68–203.

Brooks, W. K.

1886. The Life-History of the Hydromedusae: A Discussion of the Origin of the Medusae and the Significance of Metagenesis. *Memoirs of the Boston Society of Natural History,* 3(14):359–430.

Clausen, C.

1967. Morphological Studies of *Halammohydra* Remane (Hydrozoa). *Sarsia,* 29:349–370.

Dawydoff, C. N.

1930. *Protohydra caulleryi* n. sp. des eaux indochinoises. *Archives de Zoologie Expérimentale et Générale,* Notes et Revue, 70:55–57.

Delamare Deboutteville, C.

1960. *Biologie des eaux souterraines littorales et continentales.* 740 pages. Paris: Hermann.

Gosse, P. H.

1859. On *Sphenotrochus wrightii,* a New Irish Madrepore. *Natural History Review and Quarterly Journal of Science,* 6:161–163.

Hyman, L. H.

1940. *The Invertebrates: Protozoa through Ctenophora.* Volume 1, 726 pages. New York: McGraw-Hill.

Kramp, P. L.

1961. Synopsis of the Medusae of the World. *Journal of the Marine Biological Association of the United Kingdom,* 40:1–469.

Lacassagne, M.

1968a. Deux nouveaux types de nématocystes astomocnides chez les Actinulides (Hydrozoaires): les eurytéloides spirotèles et aspirotèles. *Comptes Rendus de l'Académie des Sciences,* 266:892–894.

1968b. Les anisorhizes atriches, nouveau type de nématocystes stomocnides présents chez deux formes *d'Halammohydra* (Hydrozoaires, Actinulides). *Comptes Rendus de l'Académie des Sciences,* 266:2090–2092.

1968c. Anatomie et histologie de l'Hydroméduse benthique *Armorhydra janowiczi* Swedmark et Teissier, 1958. *Cahiers de Biologie Marine,* 9:187–200.

Luther, A.

1923. Ueber das Vorkommen von *Protohydra leuckarti* Greeff bei Tvärminne nebst komplettierenden Bemerkungen über den Bau dieses Polypen. *Acta Societatis pro Fauna et Flora Fennica,* 52:1–23.

Mamkaev, J. V.

1962. Records of Interstitial Fauna from the Barents Sea. *Vestnik Leningradskogo Universiteta,* 9(2):193–224.

Monniot, F.

1962. Recherches sur les graviers à Amphioxus de la région de Banyuls-sur-Mer. *Vie et Milieu,* 13:231–322.

Nyholm, K. G.

1951. A Contribution to the Study of the Sexual Phase of *Protohydra leuckarti* Greeff. *Arkiv för Zoologi,* 2:529–530.

Omer-Cooper, J.

1957. *Protohydra* and Kinorhyncha in Africa. *Nature,* 179(4557):486.

Rao, G. C., and P. N. Ganapati

1966. A Report on the Occurrence of an Aberrant Cnidarian, *Halammohydra octopodides* Remane, in Indian Waters. *Current Science,* 35:129–130.

Rees, W. J.

1957. Evolutionary Trends in the Classification of Capitate Hydroids and Medusae. *Bulletin of the British Museum (Natural History), Zoology,* 4(9):455–534.

Remane, A.

1927. *Halammohydra,* ein eigenartiges Hydrozoon der Nord- und Ostsee. *Zeitschrift für Morphologie und Ökologie der Tiere,* 7:643–678.

Rossi, L.

1961. Morfologia e riproduzione vegetativa di un Madreporario nuovo per il Mediterraneo. *Bolletino di Zoologia,* 28:261–272.

Ruebush, T. K.

1939. The Occurrence of the Two Rare Genera, *Protohydra* and *Protodrilus,* on the East Coast of North America. *Science,* 90(2348):617–618.

Salvini Plawen, L.

1966. Zur Kenntnis der Cnidaria des nordadriatischen Mesopsammon. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:165–186.

Schulz, E.

1950a. Zur Oekologie von *Protohydra leuckarti* Greeff (studien an Hydrozoa, I). *Kieler Meeresforschungen,* 8(1):53–57.

1950b. *Psammohydra nanna,* ein neues solitäres Hydrozoon in der westlichen Beltsee (studien an Hydrozoa, II). *Kieler Meeresforschungen,* 8(2):122–137.

1952. *Halammohydra schulzei* Remane in der westlichen Ostsee. *Faunistische Mitteilungen aus Norddeutschland,* 2:6–7.

Swedmark, B.

1956. Nouveau Gastrotriches Macrodasyoides de la région de Roscoff. *Archives de Zoologie Expérimentale et Générale*, Notes et Revue, 94:43–57.

1957. Variation morphologique des différentes populations régionales *d'Halammohydra*. *Année Biologique*, 44(3/4):183–189.

1964. The Interstitial Fauna of Marine Sand. *Biological Reviews*, 39:1–42.

Swedmark, B., and G. Teissier

1950. Développement d'un Hydrozoaire aberrant *Halammohydra schulzei* Remane. *Comptes Rendus de l'Académie des Sciences*, 231:173–174.

1957a. Organisation et développement des *Halammohydra* (Hydrozoaires). *Comptes Rendus de l'Académie des Sciences*, 244:501–504.

1957b. *Halammohydra vermiformis* n. sp. et la famille des Halammohydridae Remane. *Bulletin de la Société Zoologique de France*, 82:38–49.

1958. *Otohydra vagans* n. g., n. sp., Hydrozoaire des sables, apparanté aus Halammohydridées. *Comptes Rendus de l'Académie des Sciences*, 247:238–240.

1966. The Actinulida and Their Evolutionary Significance. *Symposium of the Zoological Society of London*, 16:119–133.

Teissier, G.

1950. Notes sur quelques Hydrozaires de Roscoff. *Archives de Zoologie Expérimentale et Générale*, Notes et Revue, 87:1–10.

Thiel, M. E.

1962. Bestimmungstabellen der Polypen und Medusen der russischen Gewässer. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 60:285–324.

Valkanov, A.

1947. *Protohydra leuckarti* Greeff vom Schwarzen Meer. *Arbeiten aus der Biologischen Meeresstation in Varna*, 13:31–35.

Werner, B.

1965a. *Halammohydra* Remane, Medusennatur und Stellung im System. *Zoologischer Anzeiger*, Supplementband 28:163–168.

1965b. Die Nesselkapseln der Cnidaria, mit besonderer Berücksichtigung der Hydroida. 1. Klassifikation und Bedeutung für die Systematik und Evolution. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 12(1–2):1–39.

Westblad, E.

1929. *Protohydra leuckarti* Greeff, an der schwedischen Küste entdeckt. *Archiv för Zoologie*, 21(4):1–4.

1954. Some Hydroidea and Turbellaria from Western Norway with Descriptions of Three New Species of Turbellaria. *Universitetet i Bergen, Arbok, Naturvitenskapelig rekke*, 10:1–22.

Wieser, W.

1958. Occurrence of *Protohydra leuckarti* in Puget Sound. *Pacific Science*, 12:106–108.

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Gnathostomulida: Problems and Procedures

ABSTRACT

Procedures of sampling and extracting Gnathostomulida from sediments are evaluated. Distribution, ecology, and taxonomy are discussed. Statistical-metrical data are emphasized.

The Gnathostomulida, today a well-established group of marine meiofauna, have rapidly expanded in terms of knowledge of forms and distribution since their original description (Ax, 1956). More than 80 species and 18 genera are known to the present author, and a first approach to their systematics and evolution soon will be published (Sterrer, in press,b).

The question as to why such an abundant and cosmopolitan constituent of marine meiofauna was discovered so late is only one in a series of problems that arises when dealing with this group. Others are connected with sampling and extracting, ecology and distribution, and biology and systematics. The purpose of this paper is to give a brief synopsis of current problems as they emerge during the different procedures of investigation. More detailed technical recommendations are given in Hulings and Gray (1971), whereas a complete bibliography of the class will be found in Sterrer (in press,b).

Sampling and Extracting

Sampling and extracting procedures have to take into account the ecophysiological particularities of the group and can, in fact, take advantage of them.

Sampling can be effected with almost any device that penetrates deeply enough to get to the "black layer." A spade usually is sufficient in the intertidal, and any dredge provided with a hovel-knife to secure depth can be used in the subtidal. Small sand patches ("*Austrognathia* sand"), however, can be sampled only with skin diving methods (a smaller triangular net is pushed through the sand). For quantitative sampling, any corer can be used. The slow locomotion of gnathostomulids makes a secondary displacement in the corer during or after sampling quite improbable.

Qualitative samples, at least 1 liter in volume (but usually 10 liters), are kept in the laboratory in covered buckets for at least five days before first extraction takes place. Deterioration of climate which occurs in the sample gradually forces the vagile fauna towards the surface layers, from which they can be extracted. Gnathostomulids, however, appear very late at the surface, the density peak usually being reached in the second week. At that time the sample shows black spots at the surface due to growth of iron bacteria, and it emits a heavy H_2S smell. Hence, one more reason for the late discovery of the group: such samples were usually discarded long before gnathostomulids emerged.

For the extraction of gnathostomulids, two effective methods have been found: the seawater-ice method (Uhlig, 1964, 1968) and the magnesium chloride method (Sterrer, 1968). The author has had no personal experience with Uhlig's method, but he has found that the $MgCl_2$ method is very simple and produces high specimen numbers. Portions of surface sand from the deteriorated sample ("primary sample," about 250 ml) are placed in an Erlenmeyer flask (2 liters), and isotonic $MgCl_2$ solution is added. After mixing gently, the flask is left for 10 minutes. Then it is vigorously shaken and, when the sand has settled, the suspension is

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filtered through a 62-μ nylon monofilament sieve mounted on a plexi ring. This procedure is repeated once with $MgCl_2$ and once with seawater. After a short rinse with seawater (to get rid of the $MgCl_2$), filter and deposit are placed in a Petri dish with a little seawater. To avoid evaporation, the dish should be covered and kept in a cool place. Animals tend to move through the meshes of the filter to the bottom of the dish, where they can be collected free from sediment. This process starts immediately after extraction and may go on for several days. These "secondary samples" can be checked periodically, during which time the filter is placed in an alternate dish. Obviously based on a combination of taxes (negative phototaxis and positive geotaxis and thigmotaxis), this method works equally well for other groups of the mesopsammon (especially Gastrotricha and Turbellaria). The spaces between the meshes as well as between the filter and the bottom of the dish apparently represent equivalents of the natural interstitial habitat. This method is especially useful where large quantities of detritus make it impossible to mechanically separate larger numbers of animals.

For quantitative purposes, the same filter can be used upside down, and the deposit is washed into a dish where the animals can be sorted and counted. Otherwise, quantitative samples of usually 100 ml are treated the same way as qualitative ones, but without deterioration.

The efficiency of these extracting methods, although considered high, has not been tested as yet for Gnathostomulida, since the emphasis during the initial period of investigation was simply to obtain as much material for systematic studies as possible. It is obvious that the taxon's slow locomotory ability and its retarded response to environmental pressure make most quantitative methods rather questionable.

Ecology

The main reason for the late discovery of Gnathostomulida probably is that they have not been looked for in the right biotope. Classical research on interstitial fauna tended to concentrate on clean, well-aerated sand, and that is exactly where gnathostomulids do not occur. The typical biotope, instead, is sand with a large amount of organic detritus. (This characterization is still as vague as it sounds, since at present about 50 percent of the author's samples taken specifically for gnathostomulids do not yield a single specimen.) This type of sediment invariably occurs in sheltered positions such as (intertidally) on sand flats in sounds, or (subtidally) on small sand patches surrounded by rocks, larger plants, or coral. Such sand flats are determined by a moderate but steady rhythm of water movement and, therefore, have a rather narrow granulometrical spectrum, often with a medium grain size of 150 μ (which was thought uninhabitable for metazoa). Such a spectrum is different in the small subtidal basins. Sediment there is often extremely heterogeneous, typically composed of large shell fragments together with medium-size sand and flocculent detritus. This seems to indicate that, hydrodynamically, small subtidal basins act as more or less stagnant niches which, under a water body of varying movement and speed, collect any suspended sediment that comes under their influence. As far as the gnathostomulids are concerned, these heterogenous sands are typically inhabited by representatives of Austrognathiidae. This type of sediment should not be confused with what is known as "*Amphioxus* sand." The latter, composed of a coarse sand fraction with a high content of "mud," probably represents the only true intermediate biotope between sand and mud. "*Austrognathia* sand," however, seems to have only a very negligible fraction of silt and clay or none at all.

Another reason why gnathostomulids were so long unknown is that they prefer deeper and mostly H_2S-rich sand layers. It had been taken for granted that, except in high-energy beaches, only the uppermost sand layer was inhabited by an interstitial fauna. Recent investigations (Riedl, 1969) showed that the maximum density of the gnathostomulid population is at the discontinuity layer, i.e., often considerably below the sand surface. Recently, even living embryos, still in the egg capsule, have been found in these deep layers (Riedl and Sterrer, unpublished). Whether this means that gnathostomulids have anaerobic metabolism or that their distribution is determined by that of another organism (bacteria as food) is yet undecided.

A further interesting feature about the occurrence of the group is that a "typical" biotope almost invariably yields several species. Up to 13 species can be extracted from one sample of about 10 liters of sand. This points to a very high degree of specialization in a biotope whose characteristics we still ignore. This particular organism-biotope interrelationship should be studied from two sides: detailed analysis of the structural, chemical, and biological (including bacterial growth) properties of several "typical" substrata, and preference experiments.

Whereas the above-mentioned ecological requirements are very much the same for most gnathostomulids, the genus *Gnathostomula* Ax differs in several respects. First of all, it is rather eurytopic: species of this genus can be found on "typical" substrata as well as on pure sand, on seagrass roots, or even on mud. This unselective behavior probably also accounts for the fact that *Gnathostomula* species—contrary to the usual occurrence of several species per sample—are, in many samples, the only representatives of the class. True mass occurrence, furthermore, has been noted only in *Gnathostomula* so far, with densities so high as to outnumber even the nematodes in the sample. As to the vertical distribution in the substratum, *Gnathostomula* seems to prefer the surface layers. This agrees very well with the observation that, in a deteriorating sample, *Gnathostomula* is among the first gnathostomulids to migrate to the surface (Sterrer, 1965; Riedl, 1969). Finally, the genus *Gnathostomula* is known from all geographic regions where gnathostomulids have been found, again probably due to its eurytopic occurrence. This leads to questions of distribution and zoogeography.

Distribution

World-wide distribution of gnathostomulids was to be expected after the first descriptions had been published, and such distribution has since been well documented. The best known faunas so far are those of the North Sea (Ax, 1965; Sterrer, 1966a,b, 1968, and in press,a), the Adriatic (Sterrer, 1965), and the east coast of the United States (Reidl, 1969, 1970a,b, and in press; Sterrer, 1970, and in press,c). The author has extensive collections from the Mediterranean, Florida, and Panama. On the other hand, in the Pacific and adjacent areas the gnathostomulids are poorly known, with only a few scattered finds in the Red Sea (Riedl, 1966b), the Maldives (Gerlach, 1958), the Sea of Japan (Mamkaev, in Ax, 1965), and California (T. G. Karling, personal communication).

On the basis of the present material, an interesting zoogeographical aspect seems to emerge. As in many other taxa of the interstitial fauna (see Schöpfer-Sterrer, 1969, for Gastrotricha), the differences, for example, between the European and the American Atlantic faunas seem to be on the species level, i.e., the same genera are present on both sides of the Atlantic.

In certain species, differences may be so minute that they can be detected only by applying the statistical metric method (see under Taxonomy, below). This leads to the question of dispersal of the interstitial fauna. Since it is a common fact that most members of the interstitial fauna have no planktonic larvae, the paradox of the high similarity in geographically distant faunas becomes more and more obvious. A striking example is the gnathostomulid genus *Gnathostomaria* Ax. The first (and so far the only) described species, *G. lutheri* Ax, was found in a coastal pond ("étang") on the south coast of France (Ax, 1956). The biotope is wet sand above high water level. During the author's investigations of the North Carolina beaches, a second *Gnathostomaria* species was found in an almost identical biotope: wet sand above high water mark at a sound near Wilmington. There is no doubt about a close relation of these two species within the genus *Gnathostomaria*. A very similar case seems to be that of the Mystacocarida. The latter, however, occur on exposed beaches and have larval stages, which may present more opportunity for passive dispersal than is the case in Gnathostomulida. An investigation of such dispersal would obviously also have a bearing on the question of the relative age of the biotopes (is sand, in particular anaerobic sand, the most ancient biotope?) as well as of the origin of oceans and continents (e.g., continental drift).

It is hoped that with increasing knowledge of the distribution of the interstitial fauna it will be possible, in time, to reconstruct the mechanism of their worldwide dispersal. The possibility exists of tracing the gradual spreading of a systematic group during evolution by carefully comparing the morphological differences between species with the actual geographic distances of their distribution (see Riedl, 1966a, "Lebensorttyp").

Biology

Very few data on the biology of the Gnathostomulida are available so far (Sterrer, in press, a; Riedl, 1969). There are two reasons for this. First, the initial period of gnathostomulid research mainly was devoted to morphological studies, and biological observations were rather fragmentary. Second, it still is a difficult problem to keep animals alive in the laboratory.

Whereas some species of *Austrognatharia* Sterrer are able to form a mucous cyst in which they may survive for several days, most other gnathostomulids begin to disintegrate within hours after they have been extracted from the sediment (Sterrer, in press,a). It is not clear yet whether this is due to the extraction method (mostly with $MgCl_2$), to the lack of sediment, or to the presence of oxygen or some other unknown component of the artificial environment.

Taxonomy

Taxonomy often has to rely on minute characters which, in some cases, can be detected only by careful measurements of many members of a population. With this statement of a "splitter," for reasons of taxonomical accuracy—as well as zoogeographical information (see "Distribution")—a concept that permits one to find differences rather than similarities in a new locality is preferable to "finding the same old European species in the South Pacific." The same species may occur in the new locality but this would have to be proved (see Hulings and Gray, 1971).

Differences have to be expressed in metrical data, a method applied regularly to the macrofauna and "hard" meiofauna (Arthropoda, Nematoda) but used very little in the taxonomy of the "soft" meiofauna. As long as the criteria (such as degree of contraction and squeezing, or points of reference) remain the same, however, such measurements prove extremely valuable even in soft organisms (Sterrer, 1968). Furthermore, most "soft" taxa have at least some hard structures (such as mouthparts, stylets, scales, spines, etc.) that can easily be measured. For better comparison of relative dimensions (length-width ratio, or ratio and situation of organs) it is advisable to take the body length of a specimen as 100 units (U 0 to U 100); e.g., "ovary from U 60 to U 72," or "maximal width 33 μ (=7 U) at U 65" (Rieger and Sterrer, 1968).

One of the major problems in gnathostomulid taxonomy concerns size. This is particularly true for the most important character, the jaws. *Gnathostomula* seems to be the most difficult genus in this respect. Known from all over the world, it already comprises a considerable number of species (about 20 so far) that differ only slightly, although in a number of characters. With regard to the jaws, this means counting teeth in the dimension of one third of a micron, which coincides with the absolute limitation of the optical microscope (Figure 1*a*).

Another difficulty is that of poor delimitation between cuticular parts and surrounding tissue. This is especially true for the basal plate. In the Filospermoidea and lower Scleroperalia it often is difficult to determine whether a basal plate is present at all, and even in *Gnathostomula* the outline of the plate can be difficult to define. Cuticular parts are best studied in squeeze preparation, with increasing pressure being applied to the coverslip (Hulings and Gray, 1971). If a specimen is well oriented dorsoventrally, pictures of squeezed jaws may be obtained that allow exact counts of teeth (Figure 1*a*). It is hoped, however, that the scanning microscope will furnish a better method for the study of these structures.

A further character of high taxonomic value is the sensory organs (Figure 1*b*). Numbers, arrangement, and length of sensory cilia and bristles are important in phylogenetical considerations. But it often is extremely difficult to obtain such data, one reason being that the sensory bristles often join the ciliary beat, making them difficult to locate; furthermore, these structures disintegrate readily when the animal starts feeling uncomfortable. Recording of the above data, therefore, should be the first step in the series of observations.

Among the characters that seem to be of high taxonomic value is the pattern of the epidermal

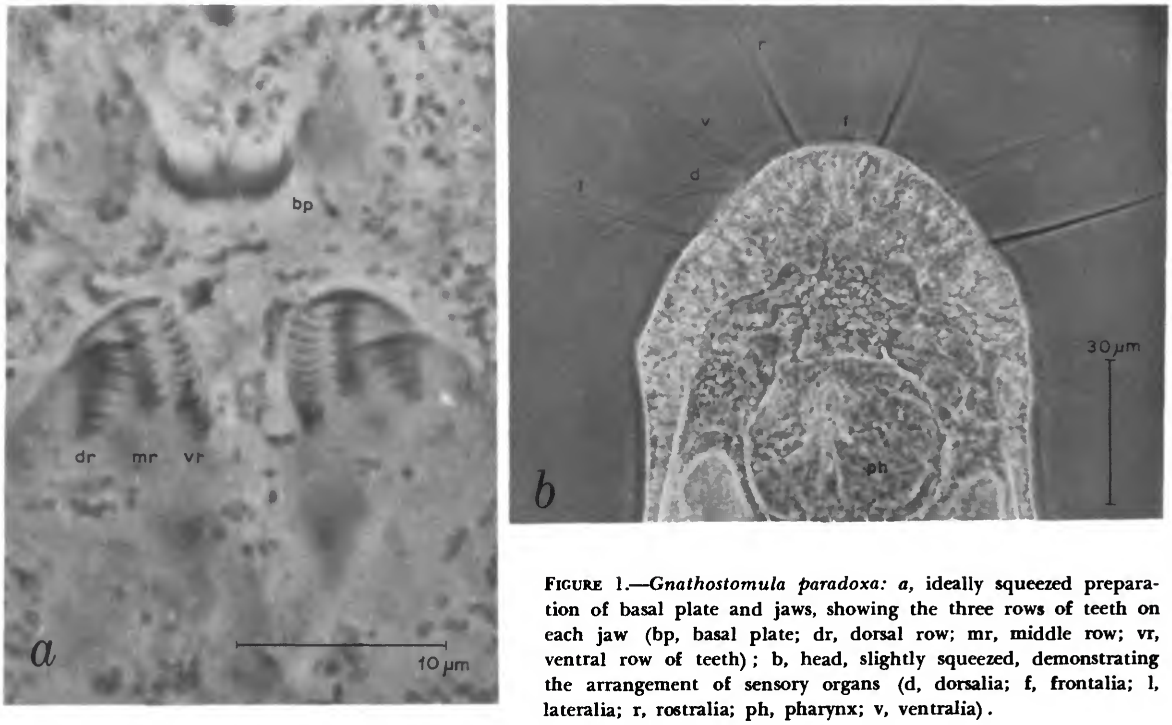

Figure 1.—*Gnathostomula paradoxa: a,* ideally squeezed preparation of basal plate and jaws, showing the three rows of teeth on each jaw (bp, basal plate; dr, dorsal row; mr, middle row; vr, ventral row of teeth); b, head, slightly squeezed, demonstrating the arrangement of sensory organs (d, dorsalia; f, frontalia; l, lateralia; r, rostralia; ph, pharynx; v, ventralia).

cells. In higher Scleroperalia as well as in the Conophoralia the cells are usually arranged in rows that converge rostrally in the ventral median line and caudally in the dorsal median line, thus forming inclined rhomb-like stripes around the body.

Sperm morphology is one of the most puzzling features in gnathostomulid research. It is, in fact, the most heterogeneous morphological character throughout the class. Known so far are three major types of sperm (filiform, dwarf, and conulus; see Sterrer, in press, b), each of which is structurally quite different from the others. It is hoped that a better knowledge of spermatogenesis, as well as special staining and ultrastructural techniques, will clarify the homology of the sperm types. An interesting aspect relevant to the clarification of gnathostomulids as a whole will be the possible homology of one of the types with sperm known from other classes: the "filiform" type of Gastrotricha and some Turbellaria, and the aberrant "conulus"-like type of Catenulida (Turbellaria).

Going into histological methods, finally, a striking contrast becomes apparent: small dimension, low level of general organization, and poor tissue differentiation on one side and the extremely complicated muscular pharynx on the other. A method of serial, ultrathin sections with subsequent three-dimensional reconstruction of electron micrographs hopefully will contribute to a better understanding of this paradox.

Taxonomic difficulties related to biology are those of life cycles. For instance, all specimens of *Gnathostomaria lutheri* collected at the type-locality in October 1966 were anterior fragments, and a study of the genital organs was impossible. Similar fragmentation seems to occur in many Filospermoidea. Another biological phenomenon occurs in Gnathostomulidae: sexual stages seem to alternate with feeding stages (Riedl, 1969), the latter being characterized by a reduction of sexual organs. All of these phenomena make taxonomy rather difficult, and they emphasize once more the necessity of getting the most out of the few available characters.

Finally, the systematic position of the taxon is far from being solved. Many features both in organization and biology are similar to those of widely distant taxa—features such as the cuticular mouthparts of Rotataria and Turbellaria, the general organization of lower Turbellaria, the sperm of Gastrotricha and Turbellaria, the quasi-lack of a parenchyma in the whole of the Aschelminthes, and the monociliary epithelium of larvae of echinoderms. This means, on the other hand, that all of these features need to be studied much more thoroughly, preferably with electron microscopy techniques. A possible relationship with the extinct Conodontophorida has been discussed recently by paleontologists (Durden et al., 1969). Careful evaluation of the available data leads the author to consider the Gnathostomulida as a class within the Platyhelminthes, with possible relationships to Turbellaria via the turbellarian order Catenulida (Sterrer, in press,b).

Summary

The problems connected with the study of Gnathostomulida (Platyhelminthes) have been briefly evaluated. Procedures of sampling (spade, corer, diver-operated net or dredge) and extracting (modified anesthetization, or Uhlig method) have been followed by remarks of distribution (worldwide), zoogeography (relation between morphological differences and geographical distances), and ecology ("black layer," hence probability of anaerobic metabolism, "typical" substratum with high species diversity). Biology is poorly known (difficulty of keeping and rearing in the laboratory). Taxonomy should rely on statistical-metrical data; the main problems are small size, as opposed to complex, frail, or poorly delimited structures, and gaps in comparability within (e.g., sperm) and without (e.g., cuticular mouthparts) the class.

Literature Cited

Ax, P.

1956. Die Gnathostomulida, eine rätselhafte Wurmgruppe aus dem Meeressand. *Abhandlungen der Akademie der Wissenschaften und der Literatur, Mathematisch-naturwissenschaftliche Klasse, Mainz,* 8:1–32.

1965. Zur Morphologie und Systematik der Gnathostomulida. Untersuchungen an *Gnathostomula paradoxa* Ax. *Zeitschrift für Zoologische Systematik und Evolutionforschung,* 3:259–276.

Durden, C.; J. Rodgers; E. Yochelson; and R. Riedl

1969. Gnathostomulida: Is there a Fossil Record? *Science,* 164:855–856.

Gerlach, S. A.

1958. Ein neuer Vertreter der Gnathostomulida (Turbellaria?) aus dem Meeressand der Malediven. *Kieler Meeresforschungen,* 14:175–176.

Hulings, N. C., and J. S. Gray

1971. A Manual for the Study of Meiofauna. *Smithsonian Contributions to Zoology,* 78:1–83.

Riedl, R.

1966a. *Biologie der Meereshöhlen. Topographie, Faunistik und Ökologie eines unterseeischen Lebensraumes.* 636 pages. Hamburg and Vienna: P. Parey.

1966b. Faunistische Studien am Roten Meer im Winter 1961/62, III. Die Aufsammlungen in Suez und Al-Ghardaqa, nebst einigen Bemerkungen über Gnathostomulida. *Zoologische Jahrbücher, Systematik,* 93:139–157.

1969. Gnathostomulida from America. *Science,* 163:445–452.

1970a. *Semaeognathia,* a New Genus of Gnathostomulida from the North American Coast. *Internationale Revue der gesamten Hydrobiologie,* 55:359–370.

1970b. On *Labidognathia Longicollis* nov. gen., nov. spec. from the West Atlantic Coast (Gnathostomulida). *Internationale Revue der gesamten Hydrobiologie,* 55:227–244.

In press. On *Onychognathia,* a New Genus of Gnathostomulida from the Tropical and Subtropical West Atlantic. *Bulletin of Marine Science.*

Rieger, R., and W. Sterrer

1968. *Megamorion brevicauda* gen. nov., spec. nov., ein Vertreter der Turbellarienordnung Macrostomida aus dem Tiefenschlamm eines norwegischen Fjords. *Sarsia,* 31:75–100.

Schöpfer-Sterrer, C.

1969. *Chordodasys riedli* gen. nov., spec. nov., a Macrodasyoid Gastrotrich with a Chordoid Organ. *Cahiers de Biologie Marine,* 10:391–404.

Sterrer, W.

1965. *Gnathostomula axi* Kirsteuer und *Austrognathia* (ein weiteres Gnathostomuliden-Genus) aus der Nordadria. *Zeitschrift für Morphologie und Ökologie der Tiere,* 55:783–795.

1966a. *Gnathostomula paradoxa* Ax und Vertreter von *Pterognathia* (Ein neues Gnathostomuliden-Genus) von der schwedischen Westküste. *Arkiv för Zoologi,* 18:405–412.

1966b. Neue Gnathostomulida. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* sonderband 2:201–207.

1968. Beiträge zur Kenntnis der Gnathostomulida. I. Anatomie und Morphologie des Genus *Pterognathia* Sterrer. *Arkiv för Zoologi,* 22:1–125.

1970. On some Species of *Austrognatharia, Pterognathia* and *Haplognathia* nov. gen. from the North Carolina Coast (Gnathostomulida). *Internationale Revue der gesamten Hydrobiologie,* 55:371–385.

In press,a. On the Biology of Gnathostomulida. In Proceedings of the Third European Marine Biology Symposium. *Vie et Milieu,* supplement 22.

In press,b. Systematics and Evolution within the Gnathostomulida. *Systematic Zoology.*

In press,c. *Agnathiella backeri* nov. gen., nov. spec. from Southern Florida: The First Gnathostomulid without Jaws. *Internationale Revue der gesamten Hydrobiologie.*

Uhlig, G.

1964. Eine einfache Methode zur Extraktion der vagilen, mesopsammalen Mikrofauna. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 11:178–185.

1968. Quantitative Methods in the Study of Interstitial Fauna. *Transactions of the American Microscopical Society,* 87(2):226–232.

Ernst Kirsteuer

The Interstitial Nemertean Fauna of Marine Sand

ABSTRACT

Lists of the interstitial nemerteans and their geographic distribution are given. The general biology, including morphology, development, and ecology, is discussed.

The acoelomate phylum Nemertina comprises about 850 species of worms with a body length between 1 mm and 30 m. Nemerteans are known from land and fresh water, from all oceans, all depths, and all major marine habitats. As far as the marine sediment bottoms are concerned, it is possible to distinguish between a mud fauna and a sand fauna. The present review, however, deals mainly with the nemerteans inhabiting the interstices of marine sand. Nemerteans living in or on mud are not characterized by small size and are generally well above the 1 to 2 mm body length limit usually applied for meiobenthic forms. Furthermore, they have, with the exception of some statocyst-bearing palaeonemerteans, no developed morphological features which would make them quite distinct from species occurring in other marine habitats such as the phytal, coral reefs, submarine caves, etc. In mud fauna, representatives of all three free-living nemertean orders are included, and when the composition of the fauna is compared with that from other biotopes it becomes evident that the Palaeonemertina have their highest frequency on mud bottoms whereas the Heteronemertina occupy an intermediate position and the Hoplonemertina are the poorest represented order (Kirsteuer, 1963).

The marine interstitial nemertean fauna, on the other hand, is systematically less diverse but the species clearly show morphological adaptation to the life in the interstitial environment. Twenty-seven species of interstitial nemerteans have been described, seven of which are palaeonemerteans:

Carinina arenaria Hylbom. Atlantic: Gullmar Fjord.
Cephalothrix arenaria Hylbom. Atlantic: Gullmar Fjord.
Cephalothrix atlantica Gerner. Atlantic: Arcachon.
Cephalothrix germanica Gerner. Atlantic: Sylt.
Cephalothrix mediterranea Gerner. Mediterranean Sea: Canet Plage.
Cephalothrix pacifica Gerner. Pacific: Washington.
Procephalothrix kiliensis Friedrich. Baltic Sea: Kiel.

The remaining species, belonging to the order Hoplonemertina and the suborder Monostilifera, are as follows:

Arenonemertes microps Friedrich. Baltic Sea: Kiel.
Arenonemertes minutus Friedrich. Baltic Sea: Fehmarn.
Prostomatella arenicola Friedrich. Baltic Sea: Kiel.
Otonemertes marcusi Corrêa. Atlantic: Brazil.
Ototyphlonemertes pallida (Keferstein). Atlantic: St. Vaast, Hörnum, Amrum. Black Sea: Suchumi, Constantza, Agigea.
Ototyphlonemertes aurita (Uljanin). Black Sea: Sevastopol, Suchumi.
Ototyphlonemertes aurantiaca (Du Plessis). Mediterranean Sea: Nice, Banyuls sur Mer, Canet Plage.
Ototyphlonemertes macintoshi Bürger. Mediterranean Sea: Naples, Villefranche sur Mer.
Ototyphlonemertes brunnea Bürger. Mediterranean Sea: Naples, Villefranche sur Mer.
Ototyphlonemertes duplex Bürger. Mediterranean Sea: Naples, Villefranche sur Mer.
Ototyphlonemertes spiralis Coe. Pacific: California.
Ototyphlonemertes pellucida Coe. Atlantic: Massachusetts, Florida.
Ototyphlonemertes evelinae Corrêa. Atlantic: Brazil, Florida.
Ototyphlonemertes brevis Corrêa. Atlantic: Brazil.
Ototyphlonemertes erneba Corrêa. Atlantic: Brazil.

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Ototyphlonemertes parmula Corrêa. Atlantic: Brazil.
Ototyphlonemertes fila Corrêa. Atlantic: Brazil, Florida.
Ototyphlonemertes lactea Corrêa. Atlantic: Brazil, Florida.
Ototyphlonemertes antipai Müller. Black Sea: Agigea, Costinesti, Vama Veche, Solotyie, Pesski, Kaba Kum.
Ototyphlonemertes americana Gerner. Pacific: Washington.

Like many other invertebrate groups the nemerteans also have their smallest representatives in the interstitial fauna. *Arenonemertes minutus,* which reaches a length of only 1 mm, is the smallest described nemertean. Several of the other species are between 2 and 10 mm long, and some, such as *Ototyphlonemertes macintoshi, O. spiralis,* and *O. evelinae,* measure from 30 to 50 mm in length. The body, however, is always extremely slender with a diameter of not more than 500 μ, thus enabling the animals to move through the interstitial system without actively replacing the sand grains; all the listed species, therefore, are considered to be mesopsammon forms sensu Boaden (1962).

Interstitial nemerteans are white, orange or brownish, yellowish white or greenish white, and they lack the elaborate color patterns so often found in other species. Generally, locomotion is effected by ciliary gliding. Locomotion by writhing, similar to that of nematodes, was described by Friedrich (1935) for *Prostomatella arenicola,* but this is an exception and atypical for nemerteans. In some species of *Ototyphlonemertes* Diesing conspicuously long tactile cirri are arranged along the anterior and posterior body margins, and near the posterior end of the body adhesive plates are formed by aggregation of epidermal gland cells. Large adhesive gland cells distributed over the whole body surface also were found in *Arenonemertes minutus* and *A. microps* by Friedrich (1949). A chordoid tissue, considered by Ax (1966) to be typical "Lebensform" characteristic of the mesopsammon, was observed in *Ototyphlonemertes antipai* by Müller (1968b), who compared the vacuolized epithelium with that in the turbellarian *Cystiplex axi* Karling.

Static organs are developed in *Carinina arenaria, Otonemertes marcusi,* and in all species of the genus *Ototyphlonemertes,* where either one or two pairs of statocysts are present. Ocelli, on the other hand, are lacking in most of the species of interstitial nemerteans.

In the stenoecious genera *Ototyphlonemertes* (recently reviewed by Müller, 1968a) and *Arenonemertes* Friedrich there is a tendency for reduction, in various degrees, of the organs otherwise typical for nemerteans. Within the *Ototyphlonemertes,* the proboscis sheath extends over the entire length of the body in *O. aurita,* whereas in the majority of the other species it reaches only for half or one third of the body length; and in *O. brevis* and *O. lactea* it is restricted to 10 percent of the body length. In the same genus the chemoreceptive cerebral sense organs also show different stages of reduction, from normal organization to the complete loss of the organ (Müller, 1968a).

Correlated with the reduction of body size, the midgut diverticula are generally less developed and are lacking in the species of *Arenonemertes* and in the smaller species of *Ototyphlonemertes.* For one of the latter, *O. brevis,* Corrêa (1950) was able to show that the loss of diverticula is compensated for by intensified enzymatic processes. Further reduction occurs in the gonads which, in accordance with observations in other mesopsammic invertebrates, are limited in number. In *Arenonemertes minutus* only six gonads, each containing just one ripe oocyte, were found (Friedrich, 1949).

The development of interstitial nemerteans is still unknown, but as only species of the orders Palaeonemertina and Hoplonemertina are present in this fauna it can be assumed that the development is of the direct type, thus omitting a pelagic larval phase, which is known only from heteronemerteans.

Interstitial nemerteans, found in the intertidal zone and in the subtidal region to a depth of 15 m, seem to prefer rather clean sand. More detailed ecological data are available for some species of *Ototyphlonemertes* (Müller, 1968a). *Ototyphlonemertes aurita* lives on sand under stones, occupying ecologically a transient position between sand epifauna and mesopsammon; interestingly, this is also the species with the unreduced proboscis sheath and normal cerebral organs. *Ototyphlonemertes pallida* occurs from the upper intertidal to 10 m. Müller (1968a) found *O. pallida* 20 mm long in fine sand only and specimens of *O. antipai* 4 to 7 mm long in coarse sand (1.2-mm grain size) only. Corrêa (1948) observed during experiments that the 30-mm specimens of *O. evelinae* and the 10-mm specimens of *O. brevis* showed no preference for either fine sand of 0.5-mm to 2-mm grain size or coarse sand of 2-mm to 5-mm grain size. Corrêa (1961) also collected *O. evelinae* (30 mm long), *O. fila* (20 mm long), *O. pellucida* (12 mm long) and *O. lactea* (4.5 mm long) from the same area of a coarse-sand beach near Miami, Florida. The present data do not indicate a specialized substratum selection for the *Ototyphlonemertes,* and obviously there is no correlation between the size of the animals and the grain size of the sand they inhabit.

The quantitative distribution of *Ototyphlonemertes evelinae* and *O. brevis* was studied by Corrêa (1949) along a transect from the line of mean high tide to that of mean low tide on a Brazilian beach. Under normal weather conditions the worms occurred mainly in the upper 10 cm of sand. The largest number of specimens was registered in samples taken from the middle part of the transect, and in this region animals also were found 20 cm deep in the substratum. No migration patterns in connection with the changing tides were observed, and only when the beach was struck occasionally by heavy waves did the animals go deeper into the sediment. The maximum number of specimens recorded for the two species combined was 555 in 1,000 cm³ of sand. Corrêa (1949), however, pointed out that this extremely high population density presumably was due to the fact that garbage from a nearby hotel was disposed in the collecting area, thus providing a rich food supply—either directly or by attracting other interstitial animals like polychaetes and crustaceans upon which nemerteans prey.

Literature Cited

Ax, P.

1966. Die Bedeutung der interstitiellen Sandfauna für allgemeine Probleme der Systematik, Ökologie und Biologie. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:15–65.

Boaden, P. J. S.

1962. Grazing in the Interstitial Habitat: A Review. *British Ecological Society Symposium Number 4,* pages 299–303.

Corrêa, D. D.

1948. *Ototyphlonemertes* from the Brazilian Coast. *Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo,* 2(49):1–12.

1949. Ecological Study of Brazilian *Ototyphlonemertes. Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo,* 3(55):1–7.

1950. Sôbre *Ototyphlonemertes* do Brasil. *Boletins da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoologia,* 15:203–233.

1961. Nemerteans from Florida and Virgin Islands. *Bulletin of Marine Science of the Gulf and Caribbean,* 11(1):1–44.

Friedrich, H.

1935. Beobachtungen über eigenartige Bewegungsweisen bei Nemertinen. *Biologisches Zentralblatt,* 55:84–86.

1949. Über zwei bemerkenswerte neue Nemertinen der Sandfauna. *Kieler Meeresforschungen,* 6:68–72.

Kirsteuer, E.

1963. Zur Ökologie systematischer Einheiten bei Nemertinen. *Zoologischer Anzeiger,* 170:343–354..

Müller, G. J.

1968a. Betrachtungen über die Gattung *Ototyphlonemertes* Diesing 1863 nebst Bestimmungsschlüssel der validen Arten (Hoplonemertini). *Senckenbergiana Biologica,* 49:461–468.

1968b. *Ototyphlonemertes antipai* n. sp., ein neues Mitglied des mediolitoralen Mesopsammals des Schwarzen Meeres. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa,"* 8:343–348.

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The Marine and Brackish-Water Gastrotricha in Perspective

ABSTRACT

The Gastrotricha are reviewed in terms of taxonomy, with generic and species criteria emphasized. The ecology of gastrotrichs, including the sampling problem, also is discussed.

Gastrotrichs are recognizable even at low magnification by their morphology and movement. Adult specimens seldom exceed 1 mm, although those of a few species reach 2 to 4 mm. They range from strap-shaped animals showing lateral and posterior adhesive tubes to bottle-shaped animals possessing a prominent caudal furca. Gastrotrichs typically move by means of ventral cilia, and they rarely, if ever, reverse direction. They are most likely to be confused with Turbellaria or Gnathostomulida, but they are easily distinguished at higher magnifications since they have a terminal mouth, an anterior pharynx, and an anus but lack both lateral and dorsal locomotor cilia and a statocyst. Densities of individuals in a single species reach as high as 2,307 in 6 cm^3 (384.5/cm^3) of substratum (Hummon, unpublished) but vary considerably and generally average less than 2/cm^3 of substratum.

The phylum, as presently defined, generally is divided into two orders, the Macrodasyida and the Chaetonotida. Macrodasyida comprises about a third of the 340 species described as of mid-1969 and is confined almost exclusively to marine or brackish-water habitats, though a few species are known to have invaded waters with salinity as low as 1 ppt. Chaetonotida includes the remaining species. Two of the six chaetonotid families are restricted to marine and brackish-water habitats; members of two additional families occur in similar habitats.

A major trend in gastrotrich systematics began during the 1930s with a shift from fresh-water to marine species. The latter forms continue to receive the most attention, their proportion currently making up about 50 percent of the described species. Published species descriptions often lack information beyond that needed to distinguish proposed species from those which preceded them. In many cases important characters have been overlooked, resulting in a need to redescribe or more fully document generic and species descriptions. Type-specimens often have been poorly preserved, or, more often, have been entirely lacking. Drawings are rarely suitable, though some very good illustrations are on record. Ecological work is generally absent or is based on cursory observations. And, far too often, the more recent reports fail to make morphological comparisons with data found in either the original description or subsequent accounts.

Several recently described forms tend to blur established distinctions between genera and even between families. As a result, criteria on which these taxa are based will have to be revised. The combined need for descriptions of new forms in neglected localities and biotopes, along with redescriptions of previously described species based on a broader spectrum of specific characters, im-

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poses an important obligation on future taxonomic research. Few persons who enter into the study of gastrotrich biology can avoid the inclusion of some serious taxonomy in their work.

With this in mind, it is important that taxonomic work be approached with the same care and preparation as needed for an experimental problem. Species descriptions should be sufficiently detailed as to provide a basis against which future species can be compared. Minimally, this means more complete descriptions based, where possible, on data derived from populations of animals. It means noting and quantifying both genetic and ontogenetic variability among specimens. It also means working with relaxed and extended specimens, and making detailed and representative drawings and supplementing them with photomicrographs and well-preserved permanent specimen mounts.

Taxonomic work on gastrotrichs, often diffuse and ill-defined, has been most valuable when based on multiple characters—metric, meristic, and what might be termed eidostic (Greek *eidos*: form, figure, thing seen). It would be helpful if, in future work, a sequence of metric-meristic-eidostic portraits could be constructed for each species. Ideally such a sequence of measured, counted, and visualized characters would be drawn from the population living in the type-locality of a species. In practice it could come from any location at which a species is sufficiently abundant as to provide adequate material with which to work. The procedure is simply to relate all metric and meristic characters to total body length of extended specimens for each of several developmental length classes, ranging from juveniles to adults. Several such length classes, including the smallest and largest, should be illustrated in detail so as to allow visualization of proportions and placement of parts (for a preliminary study of this type see Hummon, 1966). Though time-consuming, this procedure allows separation of genetic from ontogenetic variability and provides a base line against which specimens from other localities or biotopes can be compared. It also enables one to more accurately assess geographical and ecological variability and to analyze precisely cases of suspected character displacement or interspecific hybridization.

Generic characters in gastrotrichs usually involve one or more of the following: general body conformation; presence or absence of lobes, palps, or tentacles; presence or absence of entire groups of adhesive tubes; pattern of ventral cilia; type of cuticular ornamentation, if present; type and location of pharyngeal pores, if present; and the components and positions of reproductive structures. Specific characters often are related to the further definition of generic characters, but nearly as often they involve nongeneric characters which show consistent differences from population to population.

Some characters develop rather fully in the embryo prior to its hatching, whereas other characters tend to emerge in the juvenile almost as rudiments and to undergo subsequent development in the free-swimming animal throughout life. In terms of energy conservation, it is an efficient strategy for a minute animal, living within benthic sediments, to reproduce by means of a few relatively large eggs which can be attached to the substratum and from which emerge "miniatures" of the adult. Those features most necessary for survival of the newly hatched juvenile are favored by selection and hence are well developed. All systems except the reproductive are functional, though they often add numbers or increments as the juvenile matures. It is this latter group of features which provides data for the ontogenetic growth sequence, through characters such as tubule or bristle number, size, and locations; scale size; intestine length; and body proportions.

Gastrotrichs have been little studied ecologically. Of the work that has been done, most has centered on marine and brackish-water forms living in sandy intertidal or shallow subtidal substrata. Such work should be continued, and should be closely correlated with systematic studies to enhance our knowledge of gastrotrich biogeography and of the role played by various species of gastrotrichs in differing ecosystems. These studies should be broadened to include those forms living in other habitats, such as in mud bottoms, on algae or barnacles, among eelgrass roots or ascidian colonies, in estuaries, salt ponds or tidal marshes, and in benthic zones of the continental shelf or the abyssal plain.

In making intensive ecological studies, it often is productive to determine the extent of the habitat to be studied, to select a two-dimensional transect plane which lies perpendicular to the greatest number or "most important" environmental gradients, and to determine the maximum number of samples and subsamples which can be processed per collection. The samples, with their clustered subsamples, can then be allocated along the study plane. Sample and subsample size, interval between collections, duration of the study, and other features also must be considered. When possible, both biotic and physicochemical factors should be assessed in determining local distribution patterns. These should be related to laboratory determinations of species tolerances and preferences as well as to field conditions. Consideration should be given to obtaining data that will provide maximum information for use in studies of biogeography, species diversity, and population dynamics. Finally, all such ecological work should be done at the species level of identification (see Hummon, 1969; Schmidt and Teuchert, 1969).

References to the Gastrotricha are widely scattered in the literature. Rather than include an extended list of recent papers, only four additional references are cited here. Remane (1936) has provided the most comprehensive review of the entire group. The most recent reviews are those of Hyman (1951, 1959), in English; Voigt, (1958), in German; Beauchamp (1965), in French. A complete bibliography of marine and brackish-water gastrotrichs is available from the author on request.

Literature Cited

Beauchamp, P.

1965. Classe des Gastrotriches. In P. P. Grassé, editor, *Traité de Zoologie,* 4(3):1381–1430.

Hummon, W. D.

1966. Morphology, Life History, and Significance of the Marine Gastrotrich, *Chaetonotus testiculophorus* n. sp. *Transactions of the American Microscopical Society,* 85:450–457.

1969. Distributional Ecology of Marine Interstitial Gastrotricha from Woods Hole, Massachusetts, with Taxonomic Comments on Previously Described Species. Unpublished Ph.D. dissertation, University of Massachusetts.

Hyman, L. H.

1951. *The Invertebrates: Acanthocephala, Aschelminthes, and Entoprocta.* Volume 3, pages 53–59, 151–170. New York: McGraw-Hill.

1959. *The Invertebrates: Smaller Coelomate Groups.* Volume 5, pages 697–766. New York: McGraw-Hill.

Remane, A.

1936. Gastrotricha und Kinorhyncha. In H. G. Bronns, editor, *Klassen und Ordnungen des Tierreichs,* 4(2):1–242.

Schmidt, P., and G. Teuchert

1969. Quantitative Untersuchungen zur Ökologie der Gastrotrichen im Gezeiten-Sandstrand der Insel Sylt. *Marine Biology,* 4:4–23.

Voigt, M.

1958. Gastrotricha. *Tierwelt Mitteleuropas,* 1(4a):1–74.

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A Historical Overview of Kinorhynch Research

ABSTRACT

The historical development of the systematics of the Kinorhyncha from the phylum to the species level is reviewed. Procedures for collecting, extracting, study, and curating are discussed.

Considering the relative abundance of the Kinorhyncha as a constituent of the meiobenthos in marine sediments, it is difficult to understand why these invertebrates have received so little attention. Indeed, the present status of kinorhynch research seems to be as restrictive as it was more than a hundred years ago when the first kinorhynch was discovered.

While observing the meiofauna washed from algae collected along the Normandy coast in 1841, Dujardin discovered a remarkable invertebrate, less than a half millimeter in length, which he called "l'echinodere" some ten years later when he published his only paper on this subject (Dujardin, 1851). Dujardin's "l'echinodere," so named because of the animal's recurved spines on its eversible head (which Dujardin apparently considered its neck), became *Echinoderes dujardini* when Claparède (1863) described the first species. As in the case of Dujardin's short-lived interest in the new taxon, this was Claparède's only contribution to kinorhynch research. Many investigators have repeated Claparède's disinterest in continuing research on the Kinorhyncha, and this has contributed to the relative obscurity of one of the most interesting and challenging phyla of meiobenthic invertebrates.

Dujardin (1851) did not assign his newly discovered taxon to a particular group of invertebrates but suggested that "l'echinodere" was probably an intermediate between the "Worms" and the Crustacea. Prior to the publication of the nominal species by Claparède (1863), kinorhynchs were "rediscovered" by Leuchart (1854), who mistakenly assumed his specimen to be dipteran larval stage. Nonetheless, from the initial description of the first known kinorhynch until the present time, Dujardin's peculiar invertebrates have had a rather simple nomenclatorial history.

Bütschli (1876) erected the family Echinoderidae for the single species of *Echinoderes* known at that time. Soon afterwards, Greeff (1869a,b), Metschnikoff (1869), and Pagenstecher (1875) established several new species and the fact that these were, indeed, adults and not unknown larval stages of an already known invertebrate. The name Kinorhyncha was introduced by Reinhard (1881, 1887), who tried to avoid confusing this new taxon with the many other taxa whose names began with the prefix "echino-." Later authors were to use widely the name Echinodera or Echinoderida—certainly an acceptable synonym—and, more recently, the inevitable mistake "Echinorhyncha" has appeared as the phylum name (Russell-Hunter, 1968). Although it is apparent that Reinhard recognized that the Kinorhyncha constituted a major taxonomic category of invertebrates, he carefully avoided designating a level for his new name.

Not long after the first few kinorhynch papers appeared, Carl Zelinka became interested in this challenging invertebrate. Zelinka had finished his monograph on another meiofaunal taxon, the Gastrotricha (Zelinka, 1889), when he accepted the challenge offered by Dujardin's discovery. Certainly no other scientist of that time was better prepared to recognize the phylogenetic significance

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of the Kinorhyncha. Thus, Zelinka began his studies of a new invertebrate taxon. Between 1894 and 1913 he published seven preliminary papers, including a description of a new species. By 1919 Zelinka's monograph was ready for publication, but events following World War I delayed publication until his 78th year, 1928. Zelinka's *Monographie der Echinodera* still remains the most singularly important work on Kinorhyncha.

By 1908, the Kinorhyncha (Echinodera) occupied an ordinal level within Grobben's class Aschelminthes (phylum Protostomia). Twenty years later Zelinka (1928) elevated the Echinodera to a class of the phylum Aschelminthes. This classification remains satisfactory, although Pearse (1936) elected to use Reinhard's name Kinorhyncha, the name preferred by most present-day invertebrate zoologists.

While Zelinka was working on his monograph several other scientists published short papers on various aspects of kinorhynch biology. These include the papers by Haeckel (1896), Hartog (1896), and Schepotieff (1907a,b, 1908a,b). A single paper by Southern (1914) was the first to utilize Zelinka's (1896) classification in a species description.

Following the appearance of Zelinka's monograph, Remane (1928, 1929, 1936) published several summaries of the former author's work, adding some original material. Between 1922 and 1947 five papers, primarily taxonomic, appeared. Abe's (1930) description of *Echinodere masudai* from Japan was the first for a kinorhynch from the Pacific. Blake (1930) described three species from the coast of Maine (these recently were redescribed by Higgins, 1964, 1965). In 1943 Lou reported a new species, *Echinoderes tchefouensis* from Chefou (Yellow Sea); however, this species, like the one reported by Abe, remains a nomen dubium. In keeping with a series of carefully rendered descriptions on other taxa, Lang (1935) published a short paper on kinorhynchs from the Swedish coast. In later years Lang (1949, 1953) made additional noteworthy contributions, both in additional new species and phylogenetic discussion. The two other papers of the post-World War II era were those of Johnston (1938), who described a new species found by the Australian Antarctic Expedition 1911-1914, and Zaneveld (1938), who reported finding a kinorhynch on the coast of the Netherlands.

Although Zelinka and others had considerable information on the postembryonic stages of many kinorhynch taxa, the first report on the embryonic ("nonmotile") stages was made by Nyholm (1947a,b). Since 1947, very little effort has been directed toward the embryonic or postembryonic life history of the kinorhynchs. Most papers on this taxon have remained descriptive. Zelinka's introduction of larval generic names (Higgins, 1968) and the problem of recognition of the adult of certain taxa offer difficult challenges in kinorhynch research.

Despite several important new taxonomic additions to the phylum, the Kinorhyncha possess the same basic taxonomic constructs as were established by Zelinka in 1896 (Figure 1). The first of the two orders, Cyclorhagida, includes the majority of lesser taxonomic components on all levels and includes three suborders. The second order, Homalorhagida, has a much simpler taxonomic make-up.

Generally speaking, the cyclorhagids are the smallest and most difficult kinorhynchs to study, despite the fact that they are the most commonly encountered taxon. The suborder Cyclorhagae is the most common of all suborders. Within it, the monotypic family Echinoderidae, composed of 26 described species of *Echinoderes*, has only 19 species that can be properly recognized. *Echinoderes*, the most commonly encountered kinorhynch genus, often is mistaken for a copepod in preserved material.

Most closely related to the Echinoderidae is the family Centroderidae. Its nominal genus, *Centroderes* Zelinka, has two species. A second genus, *Campyloderes* Zelinka, has three species; and the third and final genus, *Condyloderes* Higgins, has two species. Species of the genus *Centroderes* are known only from the Black Sea, Mediterranean Sea, Bermuda waters, and Buzzards Bay, Massachusetts (Higgins, unpublished). *Campyloderes*, until it appeared in samples of meiofauna collected in New Caledonia, was considered to be bipolar temperate to boreal. *Condyloderes* Higgins, recently described (Higgins, 1969a,b) from material the author obtained in India, is distinctly neotenic and includes McIntyre's (1962) *Centroderes multispinosus*, found along the coast of Scotland.

Conchorhagae, a second suborder of Cyclorhagida, now contains two genera. *Semnoderes* Zelinka,

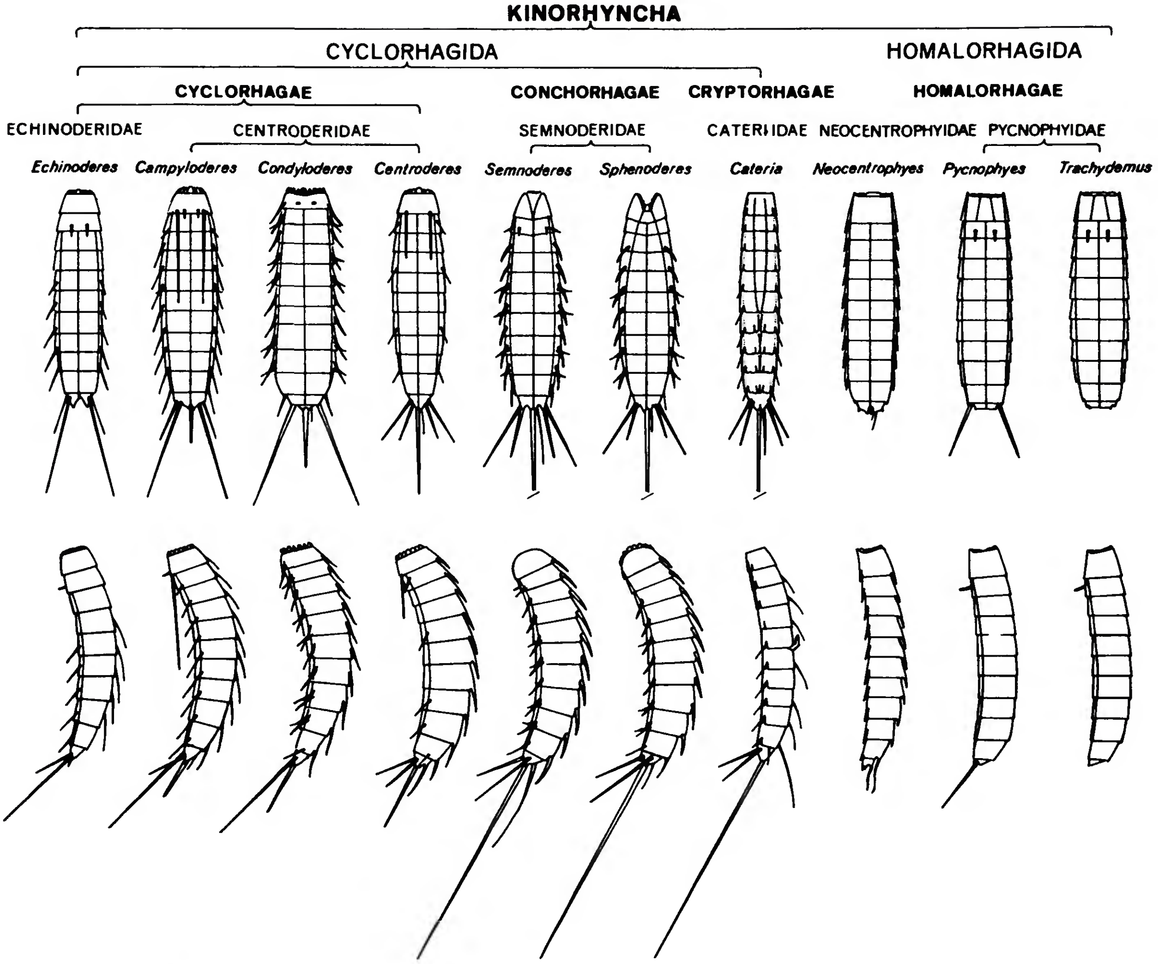

FIGURE 1.—Schematic representation of the phylum Kinorhyncha showing ventral (top row) and lateral (bottom row) aspects of adult representatives of the known genera. (Illustrations are diagrammatic and are not drawn to the same scale.)

the original conchorhagid, consists of three species. *Sphenoderes* Higgins is a monotypic genus which the author recently described from India (Higgins, 1969a). It would appear, from what little evidence is available, that the Conchorhagae more commonly are inhabitants of muddy sands as opposed to the finer marine sediment. No conclusions can be reached regarding their distribution or ecology.

The third and final cyclorhagid suborder, Cryptorhagae, is known from a single genus, *Cateria* Gerlach, discovered in the interstitial zone of a marine beach near Macaé, Brazil (Gerlach, 1956). Gerlach's species has been reported from the Angolan coast by Delamare Deboutteville (1957) and from the east coast of India by Rao and Ganapati (1966); and a second species, *Cateria gerlachi* Higgins, occurs in the latter locality as well (Higgins, 1968).

Until recently (Higgins, 1969a), the second and only other order, Homalorhagida, consisted of a single suborder, Homalohagae, a single family, Pycnophyidae, and two genera. The nominal genus, *Pycnophyes* Zelinka, consists of 20 described species, 16 of which are recognizable by their published descriptions. *Pycnophyes* species are among the largest known kinorhynchs and may approach 1 mm in length.

The genus *Trachydemus* Zelinka consists of seven easily recognized species, most of which, from evidence the author has accumulated, appear to prefer very fine sediments.

A second family of homalorhagids has been described (Higgins, 1969b) from material collected by the author in the Indian Ocean in 1964. Neocentrophyidae is a neotenic taxon made up of a single genus, *Neocentrophyes* Higgins, and two species. Phylogenetically speaking, this is an important taxon, for many of its characteristics suggest a position intermediate between the two established orders of Kinorhyncha.

The most singularly difficult problem in kinorhynch research has been the collection of sufficient material. The Kinorhyncha of marine beaches require no special technique different than that used in other studies. The great majority of kinorhynch taxa associate with subtidal sediments, particularly soft sediments—mud or mud mixed with sand with a relatively high organic content. Kinorhynchs are eurybathic, intertidal to 5,000 m or more; are euryhaline, occurring at salinities as low as 7 ppt and as high as 60 ppt; and are eurythermic, from −2° to 40°C. They usually are found within the upper few centimeters or even the upper few millimeters of marine sediments.

Qualitative collecting is best accomplished by a dredge designed to skim off the upper layer of sediment. Techniques which collect large quantities of sediment deeper than the surface layer are less likely to yield sufficient numbers of organisms for study.

Quantitative collecting is best accomplished by coring techniques. The Smith-McIntyre grab seems to be an effective sampler and can be subsampled with reasonable accuracy. The most important problem to avoid is a shock wave which dissipates the kinorhynch's habitat—the light, flocculent interface layer of soft sediments.

Removal of kinorhynchs from sediment is facilitated by introducing fine bubbles of air into a sediment sample diluted with seawater. The bubbles cause the kinorhynchs to rise to surface film where they are trapped. After the sediment is allowed to settle slightly, the kinorhynchs and several other meiofaunal taxa can be blotted off the surface by gently allowing a piece of mimeograph paper to come in momentary contact with the surface film.

By washing the adhering organisms into a small dish one can immediately determine the success of the procedure. In most cases, if kinorhynchs are present in the sample they will appear after the first few times the blotting and washing procedure is followed.

Meiofauna obtained in the above-described manner can be concentrated, by repeated bubbling, blotting, and washing, into a conical-shaped, fine-mesh (62 μ) net. The accumulated material may then be washed into a bish or directly into a suitable fixative, such as 4 to 7 percent formalin or 70 percent ethanol or isopropynol.

According to the author's best estimates, which are based on several tests, this technique extracts over 80 percent of the kinorhynchs in a large sample. It does not, however, substitute for the accuracy of meticulous sorting of the sediment, sieved through a 62-μ mesh net. The author has found that a coring tube with a cross-sectional area of about 100 cm^3 will provide reasonably accurate quantification. In a core 10 cm deep, 99 percent of the kinorhynchs occur within the upper 2 cm. Rose Bengal, liberally applied to the sample, helps in the sorting procedure, but one must be cautious since not all specimens will be penetrated by the stain. Irwin loops are most helpful in handling individual specimens.

In order to properly identify a specimen, it should be slowly transferred from alcohol or formalin to glycerin. Although glycerin mounts are satisfactory for some taxa, not all of the intricate cuticular morphology can be seen. It is necessary, therefore, to mount each animal in Hoyer's medium which contains enough Lugol's iodine to give it an amber color. Hoyer's mounted specimens clear very well for observation under oil immersion phase optics, and especially for Nomarski interference contrast optics.

The most satisfactory mounts are double coverglass preparations attached to Cobb aluminum-slide frames, an important tool of the nematologist. Such a mount with the animal positioned in a dorsal (or ventral) perspective will allow the observer to reverse the slide and view it from the opposite perspective.

Since Dujardin's discovery of the first kinorhynch almost 130 years ago, some 21 authors have been responsible for the description of the 71 species now established in the literature. Seventeen of the 21 taxonomic authors, approximately 75 percent, have published only a single paper on this subject, while two others have published two papers each. The remaining 37 species descriptions are shared by Zelinka and the author.

The preponderance of single-attempt publications, aside from having a potentially demoralizing effect on aspirant students of the taxon, often has created considerable technical problems in taxonomy. The problems do not reflect, necessarily, the qualifications of the author as a systematist; rather, they substantiate the well-known fact that extensive experience is necessary before any taxonomist can be effective in his area of specialization. Consequently, many species descriptions—most of which reflect a short-lived active interest in the kinorhynchs—are inaccurate. Few type-specimens have been established or properly curated. This necessitates re-collection from the type-locality if, indeed, that locality was noted in the original publication. In several instances the known type-localities have succumbed to the effects of pollution or other destructive forces associated with our modern world and its population expansion.

Few attempts have been made to collect sufficient quantities of kinorhynchs for proper study. Most kinorhynchs are described from only a few specimens—sometimes not by choice, but far too often more specimens could have been collected. Furthermore, few attempts have been made to study carefully the ontogeny of taxonomic characters. Which ones are stable? Which ones are reliable? Which ones are subject to environmental influences?

Similarly, there has been little interest in kinorhynch ecology. The kinorhynchs have been included with the more commonly discussed taxa of a marine sediment community by Wieser (1960) and by McIntyre (1962, 1964, 1969). Few other investigators have been concerned with the role of Kinorhyncha as a component of meiobenthos. No study has been conducted on the autecology of any species, nor has any study been made on the kinorhynch population dynamics of any meiobenthic community.

Summary

Most kinorhynch research has been in basic systematics, although Zelinka's monograph provides a considerable foundation for other disciplines. The kinorhynchs offer an interesting challenge among the taxa which remain "lesser known." Unless more researchers can be recruited to the ranks of those willing to accept such challenges, Kinorhyncha literature may continue to be as cryptic as the environment in which these animals dwell.

Literature Cited

Abe, Y.

1930. Das Vorkommen von *Echinoderes* in den japanischen Gewässern. *Journal of Science of the Hiroshima University,* series B, 1:39–44.

Blake, C. H.

1930. Three New Species of Worms Belonging to the Order Echinodera. *Biological Survey of the Mount Desert Region,* 4:3–10.

Bütschli, O.

1876. Untersuchungen über freilebende Nematoden und die Gattung *Chaetonotus. Zeitschrift für wissenschaftliche Zoologie,* 26:363–413.

Claparède, E.

1863. *Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Tiere und der Küste der Normandie angestellt.* 120 pages. Leipzig: Wilhelm Engelmann.

Delamare Deboutteville, C.

1957. Sur la présence des Echinoderes de la famille des Cateriidae Gerlach dans les eaux souterraines littorales de l'Angola. *Publicaçoes culturais de Companhia de Diamantes de Angola,* Publicações Culturais, 34:33–37.

Dujardin, F.

1851. Sur un petit animal marin, l'Echinodère, formant un type intermédiare entre les Crustacés et les Vers. *Annales des Sciences Naturelles, Zoologie,* series 3, 15:158–160.

Gerlach, S. A.

1956. Über einen aberranten Vertreter der Kinorhynchen aus dem Küstengrundwasser. *Kieler Meeresforschungen,* 12(1):120–124.

Greeff, R.

1869a. Ueber Echinoderes. *Verhandlungen naturhistorischen Vereines preussichen Rheinlande und Westfalens, physikalische und medinische Section,* 26(3)6:8–10.

1869b. Untersuchungen über einige merkwürdige Formen des Arthropoden- und Wurm-Typus. *Archiv für Naturgeschichte,* 35(1):71–100.

Grobben, K.

1908. Die systematische Einteilung des Thierreiches. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gessellschaft in Wien,* 58:491–511.

Haeckel, E.

1896. Systematische Phylogenie. Entwurf eines natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte. *Systematische Phylogenie der Wirbellosen Thiere,* 2:292–299.

Hartog, M.

1896. Rotifera, Gastrotricha and Kinorhyncha. *Cambridge Natural History,* 2:236–238.

Higgins, R. P.

1964. Redescription of the Kinorhynch *Echinoderes remanei* (Blake, 1930) Karling, 1954. *Transactions of the American Microscopical Society,* 83(2):243–247.

1965. The Homalorhagid Kinorhyncha of Northeastern U.S. Coastal Waters. *Transactions of the American Microscopical Society,* 84(1):65–72.

1967. The Kinorhyncha of New Caledonia. In *Expédition Française sur les Recifs coralliens de la Nouvelle-Calédonie,* volume 2, pages 75–90.

1968. Taxonomy and Postembryonic Development of the Cryptorhagae, a New Suborder for the Mesopsammic Kinorhynch Genus *Cateria. Transactions of the American Microscopial Society,* 87(1):21–39.

1969a. Indian Ocean Kinorhyncha: 1, *Condyloderes* and *Sphenoderes,* New Cyclorhagid Genera. *Smithsonian Contributions to Zoology,* 14:1–13.

1969b. Indian Ocean Kinorhyncha. 2. Neocentrophyidae, a New Homalorhagid Family. *Proceedings of the Biological Society of Washington,* 82:113–128.

Johnston, T. H.

1938. Report on the Echinoderida. *Scientific Reports of the Australasian Antarctic Expedition, 1911–1914,* series C, 10(7):1–13.

Lang, K.

1935. Undersökningar över Öresund. Untersuchungen aus dem Öresund XXI. Einige Kleintiere aus dem Öresund. *Lunds Universitets Årsskrift,* 31(10):1–8.

1949. Echinoderida. In J. H. Odhner, editor, *Further Zoological Results of the Swedish Antarctic Expedition, 1901–1903,* volume 4, part 2, pages 1–22.

1953. Reports of the Lund University Chile Expedition 1948–1949. 9. Echinoderida. *Lunds Universitets Årsskrift,* 49(4):1–8.

Leuckart, R.

1854. Bericht über die Leistungen in der Naturgeschichte der niederen Thiere während der Jahre 1848–1853. *Archiv für Naturgeschichte,* 20(2):289–473.

Lou, T. H.

1934. Sur la présence d'un nouveau Kinorhynque à Tchefou: *Echinoderes tchefouensis* sp. nov. *Contributions du Laboratoire de Zoologie, Académie Nationale de Péping,* 1(4):1–9.

McIntyre, A. D.

1962. The Class Kinorhyncha (Echinoderida) in British Waters. *Journal of the Marine Biological Association of the United Kingdom,* 42:503–509.

1964. Meiobenthos of Sub-Littoral Muds. *Journal of the Marine Biological Association of the United Kingdom,* 44:665–674.

1969. Ecology of Marine Meiobenthos. *Biological Reviews,* 44:245–290.

Metschnikoff, E.

1869. Bermerkungen über Echinoderes. Melanges biologiques 7. *Bulletin de l'Académie des Sciences de Saint Pétersbourg,* 4:190–194.

Nyholm, K. G.

1947a. Contributions to the Knowledge of the Postembryonic Development in Echinoderida Cyclorhagae. *Zoologiska bidrag från Uppsala,* 25:423–428.

1947b. *Campyloderes*—An "Antarctic" Genus of Echinoderida off the West Coast of Sweden. *Arkiv für Zoologi,* 39(13):1–6.

1947c. Studies in the Echinoderida. *Arkiv für Zoologi,* 39(14):1–36.

Pagenstecher, H. A.

1875. *Echinoderes Sieboldii. Zeitschrift für wissenschaftliche Zoologie,* supplement, 25(S):117–123.

Pearse, A. S.

1936. *Zoological Names. A List of Phyla, Classes, and Orders.* 24 pages. Durham, North Carolina: American Association for the Advancement of Science.

Rao, G. C., and P. N. Ganapati

1966. Occurrence of an Aberrant Kinorhynch *Cateria styx* Gerlach, in Waltair Beach Sands. *Current Science,* 35(8):212–213.

Reinhard, W.

1881. Über *Echinoderes* und *Desmoscolex* der Umgegend von Odessa. *Zoologischer Anzeiger,* 4(97):588–591.

1887. Kinorhyncha (Echinoderes), ihr anatomischer Bau und ihre Stellung im System. *Zeitschrift für wissenschaftliche Zoologie,* 45:401–467.

Remane, A.

1928. Kinorhyncha. In G. Grimpe and E. Wagler, editors, *Die Tierwelt der Nord- und Ostsee,* 7(d_2):57–84.

1929. Kinorhyncha. In W. Kükenthal and T. Krumbach, editors, *Handbuch der Zoologie,* volume 2, part 1, pages 187–248.

1936. Gastrotricha and Kinorhyncha. In G. G. Bronns, editor, *Klassen und Ordnungen des Tierreichs,* volume 4, part 2, pages 1–385.

Russell-Hunter, W. D.

1968. *Biology of Lower Invertebrates.* 181 pages. New York: Macmillan.

Schepotieff, A.

1907a. Zur Systematic der Nematoideen. *Zoologischer Anzeiger,* 31(5/6):132–161.

1907b. Die Echinoderiden. *Zeitschrift für wissenschaftliche Zoologie,* 88(2):291–326.

1908a. Zur Kenntnis der Echinoderiden. *Zoologischer Anzeiger,* 32(20/21):585–589.

1908b. Das Exkretionssytem der Echinorhynchen. *Zoologisches Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere,* 26:291–304.

Southern, R.

1914. Nemathelmia, Kinorhyncha and Chaetognatha. Clare Island Survey. *Proceedings of the Royal Irish Academy,* 31(54)69–72.

Wieser, W.

1960. Benthic Studies in Buzzards Bay. II. The Meiofauna. *Limnology and Oceanography,* 5:121–137.

Zaneveld, J. S.

1938. Marine Gastrotricha and Kinorhyncha from Scheveningen. *Zoologische Mededeelingen, Leiden,* 20:257–262.

Zelinka, C.

1889. Die Gastrotrichen.Eine monographische Darstellung ihrer Anatomie, Biologie und Systematik. *Zeitschrift für wissenschaftliche Zoologie,* 49:209–384.

1896. Demonstration von Tafeln der Echinoderes—Monographie. *Verhandlungen der Deutschen Zoologischen Gesellschaft,* 6:197–199.

1928. *Monographie der Echinodera.* 396 pages. Leipzig: Wilhelm Engelmann.

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The Current Status of the Systematics of Marine Nematodes

ABSTRACT

The systematics of marine nematodes is discussed in terms of the need for proper study, including the necessity for adequate specimens, the designation of type specimens, and the description, measurement, illustration and diagnosis of species. The need for more detailed studies of species using new techniques is emphasized.

Perhaps there is no taxon of metazoans so commonly obtained in sediment samples as marine nematodes. Nearly every sample of sediment will yield appreciable quantities of nematodes regardless of whether from abyssal depths, intertidal zones, estuaries, or tropical or polar seas. Their great abundance, adaptation to a wide diversity of habitats, and diverse morphology suggest that nematodes play a complex and significant role in the ecology of the marine environment. Yet, few major taxa have received the attention of so few taxonomists, and few taxa have been so consistently ignored by ecologists.

The reasons for this disparity are manifold and complex. For example, until recently there has not been a great deal of interest in benthic ecology; most undergraduate biology courses fail to properly introduce the student to free-living nematodes; study of marine nematodes has not been spurred by economic pressures; the animals are cryptic because of their small size and sediment-inhabitating nature; and time-consuming and laborious techniques must be employed to extract nematodes from sediment and prepare them for study. But probably the most important single reason is the difficult nature of marine nematode systematics, the difficulties having resulted from less than adequate practices in taxonomy.

In order to appreciate the magnitude of these problems, a consideration of the plight of the novice taxonomist or ecologist who for the first time attempts the identification of a collection of marine nematodes is in order. If such a person has had an adequate introduction to the anatomy of marine nematodes, he probably will be able to identify the specimens to the subfamily level by using the chapter on the systematics of the infraclass Adenophorea by de Coninck (1965). By using the extensive collection of keys in Wieser's (1953, 1954, 1956) study of the marine nematodes of the coast of Chile or the keys to the species of the suborder Oncholaimina by Kreis (1943), one may be able to assign specimens to the proper genus. But even if the novice taxonomist does make a correct generic identification, the identification at the specific level will be much more difficult—if at all possible—since so many of the keys are now obsolete. It is true that there has been some effort to keep some of these keys up to date and prepare new ones where needed, but for the almost 400 valid nominal genera, only 68 keys to species have been published in the last ten years. And, of course, many of these are now out of date because of additional new species descriptions.

Consequently, to find the correct specific name for a specimen at hand, assuming it has been described, a search must be made through various abstracting periodicals such as Biological Abstracts, Helminthological Abstracts, and Zoological Record

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in hopes of obtaining references to all work on species of the genus in question. This, of course, is a very time-consuming task and leads to problems of obtaining literature which may be scattered through 50 or more journals. But assuming this is accomplished and descriptions of all species are at hand, there is a good chance the descriptions will be incomplete or in other ways inadequate, and the illustrations may be so diagramatic that at best the identification can be narrowed only to two or three possible species. The final step then becomes an effort to borrow type material of the two or three species still in question, and in this final effort there is once more little chance of success, as a considerable number of marine nematologists have not saved specimens upon which descriptions of new taxa were based—a practice that has occurred as recently as the late 1950s and may well persist today. Or, when specimens have been set aside at the conclusion of a study, they may not have been clearly marked as types or they may have been mounted in formalin, which inevitably evaporates, leaving the specimens in poor condition. Therefore, without the benefit of large collections of correctly identified specimens to work from, an up-to-date index to the species of marine nematodes—of which there are few in the world today—and an extensive collection of literature, it is no wonder that the novice taxonomist or ecologist will turn his interests to less-exasperating taxa.

Such, then, is the plight of the novice who engages in the systematics of marine nematodes, and it depicts the status of marine nematode systematics today. Because these difficulties partially stem from less-than-adequate practices in descriptive taxonomy, it seems that a review of some of the preferred practices is appropriate and justified. These practices are considered below in approximately the same sequence as employed when describing a new taxon.

ADEQUATE MATERIAL—The first step is to judge whether specimens at hand are of sufficient quality and quantity to serve as the basis for a new species description. As a general rule, specimens fixed in alcohol are shrunken and distorted to the point where they are of doubtful value for such descriptions. Measurements of specimens fixed in such a manner are not likely to be representative of the species. Usually males must be available, for in most species they possess diagnostic characters not shared by females or juveniles. Diagnostic descriptions should be based on females in only those few genera in which species are known only from females. Never should new species of free-living marine nematodes be described and named from collections of juvenile specimens alone. Juvenile specimens lack secondary sexual characters, which are imperative for proper identification. Juveniles of a new species may be described and assigned to a genus for any of several reasons, but they should not be given a specific name. In fact, editors of journals should be discouraged from accepting for publication manuscripts that contain new species named and described on the basis of juveniles alone.

The number of specimens to be employed in a type series is rather arbitrary. New species descriptions based on single specimens, regardless of sex, are to be discouraged, however; 10 to 20 specimens of each sex would be more appropriate.

TYPE-SPECIMENS.—At some point in the preparation of a new species description, a holotype specimen must be selected. For the same reason stated above, the holotype should, in most cases, be a male. It should be the best specimen available; that is, it should display to best advantage the greatest number of diagnostic characters.

In most instances the holotype should be mounted individually in anhydrous glycerin and the coverslips sealed with some durable ringing compound such as Murrayite or Zut. Preferably, the specimen should be mounted on Cobb aluminum slides so that the specimens may be observed from either side and so the slide will not break so easily if dropped. Supports should be used to prevent the specimens from being crushed or distorted by the weight of the coverslip. This is especially important, for if such support is not used it will be impossible at later dates to accurately measure the diameter of the body and other structures. The slide should be clearly labeled with the name of the species, sex of the specimen, name of author, date of publication, collection data, identity of the mounting medium, registration or catalog number assigned by the institution in which it is to be deposited for safe keeping, and the word "holotype." A similar slide, with appropriate labeling, also should be prepared for the allotype and for each paratype.

If structures such as the spicula, gubernacula, or stomatal armature cannot be properly studied in situ from whole-mount preparations, then dissections and serial sections should be made from paratype material to obtain the best possible understanding of structural detail; also body parts should be specially oriented in glycerin jelly or other special preparations. These should be preserved with the rest of the type series. It is also advisable, if sufficient material is available, to preserve additional paratype material in small bottles containing anhydrous glycerin. These specimens may be used later for special preparations should the need arise.

DESCRIPTIONS.—Accurate and complete descriptions should be made of all structures known to have, or suspected of having, taxonomic value. While unnecessarily lengthy descriptions are to be avoided, it is even more important to avoid incomplete descriptions, often prepared under the pretenses of reducing publication costs. Such descriptions frequenly prove to be inadequate and necessitate subsequent redescriptions at greater cost and loss of time.

The characters to be included in descriptions are best determined through experience, but when description of a particular taxon is attempted for the first time it is well to compile first a list of taxonomic characters that have been used in previous descriptions of other species of the same genus. Some of the characters obtained for such a list might be of doubtful value and may be discarded, but one should also be alert to useful characters that may have been overlooked by earlier workers. While descriptions of new species should basically be of the holotype, structural variation found among the paratypes also should be given. Incidentally, it is convenient for the purpose of comparing descriptions if the same structures are consistently described in the same sequence for each species.

MEASUREMENTS.—If dimensions of structures are of taxonomic importance they should be determined and expressed in absolute units of measure (microns or millimeters). It is not sufficiently accurate to express dimensions only as fractions or multiples of the dimensions of other structures; i.e., "tail length equal to 3 anal-body diameters." Further, measurements should be given separately for the holotype and allotype, and at least the range of values, if no other statistic, for the paratypes. If new or unusual structures are being measured, the precise points between which the measurements are made should be clearly understood. A scale should be included with each illustration and photograph so that measurements given in the text may be checked against the illustration.

ILLUSTRATIONS.—Anatomical structure can almost always be represented graphically with greater accuracy and more clarity than by verbal descriptions. Consequently, descriptions of all important characters should be accompanied by accurate illustrations or photographs. Drawings should not be made free-hand, but rather with the aid of a camera lucida or other device that will provide at least comparable accuracy.

Illustrations should not be so diagrammatic that important taxonomic detail is lost, and structures should be studied until they are well understood before attempting to illustrate them, even if this necessitates special specimen preparations. Photographs are preferred to drawings, but they have limited application because of problems with depth of focus.

DIAGNOSIS.—A diagnosis should follow the description of each new species. The character or characters by which the new species differs from those to which it is judged to be most closely related must be stated precisely. Preparation of a key to the species of a genus may be useful in determining the closest affinities of a new species if they are not otherwise evident.

No doubt there are additional ways in which the general quality of the alpha taxonomy of marine nematodes can be improved, but the preceding recommendations cover some of the major problems.

In addition to the problems that exist at the level of alpha taxonomy, there is a continuing need for easier inroads into the taxonomy and systematics of marine nematodes. Here, reference is made to the need for keys, checklists, bibliographies, revisions, and monographs. Contributions of this nature are the responsibility of those working in institutions where all or most of the marine nematode literature, large collections of specimens, and species indices are available. There are few such institutions in the world today, and those that exist should encourage work in these directions.

A final trouble area to be mentioned is the higher classification of marine nematodes. For the most part, the classification used today is the same as that proposed by Filipjev (1916, 1918, 1921, 1927, 1934), with minor modifications by several ensuing nematologists. But this classification is based largely on light microscope studies of whole-mount specimens. As a result, the evolution and systematic importance of amphids, the male copulatory complex, stomatal armature, esophagus, and other features are not adequately known. Further, so little is known about other anatomical features whose detailed structure is beyond the resolution of the light microscope—such as the cuticle, muscle, and nervous system—that they may be regarded as untapped sources of taxonomic data. The electron microscope now makes these sources available. Also, the stereoscan electron microscope will provide valuable data regarding surface features of the cuticle, structure of the amphids, lips, cephalic setae, stoma, and ventromedian copulatory supplements of the male. Indeed, it is predictable that during the next several years there will be dramatic changes in the means by which nematode anatomy may be recorded for taxonomic studies, and with unprecedented accuracy.

Summary

An attempt has been made to provide an impression of the current status of marine nematode taxonomy and to identify some of the underlying problems. The approximately 6,000 nominal species known today probably represents much less than half of the species that exist. If taxonomists of marine nematodes are to move ahead in the task that lies before them, and not become mired in problems created by taxonomists themselves, they must set and attain high standards, keeping in mind that the new species and other taxa described today must be distinguished not only from those previously described but from the many that are yet to be described.

Literature Cited

de Conick, L.
1965. Systématique des Nématodes. In P. P. Grassé, editor, *Traité de Zoologie*, 4:586–726.

Filipjev, I. N.
1916. Les Nématodes libres contenus dans les collections du Musée Zoologique de l'Académie Impériale des Sciences de Petrograd. *Extrait de l'annuarie du Musée zoologique de l'Académie Impériale des Sciences*, 21:59–116.
1918. Free-Living Marine Nematodes of the Sevastopol Area. *Trudy Osoboi Zoologischeskoi Laboratorii I Sevastopol 'Skoi Biologischeskoi Stantsii Rossiiskoi Akademii Nauk*, 2(4):1–350.
1921. Free-Living Marine Nematodes of the Sevastopol Area. *Trudy Osoboi Zoologischeskoi Laboratorii I Sevastopol 'Skoi Biologischeskoi Stantsii Rossiiskoi Akademii Nauk*, 2(4):353–614.
1927. Les Nématodes libres des mers septentrionales appartenant à la Famille des Enoplidae. *Archiv für Naturgeschichte*, 91:1–216.
1934. The Classification of the Free-Living Nematodes and Their Relation to the Parasitic Nematodes. *Smithsonian Miscellaneous Collections*, 89(6):1–63.

Kreis, H. A.
1934. Oncholaiminae Filipjev 1916 eine Monographische Studie. *Capita Zoologica*, 4(5):1–271.

Wieser, W.
1953. Reports of the Lund University Chile Expedition 1948–1949. 10. Free-Living Marine Nematodes. I. Enoploidea. *Lunds Universitets Arsskrift*, 49(6): 1–155.
1954. Reports of the Lund University Chile Expedition 1948–1949. 10. Free-Living Marine Nematodes. II. Chromadoroidea. *Lunds Universitets Arsskrift*, 50(16):1–148.
1956. Reports of the Lund University Chile Expedition 1948–1949. 10. Free-Living Marine Nematodes. III. Axonolaimoidea and Monhysteroidea. *Lunds Universitets Arsskrift*, 52(13):1–115.

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The Meiobenthic Bryozoa

ABSTRACT

The morphology, ecology, and techniques for study of *Monobryozoon ambulans* and *Monobryozoon limicola* are discussed. The lunulitiform Bryozoa are considered briefly.

The Bryozoa constitute a relatively insignificant part of the meiobenthos. Like the Tunicata, however, the modifications of sedentary organisms to a relatively unstable habitat are interesting. Two groups of meiobenthic Bryozoa are known, the truly interstitial genus *Monobryozoon* Remane and the epibenthis lunulitiform species. Knowledge of both groups is scarce. *Monobryozoon* is known from Helgoland, Germany (Remane, 1936, 1938), the Gullmar Fjord, Sweden (Franzen, 1960), Robin Hood's Bay, England (Gray, in press) and Roscoff, France (Monniot, unpublished). The lunulitiform species are not well known but they appear to have a widespread distribution (Cook, 1963, 1965a–c, 1966; Lagaaij, 1963a,b; and Marcus and Marcus, 1962).

As the author is familiar only with *Monobryozoon,* the remarks are concerned mainly with this genus. Only two species are known, *Monobryozoon ambulans* Remane and *M. limicola* Franzen. Neither species is abundant. *Monobryozoon ambulans* is described from seven specimens (Remane, 1936, 1938). More recently, Gray (in press) reported the finding of 15 specimens in England. *Monobryozoon limicola* has been found at Gullmar Fjord, Sweden, in larger numbers (240 specimens) by Franzen (1960); at Roscoff, France, by F. Monniot (unpublished), and at Robin Hood's Bay, England, by Gray (unpublished). No quantitative sampling methods have been used.

Monobryozoon ambulans, when alive, is yellow-brown, the same color as the substratum it inhabits. Further, the "locomotion" exhibited is slow and cumbersome and does not aid location of specimens in a dish, as do the movements of many interstitial species. The animals are robust and are not likely to be easily damaged.

Monobryozoon ambulans lives in coarse shell-gravel whereas *M. limicola* lives in soft mud. The morphological differences between the species reflect the habitat differences. Figure 1 shows diagrammatically the differences between the two species.

Monobryozoon ambulans is small (up to 2 mm tall) and has up to 15 short, thick stolons, each less than half the width of the animal. *Monobryozoon limicola* is larger (up to 2.5 mm tall) but thinner, and has two or three long, thin stolons, each greater than the width of the animal. The collar in *M. ambulans* is short, whereas in *M. limocola* it is much longer.

Since *Monobryozoon ambulans* occurs sublittorally, samples of coarse shell-gravel can be taken with a grab or dredge. The sediment samples are then placed in large polyethylene bags which are kept in running seawater. The animals survive well within the substratum, and oxygen diffuses through the bag walls. *Monobryozoon limicola* inhabits the rich detrital layer covering mud at depths down to 55 m. Samples are best taken with an epibenthic sledge.

For extraction of both species, the traditional method of anaesthetization, with $MgCl_2$ (73.2 g/liter isotonic to 34 ppt seawater) for 10 minutes, followed by filtration of the supernatant liquid through a fine-mesh plankton net after vigorous agitation, is successful. The net is inverted in a Petri dish and the animals and substratum are washed off with normal seawater. The dish must be examined with extreme care under low-power microscope. Once extracted, both species survive well in dishes containing substratum and seawater

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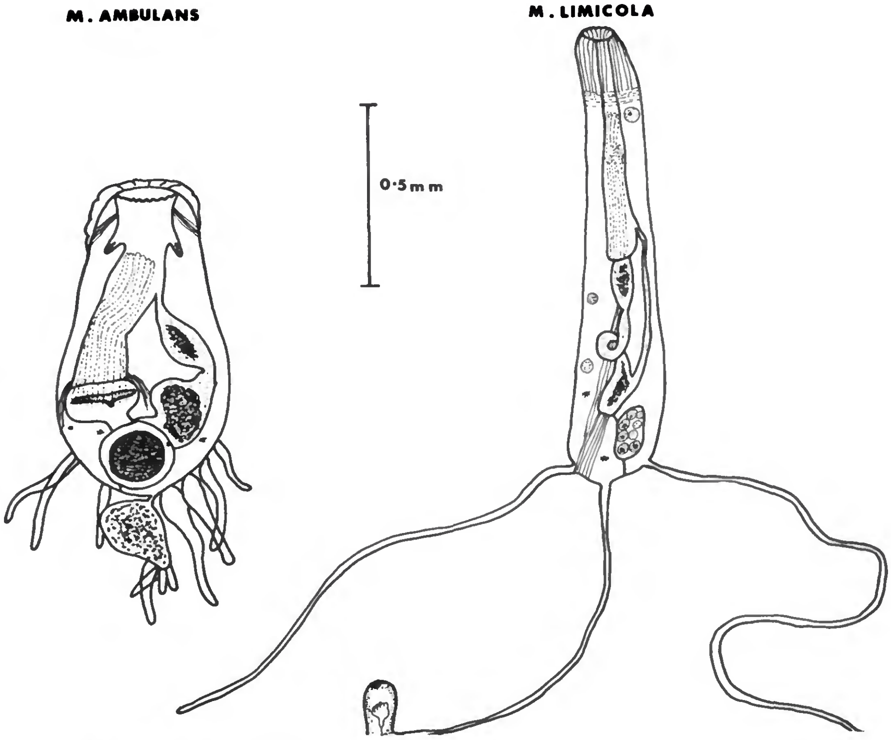

FIGURE 1.—Diagram of the two known species of *Monobryozoon,* showing morphological differences.

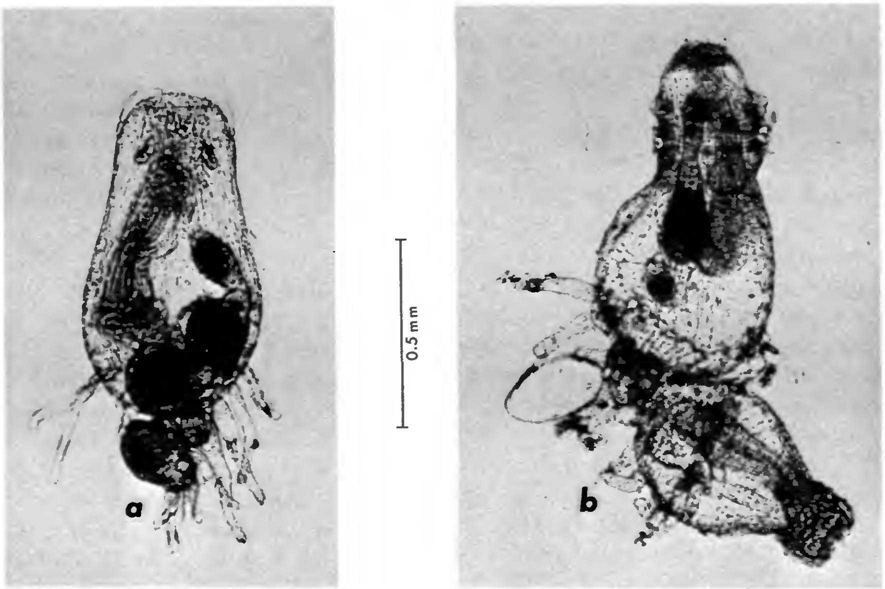

FIGURE 2.—Photomicrographs of living *Monobryozoon ambulans. a,* Individual with contracted lophophore; note egg and asexually produced bud produced from a stolon; *b,* mature, asexually produced individual still attached to parent.

kept at 8° to 10° C. It is difficult, however, to induce the animals to extend the lophophore, even under anaesthetics. For anatomical studies, relaxed animals are essential. Six percent formalin or 1.5 percent propylene phenoxetol have been used as preservatives.

As there are only two known species, keys are not necessary. Specimens of the Robin Hood's Bay population of *Monobryozoon ambulans* have been examined by the author. Figure 2 shows examples of *M. ambulans* with a ripe egg (Figure 2*a*) and with a mature asexually produced bud (Figure 2*b*). Specimens of *M. limicola* are deposited in the museum of the zoology department, University of Uppsala, Sweden.

The genus *Monobryozoon* is suspected of having a much wider sublittoral distribution pattern than is known at present. The extreme difficulty of locating nonmotile specimens of a color similar to the substratum in a dish is probably the reason for our lack of knowledge of this group.

The lunulitiform Bryozoa inhabit a variety of substrata from shell-gravel to mud. They show modifications of typically sedentary species in having discoidal or conical shapes, and they may be free-living or be attached to the substratum by rootlets. Typically, the lunulitiform Bryozoa have small numbers of zoecia in each colony, and the colonies themselves are small. Specimens have been recorded from depths of 10 to 805 m. The works of Cook (1963, 1964a,b, 1965a–c, 1966), Lagaaij (1963a,b), and Marcus and Marcus (1962) should be consulted for detailed information on the lunulitiform Bryozoa.

Literature Cited

Cook, P. L.

1963. Observations on Live Lunulitiform Zoaria of Polyzoa. *Cahiers de Biologie Marine,* 4:407–413.

1964a. Polyzoa from West Africa. 1. Notes on the Steganoporellidae, Thalamoporellidae and Onychocellidae (Anasca, Coilostega). *Annales de l'Institut Oceanographique, (Calypso, VI),* 41:43–78.

1964b. Polyzoa from West Africa. Notes on the Genera *Hipporina* Neviana, *Hippoporella* Canu, *Cleidochasma* Harmer and *Hippoporidra* Canu and Bassler (Cheilostomata, Ascophora). *Bulletin of the British Museum (Natural History), Zoology,* 12:1–35.

1965a. Notes on the Cupuladriidae (Polyzoa, Anasca). *Bulletin of the British Museum (Natural History), Zoology,* 13:151–187.

1965b. Polyzoa from West Africa. The Cupuladriidae (Cheilostomata, Anasca). *Bulletin of the British Museum (Natural History), Zoology,* 13:189–227.

1965c. Notes on Some Polyzoa with Conical Zoaria. *Cahiers de Biologie Marine,* 6:435–454.

1966. Some "Sand Fauna" Polyzoa (Bryozoa) from Eastern Africa and the Northern Indian Ocean. *Cahiers de Biologie Marine,* 7:207–223.

Franzen, A.

1960. *Monobryozoan limicola* n. sp., a Ctenostomatous Bryozoan from the Detritus Layer on Soft Sediments. *Zoologiska bidrag från Uppsala,* 33:135–148.

Gray, J. S.

In press. Occurrence of the Aberrant Bryozoan *Monobryozoan ambulans* Remane off the Yorkshire Coast. *Journal of Natural History.*

Lagaaij, R.

1963a. *Culpuladria canariensis* (Busk)—Portrait of a Bryozoan. *Paleontology,* 6:172-217.

1963b. New Additions to the Bryozoan Fauna of the Gulf of Mexico. *Publications of the Institute of Marine Science,* 9:162–236.

Marcus, Eveline, and Ernesto Marcus

1962. On Some Lunulitiform Bryozoa. *Boletim de Faculdade de Filosofia, Ciências e Letras de Universidade de São Paulo, Zoologia,* 24:281–324.

Remane, A.

1936. *Monobryozoon ambulans* n.g. n.sp., ein eigenartiges Bryozoon des Meeresandes. *Zoologischer Anzeiger,* 113:161–167.

1938. Ergänzende Mitteilungen über *Monobryozoon ambulans* Remane. *Kieler Meeresforschungen,* 2:356–358.

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A Review of Gastropoda, Brachiopoda, and Echinodermata in Marine Meiobenthos

ABSTRACT

The morphological and reproductive adaptations of the meiobenthic Gastropoda, Brachiopoda, and Echinodermata are discussed. Keys for the Pseudovermidae and the marine species of Acochlidiacea (Gastropoda, Opisthobranchia) are given.

Since small body size is unusual in gastropods, brachiopods, and echinoderms, these systematic units are minor constituents of the meiofauna. This does not mean, however, that they are unimportant for the meiobenthologist. Of general biological interest are the adaptations that these taxa have made to the ecological demands of the environment. They have a reduced or modified anatomy which may cause problems for the phylogenist and systematist who study relationships between these aberrant forms and the more-typical members of their taxa.

Up to the present time, most of the work concerning these animals has been devoted to morphology and general biology, and little is known about population densities and the particular role that these animals may play in food chains and the general dynamics of the meiobenthos. Brachiopods and echinoderms are represented in the meiobenthos by very few permanent members; the gastropods are relatively more important.

Gastropoda

Best known among the prosobranchs is the genus *Caecum* Fleming (Figure 1*a*), with two European species which are characteristic members of the interstitial fauna of the so-called "*Amphioxus* sand." The slightly curved shell of this 1-mm-long animal is an effective adaptation to living conditions in the interstitial environment. The anatomy, which presents features of reduction, is well known from the studies of Götze (1938). *Caecum* belongs to the important group of interstitial animals that feed on diatoms.

The opisthobranchs are represented in the meiobenthos by the following groups: the order Acochlidiacea with eleven species, the order Philinoglossacea with three species, and the Aeolid family Pseudovermidae with eight species.

The Acochlidiacea (Figure 1*b*) were first studied by Kowalevsky (1901) in sublittoral sand and shell debris in the eastern Mediterranean. The systematics has been studied by Thiele (1931), Odhner (1937, 1952), Marcus (1953), Challis (1968), and Swedmark (1968). Odhner derives the Acochlidiacea from the primitive family Diaphanidae, but there is no generally accepted opinion on the natural systematic position of these shell-less opisthobranchs. The small body size (0.8 to 3 mm) and the consequently small number of cells available for anatomical differentiation resulted in regressions in structure in the evolution of the Acochlidiacea. Regression is observed in several organ systems: there are no ctenidia, there is only one tubular digestive gland, the radula is simplified, the sexual apparatus is much less differentiated than is usual in opisthobranchs. The regres-

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sive characters often are combined with morphological specialization. One such character is the differentiation of spicules in certain species. In *Hedylopsis loricata* Swedmark, a species living in sublittoral shell dunes, the large epidermal spicules cover the entire surface of the visceral sac, giving it a shell-like rigidity. This secondary "shell" undoubtedly is of importance for the mechanical protection of this animal, which lives in a particularly dynamic biotope where the sediment particules are continuously displaced by the action of currents.

The Acochlidiacea also present interesting adaptations in their reproductive biology. Such adaptations are necessary for the maintenance of populations, because the animals produce very few gametes. In the Acochlidiacea, fertilization is cutaneous without copulation. The animals produce spermatophores which become attached to the epidermis of the animal to be fertilized, and the spermatozoa penetrate the mucuous base of the spermatophore and the epidermis. This type of fertilization is not known to occur in other molluscs, but it has been studied in certain Turbellaria and Archiannelida.

It is the regressive character, combined with specializations in the anatomy of the Acochlidiacea, which makes this order systematically isolated. More detailed knowledge of the anatomy is needed in order to learn the evolutionary pathways which have led to the organization of the Acochlidiacea. We can expect that more species will be discovered in the coming years and may help us in the analysis of the systematic position of these opisthobranchs.

The key for the identification of genera and species, given below, differs considerably from the one given by Odhner (1952).

Philinoglossa helgolandica Hertling (Figure 1*c*) and *Pluscula cuica* Marcus form another group of

Key to the Marine Acochlidiacea

A. Family Microhedylidae: labial tentacles of same shape or slightly larger than rhinophores; the latter may be reduced or absent; posterior region of digestive gland (liver) bent forward or looped; sexes separate; no vas deferens.
  1. Radula: *n*(2.1.2).
    a. Digestive gland without loop .... ***Microhedyle*** Hertling
      (1) With rhinophores.
        (a). $n = 34$ to 35 .... ***M. glandulifera*** (Kowalevsky)
        (b). $n = 39$ to 44 .... ***M. lactea*** Hertling
      (2) Without rhinophores .... ***M. milaschewitchii*** (Kowalevsky)
    b. Digestive gland with loop .... ***Parhedyle*** Thiele; ***P. tyrtowii*** (Kowalevsky)
  2. Radula: *n*(1.1.1).
    a. With rhinophores .... ***Unela*** Marcus
      (1) No spicules; no eyes .... ***U. remanei*** Marcus
      (2) With spicules; with eyes .... ***U. odhneri*** (Delamare Deboutteville)
    b. Without rhinophores .... ***Ganitus*** Marcus; ***G. evelinae*** Marcus
  3. Radula: *n*(0.1.0) .... ***Paraganitus*** Challis
    Digestive gland looped, male intraepidermal duct present .... ***P. ellynae*** Challis
B. Family Hedylopsidae: labial tentacles usually larger than rhinophores; digestive gland forms a straight tube; external male duct (ciliated groove from genital pore to right rhinophore); hermaphroditic; one genus, ***Hedylopsis*** Thiele.
  1. Radula: *n*(1.1.1).
    a. With eyes.
      From 3 to 4 mm long; white, opaque .... ***H. spiculifera*** (Kowalevsky)
      (***H. suecica*** Odhner = local form)
    b. Without eyes.
      From 0.8 to 1 mm long; dense epidermal spicules make the wall of visceral sac a "secondary shell" .... ***H. loricata*** Swedmark
  2. Radula: n(2.1). Without eyes .... ***H. brambelli*** Swedmark

NOTE: In the radula formula, *n* is the number of radular series. The three numbers signify elements of radular series: (2.1.2) = one median and one lateral plate at each side of the central tooth; (1.1.1) = one lateral plate at each side of the central tooth; (0.1.0) = central tooth, plates absent.

opisthobranchs belonging to the interstitial fauna of sand (Hertling, 1932; Marcus, 1953). The group, named Philinoglossacea, was erected as a distinct order by Hoffmann (1933). Both Odhner (1952) and Böttger (1955) derive Philinoglossacea from the primitive Notodiaphanidae, but here, too, regression in structure and a modified organization considerably hamper a systematic evaluation.

The eight known species belonging to the family Pseudovermidae are aeolid opisthobranchs with a peculiar, elongated shape of body. All belong to the interstitial fauna of sand. The head of *Pseudovermis* Periaslavzewa (Figure 1*d*) is acorn-like in shape and is without appendages.

All species have liver papillae, though these are more or less reduced in some species. The papillae sometimes contain nematocysts, indicating that *Pseudovermis* may prey on interstitial cnidarians such as *Psammohydra* Schulz and *Halammohydra* Remane, which usually live in the same habitat.

The biology of reproduction is of the same type as in Acochlidiacea and Philinoglossacea. In *Pseudovermis,* which is hermaphroditic, fertilization is believed to occur after copulation. The veliger larvae develop in adhesive cocoons attached to sand grains. The hatched veliger larvae swim slowly and lack photic reaction. This is evidence for a sessile development, counteracting dispersion of the larvae and keeping them within the territory of the

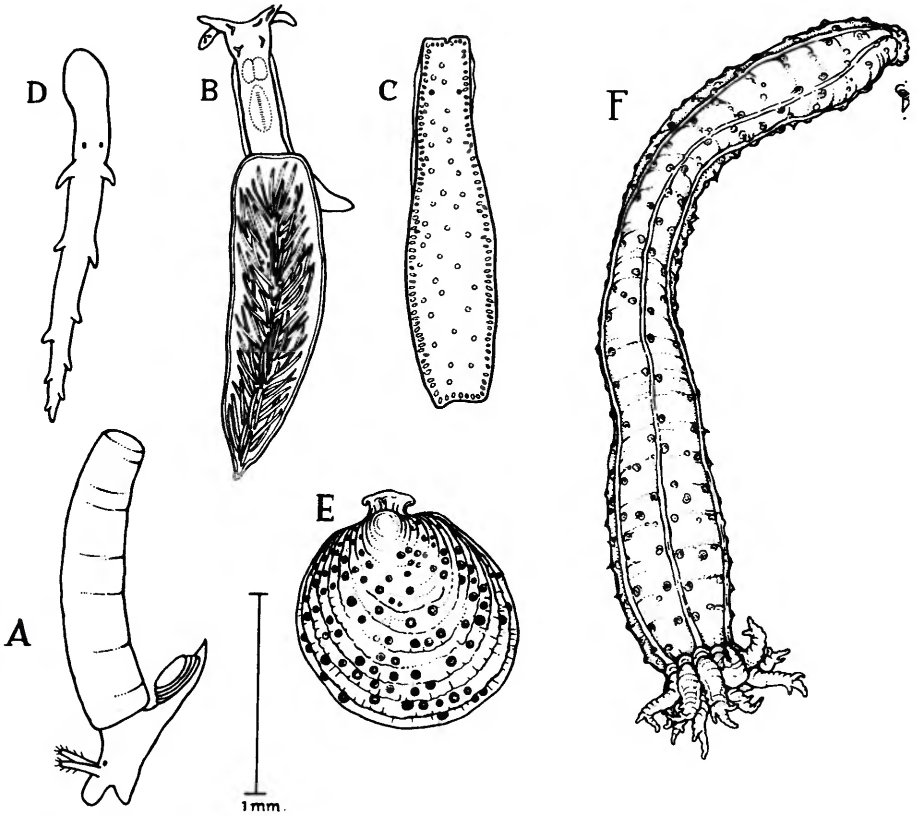

FIGURE 1.—Gastropoda, Brachiopoda, Echinodermata. *a, Caecum glabrum* (Montagu); *b, Hedylopsis brambelli* Swedmark; *c, Philinoglossa helgolandica* Hertling; *d, Pseudovermis papillifer* (Kowalevsky); *e, Gwynia capsula* Jeffreys; *f, Labidoplax buskii* (M'Intosh).

population. This can be considered a necessary adaptation in these animals, which produce few gametes (Swedmark, 1968a).

The family Pseudovermidae consists of one genus, *Pseudovermis.* The species are from 1 to 6 mm long. The head is acorn-shaped and without appendices. The pedal epidermis is ciliated and there is no distinct foot. The papillae occur in lateral rows. The pharynx has one pair of jaws. The radula formula is n (1.1.1), where $N = 26–36$. The median plate has one median denticle and from four to seven lateral denticles. The lateral plates have one or two points. The salivary gland is paired and there is one digestive gland. The genital pore is located on the right side in front of the anus. (Description from Salvini Plawen and Sterrer, 1968).

A key for the identification of seven species of the Pseudovermidae has been published by Salvini Plawen and Sterrer (1968). That key, with the addition of an eighth species, *P. setensis* Fize, is given below.

Key to Species of *Pseudovermis,* Family Pseudovermidae

1\. Without eyes 2
With eyes 3
2\. Long, finger-like papillae, median radular plate with nine denticles, lateral plates with one point .... ***P. salamandrops*** Marcus
Papillae very small, median radial plates with 11–15 denticles, lateral plates with two points .... ***P. axi*** Marcus and Marcus
3\. Papillae very small, retractile, visible on contracted animal only; anterior margin of jaws dentated 4
Long, nonretractile, finger-like papillae, distinct even on extended animals; anterior margins of jaws smooth .... ***P. papillifer*** Kowalevsky
4\. More than 10 pairs of papillae (13 pairs).......... ***P. kowalevskyi*** Salvini Plawen and Sterrer
Fewer than 10 pairs of papillae 5
5\. Not more than five papillae in total, lateral radular plates with two points ***P. schulzi*** Marcus and Marcus
Seven or eight papillae at each side 6
Five papillae at each side 7
6\. Papillae paired (symmetrically), lateral radular plates with one point ***P. paradoxus*** Periaslavzewa
Papillae in asymmetrical arrangement, lateral radular plates with two points ***P. boadeni*** Salvini Plawen and Sterrer
7\. Papillae in asymmetrical arrangement, lateral radular plates with one point....***P. setensis*** Fize

BRACHIOPODA

As far as we know, there is only one brachiopod that belongs to the meiofauna. *Gwynia capsula* Jeffreys (Figure 1*e*), with a shell diameter of only 1 mm, was described as early as 1859 by Jeffreys. Until recently, it was considered a doubtful species and perhaps the juvenile form of some larger species. The author has found mature specimens (at Bangor, North Wales) and has been able to study part of their development; therefore, it can be concluded that *Gwynia capsula* is a distinct species (Swedmark, 1967).

Gwynia Jeffreys is an articulate brachiopod and is the smallest known genus within the group. As in many other small forms in various systematic groups, the anatomy of *Gwynia* has peculiar features that perhaps are the result of a small number of cells. The lophophore is trocholophous, the simplest type in any brachiopod.

Originally, *Gwynia* was found under stones and pebbles in the littoral zone. Later it became known as a permanent member of the interstitial fauna of sand and shell debris (Menai Strait, Anglesey, North Wales). Along with some Foraminifera and coelenterates, it is one of the rare sedentary animals of this fauna.

For a brachiopod, the reproductive biology of *Gwynia* is peculiar. The eggs, 2 to 6 in number, develop in a kind of maternal pouch up to a stage when three segments are well differentiated, before the larvae are liberated.

ECHINODERMATA

In sublittoral sand and mud, juvenile ophiuroids are seasonally frequent, but other echinoderms are rare in the meiofauna. The most important echinoderms which are permanent members of the meiobenthos are apodous holothurians. Three of these synaptids are common in European waters: *Rhabdomolgus ruber* Keferstein, *Leptosynapta minuta* Becher, and *Labidoplax buskii* M'Intosh (see Becher, 1906; Nyholm, 1952). A fourth form, *Psammothuria ganapatii*, recently has been described from the Waltair coast in India (Rao, 1968). All are vermiform, and 2 to 8 mm long. *Labidoplax buskii* (Figure 1*f*) is a characteristic member of the fauna of sublittoral mud, the other three species belong to the interstitial fauna of sand.

The tentacles, digitate in *Labidoplax* Oerstergren and *Psammothuria* Rao and simple in the other two species, are of importance not only for the ingestion of food but also for locomotion.

All species are provided with statocysts, each of which contain one or more statoliths. The positive geotaxis, manifested by the synaptids of the meiofauna, is believed to be mediated by the statocysts, but these organs also serve for orientation in the interstitial environment. It is well known from the works of Remane (1952) that the interstitial fauna contains a notable fraction of species with static organs.

The animals are hermaphroditic, and the development has been studied by Becher (1906) for *Leptosynapta minuta* and by Nyholm (1952) for *Labidoplax buskii*. They produce a small number of eggs. Coelomic incubation occurs in *Leptosynapta minuta* and from 2 to 4 embryos at a time develop in the coelomic cavity of the mother.

Literature Cited

Becher, S.
1906. Über *Synapta minuta* n. sp., eine brutpflegende Synaptide der Nordsee, und über die contractilen Rosetten der Holothurien. *Zoologischer Anzeiger*, 30(11/12):505–509.

Böttger, C. R.
1955. Die Systematik der euthyneuren Schnecken. *Zoologischer Anzeiger*, Supplementband 18:253–280.

Challis, D. A.
1968. A New Genus and Species of the Order Acochlidiacea (Mollusca: Opisthobranchia) from Melanesia. *Transactions of the Royal Society of New Zealand, Zoology*, 10(20):191–197.

Götze, E.
1938. Bau und Leben von *Caecum glabrum* (Montagu). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, 71:55–122.

Hertling, H.
1932. *Philinoglossa helgolandica*, n.g., n.sp., ein neuer Opisthobranchier aus der Nordsee bei Helgoland. *Wissenschaftliche Meeresuntersuchungen*, 19(1):1–9.

Hoffman, H.
1933. Opisthobranchia. In G. C. Bronns, editor, *Klassen und Ordnungen des Tierreichs*, 3(2):1–1247.

Jeffreys, J. G.
1859. Additional Gleanings in British Conchology. *Annals and Magazine of Natural History*, series 3, 4:189–201.

Kowalevsky, A.
1901. Les Hédylides, étude anatomique. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg*, 12(6):1–32.

Marcus, Ernesto
1953. Three Brazilian Sand-Opistobranchia. *Boletim de Faculdade de Filosofia, Ciências e Letras de Universidade de São Paulo, Zoologica*, 18:165–203.

Nyholm, K.-G.
1952. The Development and Larval Form of *Labidoplax buskii*. *Zoologiska Bidrag från Uppsala*, 29:239–254.

Odhner, N. Hj.
1937. *Hedylopsis suecica* n. sp. und die Nacktschneckengruppe Acochlidiacea (Hedylacea). *Zoologischer Anzeiger*, 120:51–64.
1952. Petits Opisthobranches peu connus de la côte méditerranéenne de France. *Vie et Milieu*, 3:136–147.

Rao, G. C.
1968. On *Psammothuria ganapatii* n. gen. n. sp., an Interstitial Holothurian from the Beach Sands of Waltair Coast and Its Autoecology. *Proceedings of the Indian Academy of Sciences*, 67(5):201–206.

Remane, A.
1952. Die Besiedelung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. *Zoologischer Anzeiger*, Supplementband 16:327–339.

Salvini Plawen, L., and W. Sterrer
1968. Zur Kenntnis der mesopsammalen Gattung *Pseudovermis* (Gastropoda, Nudibranchia). *Helgoländer wissenschaftliche Meeresuntersuchungen*, 18:69–77.

Swedmark, B.
1967. *Gwynia capsula* (Jeffreys), an Articulate Brachiopod with Brood Protection. *Nature*, 213:1151–1152.
1968a. The Biology of Interstitial Mollusca. *Symposia of the Zoological Society of London*, 22:135–149.
1968b. Deux espèces nouvelles d'Acochlidiacées (Mollusques Opisthobranches) de la faune interstitielle marine. *Cahiers de Biologie Marine*, 9:175–186.

Thiele, J.
1931. *Handbuch der systematischen Weichtierkunde*. I–III. Jena: Gustav Fischer.

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Status of the Knowledge of the Systematics and Ecology of Archiannelida

ABSTRACT

The systematics and ecology of the marine Archiannelida are reviewed. Keys to the species of *Saccocirrus* and to the genera of the family Nerillidae are given.

The Archiannelida form a heterogeneous group of annelids and should be considered an order of Polychaeta (Hermans, 1969). This order is composed of five families that have few affinities with each other or with other families within the Polychaeta. From the aspect of morphology (see Figure 1), archiannelids are aberrant, some being without parapodia and setae (Polygordiidae, Protodrilidae, Dinophilidae) and others very reduced in size (Dinophilidae, Nerillidae). Formerly, archiannelids were regarded as primitive annelids, but, according to modern views, they are either regressive, secondarily altered annelids (Remane, 1932) or annelids primarily adapted for interstitial life (Hermans, 1969).

Since several of the Archiannelida can be collected in great numbers, they form suitable and interesting objects for experimental studies of ecology. These aberrant annelids have been exciting study material for morphologists and taxonomists —especially during recent years, since many new archiannelids have been discovered.

Nearly all archiannelids live in marine sediments, and most of them are small. In the Dinophilidae and Nerillidae, most species are less than 1 mm long. The species in the other three families are, as a rule, elongated. Species of *Polygordius* may become 80 mm long and 1 mm broad; consequently, they should be assigned to the macrobenthos.

Generally speaking, the larger archiannelids (*Polygordius*) are endopsammic and the smaller ones are mesopsammic except for *Paranerilla,* which is known from subtidal mud. *Nerilla* and *Dinophilus* seem to be less dependent than the others on the nature of the sediment and they live in various biotopes.

Most Protodrilidae are exclusively marine, but some species occur in brackish water and two even occur in fresh water (Pierantoni, 1908). *Troglochaetus,* which is closely related to the marine *Nerillidum* and *Thalassochaetus,* is a hypogeal form, occurring in continental fresh water.

Family POLYGORDIIDAE

Genus *Polygordius* Schneider

Twelve species of *Polygordius* are known. The specific characteristics are mainly the size of the body, the shape of the pygidium and its adhesive papillae, the nuchal organs, circulatory apparatus, and sperm. *Polygordius* lives in infralittoral sediments ("*Amphioxus* sand") or, less often, in the intertidal zone. Its geographical distribution includes the Mediterranean Sea, Adriatic Sea, Black Sea, North Sea, English Channel, Atlantic Ocean, and Indo-Pacific waters.

A key to the species has been published by Marcus (1948) but it is incomplete; other important

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works are those of Aiyar and Alikunhi (1944) and Marcus (1955).

Family PROTODRILIDAE

The family Protodrilidae is composed of two genera, *Protodrilus* Hatschek with twenty species and *Protodriloides* Jouin, with two species. Half of the species of *Protodrilus* are described in older works and are included in Pierantoni's (1908) monograph.

Jägersten (1952) has published an excellent work on the anatomy of four species from Gullmar Fjord, Sweden, in which he shows that some characteristics of the males are of great taxonomic value. When determining species of *Protodrilus*, it is always important to have sexually mature individuals available, and it is quite necessary to have such specimens at hand if new species are to be described. The following anatomic characteristics are important from the aspect of taxonomy: position of the salivary glands and the front limit of the fertile region of the body, shape and size of the lateral organs of the males, and position and number of the spermducts.

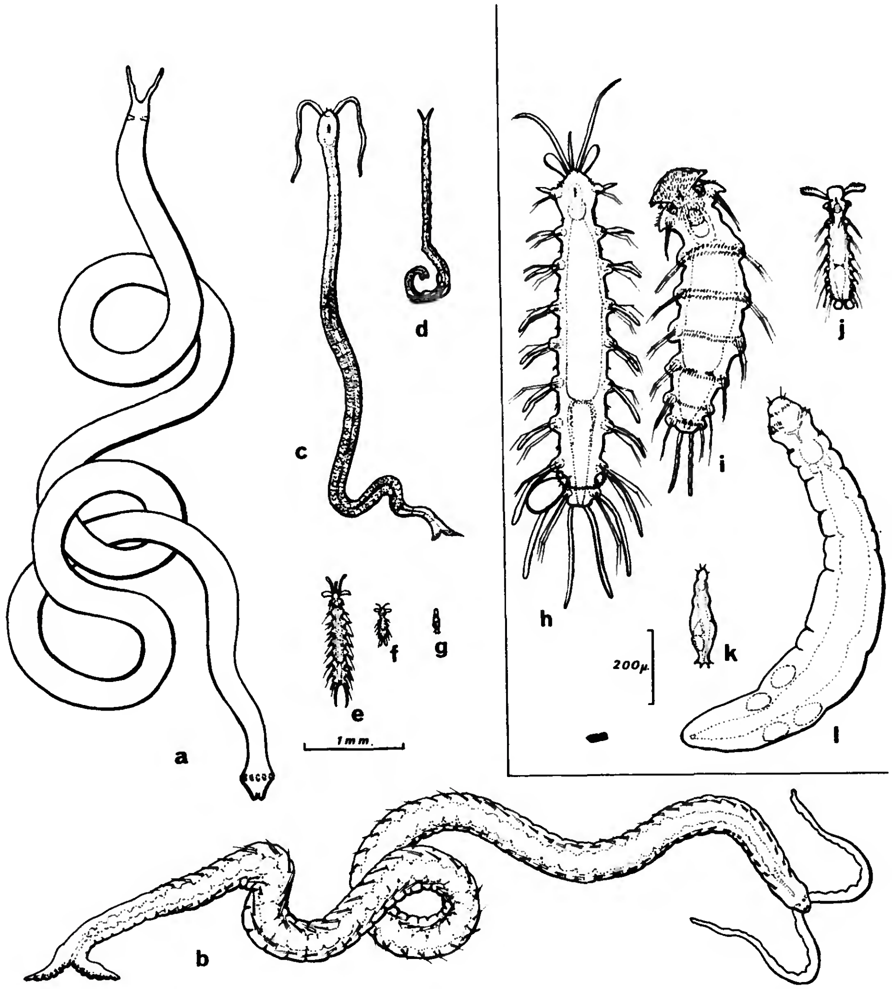

FIGURE 1.—Diagrams of typical Archiannelida. *a, Polygordius; b, Saccocirrus; c, Protodrilus; d, Protodriloides; e, Mesonerilla; f, Nerillidium; g, Diurodrilus; h, Mesonerilla intermedia; i, Paranerilla limicola; j, Nerillidum simplex; k, Diurodrilus; l, Trilobodrilus.*

Pierantoni's (1908) monograph includes the general morphological characteristics but since that work contains some errors and is incomplete in some respects there has been a need for a revision of *Protrodrilus.* In a revision by the present author (Jouin, in preparation) eleven species will be studied; among these, three will appear as new. Figure 2 shows the most important characters of the males in four species revised by the author and in four species studied by Jägersten (1952).

The genus *Protodriloides* includes only two known species (Jouin, 1966): *P. chaetifer* (Remane), which has small setae, and *P. symbioticus* (Giard), which is without setae but which has, instead, segmental adhesive organs.

Protodriloides has yellowish green inclusions in the epidermis. The tentacles, which point forward, are without the tentacle channel characteristic of *Protodrilus* and *Saccocirrus.* Both salivary glands and lateral organs are lacking; the sperm are without flagella (Jouin, 1966). The females have large, yolk-rich eggs that are deposited in a cocoon in which fertilization takes place. Development is direct (Swedmark, 1954; Jouin, 1962).

The geographic distribution of *Protodrilus* includes the Mediterranean Sea; Black Sea; North Sea; English Channel; the Skagerrak; Atlantic Ocean including Europe, Brazil, and east coast of the United States; Indo-Pacific waters, including India, South Africa (collected by C. Berrisford and

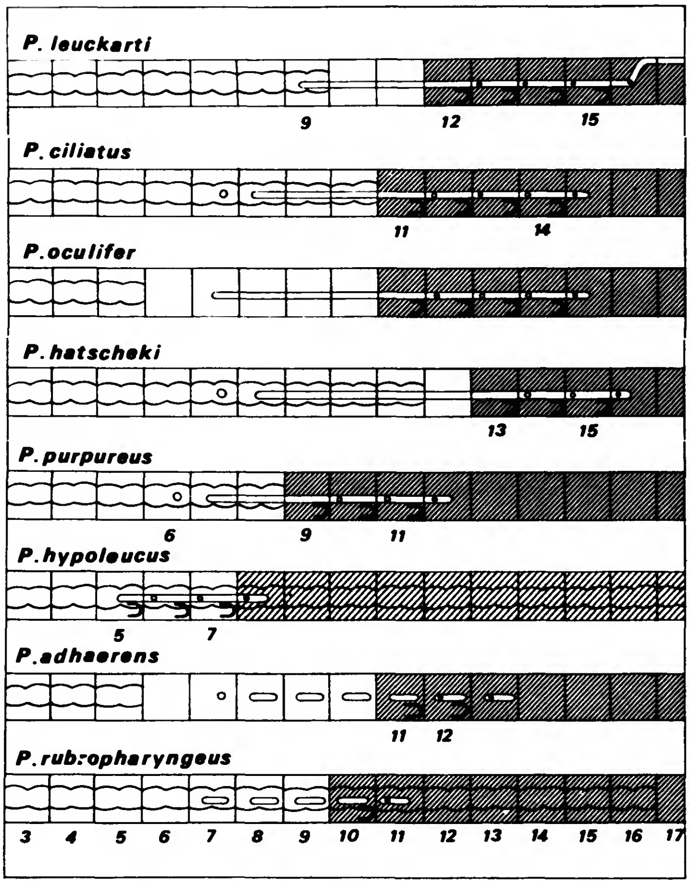

FIGURE 2.—Diagram of the male characters for eight species of *Protodrilus* (lateral view of segments 3 to 17) showing salivary glands in the anterior segments, fertile part of the body (shading) with spermaducts and lateral organs (open grooves).

determined by the author), and New Caledonia; and Pacific coast of North America. The species are cosmopolitan on the European coasts, and the same species occur in the Mediterranean Sea and Gullmar Fjord.

Protodriloides chaetifer is known from the European coasts, the Pacific coast of North America (Puget Sound, Wieser, 1957), and the east coast of South Africa (collected by C. Berrisford and determined by the author). This distribution, which implies cosmopolitanism, is interesting because the species is without a pelagic larval stage.

The Protodrilidae occur in both the intertidal zone and in infralittoral sediment. In the Mediterranean, *Protodriloides symbioticus* (A. Fize, personal communication) and *Protodrilus adhearens* Jägersten are found in coastal subsoil water ("kustengrundwasser"). In the neighborhood of Banyuls, *Protodrilus adhaerens* is found together with *P. leuckarti* Hatschek in brackish water ("etang de Salses").

Renaud-Debyser (1963) studied the vertical and horizontal distribution of *Protodrilus* in Arcachon over a period of several months. In these studies a corer was used to obtain cores of sediment 0.8 to 1 m long from various levels in the tidal area. Figure 3 shows the migrations observed. Boaden (1962) studied the significance of grain sizes for the distribution of meiofauna within the tidal area by inserting tubes containing sifted sand, representing a specific fraction into the beach sand. He was able to show that *Protodrilus adhaerens* prefers grain sizes between 500 and 1400 μ, while the preferred range for *P. chaetifer* was between 162 and 211 μ.

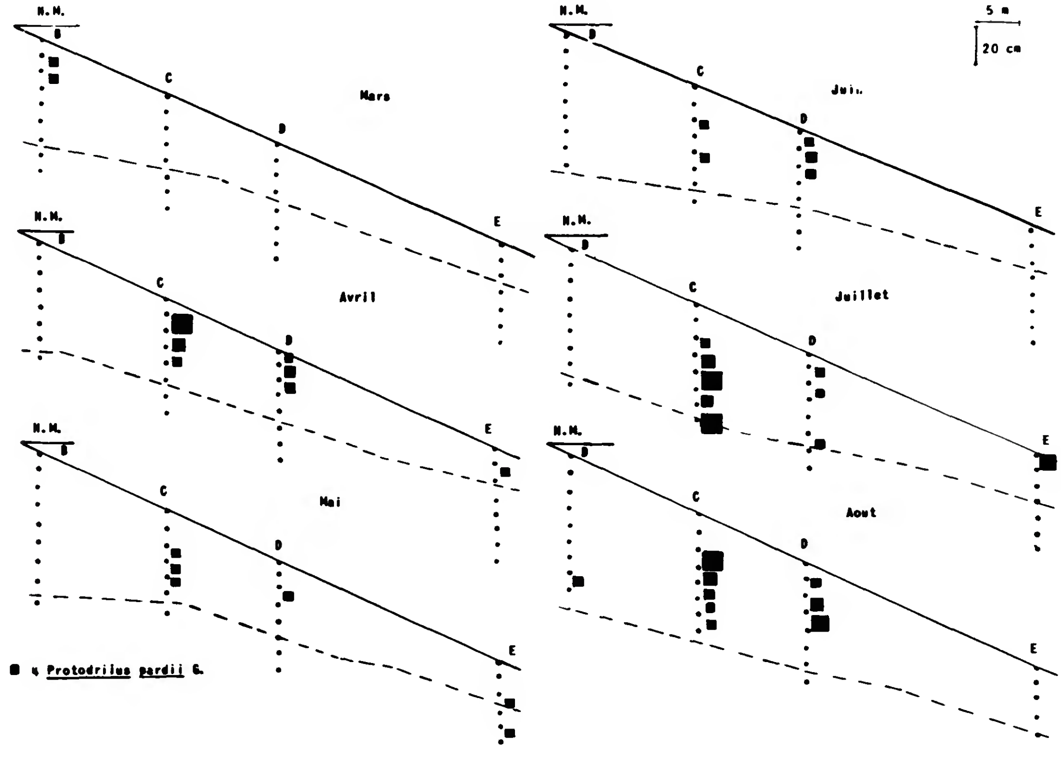

FIGURE 3.—Seasonal evolution of a population of *Protodrilus* at Arcachon, intertidal of Eyrac beach. HM, high-water mark; B–E, sampling sites; broken line, level of interstitial water. (After Renaud-Debyser, 1963.)

Gray (1965, 1966a–d, 1967a,b) experimentally investigated the preference of several species of Protodrilidae for such ecological factors as light, grain size, oxygen content, salinity, and current velocity. A hundred or so individuals were exposed to gradients of light, temperature etc., and the resulting distribution of the experimental animals was analyzed. In this way, Gray was able to determine the optimal demands made by a certain species on these ecological factors.

Jägersten (1940a,b) was the first to draw attention to the fact that larvae of *Protodrilus rubropharyngeus* Jägersten are dependent for their metamorphosis on grains of sand but he did not describe the nature of the metamorphosis-enhancing factor. Gray (1966c, 1967a,b) investigated the attractiveness of sand for three species of Protodrilidae and found that it is influenced by the thin film produced on the sand grains by certain favorable bacteria. Chemically or mechanically, the attraction to the grains of sand was reduced, but it returned successively as new films of bacteria were formed after inoculation (Figure 4).

The species of *Saccocirrus* Bobretzky are large forms, usually about 20 mm long. The largest species is 80 mm long and the smallest is 4 mm long. *Saccocirrus* has cephalic tentacles and adhesive pygidial lobes; therefore, it is somewhat similar to *Protodrilus*, but it has retractile parapodia and setae and the ventral band of cilia is absent from all species except one, *Saccocirrus eroticus* Gray.

The setae are important from the aspect of taxonomy, as are the general morphological characters of adult animals. *Saccocirrus* is dioecious and the gonads are in pairs in some animals and single in others.

The males have organs of copulation on each fertile segment, and these organs also are in pairs or single, according to the species. The females of all species, with one exception (*Saccocirrus pussicus* Marcus), have spermathecae.

The occurrence of a pharyngeal bulb in certain species is another important taxonomic feature. The existence of a pharyngeal muscular bulb was first noted by Goodrich (1901) for specimens of *Saccocirrus papillocercus* Bobretzky from Naples but, later, other authors denied the existence of such a bulb in this species. Jägersten (1947), who did not investigate the species himself, agrees with Goodrich on the existence of a muscular pharyngeal apparatus.

During a search for archiannelids at Naples, the author found two species of *Saccocirrus* in the same sediment: *S. papillocercus* without pharyn-

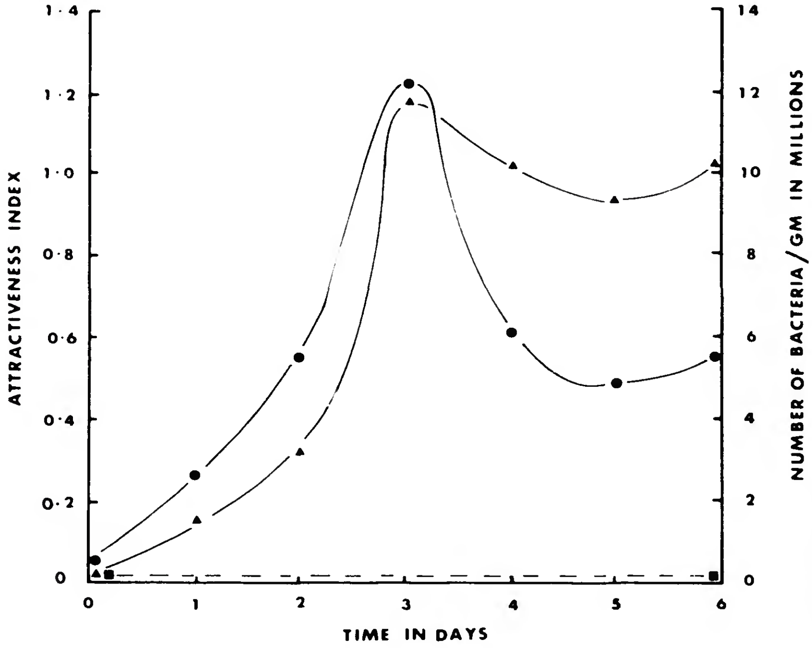

FIGURE 4.—Increase of the attractiveness index of autoclaved gravel to *Protodrilus hypoleucus* on inoculating with a culture of natural gravel bacteria: ●, number of bacteria; ▲, attractiveness index; ■, sterile controls. (After Gray, 1967a.)

geal muscular apparatus and *S. krusadensis* Alikunhi with a pharyngeal muscular pad. The specimens of *S. krusadensis* were immature and their provisory identification is based only on the setae. It is possible, therefore, that Goodrich mixed these two species, working with *S. krusadensis* for the pharyngeal apparatus and with *S. papillocercus* for the genital organs.

The following key to the species of *Saccocirrus* includes eleven known species. A twelfth species, *Saccocirrus maculatus* Tenerelli, is, in the opinion of the author, invalid, having been described from one sterile specimen having only 26 segments. Pigment granules in the epidermis very often are found in juvenile specimens in archiannelids.

There is much evidence that *Saccocirrus* is carnivorous. Marcus (1948) collected *Saccocirrus* with fish as bait, and she found remains of fish tissue in the digestive organs. In other cases, remains of copepods have been found in the intestine of *Saccocirrus*; Rao and Ganapati (1968) state that *S. minor* Aiyar and Alikunhi is carnivorous and that the intestine often contains microfauna.

Species of *Saccocirrus* have been found in the Mediterranean Sea, Black Sea, English Channel, Atlantic (Europe and Brazil), Indo-Pacific (India), and North Pacific (Japan, United States). The biotope, most often, is coarse-grained sediment in the intertidal or infralittoral zones. *Saccocirrus parvus* Gerlach lives in coastal waters. Two species, *S. papillocercus* and *S. major*, occur on the shores of the Mediterranean in the upper littoral zone.

Key to the Species of *Saccocirrus*

1. With pharyngeal muscular pad 2

Without pharyngeal muscular pad 7

2. Pygidium bifurcate, with two cirri and without adhesive papillae

S. cirratus Aiyar and Alikunhi

Pygidium bifurcate but without cirri and with numerous adhesive glands forming papillae, or else with only a few adhesive glands 3

3. Each parapodium with three types of setae: long capillary, medium with broad tip, and short 4

Each parapodium with only two types of setae (no long capillary setae)......***S. pussicus*** Marcus

4. Long setae slender and smooth at tip; only a few adhesive glands on pygidium

S. archboldi Kirsteuer

Long setae furcate at tip; adhesive papillae on pygidium 5

5. Bifid tip of the long setae symmetrical 6

Bifid tip of the long setae asymmetrical ....***S. krusadensis*** Alikunhi

6. Tip of the medium setae unequally forked; band of epidermal ventral cilia on setigerous segments 1 to 7 ....***S. eroticus*** Gray

Tip of the medium setae with a deep median notch; no band of epidermal ventral cilia

S. gabriellae Marcus

7. Pygidium without bifurcation, with two adhesive pads ....***S. minor*** Aiyar and Alikunhi

Pygidium bifurcate 8

8. No pygidial adhesive papillae; very few adhesive glands ....***S. parvus*** Gerlach

Pygidial adhesive papillae well developed 9

9. Long setae with an asymetrical, notched tip; medium setae with a broad chanelled tip

S. papillocercus Bobretzky

Long setae with a smooth tip 10

10. Medium setae with triangular section and three teeth at tip........***S. major*** Pierantoni

Medium setae with a smooth tip ....***S. orientalis*** Alikunhi

Family DINOPHILIDAE

The family Dinophilidae includes three genera: *Dinophilus* Schmidt, *Diurodrilus* Remane, and *Trilobodrilus* Remane. Each is very small, with a ventral band of cilia and without parapodia, setae, and cephalic tentacles.

The genus *Dinophilus* consists of two groups having a total of eight species. One group comprises species that are without sexual dimorphism and usually are orange colored (designated as Erythrodinophilidae by Shearer); the other group is made up of species with pronounced sexual dimorphism and usually without pigmentation (designated as Leucodinophilidae by Shearer). The females are known best in the latter group, as the males are very small (Jones and Ferguson, 1957). Jägersten (1944), in a study of a monomorphic *Dinophilus,* revealed that it spends half its life in an encysted state.

Most species live in the intertidal zone, usually among algae or on the surface of the sediment, more seldom interstitially. *Dinophilus gyrociliatus* Schmidt, however, has been found at a depth of 20 cm in sediment in the lower part of the intertidal zone (Rao and Ganapati, 1968). This species has a wide geographical distribution (Mediterranean Sea, Europen coasts of the Atlantic, and Indian Ocean).

Diurodilus, which includes five species, is among the smallest (250 to 500 μ long) of the archiannelids. The taxonomy is based on the shape of the pygidium. *Diurodrilus* moves very rapidly because of powerful ventral ciliation. The organization of the cilia grouping in cirri and membranella on the ventral side of the body is reminiscent of the arrangement in hypotrichous Ciliata.

Most species live in the intertidal zone or the littoral zone, but some are found also in submerged sand and several species inhabit coastal subsoil water. As far as known, *Diurodrilus minimus* Remane has the widest geographical distribution: North Sea, Baltic Sea, Gullmar Fjord, English Channel, Atlantic Ocean (Europe), Mediterranean

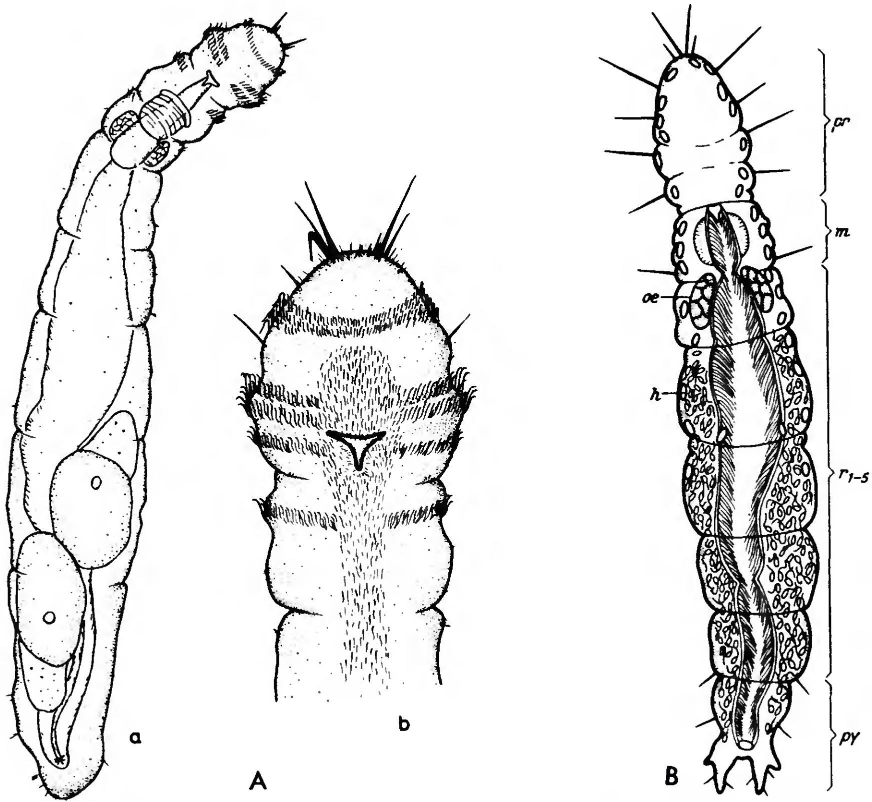

FIGURE 5.—A, *Trilobodrilus axi: a,* habitus; *b,* ventral view of head. B, *Diurodrilus ankeli: oe,* oesophagal gland; *h,* epidermal gland; *pr,* prostomium; *m,* metastomium (pharyngeal segment); r_{1-5}, trunk segments; *py,* pygidium. (After Westheide, 1967, and Ax, 1967.)

Sea, and Indian Ocean. The species is pronouncedly euryhaline. It has been found in abundance from 12 to 34 cm in the sediment (Frenchel, Jansson, and von Thun, 1967). *Diurodrilus benazzi* Gerlach is known from the Mediterranean Sea and the Indian Ocean (Rao and Ganapati, 1968). The genus *Diurodrilus* is now known from the North American coast of the Pacific, where the largest (500 μ long) known species, *D. ankeli* (Figure 5B), was found by Ax (1967).

The genus *Trilobodrilus* (Figure 5A) comprises three species, two of which, *T. heideri* Remane and *T. axi* Westheide, occur on the coasts of Europe. A third species, *T. nipponicus* Uchida and Okuda, which is very similar to *Trilobodrilus heideri,* has been found in Japan, the Bay of Bengal, and on the North American coast of the Pacific Ocean (Wieser, 1957).

Boaden (1963) has shown in laboratory experiments and field studies that *Trilobodrilus heideri* avoids light, and that it can tolerate low salinity better than high salinity. The species has tendencies towards gregariousness, with signs of a characteristic rhythm. In the course of 24 hours four periods of dispersion and four periods of concentration occur. This rhythm probably is related to that of the tides.

Family NERILLIDAE

The Nerillidae is a homogeneous family. Presently known are 10 genera and 25 species, which are distinguished taxonomically by such features as number of metameres, type of setae (capillary or composed), number of cephalic tentacles, and presence of a pharyngeal bulb with or without stilettes.

The larger species have nine metameres and the body lengths vary from 0.6 mm to 1.2 mm. Among these larger species are those of the genera *Nerilla* Schmidt, *Mesonerilla* Remane, and *Meganerilla* Boaden. Five genera have eight metameres and body lengths between 350 μ and 600 μ: *Nerillidium* Remane, *Nerillidopsis* Jouin, *Troglochaetus* Delachaux, *Thalassochaetus* Ax, and a new genus (see footnote in key to the Nerillidae). Two genera, *Psammoriedlia* Kirsteuer and *Paranerilla* Jouin and Swedmark, have only seven metameres.

Key to Genera of the Family Nerillidae

1.	Body with nine segments, including the pharyngeal segment (S1)	2
	Body with less than nine segments	4
2.	Simple capillary setae	3
	Compound setae	***Mesonerila*** Remane
3.	Three antennae, two palps	***Nerilla*** Schmidt
	One antennae or none, two large palps	***Meganerilla*** Boaden
4.	Eight segments, including the pharyngeal segment (S1)	5
	Seven segments, including the pharyngeal segment	9
5.	All segments of the body bearing the same type of setae	6
	All segments of the body not bearing the same type of setae; simple and capillary setae (S1, S5 to S8), compound setae (S2 to S4)	***Nerillidopsis*** Jouin
6.	Compound setae	7
	Simple, capillary setae	8
7.	No parapodial cirri; no antennae, two palps	***Thalassochaetus*** Ax
	Parapodial cirri well developed, often double; three antennae, two palps	New genus[1]
8.	Pharyngeal segment setigerous; two antennae or none, two palps	***Nerillidium*** Remane
	Pharyngeal segment achaetous; no antennae, two palps; fresh water and hypogeous form	***Troglochaetus*** Delachaux
9.	Compound setae; no antennae, no palps, no parapodial cirri; external ciliation well developed; limicolous form	***Paranerilla*** Jouin and Swedmark
	Capillary setae; no antennae, two palps, parapodial cirri present except on last segment; mesopsammic form	***Psammoriedlia*** Kirsteuer

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[1] With Dr. B. Swedmark's agreement, *Mesonerilla minuta* Swedmark will be placed in a new genus and species by the author (Jouin, in preparation).

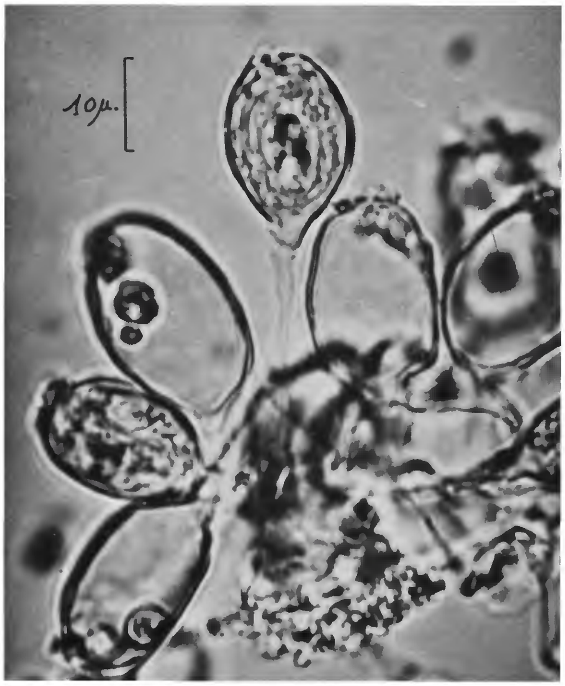

FIGURE 6.—Photomicrograph of spermatophores of *Nerilla antennata.*

The Nerillidae have colonized biotopes of widely different types. Most species are mesopsammic and marine, and are found mainly in infralittoral sediments, although some species are found in the intertidal or in the splash zone of seashores. The mesopsammic species are browsers living on diatoms and bacteria on grains of sand. The genus *Troglochaetus* is hypogeal, and is found in continental subterranean waters in Europe. The only species is closely related to *Nerillidium,* and it may be assumed that *Troglochaetus* is of marine origin.

Paranerilla Jouin and Swedmark is known in subtidal mud; it was described from the Gullmar Fjord and was found later near Bergen, Norway, on the Atlantic coast (Sterrer, 1968) and in the Atlantic Ocean (Renaud-Mornant, personal communication).

The genera *Nerilla, Nerillidium,* and *Mesonerilla* are cosmopolitan. *Nerilla antennata* Schmidt and *Nerillidium mediterraneum* Remane, described from European waters, have been found in the Indian Ocean (Rao and Ganapati, 1968). *Nerilla* is very euryoecious and depends little on the substratum. It breeds easily in aquaria. The period of egg-laying is long, and fertilization is by spermatophores (Jouin, 1968); see Figure 6. Development is direct and rapid.

Literature Cited

Aiyar, R. G., and K. H. Alikunhi

1944. On Some Archiannelids of the Madras Coast. *Proceedings of the National Institute of Sciences of India,* 10(1):113–140.

Ax, P.

1967. *Diurodhilus ankeli* nov. spec. (Archiannelida) von der Nordamerikanischen Pazifikküste. *Zeitschrift für Morphologie und Ökologie der Tiere,* 60:5–16.

Boaden, P. J. S.

1962. Colonization of Graded Sand by an Interstitial Fauna. *Cahiers de Biologie Marine,* 3:245–248.

1963. Behaviour and Distribution of the Archiannelid *Trilobodrilus heideri. Journal of the Marine Biological Association of the United Kingdom,* 43:239–250.

Fenchel, T.; B. O. Jansson; and W. von Thun

1967. Vertical and Horizontal Distribution of the Metazoan Microfauna and of some Physical Factors in a Sandy Beach in the Northern Part of the Øresund. *Ophelia,* 4:227–243.

Goodrich, E. S.

1901. On the Structure and Affinities of *Saccocirrus. The Quarterly Journal of Microscopical Science,* 44:413–428.

Gray, J. S.

1965. The Behaviour of *Protodrilus symbioticus* (Giard) in Temperature Gradients. *Journal of Animal Ecology,* 34:455–461.

1966a. The Response of *Protodrilus symbioticus* (Giard) (Archiannelida) to Light. *Journal of Animal Ecology,* 35:55–64.

1966b. Selection of Sands by *Protodrilus symbioticus* (Giard). *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband, 2:105–116.

1966c. The Attractive Factor of Intertidal Sands to *Protodrilus symbioticus. Journal of the Marine Biological Association of the United Kingdom,* 46:627–645.

1966d. Factors Controlling the Localisations of Populations of *Protodrilus symbioticus* (Giard). *Journal of Animal Ecology,* 35:435–442.

1967a. Substrate Selection by the Archiannelid *Protodrilus hypoleucus* Armenante. *Journal of Experimental Marine Biology and Ecology,* 1:47–54.

1967b. Substrate Selection by the Archiannelid *Protodrilus rubropharyngeus. Helgoländer wissenchafliche Meeresuntersuchungen,* 15:253–269.

Hermane, C. O.

1969. The Systematic Position of the Archiannelida. *Systematic Zoology,* 18(1):85-102.

Jägersten, G.

1940a. Die Abhängigkeit der Metamorphose vom Substrat des Biotops bei *Protodrilus. Arkiv för Zoologi,* 32(17):1–12.

1940b. Zur Kenntnis der äusseren Morphologie, Entwicklung und Ökologie von *Protodrilus rubropharyngeus* n.sp. *Arkiv för Zoologi,* 32(16):1–19.

1944. Zur Kenntnis der Morphologie, Enzystierung und Taxonomie von *Dinophilus. Kungliga Svenska Vetenskapsakademiens Handlingar,* 21(2):1–90.

1947. On the Structure of the Pharynx of the Archiannelida with Special Reference to There-occurring Muscle Cells of Aberrant Type. *Zoologiska bidrag från Uppsala,* 25:551–570.

1952. Studies on the Morphology, Larval Development and Biology of *Protodrilus. Zoologiska bidrag från Uppsala,* 29:425–512.

Jones, E. R., and F. F. Ferguson

1957. The Genus *Dinophilus* (Archiannelida) in the United States. *American Midland Naturalist,* 57:440–449.

Jouin, C.

1962. Le Développement larvaire de *Protodrilus chaetifer* Remane (Archiannélides). *Comptes Rendus de l'Académie des Sciences,* series D, 255:3065–3067.

1966. Morphologie et anatomie comparée de *Protodrilus chaetifer* Remane et *Protodrilus symbioticus* Giard; création du noveau genre *Protodriloïdes* (Archiannélides). *Cahiers de Biologie Marine,* 7:139–155.

1968. Sexualité et biologie de la reproduction chez *Mesonerilla* Remane et *Meganerilla* Boaden (Archiannélides Nerillidae). *Cahiers de Biologie Marine,* 9:31–52.

Marcus, E. du B.-R.

1948. Further Archiannelids from Brazil. *Communicaciones Zoologicas del Museo de Historia Natural de Montevideo,* 2(48):1–77.

1955. On Turbellaria and *Polygordius* from the Brazilian Coast. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoologia,* 20(207):19–65.

Pierantoni, U.

1908. Protodrilus. *Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte,* Monographie 31, 226 pages. Zoologische Station, Naples.

Rao, C. G., and P. N. Ganapati

1968. On some Archiannelids from the Beach Sands of Waltair Coast. *The Proceedings of the Indian Academy of Sciences,* 67(1):24–30.

Remane, A.

1932. Archiannelida. *Tierwelt der Nord- und Ostsee,* 6(22, VIa):1–36.

Renaud-Debyser, J.

1963. Recherches écologiques sur la faune interstitielle des sables. (Bassin d'Arcachon, Ile de Bimini, Bahamas.) *Vie et Milieu,* supplement 15:1–157.

Sterrer, W.

1968. *Paranerilla limicola* Jouin und Swedmark (Archiannelida) von der Norwegischen und Adriatischen Küste. *Sarsia,* 36:65–68.

Swedmark, B.

1954. Étude du développement larvaire et remarques sur la Morphologie de *Protodrilus symbioticus* Giard (Archiannélides). *Arkiv för Zoologi,* 6(25): 511–522.

Westheide, W.

1967. Die Gattung *Trilobodrilus* (Archiannelida, Polychaeta) von der deutschen Nordseeküste. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 16: 207–215.

Wieser, W.

1957. Archiannelids from the Intertidal of Puget Sound. *Transactions of the American Microscopical Society,* 76(3):275–285.

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Interstitial Polychaeta (Excluding Archiannelida)

ABSTRACT

Systematics, distribution, eidonomical and anatomical organization, and reproductive biology of interstitial polychaetes as represented in 16 families are discussed. Adaptations to interstitial life in *Pisione, Hesionides, Microphthalmus, Petitia, Psammodrilus,* and other genera are emphasized.

The class Polychaeta is a rather heterogeneous group. It includes nearly 10,000 species whose lengths range from three meters to only a few more millimeters. Many of these animals belong to the meiofauna but no real distinction can be made between the larger benthic forms and the smaller meiofaunal ones.

Only the "interstitial" polychaetes, inhabitants of sandy and sandy-muddy sediment, form a small, more or less homogeneous ecological group. More precisely, only those animals which are able to live in the interstices of sediments because of their small body dimensions, and especially because of their small diameters, are considered "interstitial." Well-known interstitial species include *Hesionides arenaria* Friedrich (length 2 mm, diameter 0.1 mm; Figure 7*a,b*), *Microphthalmus listensis* Westheide (length 2.5 mm, diameter 0.15 mm, Figure 1*b*), *Petitia amphophthalma* Siewing (length 1.5 mm, diameter 0.14 mm; Figure 1*d*), *Stygocapitella subterranea* Knöllner (length 3.5 mm, diameter 0.4 mm; Figure 2*b*), and *Psammodriloides fauveli* Swedmark (length 1 mm, diameter 0.12 mm). Many of the larger polychaetes of sandy biotopes, however, also are considered to be interstitial animals. Among these are some representatives in the families Pisionidae, Syllidae, and Glyceridae with body dimensions greater than the pore spaces of coarse sandy sediments—for example, *Pisione remota* (Southern), length 7 to 15 mm, diameter 1 mm (see Figure 2*a*)—and by pushing aside the sand grains they make space in which to move. Numerous characteristics, however, of organization and biology that have been recognized as adaptations to the sand biotope correspond to those of the smaller inhabitants of sandy environments. Thus, it is justifiable to extend the definition of the term "interstitial polychaetes" to a series of larger forms.

Accordingly, interstitial polychaetes are represented in at least 16 families (Hartmann-Schröder, 1964; Laubier, 1967a): Pisionidae (Alikunhi, 1947, 1949, 1951; Åkesson, 1961; Laubier, 1967c; Siewing, 1953, 1954, 1955a; Stecher, 1968; Storch, 1966; Tenerelli, 1965), Phyllodocidae (Hartmann-Schröder, 1963; Laubier, 1961, 1965), Hesionidae (Alikunhi, 1948; Bobretzky, 1880; Friedrich, 1937, 1956; La Greca, 1950; Westheide and Ax, 1965; Westheide, 1967, 1969; Zunarelli-Vandini, 1968), Syllidae (Cognetti, 1961, 1962, 1965; Gidholm, 1962; Hartmann-Schröder, 1956; Rao and Ganapati, 1966; Siewing, 1955b), Sphaerodoridae (Reimers, 1933), Nereidae, Nephtyidae (Marinov, 1963), Glyceridae, Goniadidae, Dorvillaeidae (Levi, 1954; Dohle, 1967), Orbiniidae (Laubier, 1962), Paraonidae, Cirratulidae, Ctenodrilidae, Stygocapitellidae (Karling, 1958; Knöllner, 1934), and Psammodrilidae (Swedmark, 1952, 1955, 1959). Only the important literature dealing with interstitial polychaetes is cited above.

Two families, the Psammodrilidae and probably the Pisionidae (Figure 3), consisting of only a few

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species, are restricted to the microfauna of sandy biotopes. Altogether, approximately 75 to 100 species that can be considered "interstitial" are known. This estimate, which is not even 1 percent of all known polychaetes, does not include those species which spend their juvenile stages in the mesopsammal, for example the younger stages of some Nereidae and Opheliidae.

Most of the interstitial species are motile forms. Many move very quickly and some, like chilopods, run by means of leg-shaped neuropodia; for example, the species of the genus *Hesionides* (Friedrich, 1937; Westheide, 1967). Ciliary gliding and swimming in the pore spaces are known to occur in the juvenile stages of some species. Sessile polychaetes are almost lacking in the mesopsammal; only *Psammodrilus balanoglossoides* Swedmark is semisessile and lives in mucous tubes between the sand grains (Swedmark, 1955).

Interstitial polychaetes occur in sandy and sandy-muddy shores in the eulittoral region as well as sandy sediments in sublittoral zones. Many mesopsammic forms (such as *Hesionides gohari* Hartmann-Schröder and *Petitia amphophthalma*) are found in both habitats. According to Tenerelli (1966a,b), a few species seem to be limited to the eulittoral shores (e.g., *Stygocapitella subterranea*) or to sublittoral regions only (e.g., *Plakosyllis brevipes* Hartmann-Schröder).

There probably are no polychaetes which characterize the "coastal subsoil water," or "Küstengrundwasser" (inter alia, Hartmann-Schröder, 1964). Like most other organisms, the polychaetes avoid that region, as has been demonstrated by many investigations on tidal as well as atidal beaches (Ax, 1969; Schmidt, 1968; Westheide, 1967). Thus, *Stygocapitella* Knöller, still regarded as a typical subsoil water animal, is not found in this region throughout most of the year, but it is found almost always in the wet sand of the upper eulittoral beach slopes. The overemphasis of the role of subsoil water in meiobenthology can be traced back to the inaccuracy of quantitative sampling techniques. Nevertheless, for limited periods the subsoil water is important for a few species. The whole population of *Hesionides arenaria* of the North Sea coast hibernates in very deep regions of subsoil water, deep enough not to be reached by the usual sampling techniques (Westheide, 1967).

Suitable habitats for most of the interstitial polychaetes are known all over the world. The distribution of six well-known, typical species of littoral sandy biotopes is shown in Figures 3–5. For the localities of these species consult the literature given above and the following: Aiyar and Alikunhi (1940), Day (1967), Delamare Deboutteville (1954, 1956, 1960), Delamare Deboutteville, Gerlach, and Siewing (1954), Fize (1963), Gerlach (1955), Hartmann-Schröder (1958, 1959, 1960a,b, 1962), Hartmann-Schröder and Hartmann (1962), Laubier (1964, 1967b, 1968), Laubier and Paris (1962), Rao and Ganapati (1967), Renaud-Debyser (1963), Renaud-Debyser and Salvat (1963), Renaud-Mornant and Serène (1967), Storch (1967), Tenerelli (1964), and Valkanov (1954).

It is quite certain that additional localities of these animals will be discovered during the next few years through further investigations on other beaches. It must be considered, however, that some of these presently recognized species are really "morphologically similar or identical natural populations that are reproductively isolated" (Mayr, 1965), thus, so-called sibling species.

An example of great external similarity of two quite different species is found in the family Hesionidae. *Microphthalmus sczelkowii* Metschnikow and *M. aberrans* (Webster and Benedict) often live in the same biotope. Their external conformity (Figure 6) is so great that it is difficult to separate the two forms, especially in fixed material. *Microphthalmus sczelkowii* lacks only a specific seta in notopodia, and its dorsal cirri are relatively longer than those of *M. aberrans;* however, its sexual organs, reproductive behavior, development, and seasonal history are quite different from those of *M. aberrans* (Westheide, 1967). There are also only slight differences between *Hesionides arenaria* and *H. gohari* (Figure 7a–d). The shape of the anal lobes and the quantitative differences in tentacles and cirri are the external characters by which these species can be differentiated. In Tunisian beaches these species live in the same littoral region; the two populations usually are separated only by approximately 25 cm of vertical distance, and individuals of *Hesionides gohari* and *H. arenaria* may be found in the same samples. There are, however, distinct differences in reproductive biology (Westheide, 1969).

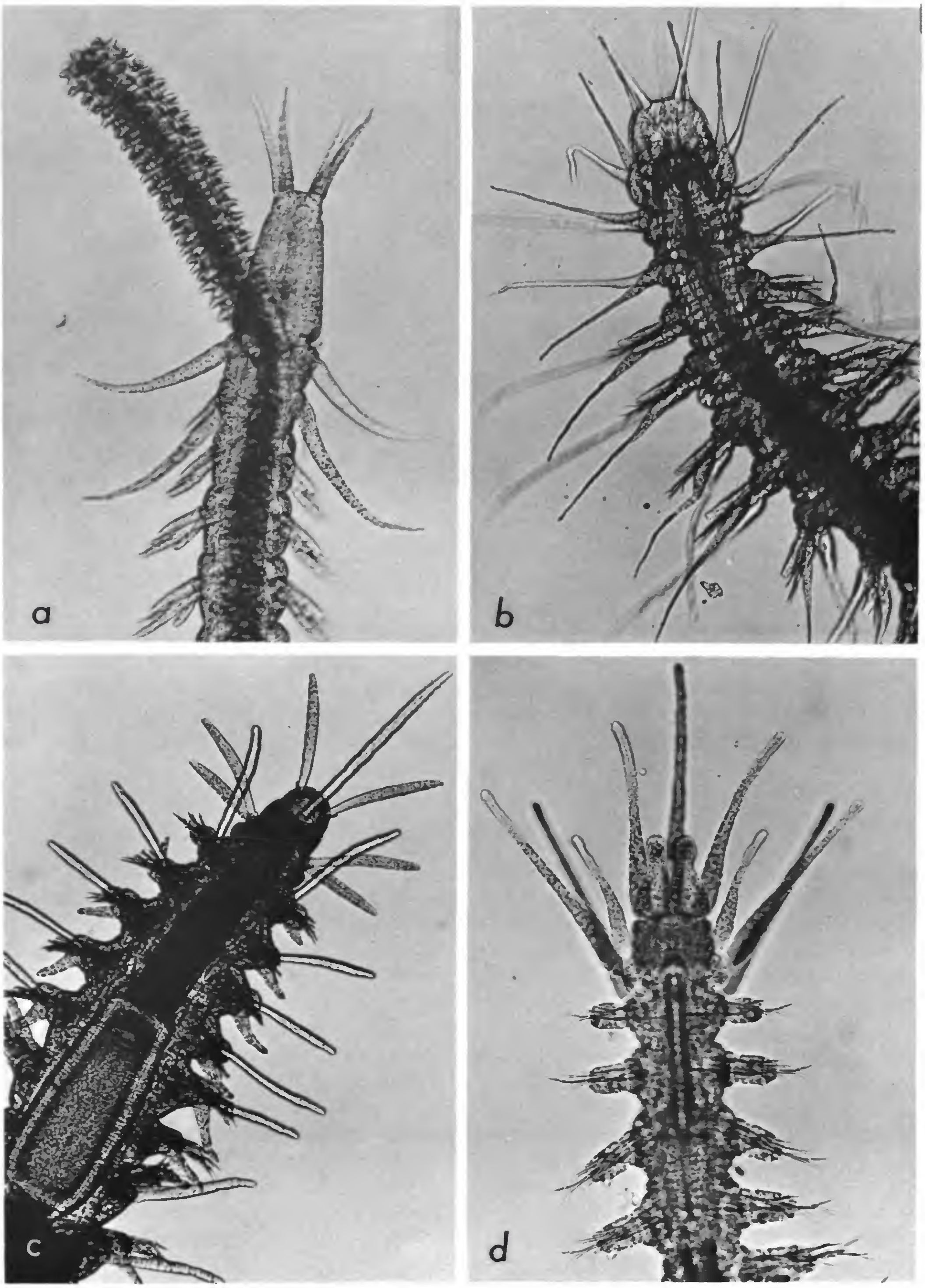

FIGURE 1.—Typical interstitial polychaetes, anterior part: *a*, *Hesionura* sp., with proboscis partly evaginated; *b*, *Microphthalmus listensis*; *c*, *Streptosyllis* sp. (Photo by P. Schmidt); *d*, *Petitia amphophthalma*.

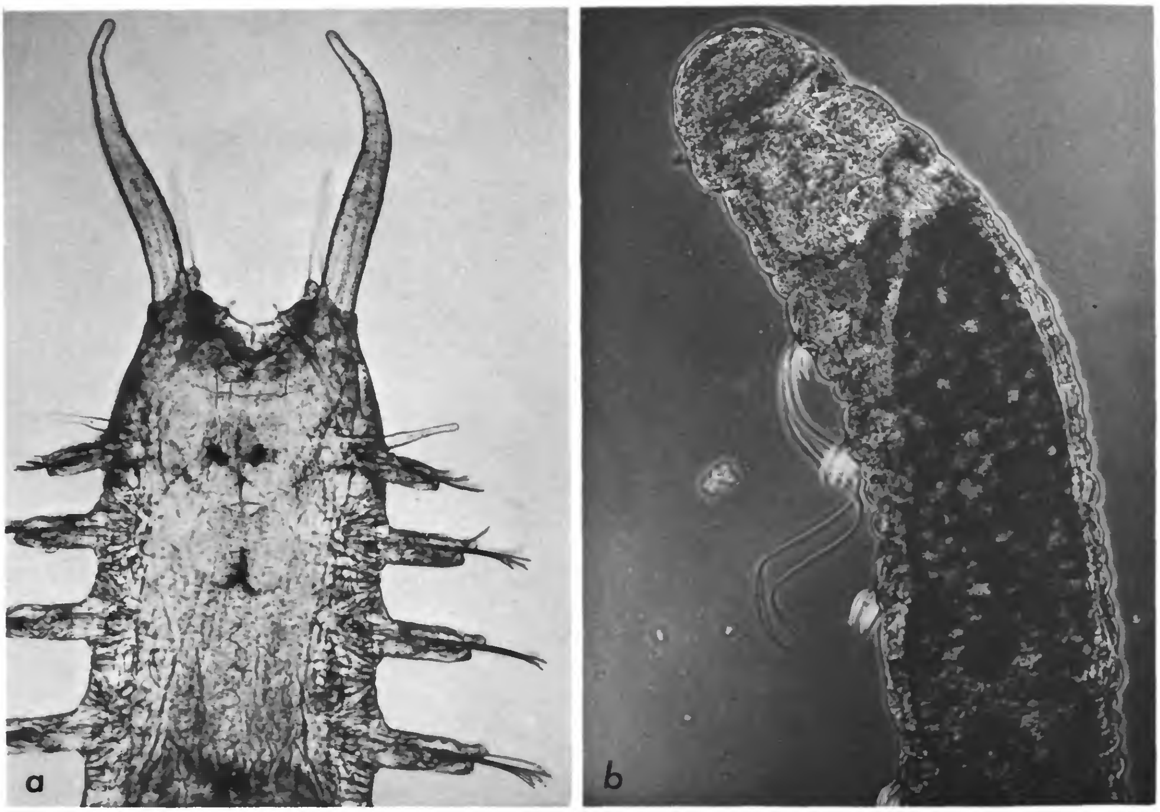

FIGURE 2.—Typical interstitial polychaetes, anterior part; *a, Pisione remota* (photo by J. Stecher); *b, Stygocapitella subterranea.*

The study of interstitial species is especially interesting for by comparison with more typical polychaetes of other biotopes, adaptations to the environmental factors of mesopsammic habitats—"Lebensformcharaktere" (Ax, 1963; Remane, 1952)—can be easily recognized.

In the external organization different kinds of reduction are found. (1) Regressive evolution in body size and number of segments and setae: Some typical mesopsammic species have an average length of 2 to 3 mm; the average number of segments in *Plakosyllis brevipes* is 40, in *Hesionides arenaria* 20, in *Hesionides gohari* 12, and in *Petitia amphophthalma* 12. (2) Modification of body appendages in number and form: Here, different types of evolution can be distinguished—increased function of appendages as sense organs (e.g., *Pisione* Grube, *Hesionides* Friedrich, *Microphthalmus* Mecznikow; Figures 1*b*, 2*a*, 6, 7,); development of extremely long filiform appendages which serve, perhaps as adhesive organs (e.g., *Microphthalmus listensis* Westheide and *Dioplosyllis cirrosa* Gidholm); reduction to small, often tubercle-shaped tentacles and cirri as seen in *Plakosyllis brevipes* and other syllids (Hartmann-Schröder, 1964); or, finally, loss of all appendages (e.g., *Stygocapitella subterranea,* Figure 2*b*). Certain external characters, such as the shape of the prostomium and ciliation, are considered to be neotenic in the genera *Ophryotrocha* Claparède and Mecznikow (inter alia, Dohle, 1967), *Psammodrilus* (Swedmark, 1955), and *Psammodriloides* (Swedmark, 1959).

Adhesive organs constitute another group of specific adaptive characters. Epidermal adhesive glands are distributed all over the body in *Pisione*

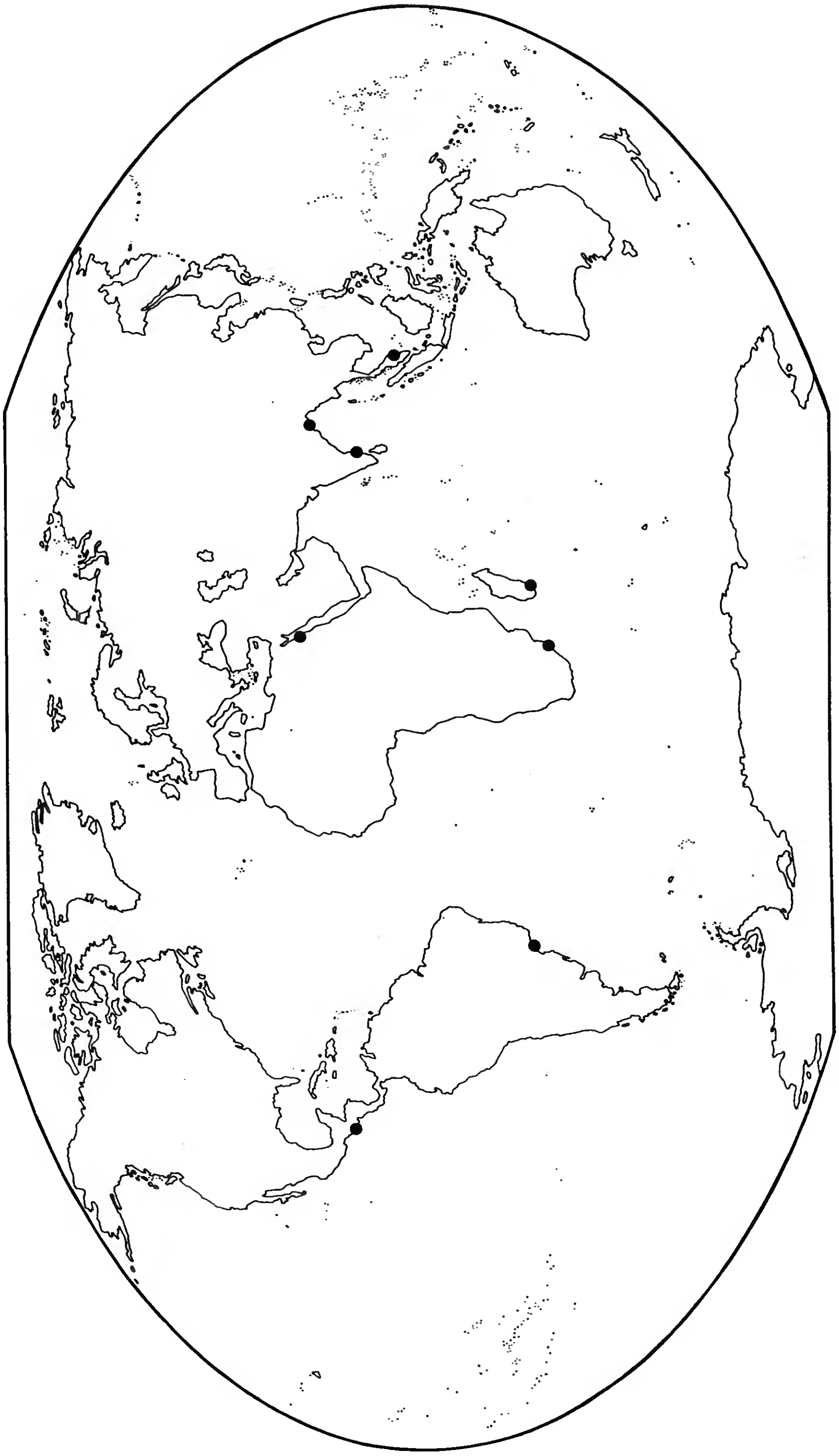

FIGURE. 3—Distribution of *Pisionidens indica* (Aiyar and Alikunhi). Pisionidae.

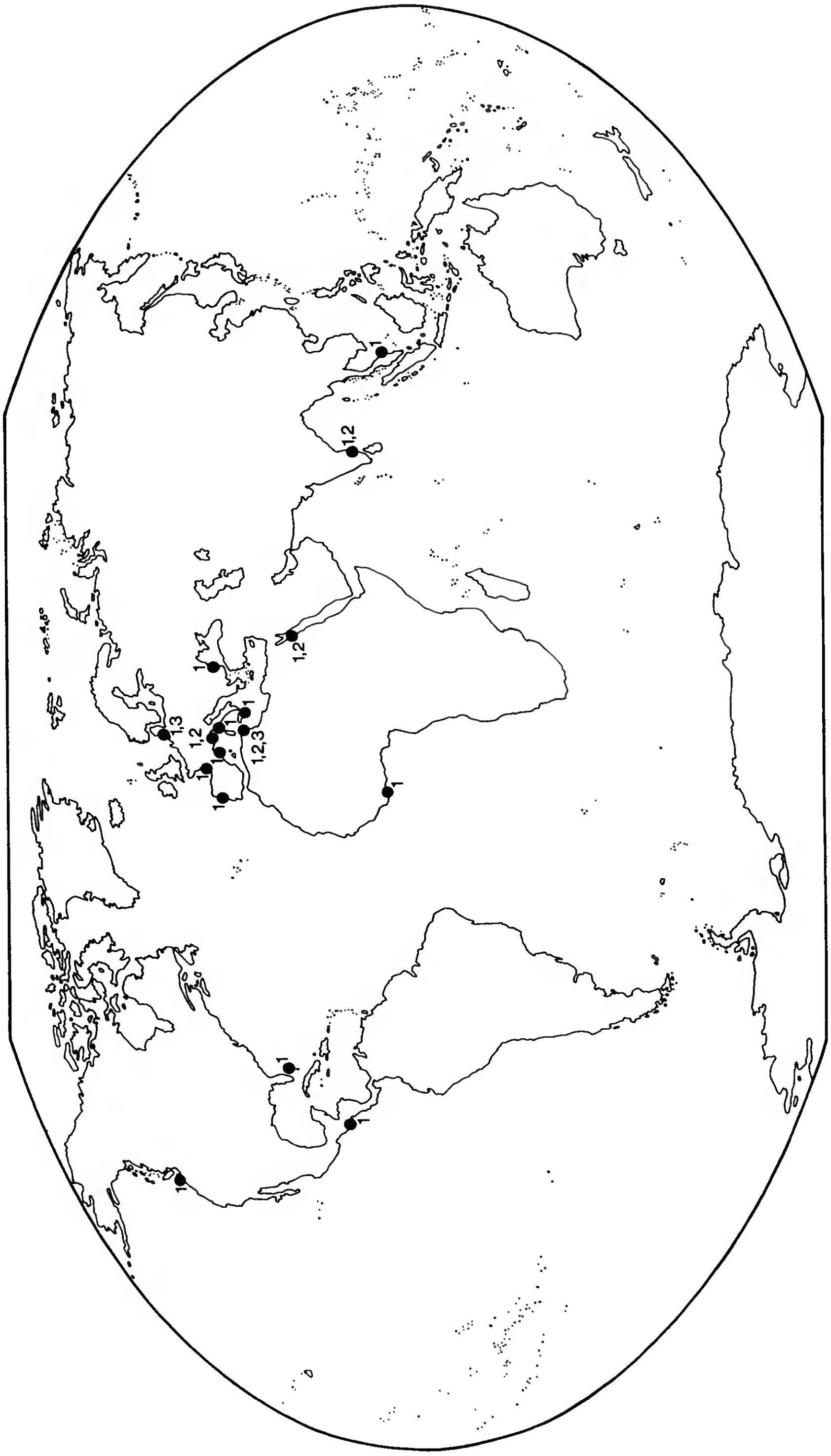

FIGURE 4.—Distribution of the genus *Hesionides*: 1, *H. arenaria* Friedrich; 2, *H. gohari* Hartmann-Schröder; 3, *H. maxima* Westheide. Hesionidae.

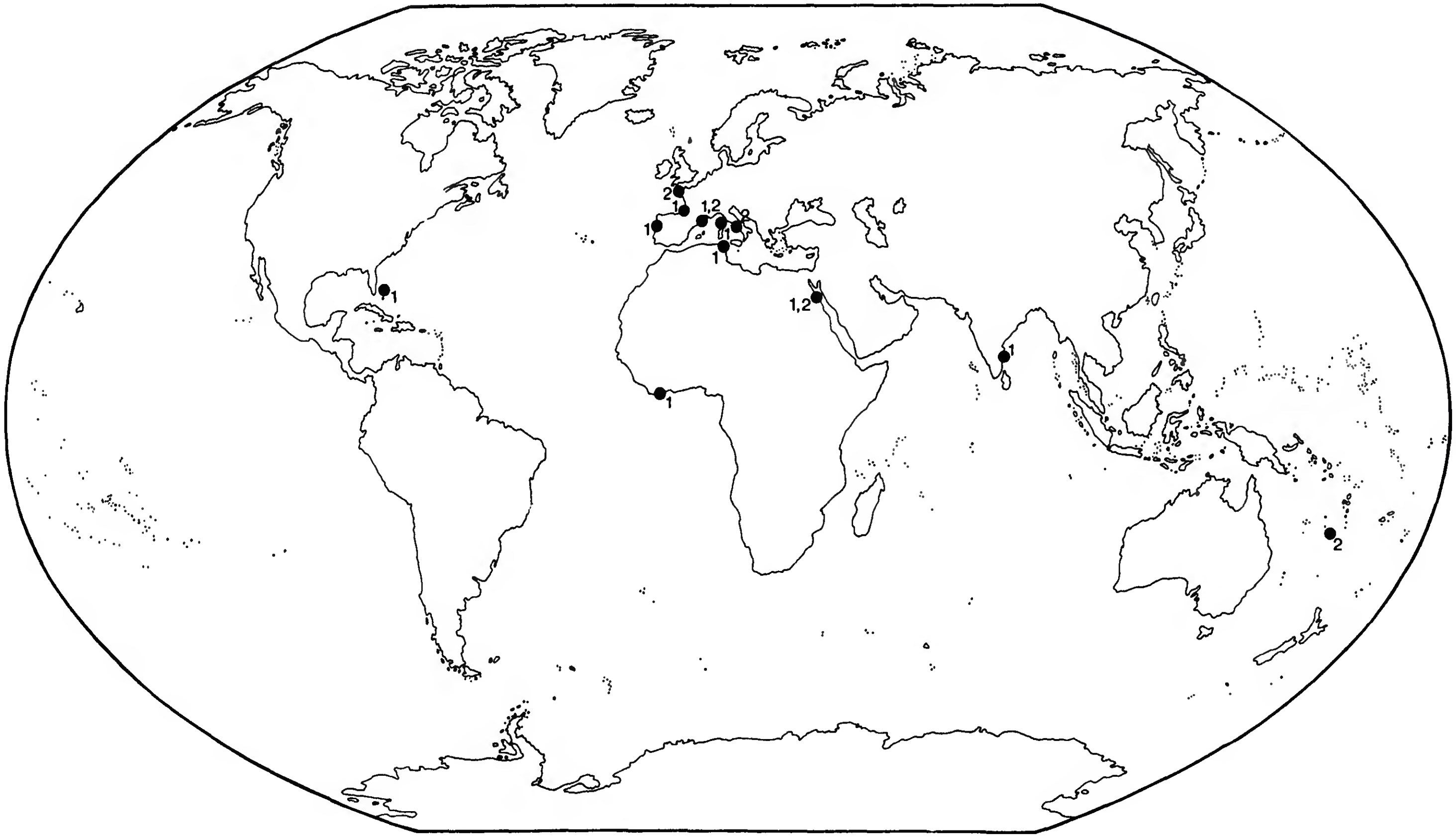

FIGURE 5.—Distribution of *Petitia amphophthalma* Siewing and *Plakosyllis brevipes* Hartmann-Schröder. Syllidae.

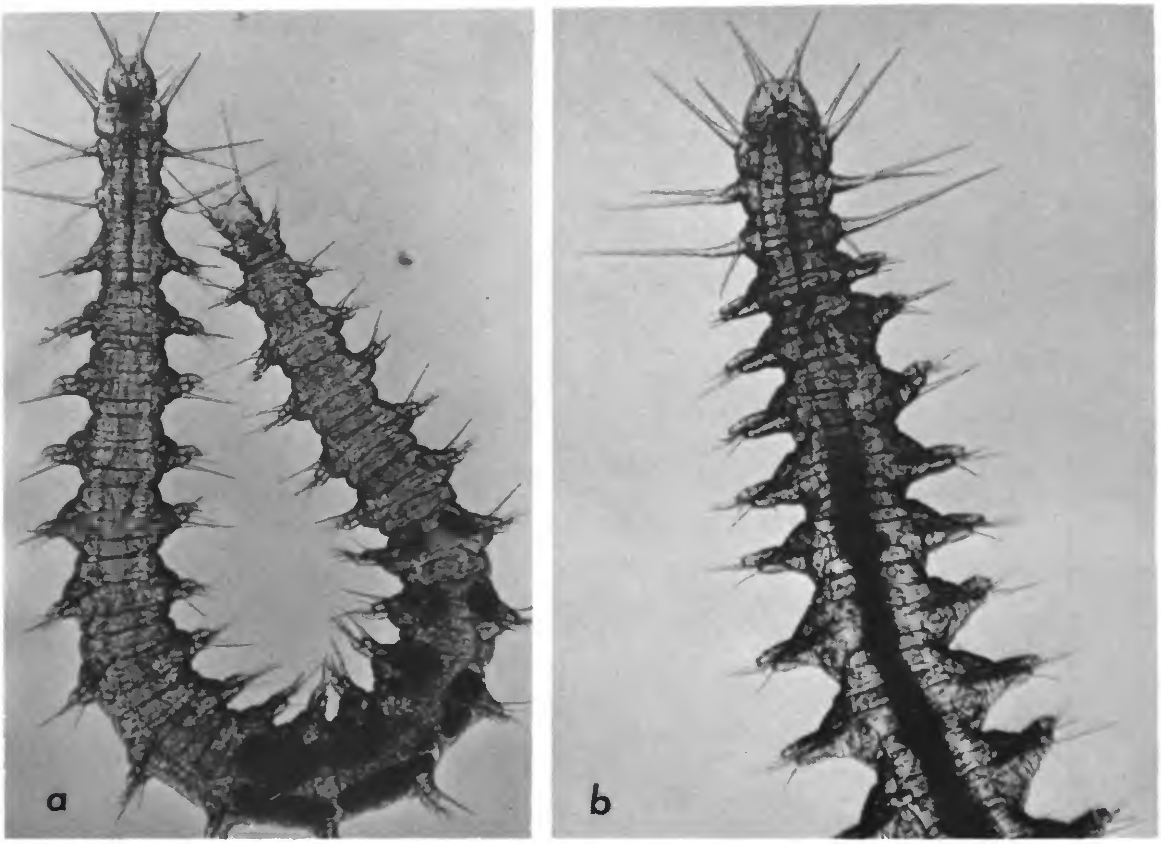

FIGURE 6.—Two species of the genus *Microphthalmus*: *a*, *M. sczelkowii*; *b*, *M. aberrans*.

remota (Stecher, 1968) and in *Microphthalmus listensis*. In the genera *Hesionides* and *Microphthalmus* characteristic caudal adhesive lobes (Figure 7*b,d*) are found. The loss of light-sensitive organs as in *Sphaerosyllis renaudae* Hartmann-Schröder, and *Parapionosyllis subterranea* Hartmann-Schröder and the loss of pigments as in *Friedericiella pacifica* (Friedrich) and *Stygocapitella subterranea* are characters considered as examples of degenerative evolution (Hartmann-Schröder, 1964). In *Petitia amphophthalma* (Siewing, 1955*b*) and *Hesionides gohari*, eyes are reduced during postembryonic development.

A second group of adaptive features is found among the psammobiontic polychaetes. There is a specific epidermis with a chorda-like layer of small vacuoles as in *Hesionides arenaria* (Ax, 1966; Westheide, 1967) or a very thick cuticula serving for mechanical protection as in *Pisione remota* (Stecher, 1968). The remarkable pharyngeal apparatus of *Psammodrilus balanoglossoides,* formed by transformation of longitudinal body muscles, serves as a suction pump for feeding on diatoms and detritus (Swedmark, 1955). Operation of the pharynx in *Hesionides* is similar (Westheide, 1967). A low production of gametes is perhaps the consequence of the few cells in interstitial animals (Swedmark, 1964). The number of eggs found at the same time in *Pisione remota* was 450 to 600, *Psammodrilus balanoglossoides* 75, *Hesionides arenaria* 30 to 80, *Microphthalmus sczelkowii* 10 to 14, *Microphthalmus listensis* 5 to 10, and *Psammodriloides fauveli* 1.

The Pisionidae (Alikunhi, 1949, 1951; Stecher, 1968) and the genera *Hesionides* and *Microphthalmus* (Bobretzky, 1880; Alikunhi, 1948; Westheide,

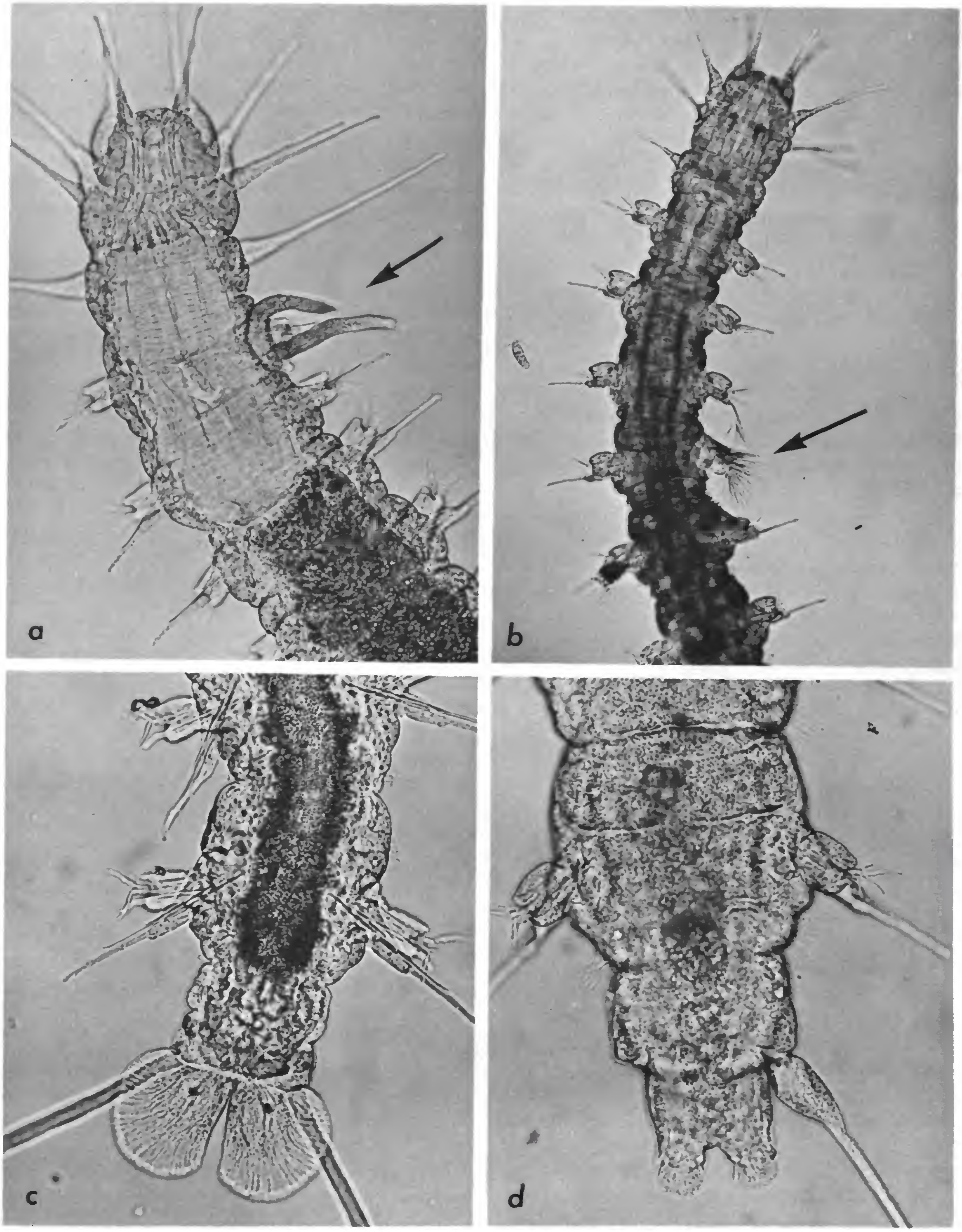

Figure 7.—Two species of the genus *Hesionides*: *a, H. arenaria,* anterior part with a double spermatophore, fixed on the epidermis; *b, H. arenaria,* posterior part with adhesive anal lobes; *c, H. gohari,* with spermatodesme (sperm bundle without any covering, fixed on the epidermis); *d, H. gohari,* posterior part with adhesive anal lobes.

1967) have complicated reproductive organs almost unknown in other polychaetes. Their structures are closely related to the reproductive biology of these species. The study of transmission of sperm, in particular, has produced new results in the biology of this class.

The best-known species of the Pisionidae is *Pisione remota.* The reproductive organs of the males are located in each parapodium in the middle part of the body (Figure 8*a*) and they consist of a copulatory organ and a modified cirrus. Sperm are transmitted by direct copulation. The male creeps over the female, and it adheres closely by means of specific glands that open at the ventral body wall. The copulatory organs are inserted into the genital pores of the female. In most cases nearly all receptacula of the female are filled in 15 minutes (Stecher, 1968).

In *Hesionides arenaria* the male has testes in the middle and posterior segments and a pair of peculiar mating organs in the anterior part. There are two vesiculae, each supplied with a partly glandular duct that opens above the prostomium. In these organs the formation of 100-μ, double spermatophores takes place (Figure 7*a*). The spermatophores are pressed out of the ducts and fixed to the body of the female and the sperm penetrate the epidermis (Westheide and Ax, 1965; Westheide, 1967).

The male organs of *Hesionides gohari* are similar to those of *H. arenaria.* The glandular parts of the spermducts, however, are much smaller. There are no real spermatophores—only sperm bundles ("spermatodesma"), without any covering, which are fixed to the integument of the sexual partner (Westheide, 1969), as in Figure 7*c.*

The genus *Microphthalmus* is hermaphroditic. Sperm are produced in the anterior half of the body, eggs in the posterior segments. All species except *M. tyrrhenicus* (Cognetti) are equipped with complicated male sexual organs in the second and third setigerous metameres (Zunarelli-Vandini, 1968). The organs of *M. sczelkowii* consist of a ciliated funnel, vesicula, ductus ejaculatorius, and a muscular bulbus that resembles a suctorial organ. In *M. aberrans* there is only an unpaired (but similar-appearing) genital organ. The terminal part is evaginated as a penis (Figure 8*b*). In *M. listensis* the mating organs are paired, with ciliated funnel, vesicula, a large glandular ductus ejaculatorius extending to setigerous segment 7, a cuticular penis, and a special muscular pump. Mating in *M. aberrans* takes place by transmission of spermatophores; in the other species, the development of copulatory organs suggests a direct mating process (Westheide, 1967).

The polychaetes of the mesopsammal do not spawn their eggs free into the water. The eggs are shed individually or in greater numbers in the pore spaces of the substratum *(Pisione remota, Hesionides arenaria)* or in a mucous mass *(Microphthalmus aberrans, M. listensis)* as seen in Figure 8*c*. *Microphthalmus sczelkowii* forms a cocoon, like an oligochaete, by means of clitellum-like glands of the epidermis (Westheide, 1967). A primitive type of brood protection has been found in the genus *Ophryotrocha,* where the female guards a cylindrical mass of 30 to 400 eggs (Åkesson, 1967). Methods of reproduction in the Syllidae (direct reproduction, viviparity, schizogamy, gestation, etc.) are summarized by Potts (1913). Investigations of the Exogoneae have been made by Haswell (1920).

The development of members of the interstitial fauna is normally direct, and free-swimming larvae are suppressed (Swedmark, 1964); see Figure 8*d.* Of the polychaetes already investigated, trochophores are found only in *Pisione remota* (Stecher, 1968; Åkesson, 1961; Banse, 1957) and *Microphthalmus aberrans* (Westheide, 1967).

Little is known about the age of interstitial polychaetes. North Sea populations of *Hesionides arenaria, Microphthalmus sczelkowii,* and *M. aberrans* probably are annual, with only one period of reproduction—in summer, autumn, or winter (Westheide, 1967). *Pisione remota* lives several years and has one reproductive period per year (Stecher, 1968).

An analysis of interstitial polychaetes shows that the evolution of particular characters has occurred in two directions: first, by regression and reduction, especially of external features; second, by formation or development of internal features and, particularly, of specific new kinds of behavior. Both groups of characters may coincide in some species.

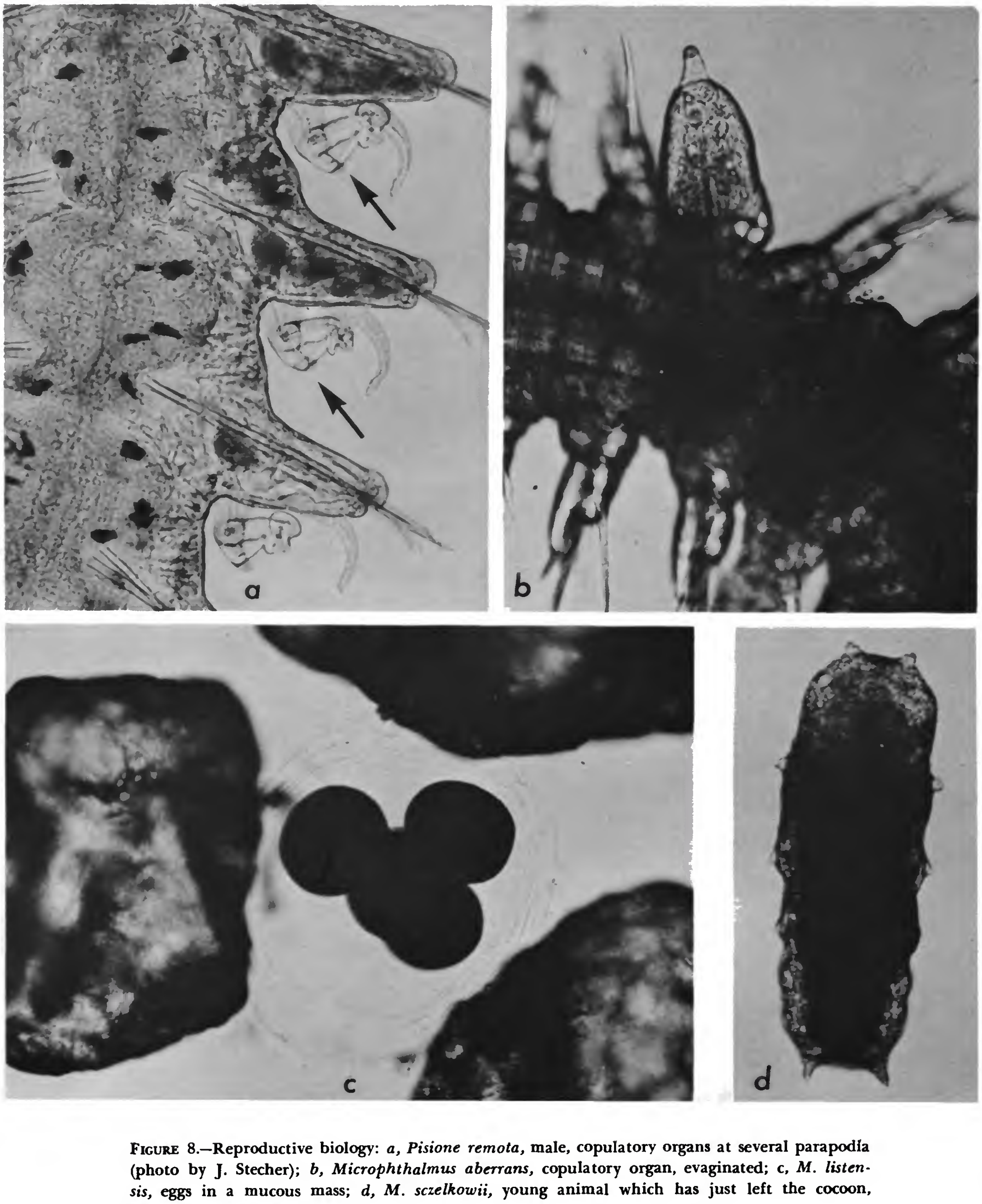

FIGURE 8.—Reproductive biology: *a, Pisione remota,* male, copulatory organs at several parapodia (photo by J. Stecher); *b, Microphthalmus aberrans,* copulatory organ, evaginated; c, *M. listensis,* eggs in a mucous mass; *d, M. sczelkowii,* young animal which has just left the cocoon, seven days after spawning.

Literature Cited

Aiyar, R. G., and K. H. Alikunhi

1940. On a New Pisionid from the Sandy Beach, Madras. *Records of the Indian Museum,* 42:89–107.

Akesson, B.

1961. On the Histological Differentiation of the Larvae of *Pisione remota* (Pisionidae, Polychaeta). *Acta Zoologica,* 42:177–225.

1967. On the Biology and Larval Morphology of *Ophryotrocha puerilis* Claparède and Metschnikov (Polychaeta). *Ophelia,* 4:111–119.

Alikunhi, K. H.

1947. On *Pisione complexa,* n.sp. from the Sandy Beach, Madras. *Proceedings of the National Institute of Sciences of India,* 13:105–127.

1948. A New Hermaphrodite Species of *Microphthalmus* (Polychaeta, Hesionidae) from the Sandy Beach, Madras. *Journal of the Royal Asiatic Society of Bengal, Science,* 14:17–25.

1949. Genital Papillae (Suckers) and Sperm-Sacs in the Pisionid Polychaete *Pisionidens indica* (Aiyar and Alikunhi). *Proceedings of the Indian Science Congress,* page 192.

1951. On the Reproductive Organs of *Pisione remota* (Southern) Together with a Review of the Family Pisionidae (Polychaeta). *Proceedings of the Indian Academy of Sciences,* 33:14–31.

Ax, P.

1963. Die Ausbildung eines Schwanzfadens in der interstitiellen Sandfauna und die Verwertbarkeit von Lebensformcharakteren für die Verwandtschaftsforschung. *Zoologischer Anzeiger,* 171:51–76.

1966. Das chordoide Gewebe als histologisches Lebensformmerkmal der Sandlückenfauna des Meeres. *Naturwissenschaftliche Rundschau,* 19:282–289.

1969. Populationsdynamik, Lebenszyklen und Fortpflanzungsbiologie der Mikrofauna des Meeressandes. *Zoologischer Anzeiger,* Supplementband 32:66–113.

Banse, K.

1957. Über die Entwicklung von *Pisione remota* (Pisionidae, Polychaeta). *Zoologischer Anzeiger,* 158:116–125.

Bobretzky, N.

1880. [Contribution to the Study of Reproductive Organs of Annelids]. *Memoires of the Natural History Society of Kiev,* 6:61–86. [In Russian.]

Cognetti, G.

1961. Les Syllidiens des côtes de Bretagne. *Cahiers de Biologie Marine,* 2:291–311.

1962. I Policheti dei fondi a sabbia grossolana del litorale livornese. *Bollettino di Zoologia,* 29:1–6.

1965. Sillidi mesopsammici delle secche della Melorina (Livorno). *Archivio Zoologico Italiano,* 50:65–72.

Day, J. H.

1967. A Monograph on the Polychaeta of Southern Africa. Part 1, Errantia; Part 2, Sedentaria. *Trustees of the British Museum (Natural History),* Publication 656:1–878.

Delamare Deboutteville, C.

1954. Eaux souterraines littorales de la Côte Catalane francaise (mise au point faunistique). *Vie et Milieu,* 5:408–451.

1956. Recherches sur la faune interstitielle des sédiments marins et d'eau douce à Madagascar. IX. Sur la présence dans les eaux souterraines littorales de Madagascar de l'Annélide polychete: *Pisionidens indica* (Aiyar et Alikunhi). *Mémoires de l'Institut Scientifique de Madagascar,* series A, 10:95–99.

1960. *Biologie des eaux souterraines littorales et continentales.* 740 pages. Paris: Hermann.

Delamare Deboutteville, C.; S. Gerlach; and R. Siewing

1954. Recherches sur la faune des eaux souterraines littorales du Golfe de Gascogne. Littoral des Landes. (3). *Vie et Milieu,* 5:373–407.

Dohle, W.

1967. Zur Morphologie und Lebensweise von *Ophryotrocha gracilis* Huth, 1934 (Polychaeta, Eunicidae). *Kieler Meeresforschungen,* 23:68–74.

Fize, A.

1963. Contribution à l'étude de la microfaune des sables littoraux du Golfe d'Aigues-Mortes. *Vie et Milieu,* 14:669–774.

Friedrich, H.

1937. Polychaetenstudien. I–III. *Kieler Meeresforschungen:* 1:343–345.

1956. Mitteilungen über neue und wenig bekannte Polychaeten aus Mittel- und Südamerika. *Senckenbergiana Biologica,* 37:57–68.

Gerlach, S. A.

1955. Die Tierwelt des Küstengrundwassers von San Rossore (Tyrrhenisches Meer). *Physiologia Comparata et Oecologia,* 4:53–73.

Gidholm, L.

1962. Sur quelques Polychètes Syllidiens des sables de la région de Roscoff avec description de deux nouvelles espèces. *Cahiers de Biologie Marine,* 3:249–260.

Hartmann-Schröder, G.

1956. Polychaetenstudien. I. *Plakosyllis brevipes* n.gen. n. sp., eine neue Syllide aus dem Mittelmeerraum. *Zoologischer Anzeiger,* 157:87–91.

1958. Einige Polychaeten aus dem Küstengrundwasser der Bimini-Inseln (Bahamas). *Kieler Meeresforschungen,* 14:233–240.

1959. Zur Ökologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador. *Beiträge zur Neotropischen Fauna,* 1:69–183.

1960a. Zur Polychaeten-Fauna von Peru. *Beiträge zur Neotropischen Fauna,* 2:1–44.

1960b. Polychaeten aus dem Roten Meer. *Kieler Meeresforschungen,* 16:69–125.

1962. Zweiter Beitrag zur Polychaetenfauna von Peru. *Kieler Meeresforschungen,* 18:109–147.

1963. Revision der Gattung *Mystides* Théel (Phyllodocidae; Polychaeta Errantia). Mit Bemerkungen zur Systematik der Gattungen *Eteonides* Hartmann-Schröder und *Protomystides* Czerniavsky und mit

Beschreibungen zweier neuer Arten aus dem Mittelmeer und einer neuen Art aus Chile. *Zoologischer Anzeiger,* 171:204–243.

1964. Zum Problem der Anpassung von Polychaeten an das Leben im Küstengrundwasser. *Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg,* 60:67–78.

Hartmann-Schröder, G., and G. Hartmann

1962. Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der argentinischen Küste Südpatagoniens unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut,* 60:5–270.

Haswell, W.

1920. The Exogoneae. *Journal of the Linnean Society, Zoology,* 34:217–245.

Karling, T. G.

1958. Zur Kenntnis von *Stygocapitella subterranea* Knöllner und *Parergodrilus heideri* Reisinger (Annelida). *Arkiv för Zoologi,* series 2, 11:307–342.

Knöllner, F.

1934. Die Tierwelt des Küstengrundwassers bei Schilksee (Kieler Bucht). V. *Stygocapitella subterranea,* nov. gen. nov. spec. *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein,* 20:468–472.

La Greca, M.

1950. Sulla presenza nel Mediterraneo di *Lycastoides pontica* (Bobr.), *Microphthalmus fragilis* Bobr. e *M. similis* Bobr. (Annelida Polychaeta). *Annuario dell'Istituto e Museo di Zoologia dell' Università di Napoli,* 2:1–16.

Laubier, L.

1961. *Mystides (Pseudomystides) coineaui* n. sp., un Phyllodocien des eaux souterraines littorales de Méditerranée occidentale. *Rapports et Proces-Verbaux des Reunions, Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée,* 16:461–464.

1962. *Schroederella pauliani* gen. nov., sp. nov., un nouvel orbiniide (polychètes sédentaires) de la faune interstitielle d'Afrique. *Annals of the Transvaal Museum,* 24:231–238.

1964. Deux polychètes interstitielles des plages de Corse. *Vie et Milieu,* 15:813–815.

1965. Sur la présence d'*Eteonides augeneri* (Friedrich, 1937) dans les sables du Bassin d'Arcachon. *Actes de la Société Linnéenne de Bordeaux,* 102:1–3.

1967a. Adaptations chez les Annélides Polychètes interstitielles. *Année Biologique,* 6:1–16.

1967b. Annélides Polychètes interstitielles de Nouvelle-Calédonie. *Expédition Française sur les Recifs coralliens de la Nouvelle-Calédonie,* 2:91-101.

1967c. Présence d'une Annélide Polychète de la famille des Pisionidae appartenant à un genre nouveau dans les eaux interstitielles littorales de Côte d'Ivoire. *Comptes Rendus de l'Académie des Sciences,* series D, 264:1431–1433.

1968. Présence au Portugal de deux Annélides Polychètes interstitielles. *Vie et Milieu,* 19:426–428.

Laubier, L., and J. Paris

1962. Annélides Polychètes. Faune marine des Pyrénées-Orientales, 4. *Vie et Milieu,* 13:1–80.

Levi, C.

1954. *Ophryotrocha minuta* nov. sp., nouveau Polychète mésopsammique. *Bulletin de la Société Zoologique de France,* 79:466–469.

Marinov, T.

1963. Über die Polychätenfauna der Sandbiozönose vor der Bulgarischen Schwarzmeerküste. *Bulletin de l'Institut Central de Recherche Scientifique de Pisciculture et de Pêcherie, Varna,* 3:61–78. [In Bulgarian.]

Mayr, E.

1965. *Animal Species and Evolution.* 797 pages. Cambridge, Massachusetts: Cambridge University Press.

Potts, F. A.

1913. Methods of Reproduction in the Syllids. *Ergebnisse und Fortschritte der Zoologie,* 3:1–72.

Rao, G. C., and P. N. Ganapati

1966. On a New Species of *Sphaerosyllis* (Polychaeta) from the Beach Sands of Waltair Coast. *Proceedings of the Indian Academy of Sciences,* 63:309–312.

1967. On Some Interstitial Polychaetes from the Beach Sands of Waltair Coast. *Proceedings of the Indian Academy of Sciences,* 65:10–15.

Reimers, H.

1933. Morphologie der Polychaetengattung *Sphaerodorum.* Monographie. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie, und Geographie der Tiere,* 64:41–110.

Remane, A.

1952. Die Besiedlung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. *Zoologischer Anzeiger,* Supplementband 16:327–359.

Renaud-Debyser, J.

1963. Recherches écologiques sur la faune interstitielle des sables. (Bassin d'Arcachon; Ile de Bimini, Bahamas). *Vie et Milieu,* supplement 15:1–157.

Renaud-Debyser, J., and B. Salvat

1963. Éléments de prosperité des biotopes des sédiments meubles intertidaux et écologie de leur populations en microfaune et macrofaune. *Vie et Milieu,* 14:463–550.

Renaud-Mornant, J., and P. Serène

1967. Note sur la microfaune de la Côte Orientale de la Malaisie. *Cahiers du Pacifique,* 11:51–73.

Schmidt, P.

1968. Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrand der Nordseeinsel Sylt. I. Faktorengefüge und biologische Gliederung des Lebensraumes. *Internationale Revue der gesamten Hydrobiologie,* 53:723–779.

Siewing, R.

1953. Morphologische Untersuchungen am "Kopf" der Pisioniden (*Pisione puzae* nov. spec., Annelida, Polychaeta). *Zoologischer Anzeiger,* 150:298–313.

1954. Zur Verbreitung von *Pisionidens indica* Aiyar and Alikunhi. *Kieler Meeresforschungen,* 10:81–83.

1955a. Ein neuer Pisionide aus Grundwasser der peruanischen Küste. *Zoologischer Anzeiger,* 154:127–135.

1955b. *Petita amphophthalma* n. gen., n.sp., ein neuer Polychaet aus dem Sandlückensystem. *Vie et Milieu,* 6:413–425.

Stecher, J.

1968. Zur Organisation und Fortpflanzung von *Pisione remota* (Southern) (Polychaeta, Pisionidae). *Zeitschrift für Morphologie der Tiere,* 61:347–410.

Storch V.

1966. Drei neue Polychaeten aus dem Litoral des Roten Meeres. *Kieler Meeresforschungen,* 22:171–175.

1967. Neue Polychaeten aus Sandfauna des Roten Meeres. *Zoologischer Anzeiger,* 178:102–110.

Swedmark, B.

1952. Note préliminaire sur un polychète sédentaire aberrant, *Psammodrilus balanoglossoides* n. gen., n. sp. *Arkiv för Zoologi,* 4:159–162.

1955. Recherches sur la morphologie, le développement et la biologie de *Psammodrilus balanoglossoides,* Polychète sédentaire de la microfaune des sables. *Archives de Zoologie Expérimentale et Générale,* 92:141–220.

1959. *Psammodriloides fauveli* n. gen, n. sp. et la famille des Psammodrilidae (Polychaeta Sedentaria). *Arkiv för Zoologi,* 12:55–64.

1964. The Interstitial Fauna of Marine Sand. *Biological Reviews,* 39:1–42.

Tenerelli, V.

1964. Su una associazione di Policheti mesopsammici del Golfo di Catania. *Bollettino delle sedute della Accademia Gioenia di Scienze Naturali in Catania,* series 4, 8:221–245.

1965. Considerazioni sul genere *Pisione* (Annelida Polichaeta) e sua presenza lungo le coste di Sicilia. *Bollettino delle sedute della Accademia Gioenia di Scienze Naturali in Catania,* series 4, 8:291–310.

1966a. Syllidae ed Hesionidaee (Annelida Polychaeta) della fauna interstiziale marina costiera. *Bollettino di Zoologia,* 33:145–146.

1966b. Considerazioni su Syllidae ed Hesionidae (Annelida Polychaeta) della fauna interstiziale marina costiera. *Atti della Accademia Gioenia di Scienze Naturali in Catania,* series 6, 18:222–239.

Valkanov, A.

1954. Zwei neue Polychaeten für das Schwarze Meer. *Arbeiten der Biologischen Meeresstation Varna,* 18:55–57. [In Bulgarian.]

Westheide, W.

1967. Monographie der Gattungen *Hesionides* Friedrich und *Microphthalmus* Mecznikow (Polychaeta, Hesionidae). Ein Beitrag zur Organisation und Biologie psammobionter Polychaeten. *Zeitschrift für Morphologie der Tiere,* 61:1–159.

1969. Spermatodesmen. Ein einfacher Spermatophorentyp bei interstitiellen Polychaeten. *Naturwissenschaften.* 12:641–642.

Westheide, W., and P. Ax

1965. Bildung und Übertragung von Spermatophoren bei Polychaeten. (Untersuchungen an *Hesionides arenarius* Friedrich). *Zoologischer Anzeiger,* Supplementband 28:196–203.

Zunarelli-Vandini, R.

1968. Reproductive Biology of *Microphthalmus* (Polychaeta, Hesionidae). *Pubblicazioni della Stazione Zoologica di Napoli,* 36:253–259.

Pierre Lasserre

Oligochaeta from the Marine Meiobenthos: Taxonomy and Ecology

ABSTRACT

The taxonomy of the marine Oligochaeta belonging to the families Aeolosomatidae, Potamodrilidae, Tubificidae, Naididae, and Enchytraeidae is discussed with emphasis on morphology. Ecology is discussed in terms of adaptations to the habitat, locomotion, reproduction, and distribution in intertidal and subtidal habitats. Distribution of intertidal species is interpreted in terms of physiological ecology.

The class Oligochaeta has both interstitial and freshwater representatives and some members have penetrated marine habitats. Certain groups that occur in estuarine muds are very abundant in terms of individuals and biomass (Brinkhurst, 1963b, 1964; Dahl, 1960; Lasserre, 1967a,b). Some groups often are dominant members of the subtidal meiobenthos, others mainly are restricted to the upper areas of sandy beaches.

It is generally accepted that the term meiofauna refers to those animals which pass through a 0.5-mm sieve. In general, adult meiobenthic oligochaetes are between 1 and 6 mm in length, with a diameter not exceeding 300 μ. There are, however, some that are larger as adults but whose juvenile forms exist as temporary members of the meiobenthos.

Many meiobenthic oligochaetes are cosmopolitan. The same species often are found on the shores of the Baltic Sea, the North Sea, around the English coast, and on both the Atlantic and Mediterranean shores of France. Recently, the author found on the eastern coast of North America many species which occur in Europe.

I thank Dr. R. Weevers, University of Bristol (England), for his linguistic revision of this manuscript.

Taxonomy

The basis for the classification of Oligochaeta is the arrangement of the genital segments and gonoducts (Avel, 1959; Stephenson, 1930). The Aeolosomatidae, Potamodrilidae, Tubificidae, Naididae, and Enchytraeidae include species living as marine meiobenthos. All of these families are plesiopora (Figure 1), that is, the vasa deferentia open on the segment posterior to the segment containing the testes. The plesiothecate plesiopora includes the Tubificidae and Naididae, in which the spermathecae are found in or near the segment containing the testes (segment 5 for Naididae, segment 10 for Tubificidae; see Figure 1). The prosothecate plesiopora includes the Enchytraeidae, in which the spermathecae are situated in segment 5, far anterior to the genital segments (Figure 1).

The Aeolosomatidae and Potamodrilidae apparently are very primitive in many respects and not closely related to the other families. Representatives of these families often look more like polychaetes or archiannelids than oligochaetes (Figure 1).

Only partial keys have been published: Bunke (1967) for Aeolosomatidae and Potamodrilidae; Sperber (1950) for Naididae; Brinkhurst (1963a) for Tubificidae; Nielsen and Christensen (1959, 1963a,b), Lasserre (1966, 1967b,c), and Tynen and Nurminen (1969) for Enchytraeidae. A review of the marine Enchytraeidae, with keys, is in preparation by the author. In many cases, original de-

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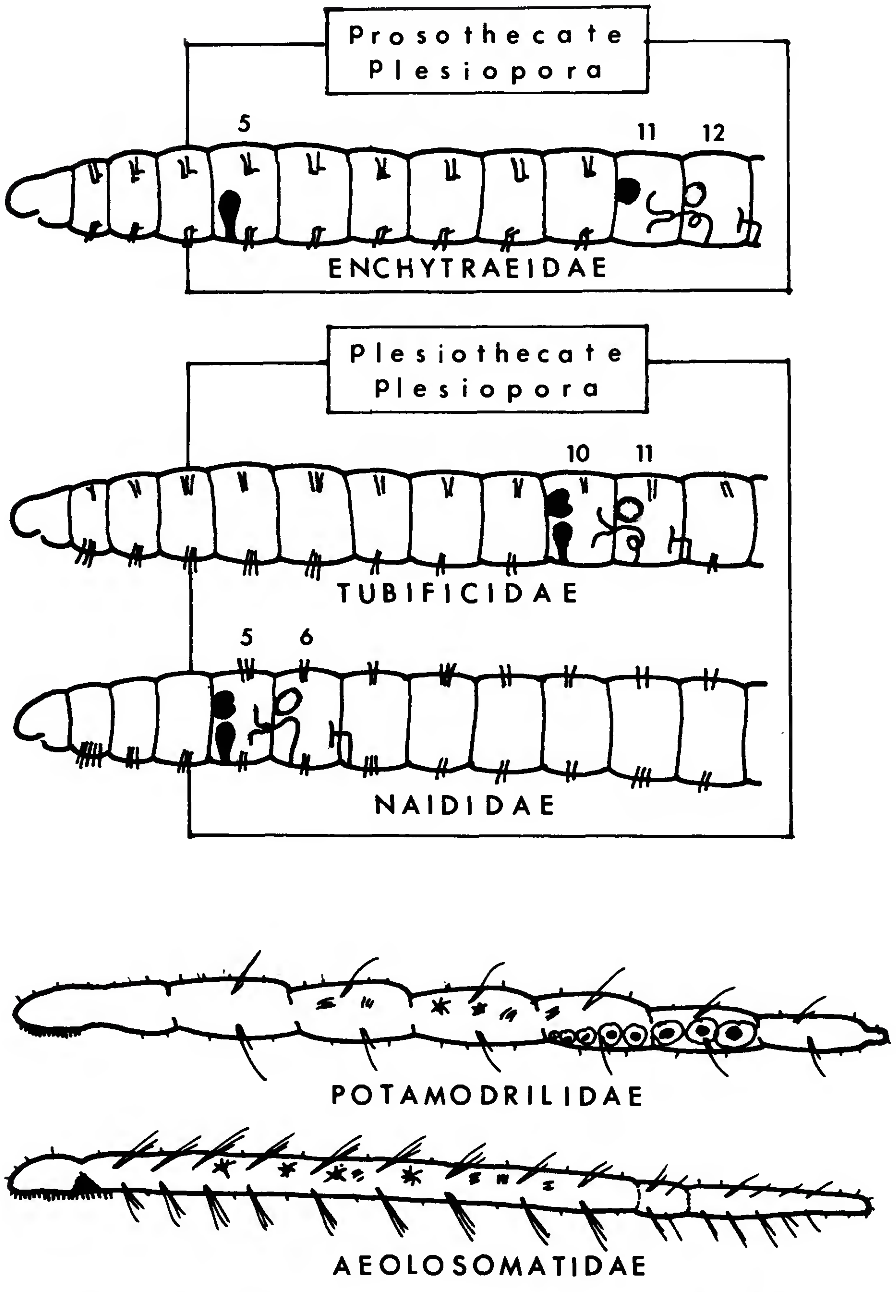


FIGURE 1.—Diagrammatic views showing arrangement of reproductive organs and setae in different families of meiobenthic Oligochaeta.

scriptions have been supplemented, emended, invalidated, and revalidated by later authors (Michaelsen, 1927; Ude, 1929; Cernosvitov, 1937; Sperber, 1950; Brinkhurst, 1963a; Nielsen and Christensen, 1959; Bunke, 1967).

The taxonomy of meiobenthic oligochaetes is difficult since careful microscopic study of live and serially sectioned animals is quite essential. Single characters generally are not diagnostic at either the generic or specific levels; their importance must be assessed in each case. The setae are the principal criteria used for identification. Of the families considered here, the setae are arranged in four bundles—two ventrolateral (termed "ventral") and two dorsolateral (termed "dorsal"). The first segment is devoid of setae.

The taxonomic difficulties encountered in descriptions of gross morphology may be overcome, with certain limitations, by the use of chromosome counts and observations on the course of the first meiotic division. Cytological investigation seems to offer a promising approach to the solution of many confusing problems in oligochaete taxonomy.

Family AEOLOSOMATIDAE

FIGURE 2G–K

The representatives of the family Aeolosomatidae have an elongated and tactile prostomium which is ciliated ventrally. Many species have prominent epidermal glands which produce a colored secretion. The color of this secretory product is an important diagnostic character which is not present after fixation in formalin or alcohol; therefore, the observation of live specimens is essential. The main colors are red and yellow-green. In some species the secretion is not colored.

Segmentation is not well marked and the number of segments is low, usually about 10. The position of the budding zone is of importance (Figure 2G).

Setae are present in the genus *Aelosoma* Ehrenberg but absent in the genus *Rheomorpha* Ruttner-Kolisko. Hair setae are dominant, and occur in both dorsal and ventral bundles. They are slender, more or less flexible filaments (Figure 2H1–K1); a serration is present on one side in some species, such as *Aeolosoma litorale* Bunke (Figure 2H2). Smaller sigmoid setae with a proximal serration are found very often (Figure 2K2).

The shape of the prostomium and the form and position of ciliated pits are important (Figure 2I,J). Since the sex organs are present only in rare individuals, they are not used for classification and do not appear in the existing keys.

Family POTAMODRILIDAE

FIGURE 2L,M

Like the previous family, Potamodrilidae has an elongated and tactile prostomium which is ciliated ventrally. Following is a characterization of the monotypic genus *(Potamodrilus)*.

The external segmentation is hardly visible. The number of segments (7) is constant, and there is a prostomium (Figure 2L). The first segment is devoid of setae, six segments have two hair setae (distally serrated) in dorsal and ventral bundles (Figure 2M1,2). The epidermal glands produce an adhesive secretion. A male pore and seminal groove are present in segment 6. The female pore is at the junction of segments 6 and 7.

Family NAIDIDAE

FIGURE 2A–C

The number, position, and shape of setae are very important for identification. In many Naididae the dorsal bundles begin on a more-posterior segment (e.g., *Paranais* Czerniavsky). Hair setae are found in the dorsal bundles; these are more or less slender filaments more common in front of the clitellum. Bifid crotchets are present in dorsal and ventral bundles (Figure 2B,C). These S-shaped setae have a distal hook or crotchet composed of two diverging teeth, and the shape and relative length of these teeth commonly are referred to in the keys. Genital setae (penial setae), differing in shape from the ordinary ventral setae, are present only in fully developed specimens. The occurrence of penial setae is a generic character, and the shape of such setae is of specific value.

The differentiation of the alimentary canal and the form of the vascular system are diagnostic characters. The alimentary canal consists of the mouth

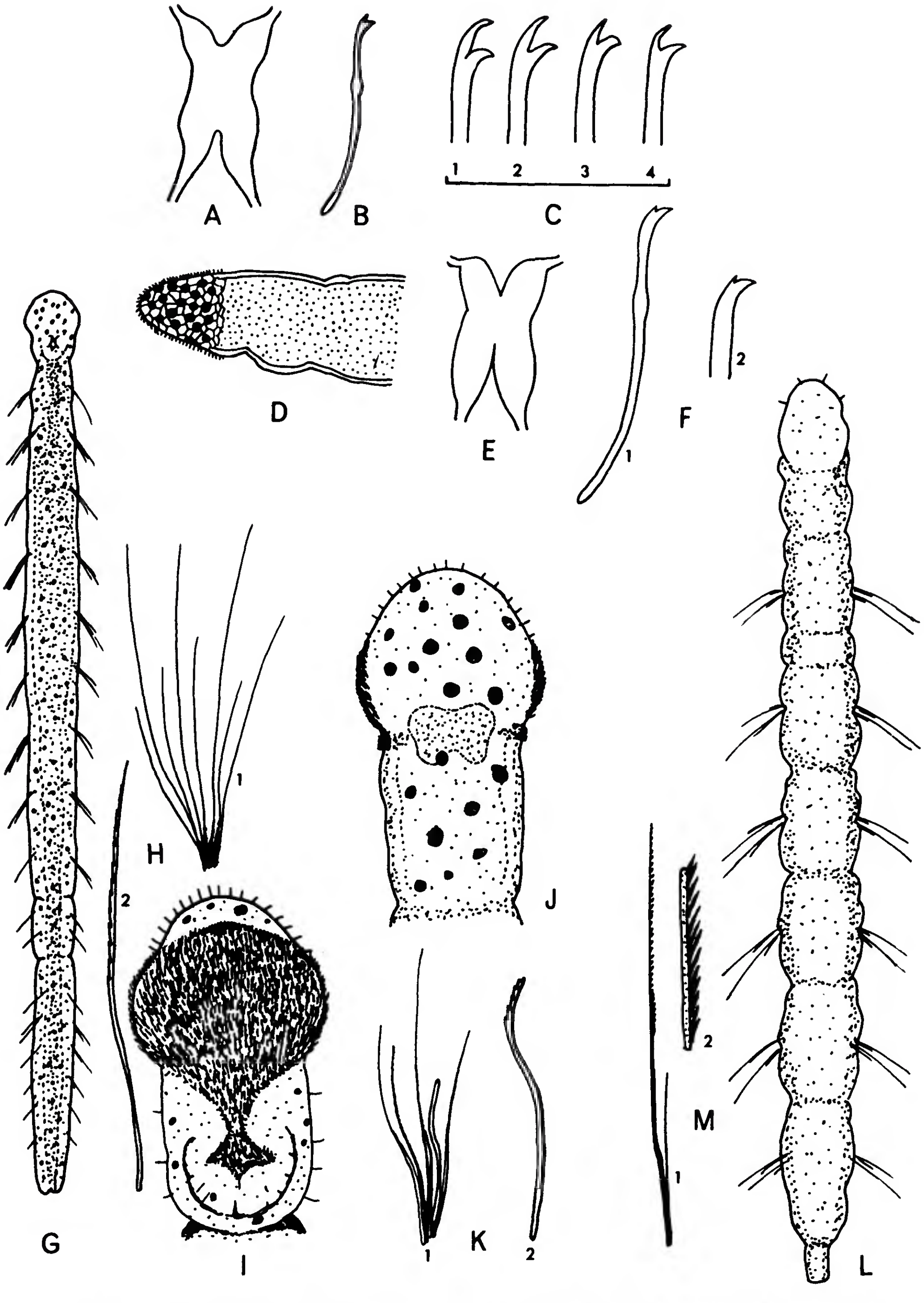


FIGURE 2.—A–C, *Paranais litoralis,* Naididae: A, brain (dorsal view); B, setae; C1–3, distal ends of ventral setae; C4, distal end of dorsal setae. D–F, *Phallodrilus monospermathecus,* Tubificidae: D, anterior part; E, brain (dorsal view);F1,2 setae. G–I, *Aeolosoma litorale:* G, habitus; H1, setal bundle; H2, hair setae; I, prostomium (ventral view). J, K, *Aeolosoma psammophilum:* J, prostomium (dorsal view); K1, setal bundle; K2, sigmoid seta. L, M, *Potamodrilus fluviatilis:* L, habitus; M1, setal bundle; M2, detail of a hair seta.

cavity, pharynx, esophagus, and intestine. The pharynx roof and parts of the esophagus are covered by gland cells and the pharyngeal and esophageal glands. In some genera there are septal glands instead of pharyngeal or esophageal glands. Behind the esophagus (segments 4–6) a dilatation of the gut forms a stomach which merges imperceptibly into the intestine. The gut behind the first three to five segments is covered by a layer of chloragogen cells that densely cover the intestine. The vascular system is composed of a contractile longitudinal vessel that divides behind the brain and unites by anastomosis to the noncontractile ventral vessel, in anterior part, to form a plexus.

The shape of the brain, as described by many authors, is of limited value (Figure 2A), and it varies much with the state of contraction, both in living and preserved material.

The reproductive organs are present only in rare individuals; consequently, they are of little use for classification and do not appear in existing keys. Immature specimens, however, should never be used for species description.

Family TUBIFICIDAE

FIGURE 2D–F

As in the previous family, the setae are very important for identification. Hair setae, when present, are found dorsally. Bifid crotchets are present in dorsal and ventral bundles (Figure 2F), and the upper tooth may be so reduced that the setae appear to be needle-like, sometimes with a trace of the reduced tooth. Pectinate setae, present in some genera, are situated in anterior bundles; the intermediate teeth may be as large as the outer teeth. Genital setae are associated with the penial or spermathecal pores; they are frequent in tubificids and their very characteristic shape is useful for identification at the generic and specific levels.

The genera and species differ chiefly in the form of the male efferent ducts. Each of these paired organs is composed of a sperm funnel and vas deferens, both of which lie in the posterior part of the testis segment. The funnel leads into the vas deferens stalk. A true penis, which may or may not be sheathed in a cuticle, may or may not be present. The presence or absence of a prostate, the shape of the atrium, and the form of the penis, when it is covered with a chitinous sheath, are generic characters. The main characters used in species diagnosis are the shape of the setae and spermatheca.

Family ENCHYTRAEIDAE

FIGURES 3–7

The genera and species of this family are not easy to identify even by experienced systematists. The difficulties encountered in the taxonomy of Enchytraeidae are due to the great intraspecific variability. A standard procedure is necessary in the description of new species. A style conforming to that of Nielsen and Christensen (1959, 1963a,b) and Lasserre (1964, 1966, 1967b,c) will facilitate identification.

The following morphological features are diagnostic for the members of this family. The number of segments remains practically constant in fully mature specimens. The number, distribution, and form of the setae furnish important clues. In the genus *Marionia* Michaelsen, which includes many meiobenthic representatives, one group of three species has ventral bundles only, and one species, *M. achaeta* Lasserre, is without setae. The setae are broad, usually simple-ended, straight or sigmoid, and with or without an ental hook (Figure 4A–C).

The brain varies widely in size and shape, but the form of the more-posterior part, more or less deeply incised or slightly concave, is of limited diagnostic value at the species level (Figures 3, 5A).

The septal glands, paired roundish organs of unknown function, are usually attached on septa 4/5, 5/6, and 6/7; and they may vary in number and shape (Figure 5D–F). The esophagus may have paired, elongate appendages which communicate with the pharynx, the peptronephridia (e.g., the genera *Enchytraeus* Henle and *Grania* Southern). These organs extend backward, floating freely in the body cavity. They are highly contractile and, hence, variable in shape. Their presence or absence is of generic value. For example, the genus *Marionia* and a new genus to be described by the author have no peptronephridia.

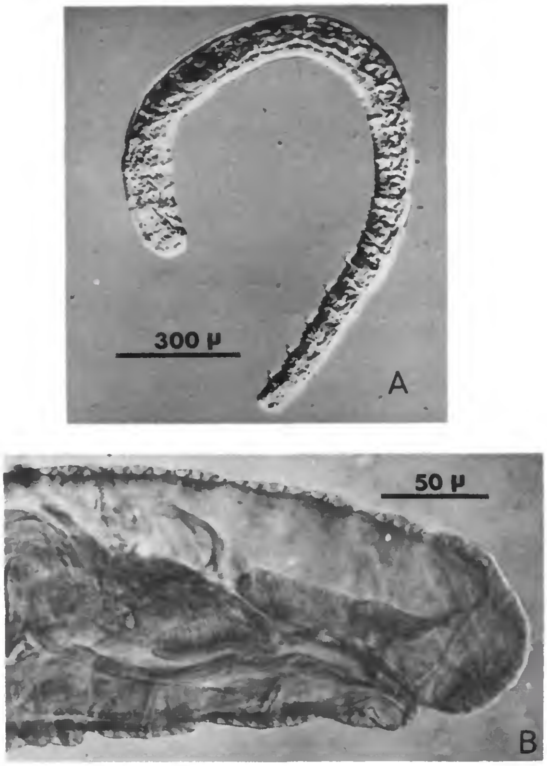


FIGURE 3.—A, An enchytraeid oligochaeta (genus *Marionina*). B, Lateral view of the anterior part of a living specimen of *Marionina* showing brain and pharynx.

Other features of taxonomic importance include the coelomocytes (= lymphocytes) and the chloragogen cells. The former float freely in the body cavity (Figure 5B1,2), while the latter are attached to the gut (Figure 5B2). The origin of the dorsal vessel, color of the blood, and form of the anteseptal portion of the nephridia are important. In *Marionina* the anteseptal portion contains one or more loops of the nephridial canal (Figure 5C1,2); in other genera (e.g., *Lumbricillus* Orsted) it consists only of the funnel.

The most important features relating to the identification of Enchytraeidae lie in the morphology of the sex organs. The sperm funnels (Figure 5G) are enlargements of the inner end of the sperm ducts and, although they float more or less freely in the body cavity, usually can be found in a position just anterior to the clitellum. The length/width ratio of the sperm funnels often is taxonomically significant. The seminal vesicles, when present, are situated just anterior to the sperm funnels, and they are good diagnostic characters at both generic and species levels. The single pair of spermathecae, situated in segment 5 and sometimes extending farther back, is a very important character (Figures 5D–F, 6A–C). In mature individuals the ampulla contains sperm, sometimes arranged in a manner typical of the species. The ampulla may or may not have an ental duct opening into the esophagus. The opening of the ectal duct to the exterior, and/or the duct itself, may be surrounded by glands, the number and form of which are important.

The principal characters used for the identification of meiobenthic *Marionina* are shown in Figure 7.

Ecology

Among oligochaetes, Aeolosomatidae and Potamodrilidae are the best adapted to the intertidal environment. Typically, they live in groundwater. These primitive oligochaetes have a prostomium which is ciliated ventrally (Figure 2), as in archiannelids, and have many epidermal glands, either scattered over the body or concentrated in the pygidium (as in *Potamodrilus*).

Meiobenthic oligochaetes other than the aelosomatids and potamodrilids have no real morphological adaptations. The degree of organization and differentiation in meiobenthic forms generally are the same as in related, larger forms. Some species of *Marionina* have greatly developed glands in place of the absent dorsal setal bundles or annexed to the posterior setae (Figure 4D–E). It seems that these glands function in promoting adhesion to sediments which often are unstable. When alive, the worms can be seen adhering to sand grains—with the middle or posterior part of the body—very probably by means of secretion(s) from these glands. Many species of Tubificidae, Naididae, and Enchÿtraeidae have developed a tolerance to brackish water and to variable salinities. Such adaptations may explain the very wide distribution of many species.

Many enchytraeids, mainly of the genus *Marion-*

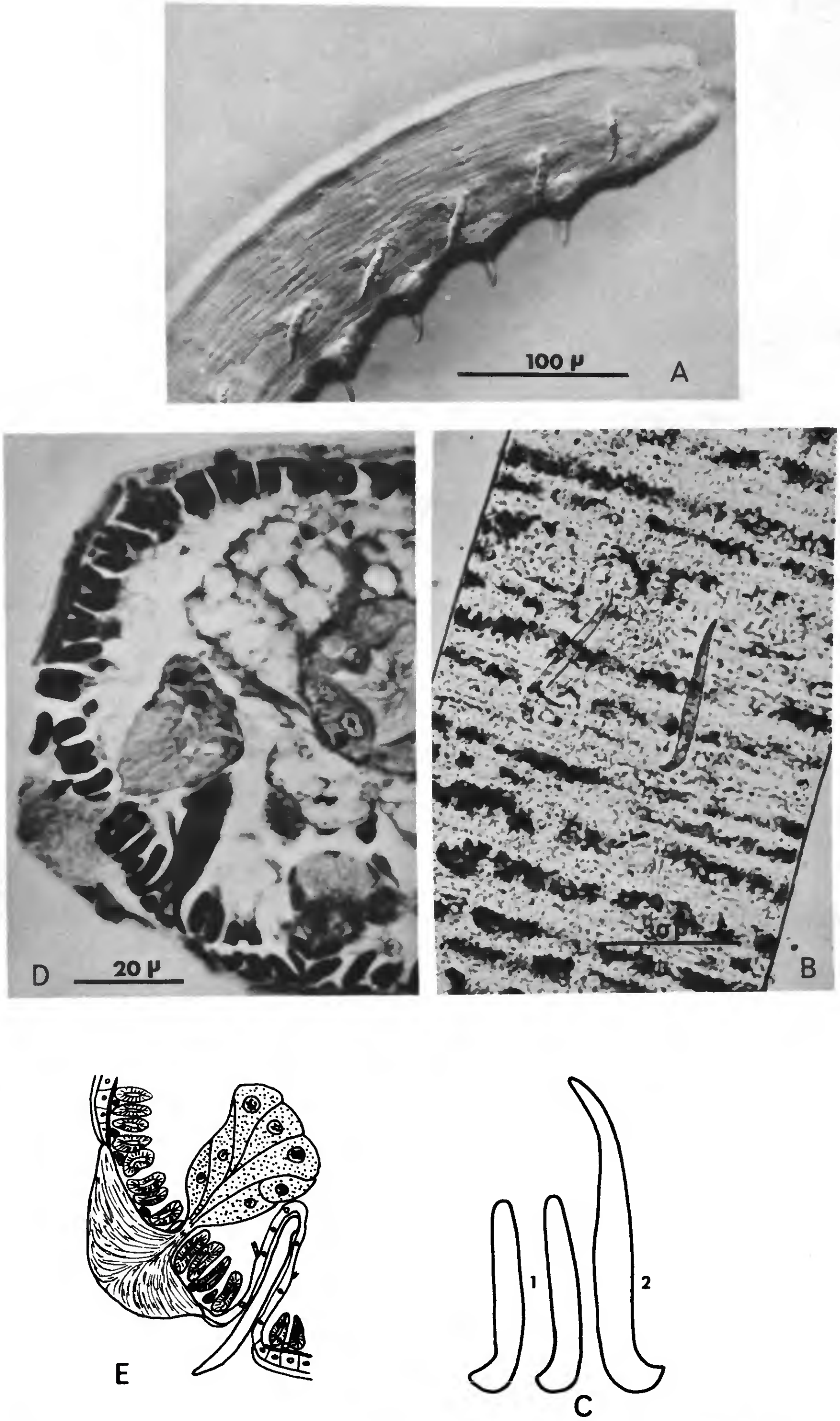
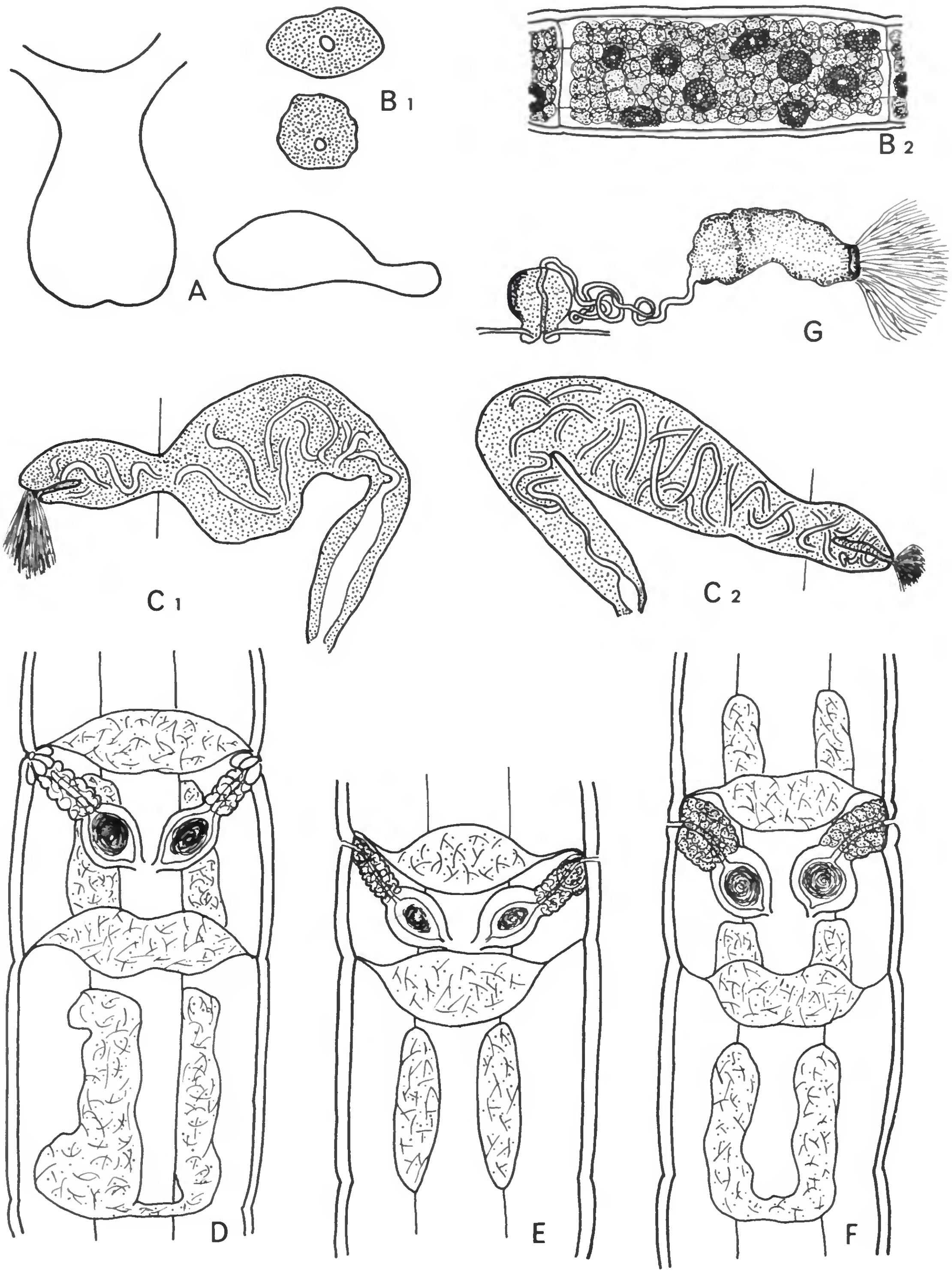


FIGURE 4.—*Marionina* sp.: A, posterior part of living specimen; B, a posterior segment showing the two ventral setae and cutaneous glands arranged in transverse rows (orcein coloration); C, an anterior bundle and posterior seta; D, E, adhesive gland annexed to a posterior seta (transverse section).


A
B 1
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C 1
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D
E
F

ina, the tubificid *Phallodrilus monospermathecus* (Knöllner), and the naidid *Paranais litoralis* are restricted to the intertidal zone of sandy beaches. The distribution of seven species of *Marionina* were studied by Lasserre (1967a) over a period of three years in the Bassin d'Arcachon.

In *Marionina,* hermaphroditism with cross-fertilization is the rule. Usually one egg is deposited in a cocoon (Figure 8c) secreted by the clitellar glands of the parent. The entire life span is benthic. The young emerge only 10 to 15 days after the laying (Lasserre, 1967a), and there are two or three generations per year. In temperate palearctic regions, the species living in the foreshores reach their maximum density in spring and autumn. Reproduction almost ceases during cold winters. No doubt a certain mortality occurs, but it seems to be moderate. As a consequence of the position of these maximum and minimum values it follows that the curves depicting the seasonal trends are asymmetrical and show a slow decrease during winter and summer and a rapid increase to maximum density in spring and autumn (Figure 9).

The populations of *Marionina achaeta* Lasserre, *M. preclitellochaeta* Nielsen and Christensen, *M. elongata* Lasserre, and *M. spicula* Leuckart live in the upper shore with *Achaeta littoralis* Lasserre and *Enchytraeus capitatus* Bulow. *Marionina subterranea* (Knöllner), *M. precilitellochaetta,* and *M. achaeta* live from the middle to the lower shore, where low salinities may occur, together with the tubificid *Phallodrilus monospermathecus* (Figure 10). Such distribution is in agreement with the observations of Jansson (1968) at Swedish beaches. In each of the middle- and upper-shore populations, 85 to 90 percent of the animals live at depths between 10 and 70 cm from the surface (Figure 11). During the period of maximum population the greatest density occurs at 30 cm depth (noted in September). The density at 50 to 70 cm depth remains quantitatively constant year round (Figure 11). The populations migrate neither daily nor seasonally. Temperature and food are tentatively concluded to be the most important factors governing the density of Enchytraeidae (Lasserre, 1967a).

Jansson (1962, 1966, 1968) has demonstrated that, on Swedish coasts, there is a clear reaction to temperature and salinity gradients for some species referred to the genus *Marionina;* however, "the preference for a certain salinity is certainly a less fixed characteristic of an animal than its tolerance" (Jansson, 1968). In some experiments the preference is outside the tolerance zone: *Marionina preclitellochaeta* tolerated 2.5 to 10 ppt salinity but preferred 0.2 to 3 ppt salinity (Jansson, 1962). *Marionina southerni* (Cernosvitov) has a great tolerance with a range of more than 15 ppt, but *M. preclitellochaeta* and *M. subterranea* have a more restricted range. The Swedish beaches studied by Jansson have salinities from 7 to 22 ppt (Jansson, 1967b).

In *Marionina,* locomotion is effected by writhing or more-coordinated burrowing. The animals force their way through the substratum. *Marionina subterranea* shows a preference for a grain size between 125 and 500 μ (Jansson, 1966). The animals are incapable of moving in sand with particle size between 1,000 and 2,000 μ and lie wriggling in the large interstices where they are initially deposited (Jansson, 1967a). The animal can cover a distance of 3 cm/minute in a thin layer of fine sand.

Marionina subterranea and many other species investigated on Atlantic coasts of France (Lasserre, 1967a,c) and eastern North America (Lasserre, in preparation) showed very great tolerance both to salinity and to temperature, with minimum ranges of more than 15 ppt and 25°C. These populations normally are subject to great fluctuations in salinity and temperature (Lasserre, 1967a,b, 1970, and in

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FIGURE 5.—A, *Marionina* sp., brain; B1, *Marionina* sp., coelomocyte; B2, *Marionina achaeta,* coelomocyte and chloragogen cells; C1, *Marionina* sp., nephridia; C2, *M. achaeta,* nephridia; D, *M. achaeta,* dorsal view of septal glands and spermathecae (segments 4–6); E, *M. spicula,* dorsal view of septal glands and spermathecae (segments 4–6); F, *M. elongata,* dorsal view of septal glands and spermathecae (segments 4–6).

press) and need wider physiological tolerance than the Swedish species. The interstitial salinities in the Atlantic sandy beaches are influenced mostly by salt concentration of the sea, evaporation from the sand, and rain.

Oligochaeta also live as subtidal meiobenthos, mainly tubificids (Cook, 1969) and naidids. The enchytraeids of the genus *Grania* and a new genus to be described by the author are characteristic of coarse sediments such as "*Amphioxus* sand" (Lasserre, 1966, 1967b).

The differences in the distribution of two species, *Marionina achaeta* and *M. spicula,* cannot be explained properly by a difference between the commonly advocated granulometric and climatic factors (Lasserre, 1967a). Therefore, the physiological preferences of each species were investigated experimentally (Lasserre, 1970 and in press). *Marionina achaeta* lives predominantly in the upper shore but sometimes in the lower part when the salinity is low (Figure 10). *Marionina spicula* is found more or less throughout the shore, though the upper

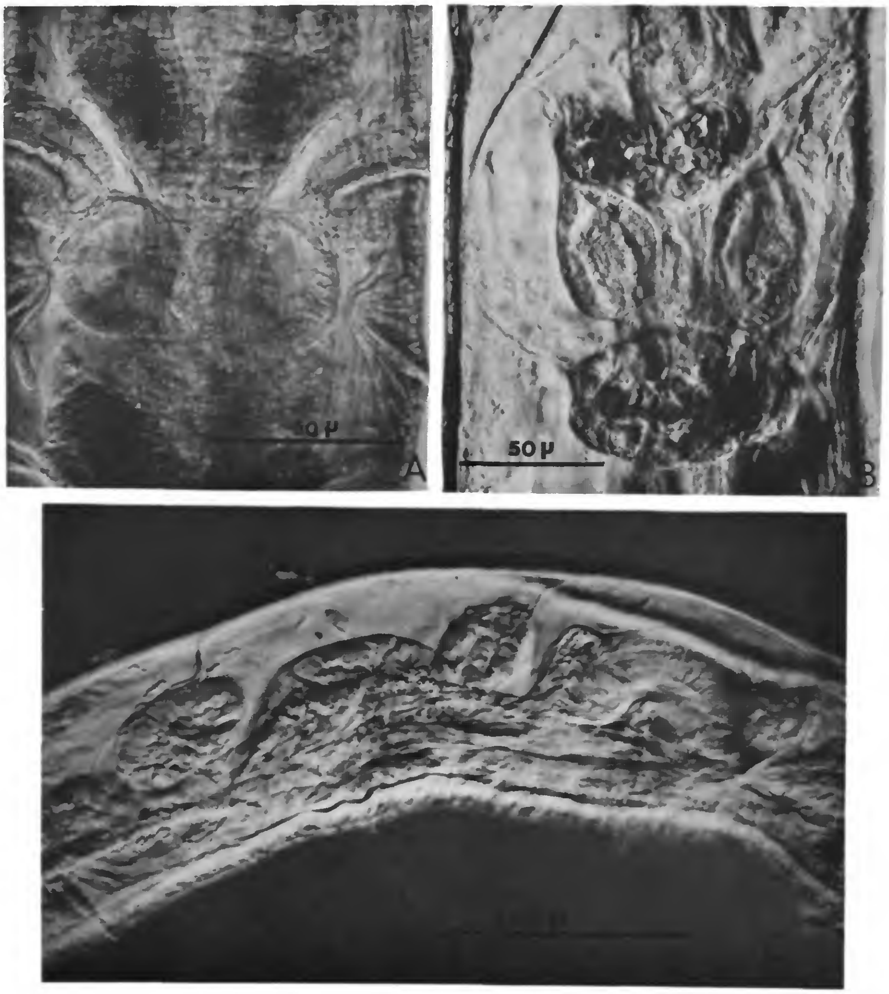

FIGURE 6.—A, *Marionina elongata,* dorsal view of septal glands and spermathecae; B, *M. spicula,* dorsal view of septal glands and spermathecae; C, *Lumbricillus* sp., lateral view of septal glands and spermathecae. All living.

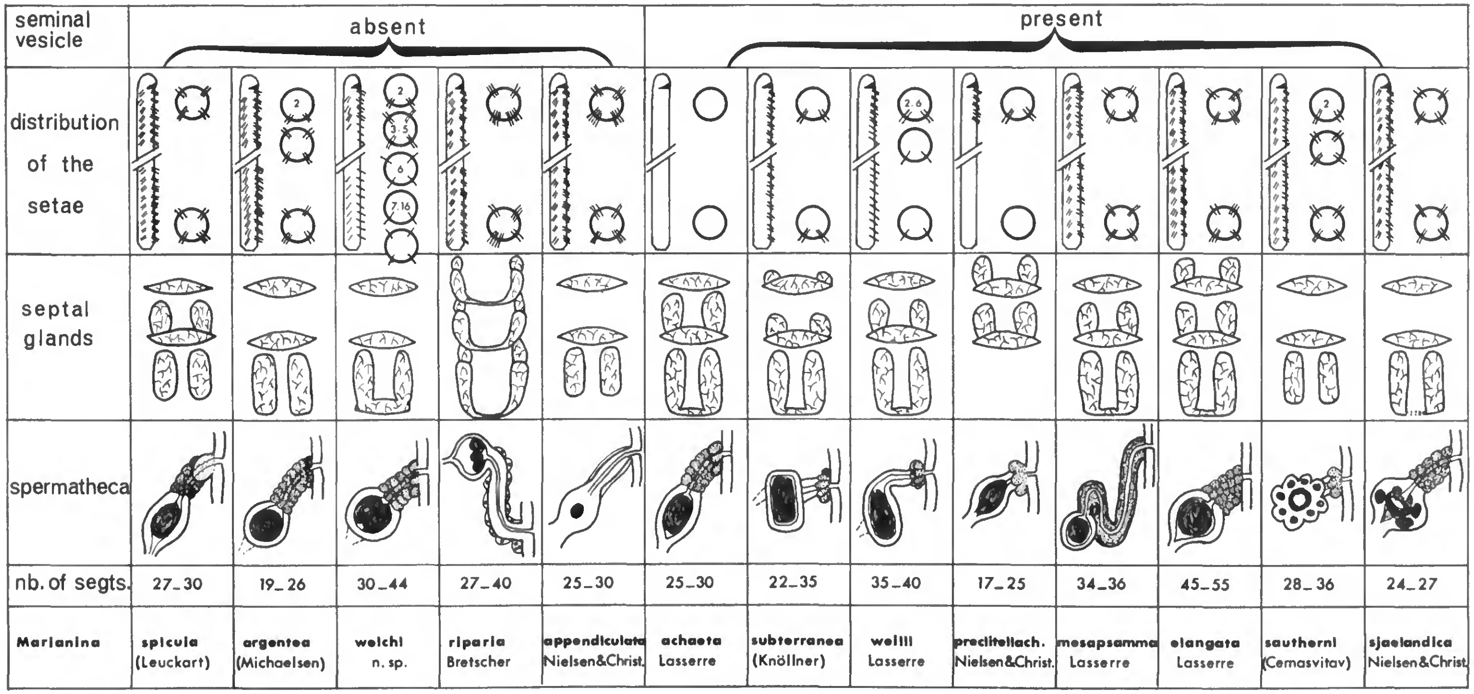

FIGURE 7.—Diagrammatic views of the genus *Marionina*.

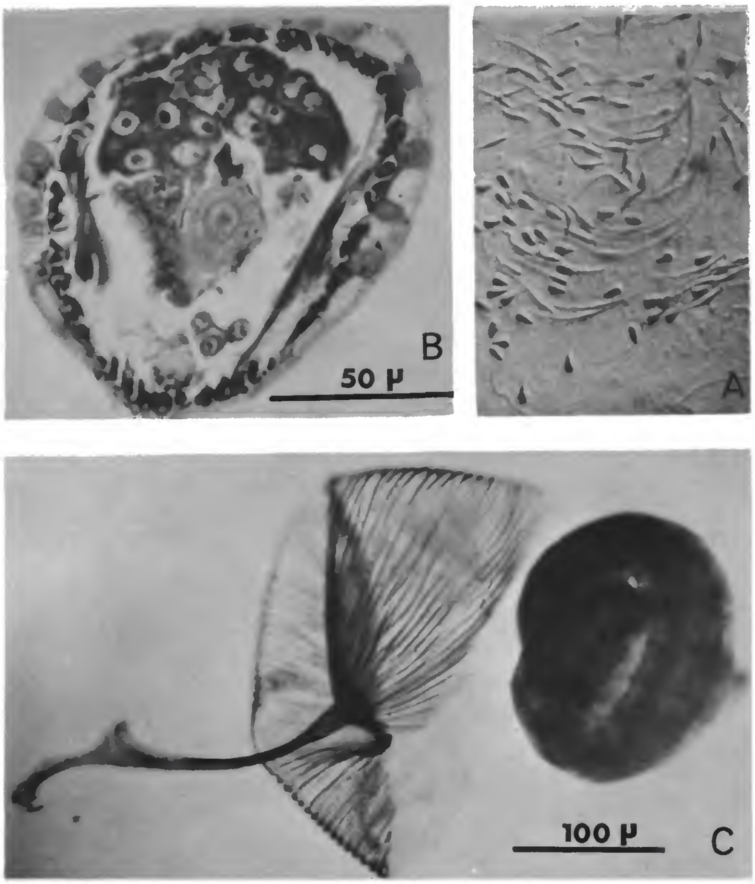

FIGURE 8.—A, Spermatids (*Marionina*), × 1200; B, transverse section through the clitellum, ovary, intestine, and sperm duct (*Marionina* sp.); C, cocoon and newly hatched worm (genus *Marionina*).

limit is slightly below that of *M. achaeta* (Figure 10). Oxygen consumption was utilized as an indication of the homeostatic capabilities of these organisms. It was found that *Marionina achaeta* could tolerate salinities somewhat above 25 ppt. but only with the expenditure of considerable metabolic energy; therefore, the animal would be at a disadvantage on the lower shore where the salinity is normally above that level. *Marionina spicula,* on the other hand, could tolerate salinities above 25 ppt without the expenditure of metabolic energy, but it was unable to survive at the high temperatures (above 30°C) which have been recorded during summer in the upper part of the range of *M. achaeta.* These last two observations, taken together, explain the relative abundance of *M. spicula* at all except the highest levels. The overall consumption of oxygen in both species is statistically constant over a range of salinities spanning those normally encountered; this phenomenon is termed an "adaptive plateau." At both very low and high salinity oxygen consumption is considerably elevated.

Further experiments (Lasserre, 1969) on *Marionina achaeta,* relating to the cellular mechanisms involved, have shown that this elevation occurs only when sodium and, to a lesser extent, potassium are present in the medium only at very low or very high ionic strengths. Chloride concentration changes have no effect on oxygen uptake. Very

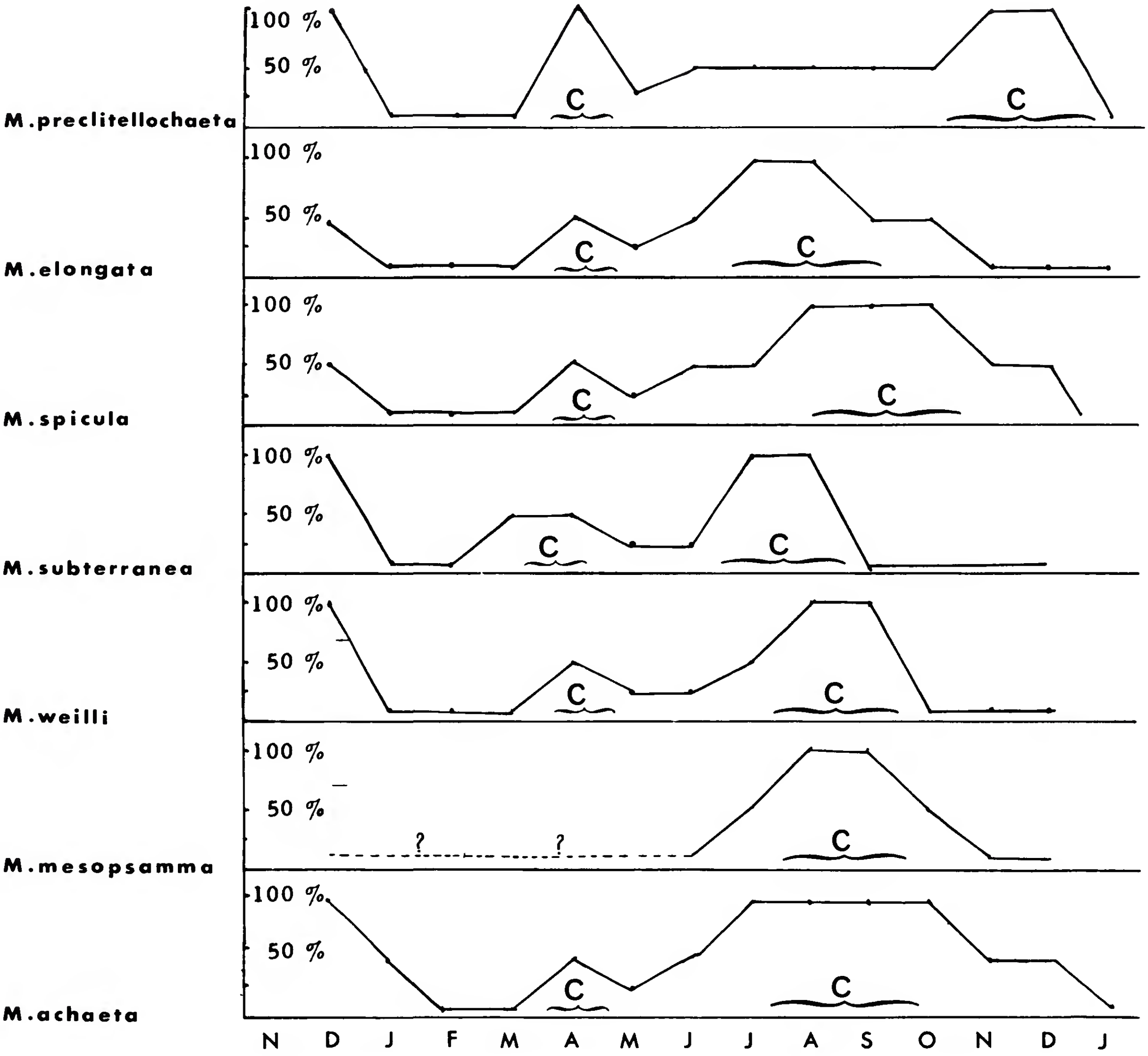

FIGURE 9.—Seasonal variations of mature animals (in percent) and deposition of cocoons (c).

high concentrations ot sodium lower the metabolic rate to a standard level which is the same as the level obtained from treatment with a metabolic inhibitor specific for sodium transport (ouabain 10–3M). The depression by ouabain reaches the same level regardless of the concentration of sodium.

The tentative conclusion is that the elevated metabolic rate in media with less or more saline than the range covered by the adaptative plateau is the result of extreme activition of a Na-K-ATPase pump system, working either inward or outward depending on the conditions. The decrease of oxygen consumption in high-salinity media is attributed to a breakdown of the ion pumps, thus producing the same depression as ouabain.

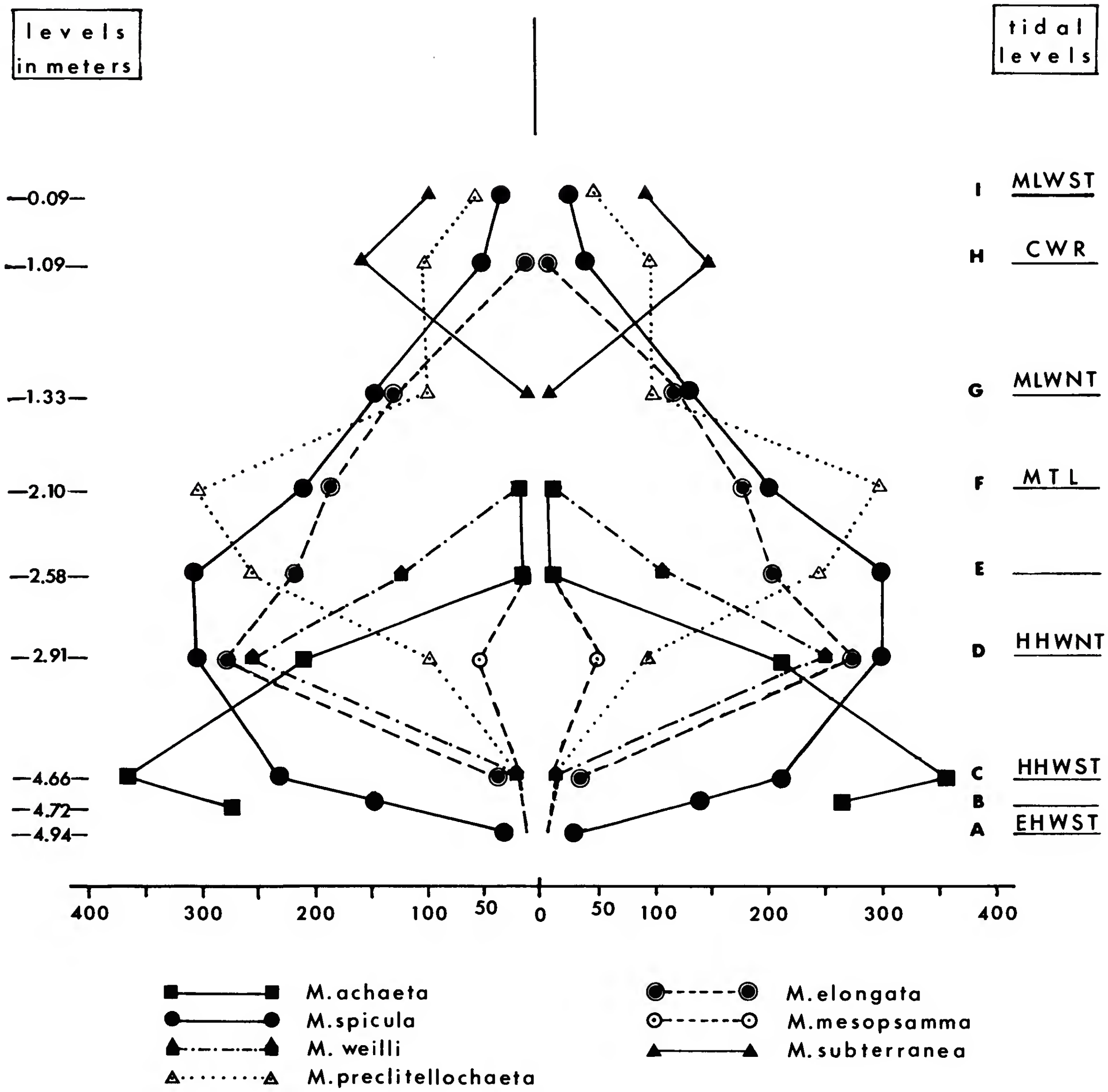

FIGURE 10.—Horizontal distribution of seven species of *Marionina* in the intertidal zone of the Bassin d'Arcachon, Atlantic coast of France (autumn 1965, Camp Américain, 30 cm depth). Tidal levels are indicated by combination of letters: E, equinoctial; M, mean; HW, high water; LW, low water; NT, neap tides; ST, spring tides; MTL, midtide level; CWR, continental water resurgence.

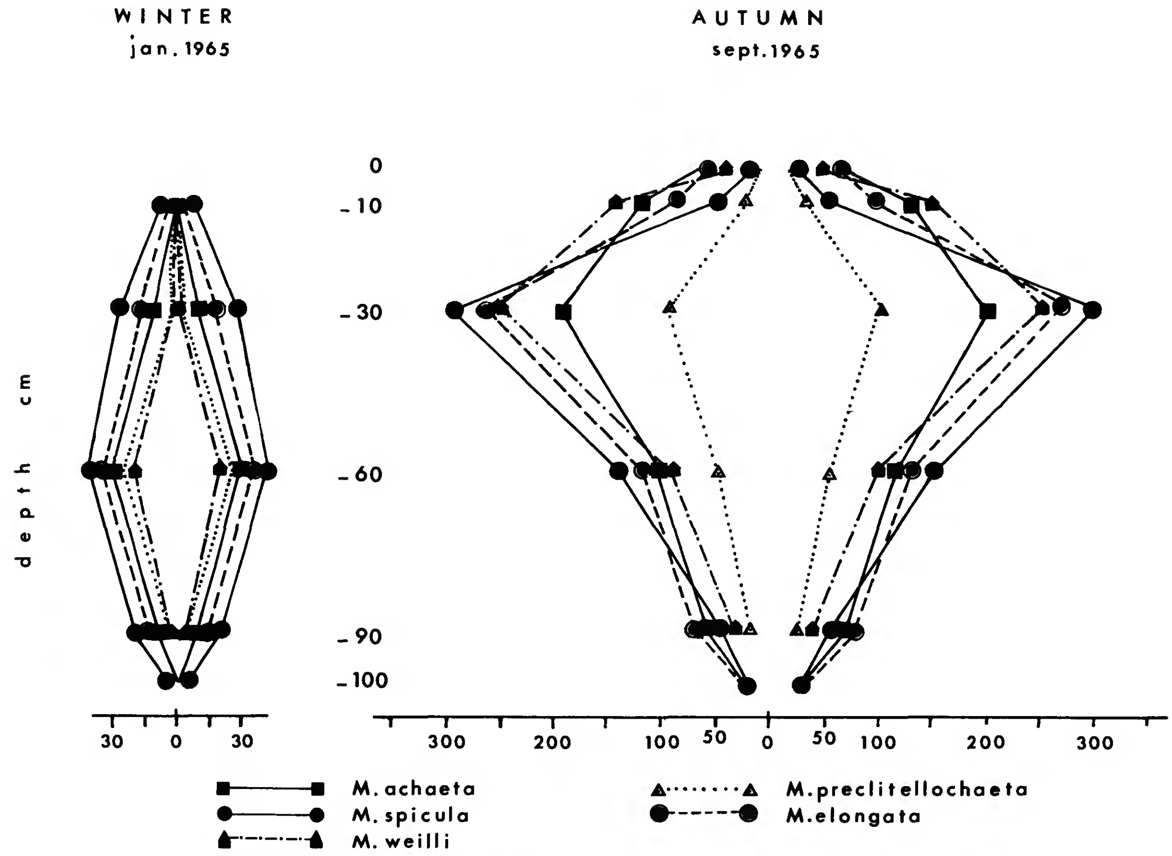

FIGURE 11.—Vertical distribution of five species of *Marionina* in the intertidal zone of the Bassin d'Arcachon: A, in winter (January, 1965); B, in autumn (September, 1965). Mean high-water/neap-tide level.

Literature Cited

Avel, M.

1959. Classe de Annélides Oligochètes. In P. P. Grassé, editor, *Traité de Zoologie*, 5(1):224–470.

Brinkhurst, R. O.

1963a. Taxonomical Studies on the Tubificidae (Annelida, Oligochaeta). *Internationale Revue der gesamten Hydrobiologie, Systematische Beihefte*, 2:1–89.

1963b. Notes on the Brackish-Water and Marine Species of Tubificidae (Annelida, Oligochaeta). *Journal of the Marine Biological Association of the United Kingdom*, 43:709–715.

1964. Observations on the Biology of the Marine Oligochaete *Tubifex costatus*. *Journal of the Marine Biological Association of the United Kingdom*, 44:11–16.

1966. A Contribution to the Systematics of the Marine Tubificidae (Annelida, Oligochaeta). *Biological Bulletin*, 30:297–303.

Bunke, D.

1967. Zur Morphologie und Systematik der Aeolosomatidae Beddard, 1895, und Potamodrilidae nov. fam. (Oligochaeta). *Zoologische Jahrbücher, Systematik Oekologie und Geographie der Tiere*, 94:187–368.

Cernosvitov, L.

1937. System der Enchytraeiden. *Bulletin de L'Association Russe pour les Recherches Scientifiques, Prague*, 5:263–295.

Cook, D. G.

1969. The Tubificidae (Annelida, Oligochaeta) of Cape Cod with a Taxonomic Revision of the Genera *Phallodrilus* Pierantoni, 1902, *Limnodriloides* Pierantoni, 1903, and *Spiridion* Knöllner, 1935. *Biological Bulletin*, 136:9–27.

Dahl, I. O.

1960. The Oligochaete Fauna of 3 Danish Water Areas (Taxonomic and Biological Observations). *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser*, 2:1–20.

Jansson, B. O.

1962. Salinity Resistance and Salinity Preference of Two Oligochaetes, *Aktedrilus monospermatecus* Knöllner and *Marionina preclitellochaeta* n. sp., from the Interstitial Fauna of Marine Sandy Beaches. *Oikos,* 13:293–305.

1966. Microdistribution of Factors and Fauna in Marine Sandy Beaches. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:77–86.

1967a. The Significance of Grain Size and Pore Water Content for the Interstitial Fauna of Sandy Beaches. *Oikos,* 18:311–322.

1967b. Diurnal and Annual Variations of Temperature and Salinity of Interstitial Water in Sandy Beaches. *Ophelia,* 4:173–201.

1968. Quantitative and Experimental Studies of the Interstitial Fauna in Four Swedish Sandy Beaches. *Ophelia,* 5:1–71.

Knöllner, F. H.

1935. Okologische und systematische Untersuchungen über litorale und marine Oligochäten der Kieler Bucht. *Zoologische Jahrbücher Systematik,* 66:425–563.

Lasserre, P.

1964. Note sur quelques oligochètes Enchytraeidae présents dans les plages du bassin d'Arcachon. *Procès-Verbaux de la Société Linnéenne de Bordeaux,* 101: 87–91.

1966. Oligochètes marins des côtes de France. I. Bassin d'Arachon: Systématique. *Cahiers de Biologie Marine,* 7:295–317.

1967a. Contribution à l'ètude des Oligochètes marins du Bassin d'Arcachon. Thèse de Biologie, Université de Bordeaux. 126 pages.

1967b. Oligochètes marins des côtes de France. II. Roscoff, Penpoull, étangs saumâtres de Concarneau: Systématique, Écologie. *Cahiers de Biologie Marine,* 8:273–293.

1967c. Présence du genre *Achaeta* Vejdovsky, 1887 (Oligochaeta, Enchytraeidae) dans des plages sableuses marines. Description de *Achaeta littoralis* n. sp. *Bulletin du Musèum d'Histoire Naturelle,* series 2, 39:979–983.

1969. Relations énergétiques entre le métabolisme respiratoire et la régulation ionique chez une Annélide Oligochète euryhaline, *Marionina achaeta* (Hagen). *Comptes Rendus de l'Académie des Sciences,* series D, 268:1541–1544.

1970. Action des variations de salinité, sur le métabolisme respiratoire d'Oligochètes euryhalins de genre *Marionina* Michaelsen, 1889. *Journal of Experimental Marine Biology and Ecology,* 4:150–155.

In Press. Données écophysiologiques sur la répartition des Oligochètes marins meiobenthiques. Proceedings of the Third European Marine Biology Symposium. *Vie et Milieu,* supplement 20.

Michaelsen, W.

1927. Oligochaeta. *Tierwelt der Nord- und Ostsee,* 6(9): 1–86.

Nielsen, C. O., and B. Christensen

1959. The Enchytraeidae, Critical Revision and Taxonomy of European Species. *Natura Jutlandica,* 8–9:1–160.

1963a. The Enchytraeidae, Critical Revision and Taxonomy of European Species. Supplement 1. *Natura Jutlandica,* 10:1–23.

1963b. The Enchytraeidae, Critical Revision and Taxonomy of European Species. Supplement 2. *Natura Jutlandica,* 10:1–20.

Sperber, C.

1948. A Taxonomical Study of European Naididae. *Zoologiska bidrag från Uppsala,* 28:1–296.

1950. A Guide for the Determination of European Naididae. *Zoologiska bidrag från Uppsala,* 29:45–78.

Stephenson, J.

1930. *The Oligochaeta.* 978 pages. Oxford: Clarendon Press.

Tynen, M. J., and M. Nurminen

1969. A Key to the European Littoral Enchytraeidae (Oligochaeta). *Annales Zoologici Fennici,* 6:150–155.

Ude, H.

1929. Oligochaeta. *Die Tierwelt Deutschlands und der angrenzenden Meeresteile,* 15:1–132.

Udekem, J. d'

1855. Nouvelle classification des Annélides sétigères abranches. *Bulletins de l'Academie Royale des Lettres des Beaux-Arts de Belgique, Classe des Sciences,* 22:533–555.

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Biology of the Mystacocarida: A Prospectus

ABSTRACT

The general biology of the Mystacocarida, including systematics, biogeography, ecology, functional morphology and life cycles, is reviewed. Many of the details of the biology remain unknown and there is a paucity of seasonal studies.

This report is a superficial review of the present knowledge of the crustacean subclass Mystacocarida. Much of what is known is summarized in Delamare Deboutteville's (1960) book on the interstitial fauna. The emphasis here is on what is not known about the Mystacocarida.

It now is generally agreed that the Mystacocarida is a distinct subclass with possible affinities with the Copepoda (Pennak and Zinn, 1943; Dahl, 1956a,b, 1963; Tiegs and Manton, 1958; Sanders, 1963; Hessler, 1964, 1969a). Some authors unite the Mystacocarida with the Copepoda, Branchiura, Cirripedia, and perhaps the Ostracoda in a single higher taxon, Maxillopoda (Dahl, 1956a, 1963; Ax, 1960; Siewing, 1963; Newman, Zullo, and Withers, 1969). Many aspects of mystacocarid anatomy are regarded as primitive, but the possible importance of neoteny in the evolution of this subclass has not been determined. The precise relationship with the other subclasses remains extremely inferential.

In the field of biogeography, Mystacocarida occur along the Pacific coast of Chile (Dahl, 1952; Noodt, 1961), the Atlantic coast of the United States (Hessler and Sanders, 1966; Hessler, 1969b) and southern Europe (Delamare Deboutteville, 1953c, 1954b, 1957; Delamare Deboutteville, Gerlach, and Siewing, 1954; Wells and Clark, 1965), the Mediterranean (summary in Delamare Deboutteville, 1960; also, Fize, 1963, and Grimaldi, 1963), the Atlantic coast of Africa (Delamare Deboutteville, 1953c; Delamare Deboutteville and Barros Machado, 1954; Delamare Deboutteville and Chappuis, 1957; Noodt, 1954), and the tip of Africa on the Indian Ocean side (Noodt, 1954), and the tip of Africa on the Indian Ocean side (Noodt, 1954). Many other portions of the world's coastlines have been searched with varying intensities but without success. This negative evidence is not published. Therefore, the presence of Mystacocarida in the rest of the world must be regarded as mostly unknown. It cannot even be guaranteed that many of the promising beaches which have been searched without success truly lacked this group, because the distribution of mystacocarids within a beach is so patchy.

Mystacocarida were thought to be absent from the cold, more-northern coastlines of the continents (Buchholz, 1953; Noodt, 1954; Delamare Deboutteville, 1960; Hessler and Sanders, 1966), but the recent discovery of *Derocheilocaris ingens* from the coast of Maine (Hessler, 1969b) raises the possibility that Mystacocarida might even occur along the coast of Canada. It also shows that each mystacocarid species does not necessarily have exclusive control of entire continental coastlines, as previous knowledge indicated (Delamare Deboutteville, 1960; Hessler, 1969b). *Derocheilocaris ingens* is separated by only 260 km from the nearest known population of *D. typicus* Pennak and Zinn, and there are no apparent climatological or physiographic barriers between them. The case of *D. remanei* Delamare Deboutteville and Chappuis along

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the Atlantic coast of Africa is an example of the general concept of the wide distribution of mystacocarid species. Only four African localities (Kayar, Senegal; Luanda and Lobito, Angola; and Swakopmund, South-West Africa) are known, and on the basis of these it is assumed that the species is found along the entire 12,000-km Atlantic coastline. That this is a very misleading extrapolation will be seen shortly.

Systematics within the Mystacocarida has always been simple. Even with the new material from Maine, there are only four known species (Pennak and Zinn, 1943; Delamare Deboutteville and Chappuis, 1951; Dahl, 1952; Hessler, 1969b). The differences between these species are slight, in spite of their complex morphology (Delamare Deboutteville, 1960; Hessler and Sanders, 1966). Clearly the Mystacocarida is an extremely conservative group. To some extent this has been ignored by past investigators. Mystacocarids from Angola and South-West Africa have been placed with certainty in *Derocheilocaris remanei* (Delamare Deboutteville, 1957; Delamare Deboutteville and Chappuis, 1957; Noodt, 1954), yet, a recent inspection of new material from these areas revealed differences that easily distinguish these populations from each other and from the Mediterranean *D. remanei.* These differences are more extensive than those which separate *D. remanei* from *D. typicus,* two species whose independence has never been questioned. From this criterion and the fact that great distances separate the known populations, I conclude that these species are distinct and that *D. remanei katesae* (Noodt, 1954) may be yet another species (Hessler, in preparation).

More has been written about the ecology of mystacocarids than any other aspect of their biology (Delamare Deboutteville, 1960; Noodt, 1961; Fize, 1963; Renaud-Debyser, 1963; Wells and Clark, 1965; Jansson, 1966; Hessler and Sanders, 1966; Hessler, 1969b). Mystacocarids tend to be described as purely interstitial organisms of intertidal or nontidal beaches. The sands are siliceous and generally are well sorted and medium-fine to medium-coarse in size. In tidal beaches, the main concentrations are at midtide to high-tide level, and in nontidal beaches are most abundant at levels where the waves soak down into the sand. Mystacocarids survive temperatures ranging from freezing to 25°C and salinities from 5 to 40 ppt.

While all this is generally valid, there already is information which indicates there are major gaps and inconsistencies in our understanding of the ecology of these animals. Grimaldi (1963) found mystacocarids in sands primarily composed of calcium carbonate and with a very low sorting coefficient. This appears to contradict some of the more important generalizations. Both *Derocheilocaris remanei* (Delamare Deboutteville, 1953b) and *D. galvarina* (Dahl, 1952) have been found subtidally. Other than these two occurrences, nothing is known about the extent, ecology, or importance of subtidal distribution. Mystacocarids are notoriously patchy in their distribution (Wells and Clark, 1965). The inability to explain this phenomenon and the absence or rarity of mystacocarids on beaches which are apparently suitable clearly indicate our ignorance of important environmental controls.

The knowledge of functional morphology is sketchy. Delamare Deboutteville (1953a) has given a brief description of movement, emphasizing the ambulatory method of progression, but the details of this activity are largely unknown. The animal bears numerous glands, setal combs, special sensory setae, toothed furrows, and other unusual structures whose function has not yet been demonstrated (Delamare Deboutteville and Chappuis, 1954; Fize, 1963; Hessler and Sanders, 1966; Cals, Delamare Deboutteville, and Renaud-Mornant, 1968; Hessler, 1969b). How mystacocarids feed is not known and there is no proof of the nature of the food, although the animal probably browses on detritus or bacterial films (Buchholz, 1953; Jansson, 1966). Internal anatomy is known in only a general way (Dahl, 1952; Tuzet and Fize, 1958; Fize, 1963; Hessler, 1964).

The life cycles of *Derocheilocaris remanei* (Delamare Deboutteville, 1954a) and *D. typicus* (Hessler and Sanders, 1966) have been documented in detail. In both cases development is gradual, beginning with a nauplius or metanauplius which is much like the adult. The eggs are proportionally large, as indicated by their great size within the body of the female (Fize, 1963), but because they are shed freely into the environment, none has been identified in this free state. Brown and Metz

(1967) have described the morphology of the sperm in detail. Tuzet and Fize (1958) and Zaffagnini (1969) have described gametogenesis. Recruitment rate of new individuals is not known, but it must be low. Reproduction may be continuous (Delamare Deboutteville, 1960) or seasonal (Hall and Hessler, in preparation), depending on the climate.

This review shows that the general features for most aspects of mystacocarid biology already are broadly known; however, almost nothing has been demonstrated in real depth, and as a result most of the existing information is vague and subject to unexplained exceptions. The paucity of careful seasonal studies is particularly noticeable. Future investigations of this subclass must employ detailed, painstaking observations if the Mystacocarida are to be used to elucidate biological principles.

Literature Cited

Ax, P.

1960. *Die Entdeckung neuer Organisationtypen im Tierreich.* 116 pages. Lutherstadt: Wittenburg.

Brown, G. G., and C. B. Metz

1967. Ultrastructural Studies on the Spermatozoa of Two Primitive Crustaceans, *Hutchinsoniella macracantha* and *Derocheilocaris typicus. Zeitschrift für Zellforschung,* 80:78–92.

Buchholz, H. A.

1953. Die Mystacocarida. Eine neue Crustaceenordnung aus dem Lückensystem der Meeressande. *Mikrokosmos,* 43:13–16.

Cals, P. C.; C. Delamare Deboutteville; and J. Renaud-Mornant

1968. Nature et adaptations à un mode de vie en milieu interstitielle des structure cuticulaires céphaliques chez *Derocheilocaris remanei* Delamare Deboutteville et Chappuis (Crustacea-Mystacocarida). *Comptes Rendus de l'Académie des Sciences,* series D, 266: 126–129.

Dahl, E.

1952. Reports of the Lunds University Chile Expedition 1948–1949. 7. Mystacocarida. *Lunds Universitets Arsskrift,* 48:1–41.

1956a. Some Crustacean Relationships. In K. G. Wingstrand, editor, *Bertil Hanstrom, Zoological Papers in Honour of His Sixty-Fifth Birthday, November 20th, 1956,* pages 138–147.

1956b. On the Differentiation of the Topography of the Crustacean Head. *Acta Zoologica,* 37:123–192.

1963. Main Evolutionary Lines among Recent Crustacea. In H. B. Whittington and W. D. I. Rolfe, editors, Phylogeny and Evolution of the Crustacea. *Special Publication of the Museum of Comparative Zoology, Harvard University,* pages 1–26.

Delamare Deboutteville, C.

1953a. Recherches sur l'écologie et la répartition du Mystacocaride *Derocheilocaris remanei* Delamare et Chappuis en Mediteranée. *Vie et Milieu,* 4:321–380.

1953b. Description d'un appareil pour la capture de la faune des eaux souterraines littorales sous la mer. Premiers résultats. *Vie et Milieu,* 4:411–422.

1953c. Révision des Mystacocarides du genre *Derocheilocaris* Pennak et Zinn. *Vie et Milieu,* 4:459–469.

1954a. Le Développement postembryonnaire des Mystacocarides. *Archives de Zoologie Expérimentale et Générale,* 91:25–34.

1954b. L'Écologie du Mystacocaride *Derocheilocaris remanei* f. *biscayensis* Delamare sur la côtes du Golfe de Gascogne. *Vie et Milieu,* 5:310–329.

1957. Le Mystacocaride *Derocheilocaris biscayensis* sur les côtes du Portugal. *Vie et Milieu,* 8:110.

1960. *Biologie des eaux souterraines littorales et continentales.* 740 pages. Paris: Hermann.

Delamare Deboutteville, C., and A. de Barros Machado

1954. Présence de la sous-classe des Mystacocarides (Crustacea) sur les côtes de l'Angola. *Companhia de Diamantes de Angola, Publicacões Culturais,* 23:119–123.

Delamare Deboutteville, C., and P. A. Chappuis.

1951. Présence de l'ordre des Mystacocarida Pennak et Zinn dans le sable des plages du Roussillon: *Derocheilocaris remanei* n. sp. *Comptes Rendus de l'Académie des Sciences,* series D, 233:437–439.

1954. Morphologie des Mystacocarides. *Archives de Zoologie Expérimentale et Générale,* 91:7–24.

1957. Contribution à l'étude de la faune interstitielle marine des Côtes d'Afrique. I. Mystacocarides, Copépodes et Isopodes. *Bulletin de l'Institut Français d'Afrique Noire,* series A, 19:491–500.

Delamare Deboutteville, C.; S. Gerlach; and R. Siewing

1954. Recherches sur la faune des eaux souterraines littorales du Golfe de Gascogne. Littoral des Landes. *Vie et Milieu,* 5:373–407.

Fize, A.

1963. Contribution à l'étude de la microfaune des sables littoraux du Golfe d'Aigues-Mortes. *Vie et Milieu,* 14:669–774.

Grimaldi, P.

1963. Primo rinvenimento di *Derocheilocaris remanei* Del. e Chapp. nel Mediterraneo orientale (Crust. Mystacocarida). *Annuario dell' Istituto e Museo de Zoologia dell' Università di Napoli,* 15:1–7.

Hessler, R. R.

1964. The Cephalocarida: Comparative Skeletomusculature. *Memoirs of the Connecticut Academy of Arts and Sciences,* 16:1–97.

1969a. Mystacocarida. In R. C. Moore, editor, *Treatise on Invertebrate Paleontology, Part R, Arthropoda, 4,* 1:192–195.

1969b. A New Species of Mystacocarida from Maine. *Vie et Milieu,* 20:105–116.

Hessler, R. R., and H. L. Sanders

1966. *Derocheilocaris typicus* Pennak and Zinn (Mystacocarida) Revisited. *Crustaceana,* 11:141–155.

Jansson, B. O.

1966. On the Ecology of *Derocheilocaris remanei* Delamare and Chappuis (Crustacea, Mystacocarida). *Vie et Milieu,* 17:143–186.

Newman, W. A.; V. A. Zullo; and T. H. Withers

1969. Cirripedia. In R. C. Moore, editor, *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4,* 1:206–295.

Noodt, W.

1954. Crustacea Mystacocarida von Süd-Afrika. *Kieler Meeresforschungen,* 10:243–246.

1961. Nuevo hallazgo de *Derocheilocaris galvarini* Dahl en Chile Central. (Crustácea, Mystacocarida). *Investigaciones Zoológicas Chilenas,* 7:97–99.

Pennak, R. W., and D. J. Zinn

1943. Mystacocarida, a New Order of Crustacea from Intertidal Beaches in Massachusetts and Connecticut. *Smithsonian Miscellaneous Collections,* 103(9):1–11.

Renaud-Debyser, J.

1963. Recherches écologiques sur la faune interstitielle des sables (Bassin d'Arcachon, Ile de Bimini, Bahamas). *Vie et Milieu,* supplement 15:1–157.

Sanders, H. L.

1963. The Cephalocarida: Functional Morphology, Larval Development, Comparative External Anatomy. *Memoirs of the Connecticut Academy of Arts and Sciences,* 15:1–80.

Siewing, R.

1960. Neuer Ergebnisse der Verwandschaftsforschungen bei den Crustaceen. *Wissenschaftliche Zeitschrift Universität Rostock, Mathematisch-naturwissenschaftliche Reihe,* 9:343–358.

1963. Discussion Following Sander's Paper. In H. B. Whittington, and W. D. I. Rolfe, editors, Phylogeny and Evolution of the Crustacea. *Special Publication of the Museum of Comparative Zoology, Harvard University,* pages 177–179.

Tiegs, O. W., and S. M. Manton

1958. The Evolution of the Arthropoda. *Biological Reviews,* 33:255–337.

Tuzet, O., and A. Fize

1958. La Spermatogenèse de *Derocheilocaris remanei* Delamare et Chappuis (Crustacé Mystacocarida). *Comptes Rendus de l'Académie des Sciences,* series D, 246:3669–3671.

Wells, J. B. J., and M. E. Clark

1965. The Interstitial Crustacea of Two Beaches in Portugal. *Revista de Biologia,* 5:87–108.

Zaffagnini, F.

1969. Quelques Observations sur l'appareil reproducteur male et femelle de *Derocheilocaris remanei* Delamare et Chappuis (Crustacea Mystacocarida). *Cahiers de Biologie Marine,* 10:103–107.

Neil C. Hulings

Summary and Current Status of the Taxonomy and Ecology of Benthic Ostracoda Including Interstitial Forms

ABSTRACT

The history of the taxonomy of Ostracoda as it applies to the evolution of the "neontological" and "paleontological" classifications is reviewed. Zoogeography, abundance, life history, and influence of environmental factors are considered. Ecology, in terms of true interstitial ostracods, and possible morphological adaptations to interstitial life are discussed.

The taxonomy of Recent ostracods had its inception in 1772 with the publication by O. F. Müller entitled "Observations of some Bivalve Insects Found in Common Water." The taxonomy of fossil ostracods began some 50 years later with the publication of a paper entitled "The Mineral Conchology of Britain" by Sowerby (1825, p. 136). The period of 1850 to 1925 was one of intense activity in ostracod taxonomy. Such investigators as G. O. Sars, G. W. Müller, G. S. Brady, D. Robertson, and A. M. Norman, to mention a few, established basic classifications of fossil and Recent ostracods. It was during this period that the use of two diverse methods for classifying ostracods evolved: (1) classification based on carapace features with little regard given to appendages, and (2) classification based on appendages with little regard given to the carapace. Results of the first method have come to be known as the "paleontological classification," although some zoologists contributed; and results of the second method are known as the "neontological classification," with some paleontologists making contributions. This divergence perhaps was unavoidable, for zoologists often and paleontologists always would have only carapaces to study. Some paleontologists working with living material have continued to base descriptions of new taxa only on carapace features, while some zoologists ignore the carapace and describe new taxa only on appendages.

The Ostracoda originally were described in 1806 by Latreille, who used both the carapace and the appendages, with emphasis on the latter. Sars (1866) divided the order into four suborders—Myodocopa, Cladocopa, Platycopa, and Podocopa—on the basis of soft parts, especially on the structure of the second antennae. Sars did not include fossil taxa in his scheme. Many paleontologists erected their own scheme, necessarily, perhaps, because in many cases they were dealing with extinct taxa. Pokorny (1958) was the first to erect a scheme of classification to include all fossil and Recent ostracods, but the emphasis was on carapace morphology. Hartmann (1963, 1964a) established a neontological and paleontological classification of ostracods, including only those families with Recent representatives; and where possible, he supplemented the diagnoses with appendage morphology. Lower taxonomic levels often included diagnosis of only the carapace (necessary in the case of fossil spe-

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cies) or appendages but, fortunately now, a diagnosis of both is included where possible. Thus, Morkhoven (1962) and Hartmann (1963, 1964a) define all taxa to the subfamily level on the basis of carapace and appendages. Morkhoven (1962, pages 96–97) has pointed out:

> It is obvious that one uniform classification for both living and fossil ostracods must be the ultimate goal, and the idea, advanced by certain authors, of having separate classifications for living and fossil forms, based on different criteria, must be rejected. Only a single uniform classification permits a comparison of Recent and fossil forms, and allows judgment of phylogenetic relationships, interpretation of ecological data, etc., without the burden of nomenclatural and taxonomic confusion.

In 1963 a Committee on Recent Ostracoda was organized during the Naples Symposium on Ostracods as Ecological and Paleoecological Indicators (see Puri, 1964). The committee was charged with the responsibility of restudying the type-species of all living genera and genera which originally were described as fossil but have living representatives, the objective being to provide a "natural" classification. Progress toward this objective was reflected in some of the papers that were presented during a symposim on The Taxonomy, Morphology and Ecology of Recent Ostracoda and that later were published in Neale (1969).

In addition to the carapace-appendage problem mentioned above, the zoogeographic distribution in intertidal and shallow water (less than 200 m) continues to be a problem in that many species have been reported as cosmopolitan. This is especially true of studies of North American ostracods, particularly the older published works (see discussion in Hulings, 1966, 1967a,b). Many of the older studies were based solely on carapace morphology, and, more often than not, specimens were not directly compared with actual type material, resulting in misindentifications and lumping of diverse taxa. Some species may be cosmopolitan, but with more detailed studies of the total organism, including comparison with type material, it probably will be found that most species have a more restricted distribution than previously reported. A reason for this is that benthic ostracods lack planktonic larval stages; thus, there is the absence of a ready mechanism for a wide geographic distribution, such as from the European coast to the Atlantic and Pacific coasts of North America.

The ontogeny and sexual dimorphism of ostracods also have led to difficulties in classification. Ostracods pass through as many as eight molt stages or instars before reaching the adult stage. Drastic changes often occur in both the carapace and appendages from one instar to the next and, in many cases, instars have been described as new species. More studies concerned with ontogenetic development such as that of Sandberg (1964) are needed to resolve this problem. Sexual dimorphism between the sexes as well as within one sex, where, in some cases, the appendages are modified for reproduction has led to different sexes of the same species being relegated to different genera.

New approaches and new techniques are adding measurably to more detailed knowledge of the taxonomy of ostracods. One such approach, numerical taxonomy, has been used by Kaesler (1969) "to obtain an initial estimate of the usefulness of numerical taxonomic methods in the classification of ostracods." Kaesler stated that the results of his study "indicate *at a minimum* that more work needs to be done"; nevertheless his results are encouraging. The scanning electron microscope is providing a new insight to carapace morphology, as shown by Sandberg and Hay (1967), Puri and Dickau (1969), and others. Techniques have also been developed to study appendages with that instrument.

That ostracods are members of the meiofauna, if the latter is defined on the basis of size, is beyond question. But to consider ostracods as members of the interstitial environment raises a question which, based on studies to date, one finds difficult to answer. Obviously the shape and the size of the grains, which determine the available pore space, must be considered. The ostracods found on a gravel bottom, where the pore space is very great, could be considered interstitial if they permanently occupy the pores. The same might be true for species found in shell bottoms, "*Amphioxus* sand," etc. But many of these species—as noted by Remane (1940), Elofson (1941), and others—climb on the large particles; and those living among shell fragments are considered burrowers and those living among shells are considered surface dwellers. Furthermore, observations have revealed that many species dwelling in siliceous sand are typically surface dwellers (episammic) and sometimes these forms burrow into the sand to a depth of 1 to 2 cm, remaining there for only a short period of time. Such burrowing forms are considered by the author as temporary members of the interstitial milieu, and, based on available information to date, these would include most of the sand-dwelling species. Thus, the author considers true interstitial ostracods as those which permanently occupy the interstitial voids of siliceous sand sediments. As defined, the author's interpretation of true interstitial ostracods is more restrictive than that of Swedmark (1964), who included shell gravel and "*Amphioxus* sand" species in his discussion of interstitial ostracods.

To date, only a few species of ostracods have been reported as truly interstitial or mesopsammic. Elofson (1941) considered *Polycope areolata* Sars, *Microcythere* sp., and *Cytherois* sp. as mesopsammon ostracoda. In the Mediterranean, Hartmann (1953) found 13 species in the interstitial, of which he considered only six—all new species—to be typically interstitial: *Microcythere subterranea* Hartmann, *Loxoconcha tuberosa* Hartmann, *Xestoleberis costata* Hartmann, *X. delamarei* Hartmann, *Microloxconcha compressa* Hartmann, and *Cytheromorpha elongata* Hartmann. In addition, Hartmann considered two new species of *Polycope* Sars to be typically interstitial.

Williams (1969), in studying four intertidal localities on the coast of Angelsey, reported four species—*Leptocythere pellucida* (Baird), *L. castenea* (Sars), *Polycope compressa* (Brady and Robertson), and *P. orbicularis* Sars as "sediment living species." He stated that he considered none of the species recorded as a true interstitial form (Williams, 1969, p. 328). Those found in the interstices were juveniles of surface dwellers. Living juvenile stages were found to a depth of 15 cm, while the adults generally were restricted to the upper 2 cm. The depth of penetration of ostracods, recorded as such and not identified to species or as living or dead, has been reported by Rees (1940) as 2 cm in sand, 5 mm in mud; by Mare (1942) as 5 mm in mud; by Moore (1931) as 7 cm in subtidal mud; by Smidt (1951) as 4 cm (maximum) in tidal sand; by Tietjen (1969) as 5 mm (maximum) in estuarine sediments. Williams also found that the "sediment living species" varied with available pore space.

Thus, only the work of Hartmann (1953) shows that true interstitial ostracods, as adults, do exist. It is interesting that, as noted by Swedmark (1964) in citing the work of Klie (1929, 1936), all the species reported by Hartmann (1953) as true interstitial forms were new species, indicating a specific interstitial ostracod fauna. But since most of Klie's species came from shell bottoms they are not considered by the present author as truly interstitial.

Certainly, Hartmann and Williams have approached the problem correctly in that they studied samples collected in a way that made it possible to determine, by coring and analyzing the core at regular intervals, whether true interstitial ostracods do exist. Beyond this, actual laboratory (or field) observations on the behavior of the individual species are necessary. Studies where the samples were collected by dredging (for example, Reys, 1961) are of little use in this context.

The possibility of special adaptations in the morphology of the carapace and appendages of the true interstitial ostracods are worth considering, although, as Hartmann (1946b) pointed out, little is known of the correlation between the morphological features of the carapace and the mode of life. Remane (1940) and Elofson (1941) have shown relationships between ornamentation of the carapace and the type of substratum on which ostrocods occur. Triebel (1941), working with fossil ostracods, also demonstrated similar relationships and noted that certain morphological features of the carapace could be understood only by considering the behavior of the ostracod in relation to substratum.

Elofson (1941) noted that for the forms he considered true mesopsammic the carapace is small and smooth; in two of the three genera it is elongated, wedge-shaped, and dorsoventrally flattened. Hartmann (1953) found essentially the same features in the species he considered truly interstitial, with the one exception of *Loxoconcha tuberosa*. The size of the species Hartmann reported (excluding *L. tuberosa*) ranged in length from 0.17 to 0.35 mm and in height from 0.06 to 0.18 mm. To use such criteria for characterizing interstitial ostracods is hazardous at the present state of knowledge because many noninterstitial ostracods exhibit similar carapace features.

Little can be said concerning whether the appendages of interstitial forms differ from noninterstitial forms. Elofson (1941)—as a result of his own work and that of Müller (1893, 1894), Remane (1933), and Klie (1936)—stated that species living in sand (and silt) do not exhibit any trends in appendage morphology. According to Elofson (1941), some species have medium-thick legs (*Microcythere* Müller and *Microxestoleberis* Müller) and others have slender appendages (*Psammocythere* Klie). The terminal claws of the appendages range from short (in *Microxestoleberis*) to long (in *Microcythere*). But, as in the case of carapace features, these criteria must be interpreted with caution because species living in other biotopes exhibit similar appendage morphology.

Abundance and distribution of ostracods vary primarily with food availability, substratum, and season. Tietjen (1969) noted that abundance of ostracods increased with the increased abundance of plant detritus. McIntyre (1969) has summarized the density of ostracods in intertidal and subtidal habitats. The average number of specimens/10 cm^2 in the intertidal from three types of sediment—sand, mud, and coral sand—is 50, with mud having a higher density (218/10 cm^2) than sand (28/10 cm^2). In the subtidal, the average number of specimens in five types of substrata—mud, sand-gravel, sea-grass mud, sand, and mixed clay-sand—was 17 specimens/10 cm^2; the average number for sand was 34/10 cm^2 and the average for mud was 14/10 cm^2.

Muus (1967) found that ostracod populations showed small annual deviations, but with the largest fluctuations being found in winter and spring. Kornicker (1964) and Kornicker and Wise (1960a) found that living ostracods were more abundant during the summer months, although the abundance of one species remained approximately constant during the year. During a year's study of New England estuaries, Tietjen (1969) found that ostracods were most abundant in late summer, fall, and winter.

Studies on the life history of benthic ostracods are very sparse. The comprehensive study of Elofson (1941) included field and laboratory observations on the reproduction and development from copulation through molting, periodicity of development, and life span of many marine species from Skagerrak. Elofson also summarized previous studies on the life history of ostracods. Theisen (1966) studied the growth and reproduction of seven brackish-water species from Denmark. Hulings (1969) determined the life cycle of a myodocopid based on field collections made weekly over a two-year period in Hadley Harbor, Massachusetts. Hagerman studied the life cycle of several species associated with algae (Hagerman, 1966, 1968) and the complete life cycle of *Hirshamannia viridis* (Müller), an algal-living species, in Øresund (Hagerman, 1969a).

The influence of environmental factors on benthic ostracods has received little attention through laboratory observations. Elofson (1941) evaluated the influence of substratum, salinity, and temperature. Kornicker and Wise (1960b), in studying a marine species, determined the salinity and temperature tolerence, response to light, and sediment preference. Ganning (1966) determined the salinity tolerance of a rockpool species found in the northern Baltic. Hagerman (1969a) evaluated various environmental factors determining the occurrence of *Hirschmannia viridis* in Øresund and later (1969b) studied the respiration, anaerobic survival, and locomotory periodicity of the same species.

In ecological studies attempting to relate distribution or abundance it is of primary importance that living specimens be used rather than dead ones. Dead specimens may represent a select population and are subject to transport and concentration by currents, especially on beaches and in shallow subtidal areas. It has been shown that living populations fluctuate considerably in certain areas, and species diversity of dead populations is generally greater than the diversity of dead populations (Kornicker and Wise, 1960a; Baker and Hulings, 1966; King and Kornicker, 1970).

Williams (1969) noted that there was considerable mixing of species from other biotopes including algae, plant detritus, and deeper water. Species belonging to the deeper-water biotope usually were represented by single valves and carapaces. It is important to be aware of potential mixing of species from other biotopes and to emphasize the presence of living specimens rather than dead ones.

It is obvious, therefore, that if valid ecological studies are to be conducted the sampling must be for living ostracods and repeated over a sufficient period of time to take into account seasonal variation in physical, chemical, and biological variables. And certainly, the taxonomic problems must be resolved so that ecological studies are meaningful.

Literature Cited

Baker, J. H., and N. C. Hulings
1966. Recent Marine Ostracod Assemblages of Puerto Rico. *Publications of the Institute of Marine Science,* 11:107–125.

Elofson, O.
1941. Zur Kenntnis der marinen Ostracoden Schwedens mit besonderer Berücksichtigung des Skageraks. *Zoologiska bidrag från Uppsala,* 19:215–534.

Ganning, B.
1966. Short Time Fluctuations of the Microfauna in a Rockpool in the Northern Baltic Proper. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* sonderband 2:149–154.

Hagerman, L.
1966. The Macro- and Microfauna Associated with *Fucus serratus* L., with some Ecological Remarks. *Ophelia,* 3:1–43.
1968. The Ostracod Fauna of *Corallina officinalis* L. in Western Norway. *Sarsia,* 36:49–54.
1969a. Environmental Factors Affecting *Hirschmannia viridis* (O. F. Müller) (Ostracoda) in Shallow Brackish Water. *Ophelia,* 7:79–99.
1969b. Respiration, Anaerobic Survival and Diel Locomotory Periodicity in *Hirschmannia viridis* Müller (Ostracoda). *Oikos,* 20:384–391.

Hartmann, G.
1953. Ostracodes des eaux souterraines littorales de la Mediterranée et de Majorque. *Vie et Milieu,* 4:238–253.
1963. Zur Phylogenie und Systematik der Ostracoden. *Zeitschrift für Zoologische Systematik und Evolution forschung,* 1:1–154.
1964a. Neontological and Paleantological Classification of Ostracoda. *Pubblicazioni della Stazione Zoologica di Napoli,* supplemento 33:550–587.
1964b. The Problem of Polyphyletic Characters in Ostracods and Its Significance to Ecology and Systematics. *Pubblicazioni della Stazione Zoologica di Napoli,* supplemento 33:32–44.

Hulings, N. C.
1966. Marine Ostracoda from the Western North Atlantic Ocean off the Virginia Coast. *Chesapeake Science,* 7:40–56.
1967a. A Review of the Recent Marine Podocopid and Platycopid Ostracods of the Gulf of Mexico. *Contributions in Marine Science,* 12:80–100.
1967b. Marine Ostracoda from the Western North Atlantic Ocean: Labrador Sea, Gulf of St. Lawrence and off Nova Scotia. *Crustaceana,* 13:310–328.
1969. The Ecology of the Marine Ostracoda of Hadley Harbor, Massachusetts, with Special Reference to the Life History of *Parasterope pollex* Kornicker, 1967. In J. W. Neale, editor, *The Taxonomy, Morphology and Ecology of Recent Ostracoda.* Pages 412–422. Edinburgh: Oliver and Boyd.

Kaesler, R. L.
1969. Numerical Taxonomy of Selected Recent British Ostracoda. In J. W. Neale, editor, *The Taxonomy, Morphology and Ecology of Recent Ostracoda.* Pages 21–47. Edinburgh: Oliver and Boyd.

King, C. E., and L. S. Kornicker
1970. Ostracoda in Texas Bays and Lagoons: An Ecologic Study. *Smithsonian Contributions to Zoology,* 24:1–92.

Klie, W.
1929. Beitrag zur Kenntnis der Ostracodes der südlichen und westlichen Ostsee, der festländischen Nordseeküste und der Insel Helgoland. *Zeitschrift für wissenschaftliche Zoologie,* 134:270–306.
1936. Ostracoden der Familie Cytheridae aus Sand und Schell von Helgoland. *Kieler Meeresforschungen,* 1:49–72.

Kornicker, L. S.
1964. A Seasonal Study of Living Ostracoda in a Texas Bay (Redfish Bay) Adjoining the Gulf of Mexico. *Pubblicazioni della Stazione Zoologica di Napoli,* supplemento 33:45–60.

Kornicker, L. S., and C. D. Wise
1960a. Seasonal Distribution of Ostracodes in Texas Bays and Lagoons. *Bulletin of the Geological Society of America,* 71:1908.
1960b. Some Environmental Boundaries of a Marine Ostracod. *Micropaleontology,* 6:393–398.

McIntyre, A. D.
1969. Ecology of Marine Meiobenthos. *Biological Reviews,* 44:245–290.

Mare, M. F.
1942. A Study of a Marine Benthic Community with Special Reference to Micro-organisms. *Journal of the Marine Biological Association of the United Kingdom,* 25:517–554.

Moore, H. B.
1931. The Muds of the Clyde Sea Area. III. Chemical and Physical Conditions; Rate and Nature of Sedimentation; and the Fauna. *Journal of the Marine Biological Association of the United Kingdom,* 17:325–358.

Morkhoven, F. P. C. M.
1962. *Post-Paleozoic Ostracoda, Their Morphology, Taxonomy, and Economic Use.* Volume 1. 204 pages. New York: Elsevier Publishing Company.

Müller, G. W.
1893. Über Lebenwise und Entwicklungsgeschichte der Ostracoden. *Sitzungsberichte der K. Preussischen Akademie der Wissenschaften,* 13:355–381.
1894. Die Ostracoden des Golfes von Neapel und der angrenzedeen Meeresabschnitte. *Fauna und Flora des Golfes von Neapel,* 21:1–404.

Müller, O. F.

1722. Observations on some Bivalve Insects Found in Common Water. *Philosophical Transactions of the Royal Society,* 61:230–246.

Muus, B. J.

1967. The Fauna of Danish Estuaries and Lagoons. *Meddelelser fra Kommissionen for Danmarks Fiskeri-og Havundersøgelser,* 5:1–316.

Neale, J. W. [Editor.]

1969. *The Taxonomy, Morphology and Ecology of Recent Ostracoda.* 553 pages. Edinburgh: Oliver and Boyd.

Pokorný, V.

1958. Grundzüge der zoologischen Mikropaläontologie. *VEB Deutscher Verlag der Wissenschaften,* 2:66–453.

Puri, H. S.

1964. Ostracods as Ecological and Paleoecological Indicators. *Pubblicazioni della Stazione Zoologica di Napoli,* supplemento 33:1–612.

Puri, H. S., and B. E. Dickau

1969. Use of Normal Pores in Taxonomy of Ostracoda. *Transactions of the Gulf Coast Association of Geological Societies,* 19:353–367.

Rees, C. B.

1940. A Preliminary Study of the Ecology of a Mud-Flat. *Journal of the Marine Biological Association of the United Kingdom,* 24:185–199.

Remane, A.

1933. Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. *Wissenschaftliche Meeresuntersuchungen,* 21:161–221.

1940. Einführung in die zoologische Ökologie der Nord- und Ostsee. Tierwelt der Nord- und Ostsee. 238 pages.

Reys, S.

1961. Recherches sur la systématique et la distribution des Ostracodes de la région de Marseille. *Recueil des Travaux de la Station Marine d'Endoume,* 22(36):53–101.

Sandberg, P. A.

1964. The Ostracod Genus Cyprideis in the Americas. *Stockholm Contributions in Geology,* 12:1–178.

Sandberg, P. A., and W. H. Hay

1967. Study of Microfossils by Means of the Scanning Electron Microscope. *Journal of Paleontology,* 41:999–1001.

Sars, G. O.

1866. Oversigt af Norges marine ostracoder. *Norske Videnskaps-Akademie Förhandlinger,* 1–130.

Smidt, E. L. B.

1951. Animal Production in the Danish Waddensea. *Meddelelser fra Kommissionen for Danmarks Fiskeri-og Havundersøgelser,* 11(6):1–151.

Sowerby, J.

1825. *The Mineral Conchology of Britain.* Volume 5.

Swedmark, B.

1964. The Interstitial Fauna of Marine Sand. *Biological Reviews,* 39:1–42.

Theisen, B. F.

1966. The Life History of Seven Species of Ostracods from a Danish Brackish-Water Locality. *Meddelelser fra Kommissionen for Danmarks Fiskeri-og Havundersøgelser,* 8:215–270.

Tietjen, J. H.

1969. The Ecology of Shallow Water Meiofauna in Two New England Estuaries. *Oecologia,* 2:251–291.

Triebel, E.

1941. Zur Morphologie und Ökologie der fossilen Ostracoden. *Senckenbergiana,* 23:294–400.

Williams, R.

1969. Ecology of the Ostracoda from Selected Marine Intertidal Localities on the Coast of Anglesey. In J. W. Neale, editor, *The Taxonomy, Morphology and Ecology of Recent Ostracoda.* Pages 299–329. Edinburgh: Oliver and Boyd.

Wolfram Noodt

Ecology of the Copepoda

ABSTRACT

The quantitative and qualitative importance of the Copepoda in the meiobenthos is discussed. Most of the families of Copedopa seem to be known but much taxonomic work remains to be done, especially in the Harpacticoida. Very little is known of the species biology of the benthic Copepoda. A number of morphological and biological evolutionary trends are defined. Based on these trends, a system of evolution of "Lebensformtypen" is given, including the origin of planktonic and parasitic forms. The ecological distribution in the marine, brackish-water, and freshwater environments is discussed briefly.

The Copepoda are quantitatively and qualitatively the most important group of the meiobenthos after the Nematoda and before the Turbellaria, Gnathostomulida, Annelida, and Ostracoda. They occur widely in the sea, quite often in brackish water and fresh water, and in semiterrestrial habitats such as moss, humus, and rotten wood.

The Copepoda do not appear to be a very old group of Crustacea. They may have originated in shallow seas in the littoral environment during the Middle Mesozoic, although sufficient information as to their origin is lacking. The only fossils known are from freshwater lake deposits of the Miocene period.

During their morphological evolution, neoteny and the tendency to dwarfism have played a part. Thus, similar to the Cladocera, a new branch of Crustacea has developed and it is still expanding. The Copepoda, with 5,000 to 6,000 species, constitute about 12 percent of Recent Crustacea (Kästner, 1967). Of the existing copepod species somewhat more than half are described. In the Harpacticoida a doubling of the list of species is to be expected. Much taxonomic work remains to be done, especially with marine copepods; nevertheless, the majority of existing families appear to be known. This situation (according to unpublished information) seems likely to hold also for the copepods of the deep-sea benthos.

Among the Copepoda is a very obvious and enormous variety of morphological forms which are adapted to special conditions in the various habitats ("Lebensformtypen," Remane, 1952; Koepcke, 1955). The analysis of this variation, however, is still in the pioneer stages. Nevertheless, it seems worthwhile to attempt a provisional classification of these forms in order to stimulate research in this area. Thus, it seems necessary to evaluate different "trends" in specialization of Copepoda. The characters given below are regarded as derived or apomorphic, as opposed to conservative or plesiomorphic (Hennig, 1950, 1957).

(a) There have been *progressive reductions* in body size to a minimum of about 180 μ; pigmentation and eyes, especially in subterranean and deep-sea forms; numbers of articles, setae, and hairs of appendages; overall egg number, from about 40 to 60 (or more) to 1 to 2 per brood; and possibly development through disappearance of certain naupliar or copepodid stages.

(b) *Progressive morphological specializations* have occurred in the body away from the basic primitive, somewhat cyclopoidean, type towards new, more specialized forms; these have included specialization of the caudal furca, the first antenna, and sometimes certain other appendages for special functions; and more efficient development of structures protecting the brood mostly formed by the fifth pereiopods.

(c) *Progressive ecological specializations* have occurred in numerous lineages through increasing

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preference for particular substrates (stenoecious forms); and probably in association with this specialization of diet, of which very little is known; increasing stenothermy; increasing euryhalinity in connection with colonization in brackish water and fresh water (cases of secondary colonization of seawater from freshwater forms are rare); loss of ability to swim (endobenthos and mesobenthos); complete independence from contact with the substrate in eupelagic forms; development of parthenogenesis, especially in freshwater forms, in which parthenogenesis may be complete, periodic or geographic; elimination of brood-sacs ("Brutpflege") with eggs deposited freely; evolution of cysts, eggs, etc., which are resistant to desiccation, especially in freshwater forms, perhaps also in certain forms of the marine and brackish littoral, and in forms of inland salt waters; and development of parasitic forms through the following stages: associated forms-ectoparasites-endoparasites.

It must be emphasized that many of these specializations are not necessarily to be seen as irreversible. Changes in specializations are, obviously, not uncommon in copepod phylogeny. Thus, the theoretically reconstructed schemes of ecological and partly morphological specialization lose their significance for evaluating particular cases. Such an evaluation will be changed only by a thorough analysis of each genus, family, etc. Toward this end, as always in systematics, it will be necessary to make the direct transformation from ecological investigations (given below) to determinations of the natural affinities, i.e., the real phylogenetic sequence.

The hypothetical ancestral form of Copepoda is envisioned to be a rather small (2 to 8 mm), free-swimming, epibiontic marine form of cyclopoidan appearance that probably feeds by seizing larger particles rather than by filtering. Ecologically and biologically, several recent groups still resemble this ancestral form and must be placed in the center of our ecological system (Figure 1). The different, derived ecological types are characterized in the following outline.

(A) *Tisbe* Lilljeborg-*Tachidius* Lilljeborg type, possibly resembling the ancestral type ecologically. Members of this group are cyclopoidean in appearance, rather small (about 1 mm), and epibiontic. They swim well, either continuously or intermittently, near the surface of the substrate; graze on algae and plant and animal detritus; and perhaps are predatory on other smaller organisms. In this group are included several frequent inhabitants of calm water and of substrates rich in detritus and diatoms and some inhabitants of brackish water. Often there is a large number of eggs. Examples of this group include Tisbidae (partim), Tachididae, and epibiontic Cyclopoida gnathostoma.

(B) Phytal living forms, possibly mostly derived from Type A:

  (1) Thalestridae type.—Forms vary from cyclopoidan to pear-shaped; the cross-section is deeply curved; size ranges from 0.4 to 1.5 mm; often there is a well-developed clinging apparatus. The forms often are brightly colored and are capable of free swimming; they feed on microalgae and detritus; and the number of eggs is large. This type lives especially in the phytal, but also in calm waters on substrates rich in detritus. Examples include Thalestridae, Harpacticidae, Diosaccidae (partim), and Cyclopoida gnathostoma (partim). More-specialized phytal-living forms (Type B2) probably are derived from this type.

  (2) *Scutellidium* Claus-*Porcellidium* Claus type.—From flattened, shield-shaped, of middle size (about 0.7 mm). These animals cling closely to the substrate but still are good swimmers; have reduced egg numbers and brood pouches; and are especially adapted to the smooth, flat surfaces of Phaeophycea. Food not known. Examples include Zausodiinae, Tisbidae (partim), Porcellidiidae, and Peltidiidae.

  (3) *Tegastes* Norman type.—Small, laterally compressed forms (less than 0.6 mm) resembling amphipods. They swim rapidly but cling closely to the substrate while feeding; they live in the phytal. Egg number is low. Group includes only Tegastidae.

(C) Sediment-living forms increasingly specialized, derived from more or less euryoecious forms.

  (1) *Ectinosoma* Boeck type.—Torpedo-shaped forms round in cross-section; size 0.5 to 1.2 mm; often brightly brownish colored; good swimmers living in the phytal, smaller forms also in the mesopsammon; crawl actively in detritus and algae; feed on detritus and algae. Egg number small to medium. Includes most of the Ectinosomidae.

  (2) *Nitocra* Boeck-*Mesochra* Boeck type.—Large and slender, vermiform, round to oval in cross-section; size 0.4 to 1 mm; without obvious specialization of appendages; mostly good swimmers; feed on detritus and microalgae; egg number medium. Live on sand, soft bottom, and in the phytal (epifauna, endofauna, and mesofauna). Examples include Ameiridae, Canthocamptidae, Diosaccidae (partim), Laophontidae (partim). Many transitional forms to Type C3.

  (3) *Lepotcaris* T. Scott-*Stenocaris* Sars type.—This type, probably derived from Type C2, appears in several families through analogous adaptations. Vermiform, slender, cross-section round; length up to twelve

times breadth, 0.25 to 0.8 mm long; poor swimmers; feed mostly on detritus; number of eggs often very low; typical vermiform, writhing inhabitants of the mesopsammon; also live in "organic" interstitial systems such as algae, wood, corals, gill chambers of Brachyura; occasionally occupy detritus layers of calm marine water, including littoral and deep sea. Includes Ectinosomidae (partim), D'Arcythompsoniidae, Diosaccidae (partim), Tetragonicepsidae (partim), Ameiridae (partim), Canthocamptidae (partim), Cylindropsyllidae, Parastenocarididae, and Laophontidae (partim).

(4) *Asellopsis* Brady and Robertson type.—Compact or more slender with arched ventral contour; with adhesive organs for clinging to and moving over the surface and sand grains; medium size (0.5 to 0.8 mm); poor swimmers; browse on the surface of sand grains (detritus and microalgae); egg number small; epipsammonic and endopsammonic, penetrate soft bottoms intermixed with sand. Includes Paramesochridae (partim), Cletodidae (partim), Laophontidae (partim), and Cyclopina (partim). Adaptational types have given rise to characteristic forms of the mesopsammon by extreme reduction of body size (Type A5).

(5) *Paramesochra* T. Scott-*Leoptopsyllus* T. Scott type.—Small, cyclopoidan to vermiform, flat in cross-section (vermiform types nearly round); 0.2 to 0.6 mm long; mostly cling to the surface of sand grains; practically unable to swim; feed on detritus; egg number small; occur in the mesopsammon, sometimes secondarily in the detritus layer of deep-sea bottoms. The extreme vermiform type, e.g., *Leptopsyllus*, must here be regarded as apomorphic. Body size of these forms is extremely reduced, approaching 200 μ. Includes Paramesochridae and *Cyclopina* (partim). Such highly developed forms in the mesopsammon have their equivalents in certain forms adopted to soft bottoms. Very little is known about the biology of these soft-bottom dwellers. It probably is necessary to distinguish at least two types, C6 and C7.

(6) *Nannopus* Brady-*Canuella* T. and A. Scott type.—Compact, vermiform, strong-bodied, burrowing forms, round to oval in cross-section; medium to large size (greater than 0.4 mm); frequently unable to swim; feed on detritus or sediment; number of eggs low; endopelos. Includes Longipediidae, Canuellidae, Cletodidae (partim), and Laophontidae (partim).

(7) *Cervinia* Norman-*Laophontodes* T. Scott type.—Cyclopoidan to elongate forms, flat to oval in cross-section; often with striking spiny processess; appendages often directed laterally to prevent sinking on soft bottom; medium to large size (0.4 to 2.5 mm); poor swimmers; feed on detritus or sediment; number of eggs questionable; live on soft bottoms, particularly in greater depths, and probably on or near the surface of the substrate. Includes Cerviniidae, Diosaccidae (partim), Cletodidae (partim), Laophontidae (partim), and Ancorabolidae.

(D) Free swimmers.—Probably derived from Type A.

(1) *Pseudocyclops* Brady type.—Cyclopoidan in form; swim near the surface of the substrate or among algae; medium to large size (1.0 to 1.5 mm, with most 0.5 to 0.8 mm); swim continuously or intermittently, or float; filter-feed on detritus stirred up by their own movements but probably also seize larger particles; egg number high; live on bottoms covered with detritus and in the phytal. Includes Pseudocyclopinae, some Cyclopoida gnathostoma, and some additional Calanoida.

(2) Euplanktonic forms.—Originating partly from Type D1, but partly (e.g., some Cyclopoida, some Harpacticoida) also in several parallel lines from already strongly specialized bottom-living forms (e.g., *Microsetella* Brady and Robertson). Closer subdivision cannot be made here. The bulk of the Calanoida is euplanktonic and forms a large and richly diversified group of copepods.

(E) Parasitic forms.—Probably some thousands of species of copepods live parasitically or in some close association with host organisms. Among free-living copepods of several different families are found so-called "association forms," some of which achieve a stronger attachment to their usually invertebrate hosts. Several lines of ectoparasites have developed from such intermediate forms, and some of these lines have given rise to highly specialized endoparasites, most of which originate from the "Cyclopoida siphonostoma." Their systematics remains to be clarified. Some interesting examples are also found in the Harpacticoida. Several main sections of the Copepoda are parasitic on fish. Little is known of the biology and ontogeny of parasitic forms (Bocquet and Stock, 1963).

Ecological distribution of the above-defined types. As in many other marine groups of animals, a great diversity of forms and species of the Copepoda lives in the marine littoral, especially in the phytal and on detritus-rich sand and soft bottoms. On such substrates in warm seas sometimes more than 60 species per association are found; such species include representatives of nearly all ecological types. Coarse marine sands, from subtidal to eulittoral, especially the detritus-rich "*Amphioxus* sand" and shell, are inhabited by many species belonging to only a few highly specialized types (C2, C3, C5). Eulittoral soft bottoms, on the other hand, may be rich in individuals but poor in numbers of species, among which are found, however, several specialized forms, such as C6 (Noodt, 1957; Lorenzen, 1968, 1969). As yet no data on the fauna of the deeper abyssal and hadal zones are available. "Littoral" soft-bottom fauna (primarily Cletodidae, Laophontidae, Ameiridae, and Diosaccidae) dominates to a depth of at least 2,000 m. Below 3,000 m the proportion of Type C7—in which are provisionally included bizarre deep-sea forms such as *Cervinia, Pontostratiotes* Brady, *Cerviniella* Smirnow, *Cerviniopsis* Sars, *Mesocletodes* Sars, and some Ancorabolidae—increases distinctly. The proportion of "littoral" types, however, still

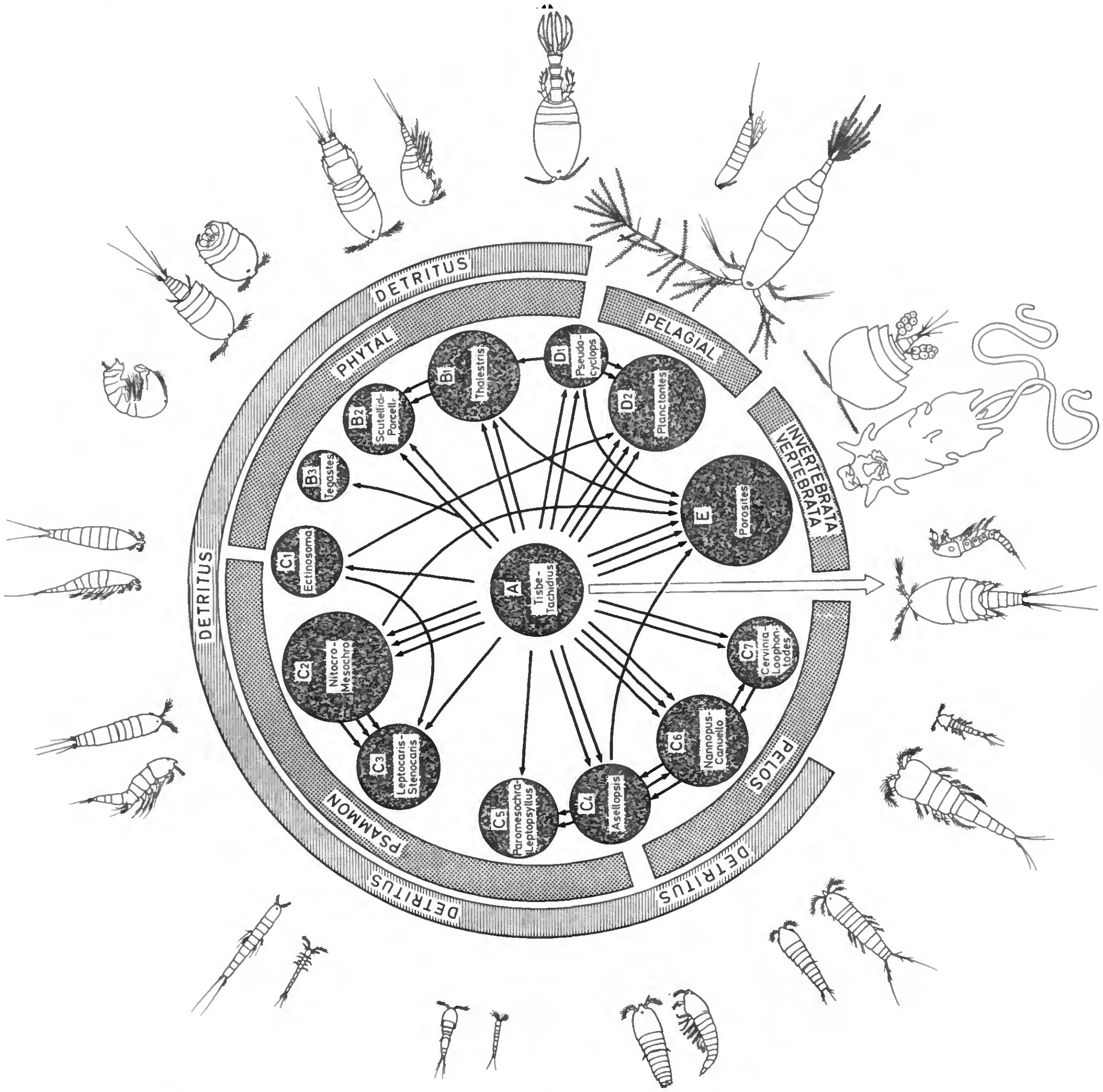

FIGURE 1.—Programmatic scheme of interrelationships between the most important types of morphological adaptation ("Lebensformtypen") of the Copepoda. The primitive ancestral type is represented in the center. The morphological types are arranged according to substrate. Note the importance of detritus in nearly all environments.

appears to outnumber the endemic specialists even in the hadal. Copepoda seem to be well represented in the greatest depths of the ocean. There is as yet no evidence for the continued occurrence of "living fossils" among copepods in the ecological refuge of the deep sea (Bodin, 1968; Pór, 1964, 1965; K. H. Becker, personal communication; Noodt, unpublished observations).

On the whole, the fauna of soft bottoms, endopelos, appears to be very rich in highly specialized forms, more so than the fauna of mesopsammon. But forms typical of the mesopsammon (C3, more of C5), obviously find adequate living conditions in the detritus layer at great depths in the deep sea, and this is of great importance in the geographical distribution of this fauna (e.g., *Leptocaris*, Cylindrotsyllidae, Paramesochridae).

How the copepod fauna changes in transition from seawater to brackish water and fresh water. It can be said that in Copepoda the reduction in ecological types parallels or even exceeds the well-known phenomenon of decrease of species number in brackish waters (Remane 1952, 1959; Remane and Schlieper, 1958). This applies in different degrees to different substrata. Most strongly affected seems to be the fauna of the phytal (C1–3). A more or less unspecialized euryoecious copepod fauna living on the surface of detritus usually dominates in the mesohaline brackish water. Exceptions occur, especially in the subterranean zones of eulittoral sandy beaches, in which a relatively large proportion of sand-living forms of marine origin (C3 and less C5) reach oligohaline and even fresh water (Noodt, 1957, 1969).

The rather monotonous picture of the copepod fauna of brackish water remains much the same in fresh water. The dominant groups here are from the Cyclopoida, some Calanoida, and Harpacticoida Canthocamptidae, whereas other groups (except for a few parasites) seldom venture into fresh water. Freshwater benthos copepods mostly belong to the less-specialized types, B1 and C2. On the other hand, tendencies to greater specialization exist, especially in the "organic" interstitial system of wood, humus, and moss (e.g., *Epactophanes* Mrázek, *Moraria* T. and A. Scott).

Again, the psammon occupies a special position. In fresh water, mesopsammon copepods of marine origin may predominate (types C2 and C3, e.g., *Nitocrella* Chappuis, *Schizopera* Sars, *Parastenocaris* Kessler, and type C5, e.g., small cyclopoids like *Graeteriella* Brehm).

In this context, the question of the duration of the phylogenetic history is of importance for biogeographic reasons. Some representatives (*Parastenocaris* and possibly *Nitocrella*) obviously are relatively old immigrants. Others (e.g., *Schizopera*), on the other hand, still have near relatives in the marine environment (Noodt, 1957, 1969).

On the whole, freshwater copepods, including the few eupelagic lines, although they do consist of a fair number of species, present a rather monotonous picture in comparison with those of the sea. Furthermore, the existing small diversity of forms in fresh water is almost entirely of marine origin. Fresh water has played no significant part as a center of evolution for benthic or planktonic copepoda.

Literature Cited

Bocquet, C., and J. H. Stock

1963. Some Recent Trends in Work on Parasitic Copepods. *Oceanography and Marine Biological Annual Review*, 1:289–300.

Bodin, P.

1968. Copépodes Harpacticoides des étages bathyal et abyssal du Golfe de Gascogne. *Mémoires du Muséum National d'Histoire Naturelle*, series A 55(1):1–107.

Hennig, W.

1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin.

1957. Systematik und Phylogenese. *Bericht über die Hundertjahrfeier der Deutschen Entomologischen Gesellschaft*, pages 50–71.

Kästner, A.

1967. *Lehrbuch der Speziellen Zoologie. I (2). Crustacea.* Jena: Verlag Fischer.

Koepcke, H. W.

1955. Las formas de vida y su significado ecologico. *Revista Pesqua y Caza*, 6:64–68. Ministerio de Agricultura, Lima.

Lorenzen, S.

1968. Die Meiofauna an der Grenze Watt/Salzwiese im Bereich der deutschen Nordseeküste. Dissertation, Universität Kiel. 191 pages.

1969. Harpacticoiden aus lem lenitischen Watt und den Salzwiesen der Nordseeküste. *Kieler Meeresforschung*, 25:215–223.

Noodt, W.

1957. Zur Ökologie der Harpacticoidea (Crust. Cop.) des Eulitorals der deutschen Meeresküste und der angrenzenden Brackgewässer. *Zeitschrift für Morphologie und Ökologie der Tiere,* 46:149–242.

1969. Substratspezifität bei Brackwasser-Copepoden. Limnologica, 7(1):139–145.

Pór, F. D.

1964. Les Harpacticoides (Crustacea, Copepoda) des fonds muebles du Skagerak. *Cahiers de Biologie Marine,* 5:233–270.

1965. Harpacticoida (Crustacea, Copepoda) from Muddy Bottoms Near Bergen. *Sarsia,* 21:1–16.

Remane, A.

1952. Die Besiedelung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. *Zoologischer Anzeiger,* Supplementband 16:327–359.

1956. *Die Grundlagen des Natürlichen Systems, der Vergleichenden Anatomie und der Phylogenetik. 2. Auflage.* Leipzig: Geest und Portig.

Remane, A., and C. Schlieper

1958. *Die Biologie des Brackwassers.* 438 pages. Stuttgart: E. Schweizerbart.

Irwin M. Newell

Problems in the Study of Subtidal Halacaridae (Acari)

ABSTRACT

Techniques of collecting, zoogeography, systematics, and preparation for study of subtidal Halacaridae are discussed. A sliding box dredge for the collection of meiobenthos is described, illustrated, and evaluated.

The Halacaridae, or marine mites, are one of the best-represented metazoan taxa in the intertidal zone, usually being outnumbered only by the Nematoda, Copepoda, and occasionally other groups of small organisms. Despite this they are poorly known by most workers on the intertidal fauna. In subtidal habitats they are even more poorly known. They generally are regarded as a "difficult group," although in reality they need not be. On the one hand, they are simpler in structure than the Copepoda, Ostracoda, and other Crustacea. On the other hand, they possess a great number of clearly definable and relatively constant structural features which make them easier to work with than such groups as the Turbellaria, Tunicata, Nemertinea, and other soft forms. In these, histological sectioning and other time-consuming techniques are frequently required to analyze the rather variable *morphos* and establish criteria for differentiating between taxa. As in other groups, the significance of variation between individuals and species of Halacaridae is not always easy to evaluate, but the variations themselves are seldom difficult to quantify. Rather clearly, then, whatever makes the Halacaridae a "difficult group" it is not their structure or their rarity, but other things which are examined here.

While the subtidal Halacaridae have been emphasized, much of what is reported here is applicable to the family as a whole. The special significance of the subtidal Halacaridae lies in the numerical relationship between the subtidal and the intertidal fauna. During Cruise 17 of the *Anton Bruun* (Southeastern Biological Oceanographic Program), 33 species of subtidal Halacaridae were collected. Yet, it is estimated that this number represented no more than 50 percent of the subtidal species in that part of the southeastern Pacific covered by the cruise (Newell, in press), and that the total subtidal forms from there eventually will reach 60 species or more. The intertidal fauna of the Peru-Chile coast and the offshore island groups of Juan Fernandez and San Felix is still largely undescribed, but a large part of it has been examined and it appears unlikely that this intertidal fauna will exceed 60 species, if indeed it reaches that number. There is some overlap between intertidal and subtidal forms, but the majority probably will be distinct. If the same generalizations can be applied to other parts of the world, then it would appear that one-half or more of the living species of Halacaridae are found only below tidal depths. Clearly, no study of the world fauna of marine mites can be complete without vastly greater attention being given to the subtidal fauna than it has received heretofore.

Collecting Techniques

The specific gear for subtidal collecting will not be discussed here, but only those principles which should be incorporated into devices to improve the

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efficiency of collecting meiobenthos, including Halacaridae. Subtidal Halacaridae are collected in a variety of sampling devices. For nonquantitive studies, the best results are obtained with devices which cover a large area without digging deeply into the sediment. In very deep waters (to 5,000 m or more), some Halacaridae may live on the soft sediments themselves, but it is more likely that most of them will be found to be more abundant on substrates like bryozoan-encrusted rocks, clumps of hydroids, shells, etc., which are widely and unevenly scattered over the bottom. Small-diameter coring devices are not suitable for collecting organisms with this type of distribution. Since the Halacaridae are probably limited to the upper few millimeters of the bottom, grabs or other devices which go deep into the sediments produce samples which are difficult to process because the great bulk of the sample consists of substrate unoccupied by surface-dwelling forms. Trawls or sliding dredges which collect only the thin surface layer should give the best results in nonquantitative studies. But here it must be remembered that the small size of subtidal Halacaridae (500 μ down to 90 μ) requires that mesh size be much smaller than that usually used. The best single haul of Cruise 17 of the *Anton Bruun* was made with a canvas bag cut to fit the frame of a Menzies trawl. This device brought up 307 Halacaridae, belonging to 10 species, and many other animals from a depth of 485 m (Newell, in press). Moreover, the mud, which is washed out in coarse-mesh dredges, provided a protective matrix that resulted in far better preservation of mites and other delicate organisms.

Rigid metal box dredges of one design or another would have certain advantages over bag-type dredges. They would minimize abrasion of the specimens, reduce exposure to "winnowing" during recovery, and protect the animals from extreme temperature changes during the ascent. The latter feature could be improved even further by insulated linings, but these have the disadvantage of producing "bow-wave" effects, and many, but certainly not all, of the lighter organisms would be pushed aside as the dredge moved over the bottom. This disadvantage probably can be found in filter-type dredges to a greater degree than realized. Very likely such dredges become so clogged with fine sediments after a short time on the bottom that little filtration occurs anyway, until the bag is on its way to the surface.

A type of sliding box dredge recently developed by the author for the collection of meiobenthos is shown in Figure 1. This is a small prototype model made for use from a small boat in shallow waters, but the same principles could be incorporated in larger dredges operated from deep-sea research vessels. Thus far it has been used only on sandy and rocky bottoms, and has brought up large numbers of meiobenthos in an excellent state of preservation. The box is of quarter-inch welded aluminum, 21 by 10.5 by 3.5 inches outside dimensions, with the leading edges beveled. The baffled plastic insert is designed to minimize winnowing during recovery and also to prevent loss of the sample while the dredge is passing over irregular bottoms. The insert is held in place by a transverse rod. The leading edge of the insert is fitted with short metal "teeth" which keep rocks or sponges from fouling the throat of the dredge. Thus, the front section is essentially a rock dredge (Figure 1*b*). Sediments move into the dredge, sliding over the bottom. Displaced water moves through the holes in the plastic insert and exits at the front. When the bottom chamber is filled, the top chamber then becomes filled, although retention of lighter sediments probably is less efficient here. The interior of the dredge is spray-coated with "Teflon" to minimize adhesion of mud. The dredge is shackled to the cable centrally (Figure 1*b*) so that most of the working edge passes over undisturbed bottom. This dredge is not a quantitative sampler, but it is more effective in getting a good sample of the meiofauna than are quantitative samplers.

Processing of samples on board is another critical phase in meiofaunal studies. Reports of most deep-sea expeditions are notably lacking in records of Halacaridae. Yet it is known that Halacaridae occur to depths of over 5,000 m, which means that at least 80 percent of the area of the world oceans provides potential habitats for Halacaridae (Newell, 1967 and in press; Sokolov and Iankovskaya, 1968). In many expeditions it has been standard practice to place the haul on a shaker table or fixed screen of 1-mm mesh and "wash out the silt." This removes the great majority of the meiofauna, of course, leaving only the macrofauna. Clearly, such routine practices must be discontinued if anything is to be

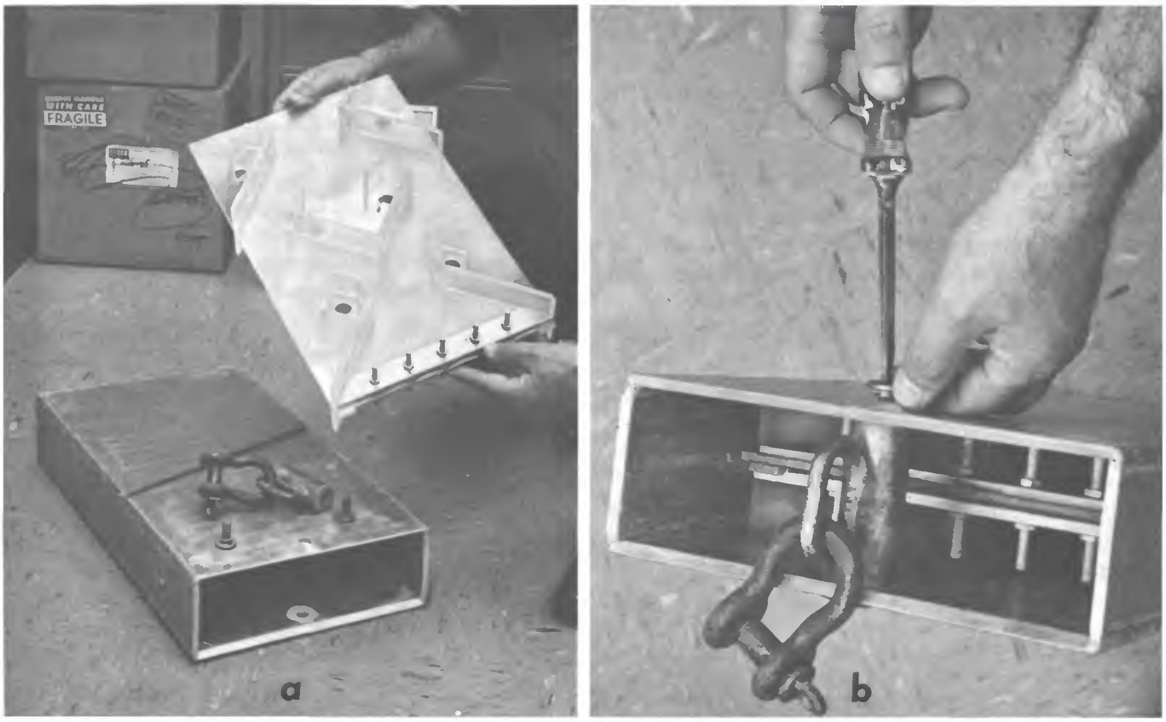

FIGURE 1.—*a*, Sliding box dredge with baffle plate removed. The baffle plate is held in place by the long threaded rod. *b*, Attaching the shackle assemblage to the dredge. The eye of the shackle assemblage turns freely on a central rod which is tapped to receive the heavy retaining bolts. The weight (not shown) is "in line" with the cable.

learned about total fauna. Considering the great cost of deep-sea work, it is doubtful if any biological expedition can be justified on the basis of study of macrobenthos alone. At least a portion of the effort must be allotted to the meiobenthos.

Zoogeographic Problems in Subtidal Halacaridae

From the foregoing remarks it should be apparent that not enough has been learned of subtidal Halacaridae to provide more than the slighest glimpse of the total picture of the world fauna. The following discussion is based in part on unpublished information, undescribed species, and a certain amount of conjecture. Nevertheless, it serves to pinpoint some of the directions in which future efforts should be aimed.

To what extent is endemism developed in the subtidal fauna? The author has seen collections from subtidal faunas from several parts of the world, including the Antarctic, southeastern Pacific, Indian Ocean, Bering Sea, and Artic Ocean. These collections are by no means complete, but they indicate that the differences between faunas in these widely separated parts of the world are so considerable that endemism must be quite high. It is doubtful that there is any appreciable number of cosmopolitan species, if any, even in the deep sea. Most genera appear to be cosmopolitan in subtidal habitats, but even here there are notable exceptions—for example, in the genus *Werthella* Lohmann, confined to the southern hemisphere on the basis of present information.

There are other interesting patterns in the distribution of certain taxa. *Arhodeoporus* Newell has been seen subtidally from the Arctic, Indian Ocean, southeastern Pacific, North Atlantic, and Mediterranean (Newell, 1947). In the North Atlantic and Mediterranean it is represented by intertidal forms as well. This raises the question whether the intertidal occurrence in the North Atlantic is a primitive or a recent development. In line with the hypothesis that the North Atlantic is a relatively young ocean, it would appear that the latter might be the case. This also parallels the distribution of the genera *Rhombognathides* Viets and *Metarhombognathus* Newell, both restricted to intertidal and shallow subtidal waters of the North Atlantic, which would mark them as relatively recent groups (Viets, 1927; Newell, 1947). These are somewhat speculative points, but the alternatives appear to be few and somewhat less probable. Recent developments in marine and terrestrial geology, paleomagnetism, etc., strongly support Wegener's theory of the origin of the Atlantic through continental drift. The Halacaridae promise to be an excellent group in which to study the faunistic effects of continental drift.

Systematic Problems

One of the indispensable ingredients of good zoogeography is good systematics. The principal systematic problems in the Halacaridae stem from the lack of accurate descriptions and illustrations. Many of the best structural characters that could be used in this group have never appeared in published keys or descriptions. For example, earlier writers paid almost no attention to the setae of Halacaridae, except some of the more obvious ones on the palpi and on the legs. The setae of the idiosoma (body), the rostrum, and the specialized setae of the tarsi essentially went unnoticed. The setae of the idiosoma show important interspecific differences in position relative to the plates and in length and form, and these must be carefully described. The same also is true of the setae of the gnathosoma, some of which have significance at the generic level, yet they are not even mentioned in keys and diagnoses, nor shown in figures, except in occasional and sporadic instances. As a consequence, there are a number of species whose true generic position cannot be resolved without reference to types or topotypic material, both of which are expensive and time-consuming. The alternative is to postpone final resolution of these problems, which lead to perpetuation of errors in the literature. Examples of such errors are found in relation to *Agaue aculeata* (Trouessart), *Werthella bouvieri* Trouessart, and *Agaue affinis* Sokolov. It is suspected that all of these belong in genera other than the ones to which they are presently assigned, but there is no way this can be resolved from existing descriptions, simply because the critical characters have been overlooked.

Mounting Problems

Unquestionably, the source of many of the systematic problems in the Halacaridae is in the techniques used in preparation of material for study. Standard practice of many workers in the Halacaridae is to mount specimens in Hoyer's (or Marc Andre's) medium, or similar media. The refractive index of these media is such that many important setal characters have gone unobserved. The advent of phase microscopy has made such preparations easier to study, but the important problem of permanence still remains. Hoyer's mounts simply are not permanent, and while, presumably, there are techniques to make them permanent, none has ever stood the test of time. Ringing is the procedure usually recommended, but the results are inconsistent. Trouessart's vitally important type slides of Halacaridae were faithfully ringed (with black asphaltum or shellac?), and the closest examination of most of these slides reveals no visible cracks or separation between glass and sealant. Yet, without exception, these mounts have dried so completely that the coverslip in all cases is deformed even to the point of cracking over the specimen, and more than 90 percent of the specimens are completely surrounded by air. Even when successful, ringing is a time-consuming process, which often must be repeated two or three times.

Remounting is always possible, but it is time-consuming and risky. Again, in the Trouessart collection of Halacaridae several specimens have been remounted with disastrous results. Appendages are lost, setae broken, rostrums are badly deformed, etc., making specimens truly worthless for descriptive purposes. Over-compression of the specimens by shrinkage of the medium has obliterated setae, destroyed surface detail, and produced artifacts of many kinds. These changes are irreversible, and even careful remounting by an experienced worker cannot restore the details.

Polyvinyl alcohol, lactophenol media, all have their adherents, but none of these media has yet withstood the test of time. A large portion of the mite collection of the South Australia Museum, including many types, is totally unusable because it was mounted in polyvinyl alcohol. In the writer's experience, only two media of acceptable refractive index have withstood the test of time, namely Hyrax and glycerin. Of these, Hyrax is preferable because it gives more rigid support, is easily adaptable to reversible-mount techniques, and is permanent. A question frequently asked is whether it is easy to remount from Hyrax. The answer is yes, but remounting usually is unnecessary. Ringing is not required, either. The specimens are held rigidly so that oil immersion examination is possible immediately after labeling. Changes in position of the mites, or the legs, can be achieved, while examining under the microscope, simply by heating the slide and pushing and/or compressing the coverslip until the desired position is achieved. Upon cooling, the mount is rigid again. Compression of specimens to enhance resolution is accomplished in the same way. Remounting is necessary only if a dissection of a previously mounted specimen is desired. The oldest Hyrax preparations were made by the author 30 years ago, and they are as good as the day they were made, in all respects.

The only disadvantage of the Hyrax technique is that it requires considerable "tooling up." But once this has been done, mites can be put into Hyrax as quickly as into Hoyer's medium on a per-specimen basis, and this has been tested by detailed time analyses. In 30 years more than 200,000 mites have been mounted in Hyrax by the author and his assistants. Evidently the Hyrax technique is not as time-consuming as generally thought. When one considers the time saved in remounting, the elimination of ringing, the superior optical qualities of Hyrax, the simplicity of making reversible mounts, and the total lack of crystallization and other forms of deterioration which plague the "simpler" techniques, there appears to be no good reason for using any mounting medium which is less durable, has less desirable optical properties, and which requires just as much time as Hyrax.

The details of the Hyrax technique are given in Hulings and Gray (1971).

Literature Cited

Hulings, N. C., and J. S. Gray
1971. A Manual for the Study of Meiofauna. *Smithsonian Contributions to Zoology,* 78:1–83.

Lohmann, H.
1907. Die Meeresmilben der deutschen Südpolar-Expedition 1901–1903. *Deutschen Südpolar-Expedition,* 1(5): 361–413.

Newell, I. M.
1947. A Systematic and Ecological Study of the Halacaridae of Eastern North America. *Bulletin of the Bingham Oceanographic Collection,* 10(3):1–266.
1967. Abyssal Halacaridae (Acari) from the Southeast Pacific. *Pacific Insects,* 9(4):693–708.
In press. Halacaridae (Acari) Collected During Cruise 17 of the *Anton Bruun,* in the Southeastern Pacific Ocean. *Anton Bruun Reports.*

Sokolov, I.
1962. New Species of Halacarids from the Antarctic. *Academy of Science of the U.S.S.R., Explorations of the Fauna of the Seas, Biological Results of the Soviet Antarctic Expedition (1955–1958),* 1(9):190–195.

Sokolov, I., and A. I. Iankovskaya
1968. Pervii abyssalnyi predstravitel Halacaridae (Acari) is raiiona Kurilo-Kamchatskoii vladiny. *Doklady Akademii Nauk SSSR,* 179(2):486–488.

Trouessart, E.
1896. Note préliminaire sur les Acariens marins dragué à de grandes profondeurs par M. Koehler dans le Golfe de Gascogne (Août-Septembre 1895). *Bulletin de la Société Zoologique de France,* 21:102–105.
1914. Acariens. *Deuxième Expedition Antartique Française (1908–1910),* pages 1–16.

Viets, K.
1927. Die Halacaridie der Nordsee. *Zeitschrift für wissenschaftliche Zoologie,* 130(1–2):83–173.

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A Review of the Systematics and Ecology of Marine Tardigrada

ABSTRACT

The affinities, morphology, embryonic development, systematics, and ecology of the phylum Tardigrada are discussed. A key to the genera is given.

The Tardigrada comprise a well-defined group of uncertain position, perhaps near the base of the arthropod branch but with affinities suggesting aschelminth relationships. The size rarely exceeds one millimeter, and the body is stout, bilaterally symmetrical, superficially annulated, enveloped in a cuticle, and possesses four pairs of legs with toes or claws. There are no nephridia (although lateral and/or dorsal "excretory" structures are found in most freshwater taxa), no circulatory apparatus, and no respiratory structures.

The phylum consists of few genera and many species—especially in freshwater and semiterrestral habitats—whose affinities are uncertain and whose characters show similarity to aschelminths, annelids, and arthropods. The aschelminth characters include several embryological features, nonchitinous cuticle, absence of circular muscles, similarity in feeding parts and digestive system, and a pseudocoelous body cavity in adults. The annelid characters include a ladder-shaped nervous system and cephalic appendages. Arthropod characters include metamerism of the cuticle, growth through molting, and absence of cilia.

In the general scheme of organization, the cuticle is thin, transparent, and (in most marine species) punctate. It can form into thick ornamented plates in semiterrestral species (plated Echiniscoidea). Cuticular expansions may be very important in marine Heterotardigrada such as *Florarctus* Delamare Deboutteville and Renaud-Mornant, *Actinarctus* Schulz, and *Parastygarctus* Renaud-Debyser. In most genera, long cirri (cirrus E) are located laterally in the posterior portion of the body. In addition, cephalic appendages in the form of cirri are present only in the Heterotardigrada and separate them from the Eutardigrada (Figures 1 and 2). The cephalic appendages include unpaired median cirrus, paired internal median cirri, paired external median cirri, and paired lateral cirri, each associated with a clava.

There are four pairs of legs, of which the first three pairs are anteriorly directed and the terminal pair is posteriorly directed. Each leg terminates with claws or papillae-bearing toes, or both. Legs usually are retractable and telescope to the point that the claws disappear within the leg sheath.

The muscles are composed of striated fibers forming ventral and dorsal longitudinal bands as well as dorsolateral and ventrolateral bands. Circular muscles do not occur. There are pedal retractor muscles and pharyngeal muscles which control the buccal apparatus.

The nervous system consists of a brain that is relatively large and is formed in four or five dorsal lobes. A circumesophageal ring connects the brain to a ventral nerve chain, which includes two main trunks connecting ganglia corresponding to each leg pair. The brain innervates the cephalic appendages (cirri) and possibly the clava. Some tardigrades possess eyes inserted directly on the brain.

The digestive tract consists of a foregut, midgut, and hindgut. The foregut and midgut are lined

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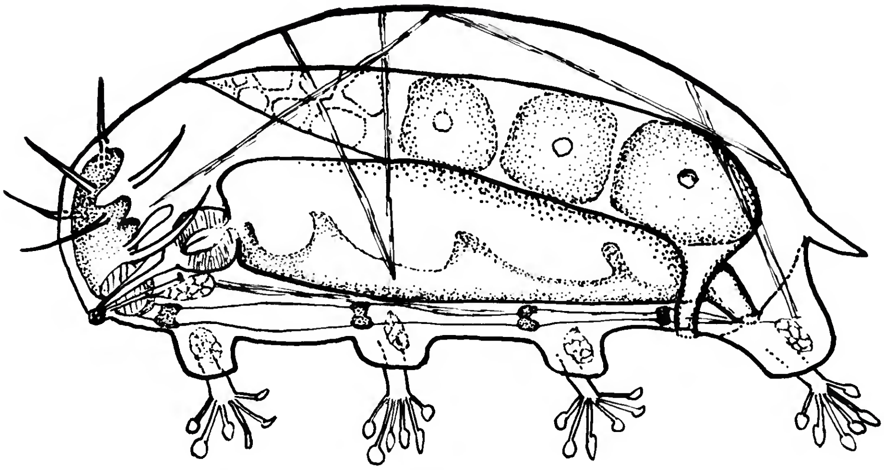

FIGURE 1.—*Batillipes mirus*, a primitive marine tardigrade with cephalic cirri and toes.

with cuticle and a buccal canal with a pharyngeal bulb and stylets followed by a short esophagus leading to a large diverticulated intestine. The buccal apparatus is complex and important in systematics. In Heterotardigrada stylet supports may or may not be present. In Eutardigrada (Figure 3) the cuticular pieces within the bulb ("placoids") differ in shape and number among the species. On each side of the buccal canal are two large "salivary glands." These glands play a role in the reformation of a new buccal apparatus during molting. The intestine is usually filled with a reserve of nutritive material, of vegetal origin, colored brown, green, or red. In the Heterotardigrada defecation occurs during molting and products are deposited in the shed cuticle. The digestive system terminates in an anus in Heterotardigrada and a cloaca in Eutardigrada.

The body cavity of adult tardigrades may be a pseudocoel, although one study suggests that enterocoelic pouches form and then disappear in early embryology. A coelomic fluid containing numerous free cells in suspension fills the cavity of eutardigrades. Constant agitation of these cells by the movements of the body and internal organs functions as a circulatory system. Glands of unknown function are connected to the posterior part of the intestine in Eutardigrada only.

Reproductive organs are located dorsally above the intestine. In tardigrades sexes are always separate. From the sack-shaped gonad leads two vasa deferentia in males or a single oviduct in females.

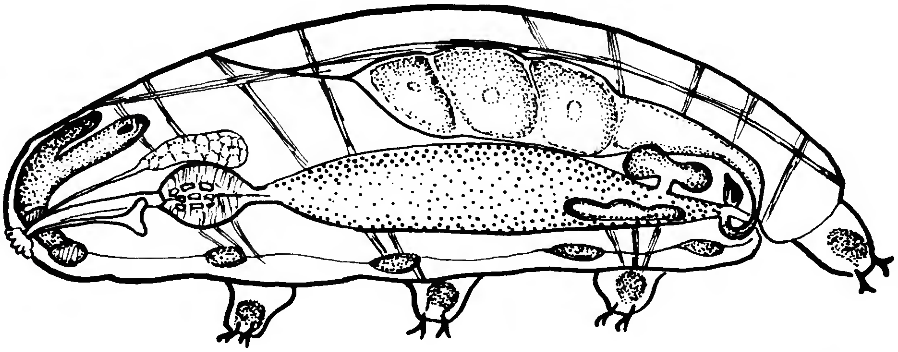

FIGURE 2.—*Macrobiotus* sp., a terrestrial tardigrade without cephalic cirri and toes.

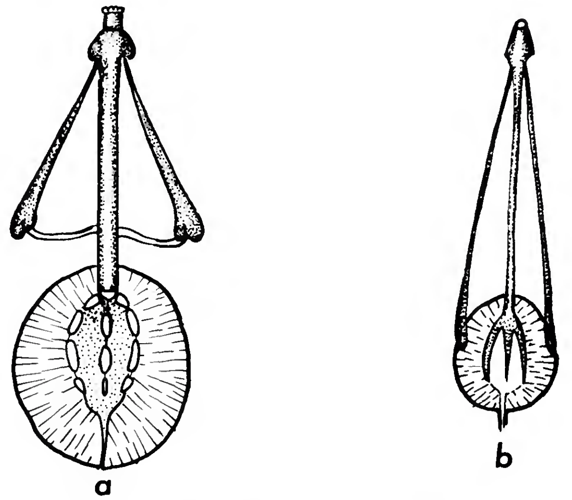

FIGURE 3.—Buccal apparatus. *a,* Eutardigrada; *b,* Heterotardigrada.

These ducts pass around the intestine and rectum and exit ventrally. In some Heterotardigrada there is dimorphism in the shape and location of gonopores, which are located anterior to the anus. In Eutardigrada gonoducts open directly into the intestine, forming a cloaca.

Methods of fertilization and egg deposition are unknown in marine heterotardigrades. In eutardigrades, which are mostly semiterrestrial, eggs are deposited into a recently shed cuticle or in some other similarly protective location. Other eutardigrades produce highly ornamented eggs which become entrapped in the substratum and are protected from damage. The pattern of these egg-shell elaborations is used in taxonomy of these species.

Postembryonic development is direct in Eutardigrada, and the young closely resemble the adults. In Heterotardigrada, acquisition of the trunk and caudal appendages is accomplished in several successive molts. The number of toes or claws is always reduced in the young. During molting, egress occurs through an opening in the head region. The old buccal apparatus is lost and a new one forms during molting. The pedal glands play an important role in the production of new feet, toes, and claws.

Table 1 shows the major lines of classification of Tardigrada suggested by Ramazzotti (1962). A key to the genera is given below. Two large orders include most of the genera, while an intermediate order possesses only one species from a single locality. Nearly all marine Tardigrada belong to the Heterotardigrada and are found in the most primitive families of the suborder Arthrotardigrada. In the suborder Echiniscoides only *Archechiniscus* Schulz and *Echiniscoides* Plate are marine (Figure 4).

TABLE 1.—*Major lines of classification of phylum Tardigrada. (Modified from Ramazzotti, 1962.)*

1. Order Heterotardigrada
    1. Suborder Arthrotardigrada
        1. Family Halechiniscidae
            1. *Florarctus*
            2. *Halechiniscus*
            3. *Pleocola*
            4. *Actinarctus*
            5. *Tetrakentron*
            6. *Styraconyx*
            7. *Tanarctus*
        2. Family Batillipedidae
            1. *Batillipes*
            2. *Orzeliscus*
        3. Family Stygarctidae
            1. *Stygarctus*
            2. *Parastygarctus*
    2. Suborder Echiniscoidea
        1. Family Oreellidae
            1. *Oreella*
            2. *Echiniscoides*
            3. *Archechiniscus*
        2. Family Echiniscidae
            1. *Echiniscus*
            2. *Parechiniscus*
            3. *Pseudechiniscus*
            4. *Mopsechiniscus*
2. Order Mesotardigrada
    1. Family Thermozodiidae
        1. *Thermozodium*
3. Order Eutardigrada
    1. Family Macrobiotidae
        1. *Macrobiotus*
        2. *Haplomacrobiotus*
        3. *Hypsibius*
        4. *Itaquascon*
    2. Family Milnesiidae
        1. *Milnesium*

Principal characters used in systematics include the following: presence or absence of the median cirrus separates the suborders of the Heterotardigrada, as does the presence or absence of toes (Figures 5 and 6); distinctive characters of the Eutardigrada are limited to the pharynx placoids and the claw shape (Figures 7 and 8). There are no sub-

Key to the Genera of Tardigrada

1. With lateral cephalic cirri (cirrus A) 2
Without lateral cephalic cirri (cirrus A). (Order Eutardigrada) 20
2. Bulbus including clearly separated placoids. (Order Mesotardigrada).... ***Thermozodium*** Rahn
Clearly separated placoids lacking. (Order Heterotardigrada) 3
3. With median cephalic cirrus. (Marine) 4
Without median cephalic cirrus 13
4. Body surface with a gelatinous coating including spines .... ***Actinarctus*** Schulz
Body surface without such coating and processes 5
5. Distal end of leg without toes, claws inserted on foot; dorsal plates present on body........ 6
Distal end of legs with toes 7
6. Head transversally separated in two parts; posterior cephalic plate bearing expanded lateral processes .... ***Parastygarctus*** Renaud-Debyser
Head not separated into plates; cephalic plate simple without expanded lateral process
Stygarctus Schulz
7. Distal end of toes bearing adhesory discs, or rodlike appendages 8
Distal end of toes bearing claws 9
8. Six toes of different size with spoon-shaped appendages........ ***Batillipes*** Richters
Four toes of similar size with rodlike appendages........ ***Orzeliscus*** Bois-Reymond-Marcus
9. Four toes arranged in two different pairs with heterogenous claws; body cuticle with large lateral aliform processes........ ***Florarctus*** Delamare Deboutteville and Renaud-Mornant
Four similar toes (homodactylous) 10
10. Claws with accessory spurs 11
Claws without accessory spurs 12
11. Body dorsoventrally flattened: lives on *Synapta* tentacles .... ***Tetrakentron*** Cuénot
Body not dorsoventrally flattened .... ***Styraconyx*** Thulin
12. Clava shorter than lateral cirrus (A), 16 µ maximum........ ***Pleocola*** Cantacuzène
Clava longer than lateral cirrus (A), more than 15 µ .... ***Halechiniscus*** Richters
13. Distal end of leg with unequally long toes; or even toes reduced to a small membrane. (Marine) 14
Distal end of leg without toes, bearing only unstalked claws 15
14. Distal end of leg with two median toes bearing claws, and two lateral claws inserted on the leg on a short membrane or papillae .... ***Archechiniscus*** Schulz
All claws inserted on toes; hind end bilobed with long cirri........ ***Tanarctus*** Renaud-Debyser
15. Dorsal plates of body cuticle poorly delimited 16
Dorsal cuticle partially or fully covered with thickened plates 17
16. With four claws on each leg .... ***Oreela*** Murray
With five to eleven claws on each leg. (Marine) .... ***Echiniscoides*** Plate
17. Dorsal plates not fully developed, only the posterior one is wholly thickened
Parechiniscus Cuénot
Dorsal plates fully developed, including a cephalic plate 18
18. Posterior plate adjacent to second paired plate or third unpaired plate.... ***Echiniscus*** Schultze
Posterior plate separated from second paired plate or third unpaired plate by a transverse paired or unpaired plate 19
19. Without buccal internal and external paired cirri........ ***Mopsechiniscus*** Bois-Reymond-Marcus
With buccal internal and external cirri .... ***Pseudechiniscus*** Thulin
20. Mouth surrounded by six rostral and two lateral or ventrolateral papillae; bulbus without placoids .... ***Milnesium*** Doyère
Mouth not surrounded by papillae 21
21. Legs with two simple, distally bifid claws .... ***Haplomacrobiotus*** May
Legs with two double claws 22
22. The two double-claws are of the same size and symmetrically distributed from the median axis of the leg .... ***Macrobiotus*** Schultze
The two double-claws are a little or very much different in size and shape and always asymmetrical from the median axis of the leg 23
23. Bulbus always without placoids .... ***Itaquascon*** Barros
Bulbus with placoids (except in larval stages or during pre-ecdysis time)
Hypsibius Ehrenberg

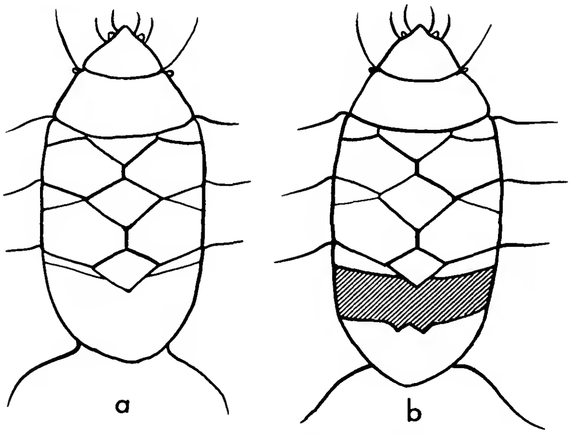

FIGURE 4.—Plates of echiniscids. *Pseudechiniscus* (right, shaded area) has an additional plate.

borders of Eutardigrada because it is a very homogenous group.

Until recently, marine tardigrades have been reported rarely, and studies of their ecology are few. Extensive studies of Tardigrada populations appear in the works of Renaud-Debyser (1956, 1959a,b, 1963) and de Zio and Grimaldi (1966).

At present marine tardigrades may be grouped generally according to habitat: (1) some genera are limited strictly to interstitial spaces, leading a subterranean life within the sediment; (2) others live on algae or vegetal debris, usually in surface sediments; and (3) others appear to be commensal on marine invertebrates.

Interstitial or subterranean species which form a part of the mesopsammon are not always strictly limited to a specific type of sediment but are able to colonize sands of different composition. In silicious sand *Halechiniscus* Richters, *Batillipes* Richters, and *Stygarctus* Schulz are frequently found, but all three also are found in entirely calcareous coralline sands. Other genera seem more restricted. *Orzeliscus* Bois-Reymond-Marcus and *Actinarctus* are most frequent in "*Amphioxus* sand," which is silicious but contains a large proportion of shell debris and other calcareous materials. To date, *Tanarctus* Renaud-Debyser and *Florarctus* have been found only at the surface or in deeper layers of coralline sands. *Parastygarctus* can be found in coralline sand containing a relatively large fraction of silicious elements.

Certain genera and species are epizoic and are not limited to intragranular spaces. One often finds them associated with algal debris settling at the sediment surface. Included here are *Styraconyx* Thulin, *Echiniscoides,* and *Archechiniscus.*

Finally, among marine tardigrades are commensal species such as *Tetrakentron synaptae* Cuénot, which lives on the tentacles of *Synapta galliennii* Herapath. Three other species have been reported in apparently commensal relationships and are free-living as well. *Echiniscoides sigismundi* (Schulz) has been found within the mantle cavity of mussels, and *Actinarctus doryphorus* Schulz has been recorded as an ectoparasite of the echinoid *Echinocyamus pusillus* (O.F. Müller). Recently, the junior author found free-living *Plecola limnoriae* Cantacuzène in coralline sand from the Bahamas. This species originally was described from the pleopods of the isopod *Limnoria lignorum* (Rathke).

Mesopsammic tardigrades are found from the high-tide region to the low-tide region along intertidal beaches, and as deep as 1.5 m in the sand. They show a continuous pattern of distribution where the settling of sand and the circulation of water (permeability and slope) permit good oxygenation of the "milieu." For example, *Halechiniscus* can be found in higher levels of the shore and *Stygarctus* occurs in great density at 40 to 60 cm depth in the sand at the midtide level. *Batillipes* is most common in the lower half of the beach, as are *Parastygarctus* and *Archechiniscus.* In atidal beaches, *Batillipes* is found near the water's edge and follows seasonal fluctuations of the water level.

Other genera are characterized by subtidal distributions. *Actinarctus, Orzeliscus,* and *Halechiniscus* are found at several meters depth in "*Amphioxus* sand" of the North Atlantic (North Sea, Gullmar Fjord, and English Channel); and *Florarctus, Archechiniscus,* and *Styraconyx* are found in subtidal corraline sand at depths between 2 and 4 m.

It appears that tardigrades may be rare in the neritic zone. To date the only representative has been *Styraconyx,* collected at 380 m. It is likely that sampling gear and sorting methods are not well adapted to collecting meiobenthos, and especially tardigrades. The use of such methods may well be the reason for our lack of knowledge of deep-sea tardigrades, which have been reported from depths of 4,690 m.

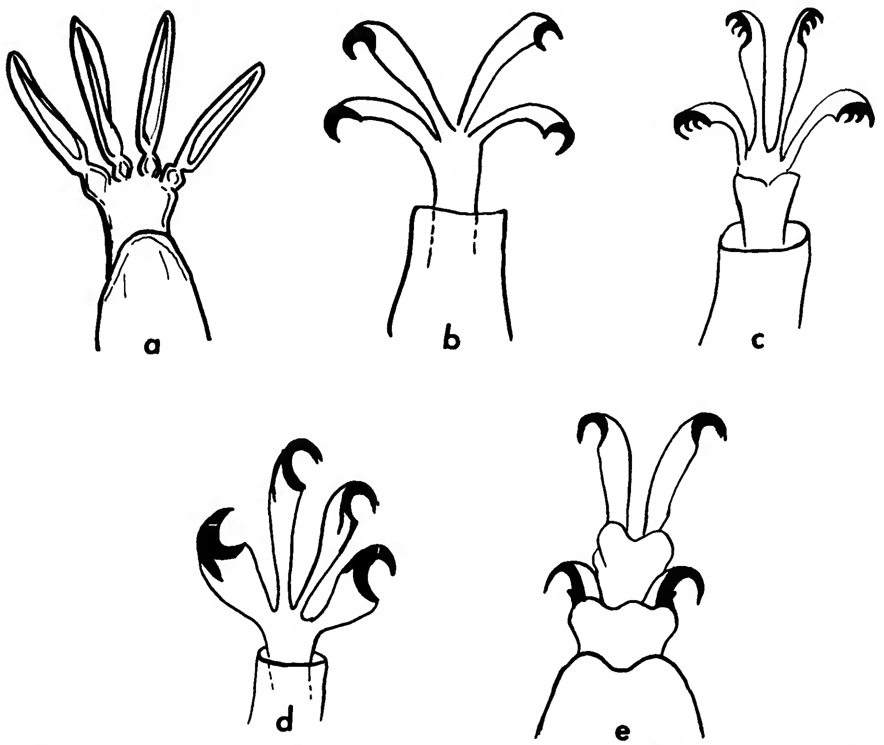

FIGURE 5.—Claws of Heterotardigrada, mounted on toes. *a, Orzeliscus* sp.; *b, Halechiniscus* sp.; *c, Styraconyx* sp.; *d, Florarctus* sp.; *e, Archechiniscus* sp.

Concerning geographical distribution, *Batillipes, Actinarctus, Tanarctus, Tetrakentron, Pleocola, Stygarctus,* and *Florarctus* are Atlantic or Mediterranean; *Florarctus, Parastygarctus, Archechiniscus,* and *Batillipes* have been found in the Indo-Pacific region; and *Halechiniscus, Styraconyx, Orzeliscus,* and *Batillipes* are cosmopolitan.

Among ecological factors, granulometric characteristics are important. Authors have recorded tardigrade populations in silicious sand beaches of grain sizes varying from 250 to 350 μ in mean diameter at Arcachon (Renaud-Debyser, 1963) to 800 μ or larger on the east coast of the United States (Pollock, manuscript in preparation). In Malaysia, *Parastygarctus* was found in sand of relatively large grain, of 770 μ diameter. Within broad limits, it does not seem that grain size by itself plays a fundamental role in determining tardigrade distribution; however, the shape and arrangement of sediment components primarily determine intragranular living spaces.

The arrangement of sand grains is determined by the shape of the particles and their settling. Sorting and homogeneity also are important. Very tight packing (rhombohedral) and clogging of interstices by fine elements are factors unfavorable to colonization by tardigrades. It is important, therefore, to know the quantity of very small size particles present in the sediment. Renaud-Debyser and Salvat (1963) expressed the results of their granulometric analyses as the number of grains in each fraction clearly showing the amount of finer elements.

In tidal beaches, interstitial water is replaced by each tide change, providing a fresh supply of oxygen-rich water throughout the beach. Important displacements of fauna may be caused by this circulation, as shown by Renaud-Debyser (1963) particularly for *Stygarctus* at Arcachon. Other species are influenced by the circulation of subterranean water, especially in atidal beaches.

Seasonal changes affect both population densities

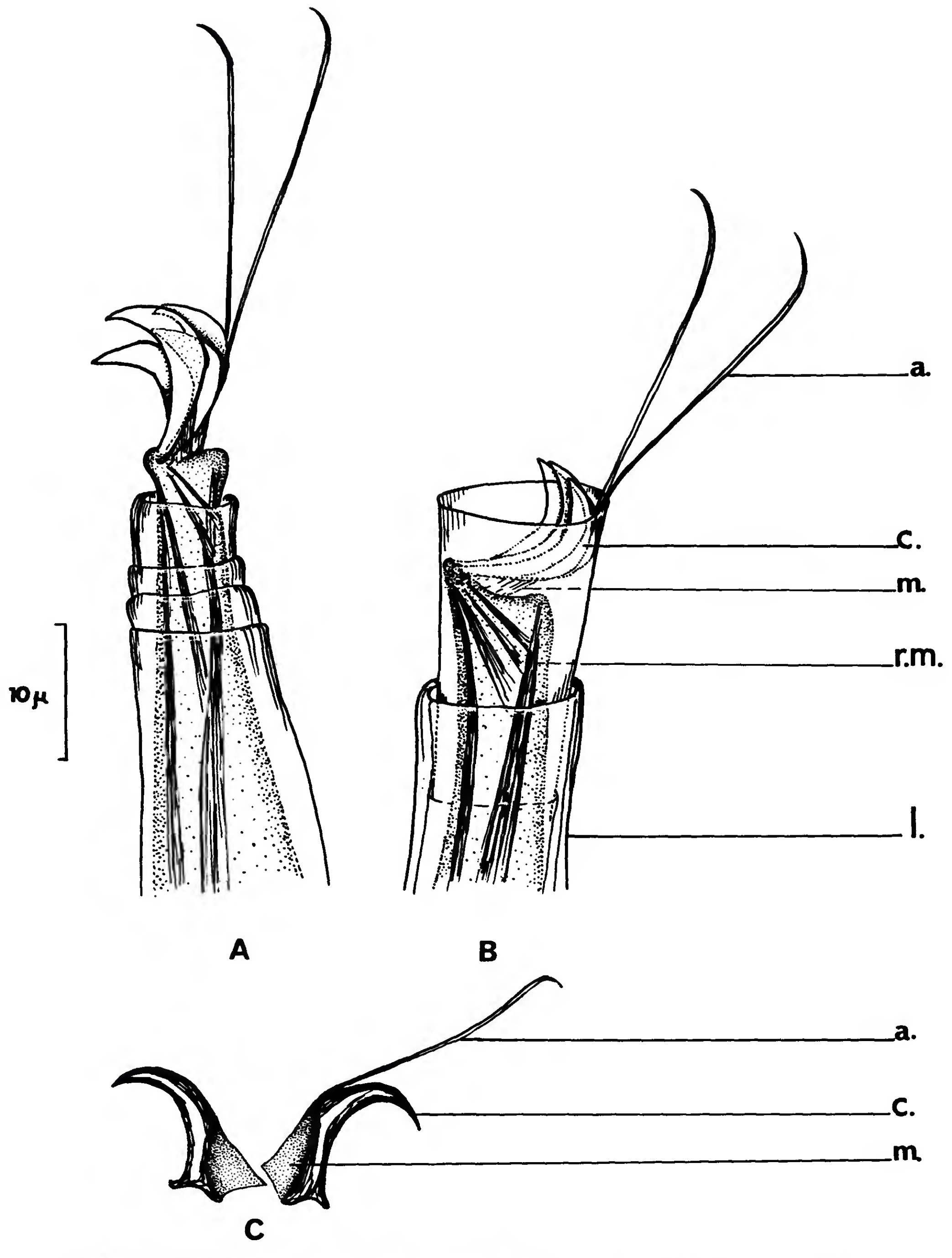

FIGURE 6.—Claws of stygarctids, with basal membranes but without toes. A, extended; B, retracted; C, detached from legs, showing membranes. Symbols: *a*, appendage on median claws; *c*, claws; *l*, leg; *m*, membrane; *r.m.*, retractor muscle.

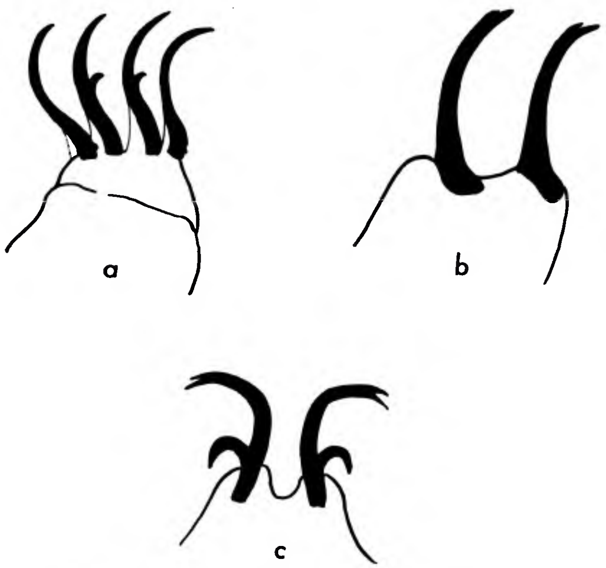

FIGURE 7.—Claws: *a,* of echiniscids; *b,* of *Haplomacrobiotus;* *c,* of *Macrobiotus.*

and distributions. Numerical variations may be extremely large. At Arcachon an extreme cold spell severely reduced interstitial populations. Progressive repopulation occurred through the spring months and resulted in maxima in May and autumn.

Thorough studies of tardigrade populations have been developed only recently. Reasons for this are the difficulties of sampling, extraction, and sorting; the small size of the animals (especially larval stages); and difficulty in distinguishing sexes of immature animals.

Marine Tardigrada are phytophagous "pump-suckers," as shown by their buccal apparatus. The stylets extrude through the mouth opening and pierce the phytal material, the liquid contents of which are pumped out by means of the muscular pharynx. This food is stored in the intestinal diverticulae, where it is given a green, red, or brown color. It is likely that the distribution of intertidal *Stygarctus bradypus* Schulz is determined by the presence or absence of abundant appropriate food within the sediment. Large populations have been found only within sheltered beaches located close to abundant beds of *Zostera* Linné at Arcachon and of *Sargassum* C. Agardh or *Thalassia* Koenig and Sims in the Bahamas. These plants are frequently detached from their substrate and washed onto beaches where they provide abundant vegetal debris for phytophagous tardigrades.

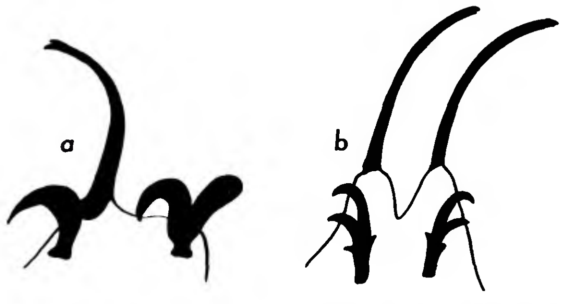

FIGURE 8.—Asymmetrical claws in two genera of Eutardigrada: *a, Hypsibius; b, Milnesium.*

Regarding salinity, Renaud-Debyser and Salvat (1963) have observed that tardigrades cannot withstand direct exposure on a beach where an outflow of fresh water occurs. In the outflow area, the salinity is lowered during the ebb tide from 31 to 8 ppt, and the tardigrades disappear; however, in a station immediately below, where mixing with the water of imbibition elevates the salinity to 16 ppt, the tardigrades recolonize the sediment. The remainder of the selective distribution of different species along the tidal beach possibly is related to tolerances of different species to changes in salinity and other factors produced by the rhythm of tidal variations.

A comprehensive bibliography on marine tardigrades including general and review articles, original species descriptions, ecological studies, etc., is available from the authors upon request.

Literature Cited

Ramazzotti, G.

1962. Il Phylum Tardigrada. *Memoire dell'Istituto Italiano di Idrobiologia,* 14:1–595.

Renaud-Debyser, J.

1956. Répartition de deux Tardigrades, *Batillipes mirus* Richters et *Stygarctus bradypus* Schulz dans un segment de plage du Bassin d'Arcachon. *Comptes Rendus de l'Académie des Sciences,* 243:1365–1369.

1959a. Sur quelque Tardigrades du Bassin d'Arcachon. *Vie et Milieu,* 10:135–146.

1959b. Études sur la faune interstitielle des Iles Bahamas. III. Tardigrades. *Vie et Milieu,* 10:296–302.

1963. Recherches écologique sur la faune interstitielle des sables. (Bassin d'Arcachon, Ile de Bimini, Bahamas). *Vie et Milieu,* supplement 15:1–157.

Renaud-Debyser, J., and B. Salvat

1963. Éléments de prospérité des biotopes des sédiments meubles intertidaux et écologie de leurs populations en microfaune et macrofaune. *Vie et Milieu,* 14:463–550.

de Zio, S., and P. Grimaldi

1966. Ecological Aspects of Tardigrada Distribution in South Adriatic Beaches. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Supplementband 2:87–94.

F. Monniot

Les Ascidies littorales et profondes des sédiments meubles

ABSTRACT

The anatomy, methods of collecting and fixing, techniques for studying, systematics, and ecology of interstitial ascidians are reviewed. Consideration is given to shallow-water and deep-sea species.

Les Ascidies du meiobenthos sont de découverte récente. Les premières Ascidies interstitielles ont été décrites en 1961 par Weinstein. Elles provenaient de la zone littorale Méditerranéenne du Golfe du Lion. Les petites Ascidies des grandes profondeurs, vivant dans les vases à Globigérines ont été décrites d'une part à la suite de l'expédition de la Galathea, d'autre part tout récemment après les récoltes des navires américains Atlantis, Atlantis II et Chain.

Ces Ascidies vivent dans tous les cas sur des fonds meubles. Elles sont de trés petite taille et habitent les interstices entre les grains de sable pour les Ascidies "interstitielles" ou entre les tests de Foraminifères pour les Ascidies des grandes profondeurs. Les convergences de formes sont frappantes à première vue. Les convergences anatomiques sont plus étonnantes encore. La découverte d'une méiofaune de petits Procordés, bien que très récente, a déjà permis une bien meilleure compréhension du groupe des Ascidies grâce à des échelons évolutifs qui manquaient et à des formes d'organisation insoupçonnées jusqu'à présent. Pour mieux comprendre l'apport des Ascidies de la méiofaune à l'ensemble de ce groupe, il est nécessaire de rappeler leur schéma d'organisation générale avec les caractères les plus fréquemment utilisés en systématique.

Schéma anatomique

Les Ascidies ont une structure générale assez simple, bien que chaque organe soit susceptible de se compliquer énormément, je ne parlerai ici que des Ascidies simples, les Ascidies composées étant exceptionnelles dans la méiofaune.

L'animal (Figure 1) se compose d'un sac constitué par le manteau percé de deux orifices: les siphons. L'un sert à l'entrée, l'autre à la sortie de l'eau. Les Ascidies fonctionnent comme un filtre. Le manteau contient des fibres musculaires entrecroisées et secrète sur sa face externe une tunique plus ou moins rigide et plus ou moins epaisse. Sur sa face interne, le manteau supporte tous les organes, à l'entrée de l'orifice buccal il porte une couronne de tentacules qui arrêtent les particules de trop grande taille. Sous ces tentacules est suspendue une sorte de poche à parois perforées: la branchie, au fond de la poche s'ouvre l'oesophage. L'eau est aspirée par des battements ciliaires dans la poche branchiale. Elle est filtrée au niveau de multiples orifices à bordure ciliée: les stigmates; elle sort dans la cavité générale du corps ou cavité péribranchiale, puis à l'extérieur par l'orifice ou le siphon cloacal. La ciliature retient au passage les particules nutritives engluées sur un film de mucus qui est, lui, dirigé entre les stigmates vers l'oesophage. Le tube digestif est relativement simple. L'estomac globuleux, couvert ou non de glandes hépatiques, débouche dans un intestin tubulaire. Ce tube digestif décrit une boucle. Il est attaché de façon plus ou moins lâche au manteau. La branchie est retenue par quelques trabécules minces à la paroi du manteau. A l'état adulte des gonades hermaphrodites plus ou moins

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nombreuses se développent sur la face interne du manteau faisant saillie dans la cavité générale. Oeufs et spermatozoïdes sont évacués par le siphon cloacal avec l'eau sortant de la branchie et les pelotes fécales.

Les systèmes nerveux et vasculaire sont complexes; nous ne pouvons en parler ici en détail, ils ne sont pas utilisés en systématique. Il existe un ganglion nerveux ou cerveau qui détermine la face dorsale de l'animal. L'excrétion est assurée par des cellules à accumulation. Il existe un rein chez les Molgulidae seulement, il s'agit d'un organe clos.

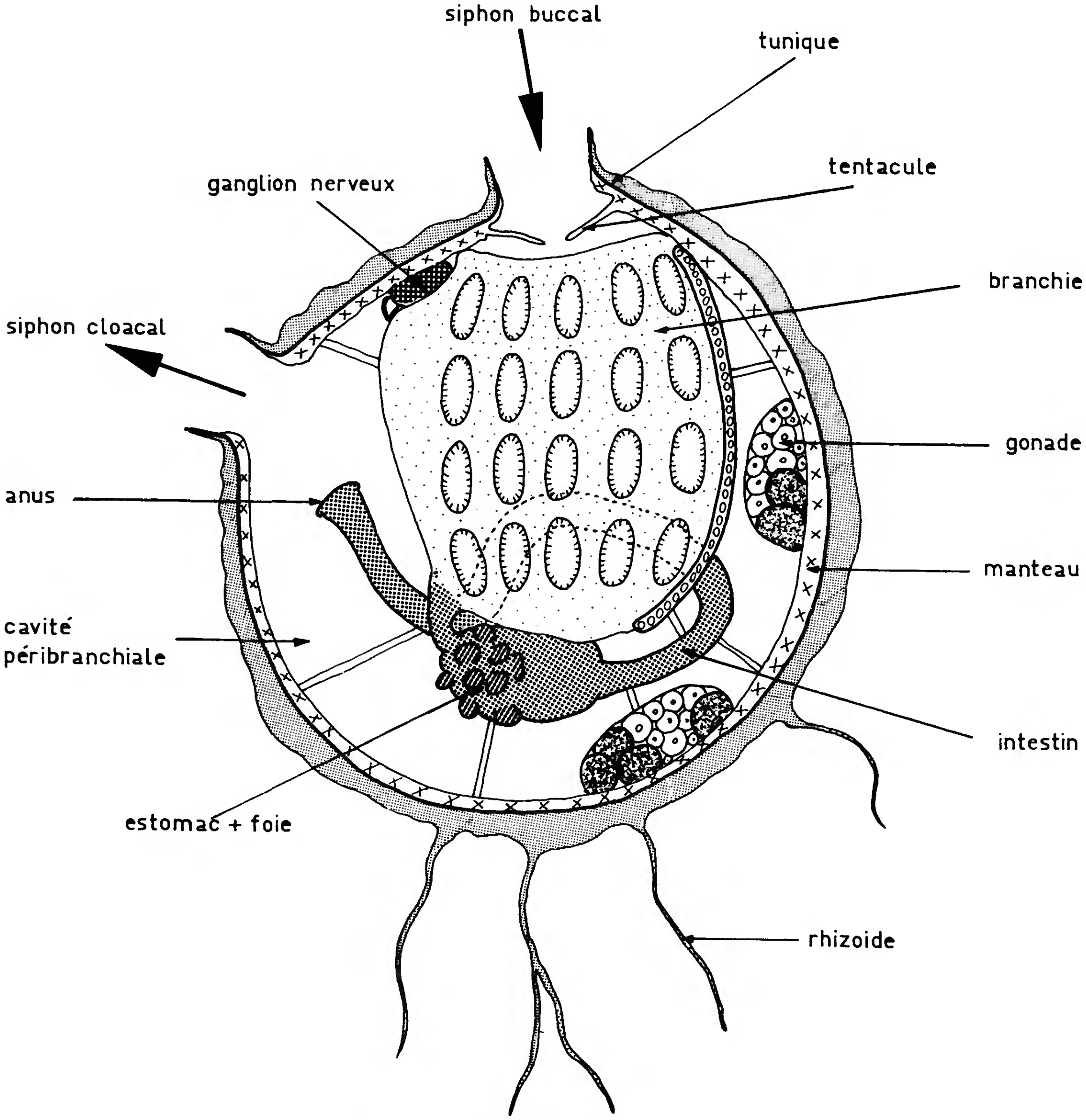

FIGURE 1.—Schéma anatomique d'une Ascidie.

Ce bref schéma montre qu'il s'agit d'un animal mou, déformable en tous sens, creux—les organes ont toujours des épaisseurs tissulaires très faibles. Par contre, chacun d'eux, y compris la branchie, contient des fibrilles musculaires entrecroisées qui peuvent se contracter indépendamment les unes des autres. L'animal richement innervé peut devenir méconnaissable en état de contraction. Cette contractibilité, bien connue chez les Ascidies, a de très nombreux inconvénients: La taille des animaux peut varier énormément (de 1 à 10); la forme du corps ne peut que rarement être précisée; une anesthésie est indispensable pour une étude correcte; et l'étude systématique ne peut avoir lieu qu'après fixation (48 heures minimum) pour durcir les tissus, et surtout après dissection. Une coloration est nécessaire à cause de la minceur et souvent de la transparence des tissus.

Méthodes pratiques de récolte et de fixation

Comme nous l'avons vu précédemment, les tissus très minces des Ascidies sont enfermés dans une tunique épaisse, imperméable, hermétiquement close par la musculature puissante des siphons. Ces tissus s'histolysent quand l'animal meurt et en premier lieu la branchie. Il y a une action importante des bactéries qui sont très abondantes dans toutes les cavités des Ascidies. Les animaux peuvent être totalement liquéfiés sans que leur apparence externe aie changé. Ce stade est atteint d'autant plus vite que la température est plus élevée.

Mais avant que l'histolyse ait commencé, l'état des animaux peut être très mauvais: la contraction musculaire est souvent irréversible et les tissus très minces restent définitivement plissés après la fixation, interdisant toute étude anatomique précise.

Les Ascidies du méiobenthos contiennent très souvent dans leur branchie, leur cavité cloacale ou leur tube digestif des particules sédimentaires. Au cours des dragages, du tri, ou après une forte contraction, ces particules minérales lèsent les tissus qui les contiennent.

La récolte des Ascidies s'effectue à la drague. Pour que les animaux soient moins abîmés il faut que le coup de drague soit court, que le sédiment ne subisse pas un trop grand échauffement avant le tri. Il ne doit donc pas être gardé au soleil et être conservé dans l'eau si possible. Le tri doit s'effectuer dans les 24 heures qui suivent le dragage pour le matériel vivant. Le tamisage abîme beaucoup les Ascidies. La méthode de tri par lavage et flottation a donné les meilleurs résultats. Le fixateur est le formol neutre salé 5 pourcent. Les animaux peuvent être conservés indéfiniment dans le fixateur, mais il est préférable de les transférer après 15 jours de fixation dans l'alcool 75 pourcent quarante-huit heures de fixation sont suffisantes pour des animaux de très petite taille. Tous les fixateurs pour histologie conviennent, mails ils donnent de moins bons résultats pour une étude anatomique, les tissus sont généralement trop durcis. Les fixateurs acides sont à éviter pour préserver les spicules éventuels.

Techniques de préparation

Les Ascidies fixées au formol neutre pendant plusieurs jours sont conservées dans l'alcool 75 pourcent. Pour la dissection et la coloration elles doivent être progressivement réhydratées.

1. La tunique est débarrassée des particules sableuses qui la couvrent. Cette opération doit être fait à la pince délicatement afin de ne pas déchirer la tunique qui y adhère parfois fortement.
2. La tunique est enlevée avec précaution sans déchirer le manteau qu'elle recouvre. Elle possède parfois plusieurs couches. La région des siphons (tunique interne et externe) est montée directement entre lame et lamelle dans une goutte de gomme au chloral; les tissus sont éclaircis et les spicules s'ils existent peuvent être observés au microscope.
3. Le manteau est ouvert d'un siphon à l'autre selon la ligne medio-ventrale, au-dessus de l'endostyle.
4. La branchie est détachée du manteau et des différents organes en coupant les ponts dermatobranchiaux qui la retiennent.
5. Coloration.
    - (a) Branchie: 3 à 5 minutes dans l'hémalun d/Masson. Rinçage 10 minutes dans l'eau; deshydratation progressive à l'alcool jusqu'à l'alcool 95 pourcent seulement. Passage à l'alcool butylique 5 à 10 minutes. Montgage au baume de canada entre lame et lamelle.
    - (b) Manteau: Les gonades et le tube digestif doivent y rester accrochés de façon à conserver leur place respective. Le deux siphons doivent être bien écartés pour observer les tentacules. Coloration de 1 à 3 minutes seulement, selon l'âge du colorant. Les différents organes se colorent plus ou moins intensément selon la proportion des tissus en

matière nucléaire. Le manteau reste assez pâle tandis que les gonades sont très foncées. Par contre les conduits génitaux restent clairs et deviennent visibles sur les gonades. Après rinçage à l'eau, deshydratation jusqu'à l'alcool 95 pourcent puis alcool butylique. Montage au baume de canada.

Caractères des Ascidies de la méiofaune: leur reconnaissance dans le sédiment

La taille des animaux est extrêmement réduite. Les Ascidies interstitielles mesurent 1 à 3 mm dans leur grande longueur en extension. Les Ascidies des vases à Globigérines de 1 à 4 mm.

La forme est généralement arrondie ou en fuseau. Certains animaux présentent des excroissances tunicales (Rhizoïdes) qui servent à leur ancrage dans le sédiment. Certaines espèces peuvent fixer sur leur tunique des grains de sable ou des Foraminifères et s'en couvrir complètement;

La coloration des Ascidies de la méiofaune est très terne, grise ou jaunâtre. Il est rare que la tunique soit transparente.

Certaines espèces sont capables de mouvements de reptation par allongement et rétraction des siphons et contractions alternées des diverses parties du corps.

On confond souvent les Ascidies interstitielles avec les jeunes Molgulidae dont les premiers stades sont tout à fait comparables. Souvent, seule la dissection permet de les distinguer. Leur aspect et leur mode de contraction dès qu'on les excite les fait ressembler également à de jeunes Siponcles ou à des petites Actinies rétractées.

La systématique

La systématique des Ascidies simples (les Ascidies composées sont des exceptions dans la méiofaune) est basée essentiellement sur la structure fine de la branchie, la présence ou l'absence d'un rein, la structure du tube digestif et des gonades. La branchie joue un rôle prépondérant. Elle peut se présenter sous diverses formes (Figure 2 de gauche à droite):

(a) Une lame tissulaire très mince perforée d'orifices ciliés (Figure 2). Il s'agit de la famille des Aplousobranches à laquelle appartiennent la plupart des Ascidies composées. Aucune Ascidie de la méiofaune n'appartient à cette famille jusqu'à présent.

(b) Sur la lame branchiale dite fondamentale poussent des papilles entre les stigmates du côté interne. Ces papilles s'élèvent au-dessus de la lame fondamentale, se bifurquent, se rejoignent formant des sortes de ponts au-dessus des rangées de stigmate. Les stigmates peuvent être des simples trous ronds ou allongés mais ils peuvent aussi s'enrouler en spirale. Dans ces ponts passent des sinus sanguins. On appelle l'ensemble de ces formations sinus longitudinaux.

L'ordre des Phlebobranches possède une branchie avec des papilles ou des sinus longitudinaux.

Chez les Stolidobranches les sinus longitudinaux peuvent se grouper, la branchie se plisse, les tissus faisant saillie à l'intérieur du sac branchial. La surface de la lame branchiale est considérablement augmentée.

Parmi les Stolidobranches on distingue trois familles.

Les Styelidae dont les stigmates sont droits c'est-à-dire parallèles aux sinus longitudinaux comme ce qui a été figuré jusqu'à présent. Les animaux ont un estomac à côtes longitudinales, pas de foie, des gonades hermaphrodites dispersées sur le manteau, pas de rein.

Les Pyuridae ont elles, des stigmates spiralés à l'origine, qui souvent sont tellement recoupés qu'ils donnent l'impression d'être droits. L'estomac est partiellement couvert d'une glande hépatique. Il n'y a pas de rein. Dans cette famille la tunique possède des spicules cornés. Il y a parfois des spicules calcaires.

Les Molgulidae ont toujours des stigmates spiralés, une glande hépatique et un rein.

Place des Ascidies du Méiobenthos dans la systématique du groupe

Les Ascidies interstitielles et celles des grands fonds apparienent aux 2 ordres des Phlebobranches et des Stolidobranches, c'est-à-dire aux Ascidies qui possèden des sinus longitudinaux. Tous les grands types d'organisation sont représentés. Quelques exemples:

Phlebobranches
  Interstitielles
    Psammascidia teissieri Monniot
    Dextrogaster suecica Monniot
    Corella halli Kott
  Grands fonds
    Namiella bistigmata Monniot et Monniot

Stolidobranches
  Styelidae
    Interstitielles
      Psammostyela delamarei Weinstein
      Polycarpa pentarhiza Monniot
      Polycarpa arnbackae Monniot
    Grands fonds
      Polycarpa pseudoalbatrossi Monniot et Monniot
      Polycarpa delta Monniot et Monniot
      Cnemidocarpa digonas Monniot et Monniot
      Styela loculosa Monniot et Monniot
      Bathystyeloides enderbyanus (Michaelsen)
  Pyuridae
    Interstitielles
      Heterostigma fagei Monniot et Monniot
      Heterostigma separ Arnback-Christie-Linde
      Heterostigma reptans Monniot et Monniot
      Heterostigma gonochorica Monniot
  Molgulidae
    Interstitielles
      Molgula hirta Monniot

A ces Ascidies s'ajoutent une catégorie d'animaux des grandes fonds sans branchie qui sont classés à part dans la famille des Hexacrobylidae: *Hexacrobylus indicus* Oka et *Gasterascidia sandersi* Monniot et Monniot.

Les Ascidies du méiobenthos ne rentrent pas toujours facilement dans les cadres systématiques. On peut les attribuer à une famille assez facilement (après coloration, dissection et montage des différents organes sur lame histologique). Il est souvent difficile de les placer dans un genre. Leur branchie est souvent réduite, avec quelques sinus longitudinaux, sans plis. Mais il s'agit d'une réduction secondaire ou d'un caractère resté juvénile. Il arrive très souvent aussi que la branchie ne possède pas encore de vrais stigmates. La systématique ne peut plus s'effectuer avec la branchie pour base. Le tube digestif est très simplifié et le foie n'est parfois visible que sur coupes histologiques. La taille des animaux est si réduite qu'il est parfois difficile de décider, même après coloration, si une formation globuleuse transparente est un coeur ou un rein. Là encore il faut recourir aux coupes.

L'étude systématique de très petites ascidies des fonds meubles présente, par contre, un grand intérêt dans l'explication de certaines structures, le manque de place ne permettant de conserver que les différenciations essentielles pour chaque groupe. Beaucoup de formes nouvelles sont certainement à découvrir. Les Ascidies interstitielles ont en tous cas permis de démontrer la structure essentielle et les directions évolutives de Pyuridae.

Intérêt des Ascidies des fonds meubles du point de vue écologique

Elles existent à toutes les profondeurs: ascidies interstitielles littorales et ascidies interstitielles retrouvées sur talus continental (exemple: *Heterostigma reptans* à 300 m). Mais ce milieu n'est pratiquement pas encore prospecté. Actuellement, seule la zone tout à fait littorale et quelques prélèvements dans les fosses océaniques sont étudiés. La prospection des fonds meubles est extrêmement restreinte, surtout pour les sédiments sableux. La zone entre 50 et 1,000 m n'est absolument pas prospectée. Or, la faune ascidiologique à ces profondeurs s'est révélée très riche et très variée sur les roches dures; il n'y a aucune raison pour qu'il n'y ait pas d'ascidies sur les fonds meubles, en particulier à la base du talus continental.

Elles existent dans toutes les mers: On a retrouvé les ascidies interstitielles sur toutes les côtes d'Europe, partout où elles ont été recherchées. Les navires américains Atlantis, Atlantis II et Chain ont récolté des Ascidies des grands fonds dans l'Atlantique Nord, près des Bermudes, au large des côtes du Brésil et au large du Sénégal. Seul le petit nombre de prélèvements effectués a limité l'abondance et la variété des Ascidies répertoriées.

Les Ascidies du méiobenthos sont liées à des conditions écologiques précises. Pour les Ascidies intertitielles, la granulométrie a une importance prépondérante. Elles vivent dans des zones de courants importants et la présence dans l'eau d'une suspension de particules trop fines limite leur développement. Aux grandes profondeurs on ne sait rien des conditions écologiques: ou bien les courants sont presque nuls et la branchie n'est pas encrassée par des suspensions vaseuses, ou bien la couche de Foraminifères sur la vase du fond est suffisamment épaisse pour que ces organismes jouent le rôle des particules sédimentaires plus grosses qui existent au littoral. Les Ascidies étant des animaux filtreurs très actifs, il est logique de supposer qu'il existe toute de même un courant de fond suffisant pour assurer l'apport de nourriture. Les Ascidies de la

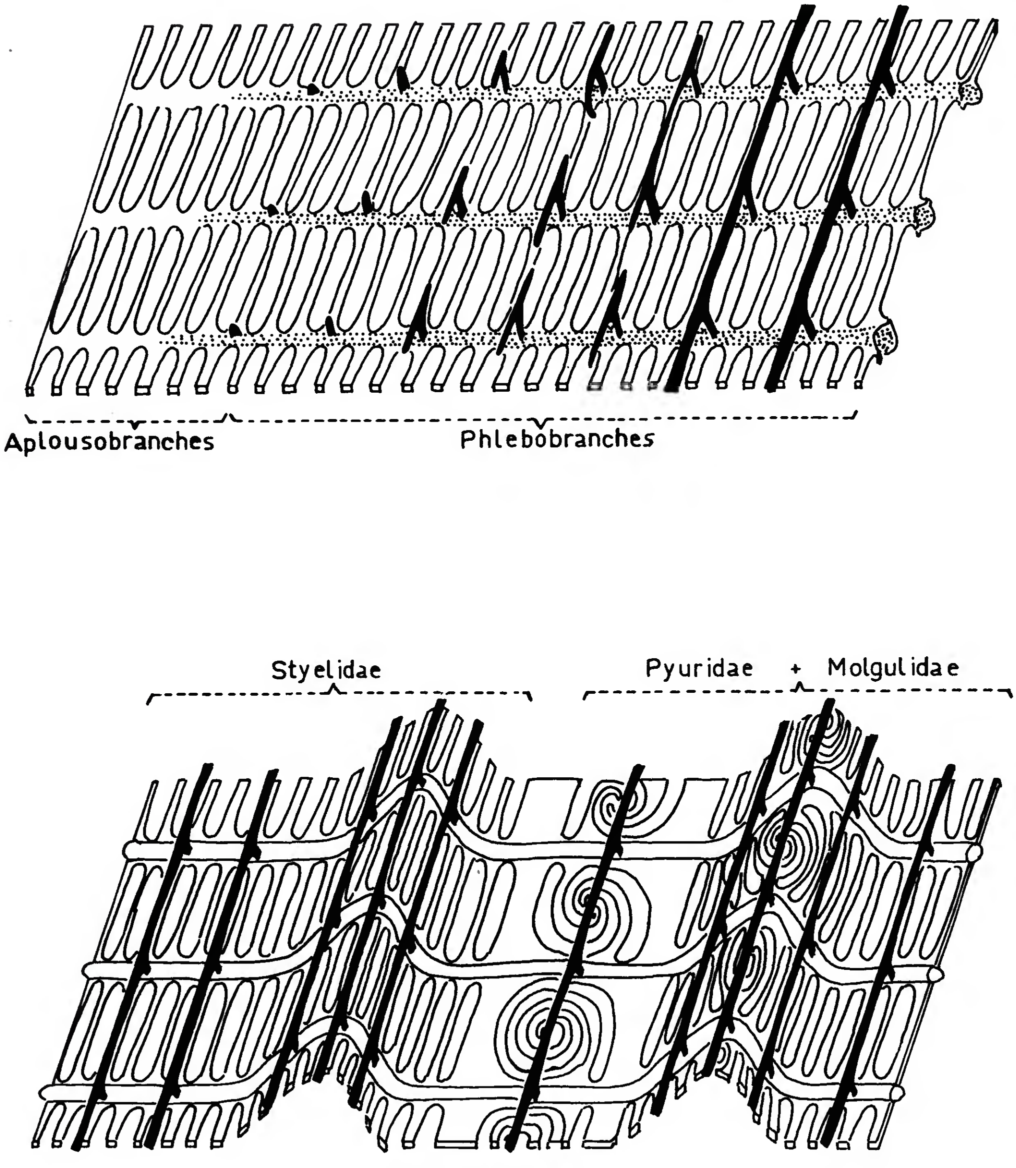

FIGURE 2.—Schéma de l'évolution branchiale dans les divers ordres d'Ascidies.

méiofaune sont toujours liées à une microfaune variée: Ostracodes, Polychètes, Copépodes, Isopodes, Amphipodes, Nématodes.

Un autre caractère plus discutable mérite cependant d'être signalé: l'abondance des Ascidies intertitielles paraît liée à une teneur élevée du sédiment en ions métalliques. Les microascidies sont très abondantes dans les grands fonds atlantiques, au voisinage des volcans (Sicile) et dans les zones schisteuses (Méditerranée occidentale); par contre, elles sont rares dans les sables quartziques, les sables coquilliers. On ignore si la composition chimique du sédiment agit directement sur les Ascidies ou sur les micro-organismes qui composent leur nourriture.

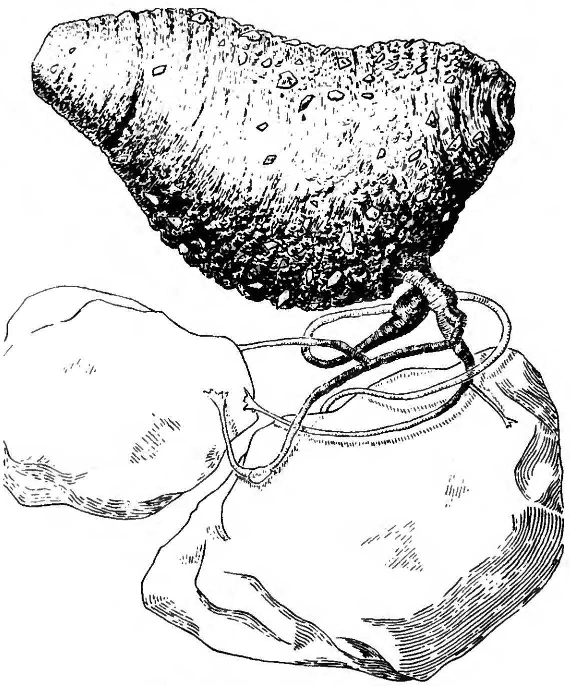

FIGURE 3.—*Heterostigma fagei.*

Conclusion

Les Ascidies forment un groupe dans l'ensemble difficile à étudier. Leur systématique est mal fixée. Ces difficultés s'accentuent quand il s'agit d'animaux microscopiques.

Le travail technique de récolte et de préparation étant effectué, la détermination reste encore délicate. Il n'existe pas de clés utilisables, même au niveau de la famille comme nous l'avons vu précédemment. Il faut signaler encore, après toutes les difficultés précédentes, la présence de cas tératologique fréquents: dédoublement d'organes, malformations, etc.

Beaucoup de difficultés de détermination disparaîtront quand une collection de préparations microscopiques sur lames sera constituée et pourra être communiquée. Le travail est en cours, mais les ascidiologiques ont l'habitude de ne pas faire de préparations permanentes!

Il n'existe aucune clef générale pour la détermination des Ascidies. L'ouvrage systématique le plus complet est Van Name (1945). Il peut être utilisé pour les caractères familiaux et les grands genres. Harant et Vernieres (1933) et Berrill (1950) sont inutilisables pour faire une détermination. Faute d'ouvrages généraux quelques publications d'importance variable peuvent être facilement utilisées (Hartmeyer, 1911, 1912; Herdman, 1882; Michaelsen, 1904; Millar, 1955, 1959, 1960, 1962, 1964; Monniot, 1965, and in press; Monniot et Monniot, 1968, 1970; Tokioka, 1953, 1967).

Auteurs Cités

Berrill, N. J.

1950. *The Tunicata with an Account of the British Species.* London: Ray Society.

Harant, H., et P. Vernières

1933. *Faune de France.* Paris: Tuniciers.

Hartmeyer, R.

1911. Die Ascidien der Deutschen Südpolar-Expedition 1901-1903. *Deutsche Südpolar Expedition,* 12(Zoologie 4):407–606.

1912. Die Ascidien der Deutschen Tiefsee-Expedition. *Wissenschaftliche ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer, "Valdivia" 1898-1899,* 16:223–392.

Herdman, W. A.

1882. Report on the Tunicata Collected during the Voyage of H.M.S. *Challenger* During the Years 1873–1876. Part I. Ascidiae Simplices. *Report on the Scientific Research Voyage of H.M.S. Challenger,* 6:1–285.

Michaelsen, W.

1904. Dis stolidobranchiaten Ascidien der deutschen Tiefsee-Expedition. *Wissenschaftliche ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899,* 7:181–260.

Millar, R. H.

1955. On a Collection of Ascidians from South Africa. *Proceedings of the Zoological Society of London,* 125:169–221.

1959. Ascidiacea. *Galathea Report,* 1:189–209.

1960. Ascidiacea. *Discovery Reports,* 30:1–159.

1962. Further Descriptions of South African Ascidians. *Annals of the South African Museum,* 46(7):113–221.

1964. Ascidiacea: Additional Material. *Galathea Report,* 7:59–62.

Monniot, C., et F. Monniot

1968. Les Ascidies de grande profondeurs récoltées par le le navire océanographique américain "Atlantis II." *Bulletin de l'Institut Océanographique, Monaco,* 67(1379):1–48.

1970. Les Ascidies des grandes profondeurs récoltées par les navires *Atlantis, Atlantis II* et *Chain* (2ème note). *Deep-Sea Research,* 17:317–336.

Monniot, F.

1965. Ascidies interstitielles des côtes d'Europe. *Mémoires du Muséum National d'Histoire Naturelle,* série A, 35:1–154.

In press. Les Ascidies des grandes profondeurs récoltées par les navires *Atlantis II* et *Chain* (3ème note). *Deep-Sea Research.*

Tokioka, T.

1953. *Ascidians of Sagami Bay Collected by His Majesty the Emperor of Japan.* Tokyo.

1967. Pacific Tunicata of the United States National Museum. *Bulletin of the United States National Museum,* 251:1–247.

Van Name, W. G.

1945. The North and South American Ascidians. *Bulletin of the American Museum of Natural History,* 84:1–476.

Weinsten, F.

1961. *Psammostyela delamarei* n. g., n. sp., Ascidie interstitielle des sables a Amphioxus. *Comptes Rendus de l'Academie des Sciences,* serie D, 252:1843–1844.

ECOLOGY OF MEIOFAUNA

Bengt-Owe Jansson

The "Umwelt" of the Interstitial Fauna

ABSTRACT

The biotic and abiotic parameters that are considered to be of greatest functional significance to the sense organs of interstitial animals are discussed. Such parameters include the surface of sand grains, pore and grain size, pore water, temperature, salinity, oxygen, detritus, light, and currents. The interaction of the parameters is discussed briefly.

Though living in the same environment ("Umgebung"), the pigeon and the tick in the same tree experience their habitat in quite different ways—the "Umwelt" of the bird is quite different from that of the arthropod. To exemplify this concept, stated by the German biologist Jackob von Uexküll, I shall tell the story of the cheated tick, based on the facts given by von Uxküll in his book of 1956.

Once upon a time there was a little female tick sitting in a tree high over the green pasture with grazing cattle. She waited and waited. All of a sudden she felt that wonderful smell of sweat, she loosened her grip and, landing on something hairy she crawled to the barest and warmest spot, pushed out her proboscis, and started to suck. When she was several times her original size she fell to the ground and her life cycle came to an end.

But she was not going to have any young because it was not a cow she had landed upon. It was the apparatus of a nasty ecologist who had walked under the tree with a plastic sheet, prepared with butyric acid and cattle hairs which covered a plastic tube filled with body-temperature water.

The "Umwelt" of that tick, the components of the environment that are really perceived, is not the richly colored and odorous pasture with flowers and cattle but the smell of butyric acid, releasing the fall reflex; the perception of hair, repelling the tick to the most naked area; the highest temperature of a warm-blooded animal, leading the tick to a blood vessel where the sucking reflex is released. The tick does not even react to the taste of the fluid, as it sucks blood and water with the same intensity. The "Umwelt" corresponds to "functional environment," the "Umbebung" to "generalized environment" of Platt and Griffiths (1965).

As ecologists we must measure those parameters that are the real components of the "Umwelt" of the organisms, thereby stimulating taxonomists and physiologists to obtain sufficient data on the sense organs and their function in the separate organisms. The present survey attempts to present the various components of the interstitial habitat along such lines.

Environmental Components

The Surface of the Sand Grains

Interstitial animals, moving over the proportionally vast surface areas of sand grains will naturally perceive many different properties of the internal surface, which is very great. Fenchel (1969) calculated the internal surface as $K(1/Md)$, where K is a constant dependent on geometrical packing and Md the median grain size of a sediment of equally large spheres. Thus, the internal surface of a sediment with a medium grain size of 300 μ, a surface of 1.0 cm^2, and a depth of 20 cm is about 0.1 m^2. Zobell and Anderson (1936) pointed out the enormous capacity of the sand for carrying bacteria, and the investigations of Meadows and Anderson (1966, 1968) showed the grain surfaces to be anal-

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ogous to "landscapes" with green hills of diatoms or blue-green algae and vast meadows of bacteria. Round (1965) studied the freshwater algal associations of sand grains; and Westheide (1968) made careful investigations on the quantitative distribution of bacteria and yeasts on a tidal beach in the North Sea. Both authors showed maxima of bacteria at the sand surface in the sandy mud flats and in the supralittoral zone but no correlation was found to either oxygen availability or organic content. In his work with marine microbenthos, Fenchel (1968) pointed out the great importance of the sessile diatoms as food for the ciliates. That the meiofauna can thrive on microbial populations utilizing soluble material was shown experimentally by McIntyre, Munro, and Steele (1970).

Jansson (1966b), in his study of the ecology of *Derocheilocaris remanei* Delamare and Chappuis, suggested the great importance of the bacteria as food for the interstitial fauna. This, confirmed by Gray in a series of important studies from 1966 to 1968, may also explain the possible contradiction of a rich fauna in samples with no visible organic content (Jansson, 1968; Pennak, 1942; Renaud-Debyser, 1963). The importance of the bacterial film was shown as a decisive factor for the metamorphosis of certain polychaetes (Wilson, 1955), archiannelids (Jägersten, 1940), and gastropods (Scheltema, 1961) but Gray showed that certain archiannelids were so specific in their preferences that they preferred sand inoculated with a certain species of bacteria. This certainly broadens the "Umwelt" of the interstitial fauna.

How the adsorbed ions on the sand grains are perceived by organisms is difficult to judge, as has been pointed out by Stowel (1927). The perception of ions by the organism may be a serious problem, especially in polluted areas. Dissolved organic matter may precipitate around the sand grains, especially at the supralittoral fringe, in a manner similar to the precipitation of organic matter around small air bubbles, as shown by Sutcliff, Baylor, and Menzel (1963).

The surface texture of the sand grains, whether smooth or rough, may also be of importance to interstitial fauna though it has not yet been investigated. The roundness of the grains will affect the size of the interstices.

The Interstices

PORE SIZE.—Pore space limits the size distribution of the inhabiting fauna. Fraser (1935) proposed the important concepts of "critical ratio of entrance" and "critical ratio of occupation," both of which were then used by Renaud-Debyser (1963) and Jansson (1967a). Measurements in the field of the diameter and area of pores in soil were made by Haarløv and Weis-Fogh (1953). By means of these measurements Haarløv (1959) showed how microarthropods were distributed in soils. Williams (in a paper in these proceedings) has shown, by imbedding techniques, that larger interstitial forms were restricted by the sizes of the pores, whereas smaller forms were more influenced by biological factors.

The movement of the nematode *Heterodera schachtii* Schmidt in soil of different pore sizes and water films was studied by Wallace (1958, 1959). This type of experiment should be repeated with interstitial animals.

GRAIN SIZE.—Granulometry has long been the method most frequently used by the ecologist to measure the pore size of sands, and it has led to an overestimation of grain size as a biological factor. Fraser (1935) and Graton and Fraser (1935) discussed the relation between grain size, porosity, and permeability. Prenant (1960) gave a detailed bibliography on granulometric literature. In a later work Prenant (1962) gave a method of translating frequency diagrams of the sizes into number of grains. This method then was used by Renaud-Debyser and Salvat (1963) in their study of the microfauna and macrofauna of intertidal beaches. A principal study of the determination of grain size was made by Morgans (1956). Much information on grain size distribution in the field is scattered in the vast taxonomical literature on interstitial fauna. Much of the literature is summarized in the reviews of Delamare Deboutteville (1960), Swedmark (1964), and Jansson (1967a). Following are examples of studies stressing a correlation between a certain animal group and grain size: foraminiferans, Blanc-Vernet (1958); cnidarians, Salvini Plawen (1966); turbellarians, Sterrer (1965); gastrotrichs, Schrom (1966); polychaetes, Soika (1955), Sourie (1957), Amoureux (1966); tardigrades, de Zio (1964) de Zio and Grimaldi (1964, 1966); crustaceans, Wells and Clark (1965); and several groups of limnopsammon, Tilzer (1968).

It is very difficult, however, to determine a relationship between grain size and animal distribution without controlling other important parameters. No correlation between grain size and the distribution of the fauna was found by Schmidt and Westheide (in press), who stressed the significance of other factors as being responsible for the faunal distributions.

In general, studies show maximum grain sizes in the vicinity of the water line and a successively decreasing coarseness of the sand landward. Beaches, however, can be rather homogeneous, as the tidal beach of Arcachon (Renaud-Debyser, 1963), the atidal Canet Plage in the Mediterranean (Delamare Deboutteville, 1960), and the atidal Simrishamn beach in the Baltic (Jansson, 1967a). The vertical distribution of the grain size may be quite different. Laterally (i.e., parallel to the water line), the sand appears to be more homogeneous.

The picture of the grain size frequency distribution of sediments is dependent on the number of different-size sieves used in the analysis, but more importantly it is dependent on the size of sample (Jansson, 1966a, 1967a). The sample size must always be related to the size of the animals. Sorting must also be determined, because the animals might react not to the sizes of the grains but to the size of the pores.

The correlation between the true sand fauna and their substrate was first stressed by Remane (1933). Locomotory behavior, termed "Stemmschlageln," was shown for numerous animals by Remane (1933). A recent analysis of the adaptive features of sand fauna was given by Ax (1966). Renaud-Debyser (1963) and Boaden (1962) used the experimental approach to show the correlation between grain size and animal distribution by inserting cylinders of graded sand into beach sand and analyzing the invasion of the fauna into the cylinders. Because other parameters were not controlled, the results of Renaud-Debyser and Boaden may not give the definite response to the space-restricting property of the sand. The same criticism can be made of the Puget Sound studies by Wieser (1959), who stressed the correlation between grain size distribution and occurrence of the animals. Husmann (1968) applied a "substrate organ" in his work with biological filters as biotope models. Husmann's device provides important data on the affinities of the interstitial freshwater fauna in conjunction with the simultaneous control of the chemistry of the interstitial water.

Laboratory experiments under controlled conditions have shown a definite correlation between grain size as a space-restricting measure and the occurrence of several animals. The enchytraeid *Marionina subterranea* (Knöllner) preferred sand of 125 to 500 μ (Jansson, 1966a). Three species of *Protodrilus*—*P. symbioticus* (Giard), *P. rubropharyngeus* Jägersten, and *P. hypoleucus* Armenante—chose 200 to 300, 500 to 1,000, and 250 to 500 μ respectively (Gray, 1966a,b, 1967a,b). Similarly, the harpacticoids *Parastenocaris vicesima* Kunz (Jansson, 1967b) and *Lepatastacus constrictus* Lang (Gray, 1968) preferred 150 to 250 and 246 to 500 μ grains respectively. These experiments surely reflect the types of locomotion of the experimental animals, because animals which move by peristalsis (e.g., *Aktedrilus monospermatecus* Knöllner) or by gliding (e.g., *Coelogynopora schulzii* Meixner) exhibit no preference for sand of a definite porosity (Jansson, 1967a).

Pore Water

Amount of pore water.—When pores are not totally filled with water, the water meniscus takes over the role as the space-restricting component. The amount of pore water is a primary requirement for interstitial life (Jansson, 1967a). Most studies deal with the capillarity and saturation of sand with different grain sizes rather than with the actual amount of pore water (Bruce, 1928; Wiszniewski, 1934, 1947; Pennak, 1940, 1942, 1951; Neel, 1948; Davant and Salvat, 1961; Ganapati and Rao, 1962; Ruttner-Kolisko, 1962; Callame, 1963).

The quantity of different grades of sand is the determining factor for the amount of pore water rather than the medium grain size (Fraser, 1935; Ruttner-Kolisko, 1962). Porosity is determined by both the coarseness and the sorting of sand. A superficial layer of sand may, therefore, contain more water than a deeper layer that is near the groundwater table (Jansson, 1967a; Rullier, 1957). The space available for the animals may be adequately determined from mean grain size, sorting, and water content of the different layers of sediment.

A correlation between the distribution of tardigrades and the amount of interstitial water was found by de Zio and Grimaldi (1964, 1966). Salvat (1964) divided a tidal beach into four zones in his work with sand isopods. In soil habitats Wallace (1959) studied the movement of eelworms in water films and found a strong correlation between the length of the worms, the amplitude of their "Stemm-schlageln," and the thickness of the water films. In Swedish sandy beaches Jansson (1968) showed a stratification of the fauna. The harpacticoids, being the group most sensitive to pore water, were limited by a water content of about 7 percent net weight. The harpacticoids, which dominated the deepest layers, were followed in abundance by turbellarians. The oligochaetes, which are able to live in sand with a very small content of water, occupied the top layers of sand. A similar limit of pore water for the harpacticoids can be calculated from the tables of Pennak (1942). This limit for harpacticoids was confirmed by Enckell (1968) in his studies of meiofauna from Swedish freshwater beaches. A landward submergence of beaches because of decreasing amounts of pore water in the upper layers of sand was reported by Pennak (1940), Ganapati and Rao (1962), and Schmidt (1969). The abundance of animals decreased towards the groundwater table more rapidly in the atidal beaches (Fenchel, Jansson, and von Thun, 1967; Jansson, 1968; Enckell, 1968; Pennak, 1940) than in tidal beaches (Renaud-Debyser, 1963; Ganapati and Rao, 1962; Schmidt, 1968). This may be due to greater oxygen availability in the tidal groundwater resulting from tidal movements (Emery and Foster, 1948; Davant and Salvat, 1961; Renaud-Debyser, 1963).

Temperature of pore water.—Temperature affects both sand and water (Kinne, 1963). Detailed temperature measurements from sandy beaches are rather scarce. Pennak (1940), Wiszniewski (1934), Angelier (1953), and Ruttner-Kolisko (1953, 1954) have given measurements from freshwater beaches. Linke (1937) gave values for the heat conductivity of sand containing different amounts of mud. McIntyre (1963) reported very high temperatures from New Zealand beaches, and Swedmark (1955) studied the temperature variations in a tidal beach at Roscoff during different intensities of insolation. Annual variations of temperature in beaches were measured at Arcachon by Renaud-Debyser (1963), in California by Johnson (1965), and on the island of Sylt, North Sea, by Schmidt (1968). The influence of air and seawater temperatures upon sand temperatures was shown by Salvat (1967). A detailed analysis of the diurnal and seasonal temperature variations at different depths in a Baltic sandy beach was made by Jansson (1967b). These studies and the investigations of others support the following generalizations for temperatures of sandy beaches of the boreal region.

The seasonal minima occur during the winter, when frost often occurs to 1 m depth in northern countries. In the spring diurnal, temperature often fluctuates as much as 40 degrees. The highest temperatures are found during the summer, when the temperature of the sand, even in temperate areas, may reach values of 50° C. Vertical stratification is very pronounced, and a decrease in temperature of more than 10° C within the upper 2 cm of sand is by no means uncommon. In the autumn, in northern countries, temperatures decrease and night frosts appear, resulting in high diurnal ranges. Annual ranges of temperature taken in the sand of a Swedish sandy beach were 49.7° C for the surface, 27° C for 10 cm depth, and 18.1° C for 70 cm depth (Jansson, 1967d). The more seaward parts of the beach showed smaller amplitudes of temperature. Higher values may be found at higher altitudes during the summer; for example, 55° C at the sand surface on New Zealand beaches (McIntyre, 1963).

Interstitial fauna is subjected to great temperature variations both in space and time. In northern countries interstitial fauna may be captured in frozen sand for long periods but evidently may thaw out and show a high percent survival (Barnett, 1968; Jansson, 1968). Specimens of *Protodrilus symbioticus* survived negative temperatures without ice formation (Gray, 1965). Schmidt (1968) considered temperatures of 5° to 10° C as the lower limit for the spawning of interstitial fauna. This temperature limit for spawning resulted in a minimum of animals in the spring and a maximum in the autumn. Seasonal fluctuations of interstitial fauna also were found by Brenowitz (in press) in Long Island beaches. As was shown by Renaud-

Debyser (1963) for the Arcachon beaches and by Schmidt (1969) for the beaches of Sylt, the fauna was abundant throughout the year but migrated downward during the coldest period.

The temperature tolerance of several turbellarians, oligochaetes, and harpacticoids was investigated by Jansson (1966a, 1967b, 1968). Most of the species survived for three or four days when kept in their optimal salinities. Exceptions were the turbellarian *Haplovejdovskya subterranea* Delamare Deboutteville and the enchytraeid *Marionina subterranea,* both of which survived only two to three hours, and the harpacticoid *Parastenocaris phyllura* Kunz, which survived nearly one week.

A well-established horizontal and vertical gradient of temperature in the beach and a sensitivity to high temperatures of the organisms were shown in experiments with *Marionina subterranea* by Jansson (1966a) and with *Protodrilus symbioticus* by Gray (1965). More of these kinds of experiments should be attempted.

Salinity of pore water.—The significance of salinity for aquatic organisms was summarized for numerous animals in various habitats (Kinne, 1964a–c, 1966). Salinity records from sandy beaches are presented in many taxonomic papers but more detailed studies of salinity are few. In atidal beaches the salinity decreases landward (Brinck, Dahl, and Wiser, 1955; Ax, 1954; Münch and Petzold, 1956; Jansson, 1966a,b, 1967b,d, 1968; Fenchel, Jansson, and von Thun, 1967). In tidal beaches a landward decree of salinity is affected by the tidal movements (Bruce, 1928; Linke, 1937; Sourie, 1957; Ganapati and Rao, 1962; Davant and Salvat, 1961; Renaud-Debyser, 1963; Govindankutty and Nair, 1966; Johnson, 1967; Salvat, 1967; Schmidt, 1968). The surface layers of the submerged part of the beach may show hypersalinites because of evaporation (Gerlach, 1954; McIntyre, 1963; Jansson, 1967d; Barnett, 1968). The effect of rain is minimal in temperate, sandy beaches (Linke, 1937) but more important in mud flats (Barnett, 1968), freshwater beaches (Pennak, 1951), and tropical beaches (Ganapati and Rao, 1962. When the overflowing water was hyposaline the interaction between the interstitial water and an overflowing water of different salinity was minimal (Reid, 1930; Callame, 1963). Jansson (1967d) found that the influence of intermediate waves on the salinity of water-filled interstices of beach sands was small. Complex interactions between seawater, groundwater, and rain anomalies may occur in the beach with "tongues" of saltier water in intermediate layers (Fenchel, Jansson, and von Thun, 1967).

Wide fluctuations in salinity exert a great stress upon interstitital organisms, as shown by simple tolerance experiments on ciliates (Ax and Ax, 1954), turbellarians (Jansson, 1968), archiannelids (Boaden, 1962, 1963; Gray, 1966c), and crustaceans (Jansson, 1966a,b, 1967b, 1968). Many interstitial animals, including the mystacocarid *Derocheilocaris remanei* and the enchytraeid *Marionina southerni* (Cernosvitov), have a physiological tolerance of salinity ranges of more than 15 ppt (Jansson, 1966b, 1968). Others, including the harpacticoids *Paraleptastacus spinicauda* (T. and A Scott), *Parastenocaris vicesima* Klie and *P. phyllura* Kiefer, have a rather restricted range of less than 7.5 ppt (Jansson 1967d, 1968). Some animals (e.g., *Marionina southerni* and *Schizopera baltica* Lang) may display a strong preference for narrow salinity ranges in spite of their euryhalinity (Jansson, 1968). Specimens of *Protodrilus symbioticus,* however, showed no preference reaction to salinity (Gray, 1966c).

The ecological tolerances may not always coincide with the physiological tolerances. *Paraleptastacus spinicauda, Marionina subterranea,* and *M. preclitellochaeta* Nielsen and Christensen show a wide geographical distribution (Noodt, 1957; Remane, 1958; Lasserre, 1966, 1967) but a small physiological tolerance (Jansson, 1962, 1968). This raises the question of nongenetic and genetic adaptation (Kinne, 1964b). Reuter (1961) has shown genetic adaptation to different salinities for three populations of the turbellarian *Gyratirix hermaphroditus* (Ehrenberg).

Oxygen in pore water.—The dissolved oxygen (DO) content of interstitial sediments has been little studied. Most oxygen values refer to tidal beaches (Ganapati and Rao, 1962; Renaud-Debyser, 1963; Amoureux, 1963; Brafield, 1964, 1965), and few oxygen determinations have been taken from atidal beaches (Pennak, 1940; Angelier, 1953; Münch and Petzold, 1956; Ruttner-Kolisko, 1954, 1962). The oxygen valves for tidal sand flats at 5 to 15 cm depth often are below 0.5 ml/liter but vary with grain size, drainage, amount of organic matter, and slope. Atidal beaches have oxygen values comparable to those of tidal beaches with good drainage. Severe fluctuations of oxygen, pH, temperature, and salinity have been reported in tidal pools of a sandy mud flat in the Elbe estuary (Kühl, 1964). The changes were correlated with the occurrence of benthic diatoms.

Stressing the fact that interstitial organisms perceive oxygen not as concentration but as availability, Jansson (1966a,b) introduced a method from soil science to marine biology, namely, the oxygen diffusion rate (ODR). This measure, expressed as $g0_2/cm_2$ electrode surface/minute, incorporates not only oxygen concentration but also temperature, porosity, and interstitial water flow. Therefore, the ODR constitutes a more important ecological measure of the oxygen conditions than DO. The distributions of ODR both in atidal (Jansson 1966a,b; 1967b,c; 1968; Fenchel and Jansson, 1966; Fenchel, Jansson, and von Thun, 1967; Enckell, 1968) and tidal (Westheide, 1968) beaches show low values in and below the groundwater table, high values in intermediate layers, and low values at the sand surface. The latter are sometimes artifacts, caused by the small amounts of interstitial water present which are not sufficient to totally moisten the electrode. The somewhat higher values of oxygen in the groundwater of tidal beaches are explained by the better ventilation due to tidal movements (Schmidt, 1968). The direct effect of waves upon the ODR has been shown by both field measurements and laboratory experiments (Jansson, 1967c).

A correlation between the oxygen content of interstitial water and the distribution of interstitial fauna was found by Pennak (1940), Jansson (1966b, 1967b,c), Fenchel and Jansson (1966), and Fenchel, Jansson, and von Thun (1967). Very little is known of the response of the interstitial animals to oxygen. Gray (1966c, 1967a) found that *Protodrilus symbioticus* and *P. rubropharyngeus* moved towards the highest oxygen concentration when placed in an oxygen gradient. The lower ODR limit for the harpacticoid *Parastenocaris vicesima* was found by Jansson (1967b) to be around $1g^{-7}$ cm^{-2}min^{-1}. This harpacticoid was absent at the low values in the field, as were harpacticoids investigated by Enckell (1968) in a Swedish freshwater beach. The enchytraeids *Marionina achaeta* Lasserre and *M. spicula* (Leuckart) colonize different parts of the beach because they have different respiration rates at high temperatures (Lasserre, in press).

Detritus in pore water.—Animals perceive detritus partly as food and partly as a space-restricting medium. Besides the important work of Perkins (1958), few investigations have been carried out concerning the food of interstitial fauna. Bacteria have been mentioned previously as an important food resource. In his comprehensive study of the harpacticoids of the German coasts Noodt (1957) mentioned detritus as a frequent food. The importance of detritus for the total fauna was stressed by Remane and Schultz (1934), Remane (1952), and Renaud-Debyser and Salvat (1963); however, no correlation between the amount of detritus and the interstitial fauna was found by Ganapati and Rao (1962) or by Renaud-Debyser (1963). The suggestion by Jansson (1966a) that the amount of bacteria in the beach is not necessarily correlated to the detritus factor was supported by Westheide (1968).

Detritus often is irregularly distributed within the beach (Jansson, 1967a,b, 1968; Schmidt, 1968), but it may show a maximum in the sand flats (Westheide, 1968) or in the back-shore (Pennak, 1940; Salvat, 1967). Sometimes dark, concentrated bands of decaying organic material is found in the sand, thus excluding most interstitial life (Jansson, 1966a, 1967a,b). The finer particles may show an increase towards the groundwater level (Westheide, 1968).

Increased organic material favors increased bacterial activity and, as a consequence, the ODR values and the redox potential (Eh) fall. Under anaerobic conditions H_2S formation will occur, eliminating much of the meiofauna, which usually concentrates in the upper layers (Fenchel and Jansson, 1966). Elimination of meiofauna by H_2S also has been recorded in freshwater beaches by Enckell (1968). The dynamics of detritus-rich sediments are exhaustively treated in the important study of Fenchel (1969).

Other parameters in pore water—Because the maximum penetration of light into the sand is 5 to 15 mm (Neel, 1948; Pennak, 1951; Gray, 1966b), few animals are subjected to strong insolation. The archiannelids *Trilobodrilus heideri* Remane, *Protodrilus symbioticus,* and *P. rubropharyngeus,* however, show a negative klinokinesis (Boaden, 1963; Gray 1966b, 1967a). A photonegative response also is exhibited by the harpacticoids *Schizopera baltica* and *Nitochra fallaciosa* Klie f. *baltica* Lang and *Leptastacus constrictus* (Jansson, 1968; Gray, 1968).

Currents are a common phenomenon of tidal beaches. A rheoactive behavior has been found in *Trilobodrilus heideri* (Boaden, 1963). Boaden (1968) showed the negative influence of turbulence upon interstitial animals. Similarly, the seaward limit for the distribution of *Derocheilocaris remanei* in Canet Plage was found to be controlled by turbulence (Jansson, 1966b). Tilzer (1968) found that the interstitial fauna of mountain streams migrated better along the water flow than against it, although examples of upstream migration also were noted.

Boaden (1963) demonstrated gregarious behavior by *Trilobodrilus heideri.* Gray (1967a) showed that *Ptotodrilus rubropharyngeus* is attracted to members of the same species and to sand recently inhabited by members of the same species. Similarly, Boaden and Erwin (in press) found that *Protodrilus symbioticus* produced a substance that made sand unattractive to the gastrotrich *Turbanella hyalina* Schultze.

Negative geotaxis was shown for *Protodrilus symbioticus, P. rubropharyngeus,* and *Leptastacus constrictus* by Gray (1966a, 1967a, 1968).

Interaction Between Parameters

This presentation is not totally adequate, as the different parameters of the interstitial animals' "Umwelt" do not interact with each other or upon the animals singly but in aggregate. Often, several parameters may dominate in a given situation or act synergistically. The sizes and shapes of the sand grains indirectly affect the oxygen availability, which, in turn, determines the aeration of the interstitial water (Jansson, 1967a). If 30 percent of the sand consists of grains of 250 μ the oxygen drops to near zero (Ruttner-Kolisko, 1961). A close correlation between oxygen content and grain size also was found by Brafield (1965). Jansson (1966b) showed high ODR values in sand of 200 to 300 μ. Wieser (1959) showed from field studies that "the critical grain size" of 200 μ was the lower limit of grain sizes for the occurrence of interstitial animals. When tested in the laboratory for their space-restricting property, however, 200-μ sands could not be shown to affect the animals (Jansson, 1967a).

It has been proved clearly that animals react to gradients of temperature, salinity, oxygen, and light and that they perceive pore space, gravity, currents, and chemical substances from their own species. The aggregate and intensities of the various parameters will determine the field distribution of interstitial fauna. The patchy distribution of the harpacticoid *Parastenocaris vicesima* was attributed to its preference for salinities below 5 ppt, sensitivity to ODR values below $\lg^{-7}$ $cm^{-2}min^{-1}$, and preference for grain sizes between 250 and 125 μ (Jansson, 1967b).

But preferences may change. As for certain terrestrial invertebrates, the intensity of a certain factor may displace the preference zone of another. Salinity preference may change if the animal is able to adapt to other salinities. Efforts to displace the preference zone of the tubificid *Aktedrilus monospermatecus,* however, were in vain (Jansson, 1962). The euryhaline enchytraeid *Marionina southerni* was shown to have a narrow preference zone, but this could be affected by keeping the animals in higher salinities for more than eleven days, as shown in Figure 1*a* (Elmgren and Jansson, unpublished).

Salinity may be perceived by animals not as a salt concentration but as osmotic pressure. Oxygen availability also is involved, because osmotic work of an organism requires oxygen. The preference zone for three groups of specimens of *Marionina southerni* from the same population was found to be clearly dependent upon temperature (Figure 1*b*). While the animals held at 15° C showed distinct preference for neither 1 nor 5 ppt, those held at 5° C clearly preferred 1 ppt and those held at 30° C preferred 5 ppt (Elmgren and Jansson).

One must not only know the ranges of the different environmental parameters and how the animals react to them but also the intensities to which the animals have become acclimated in the field.

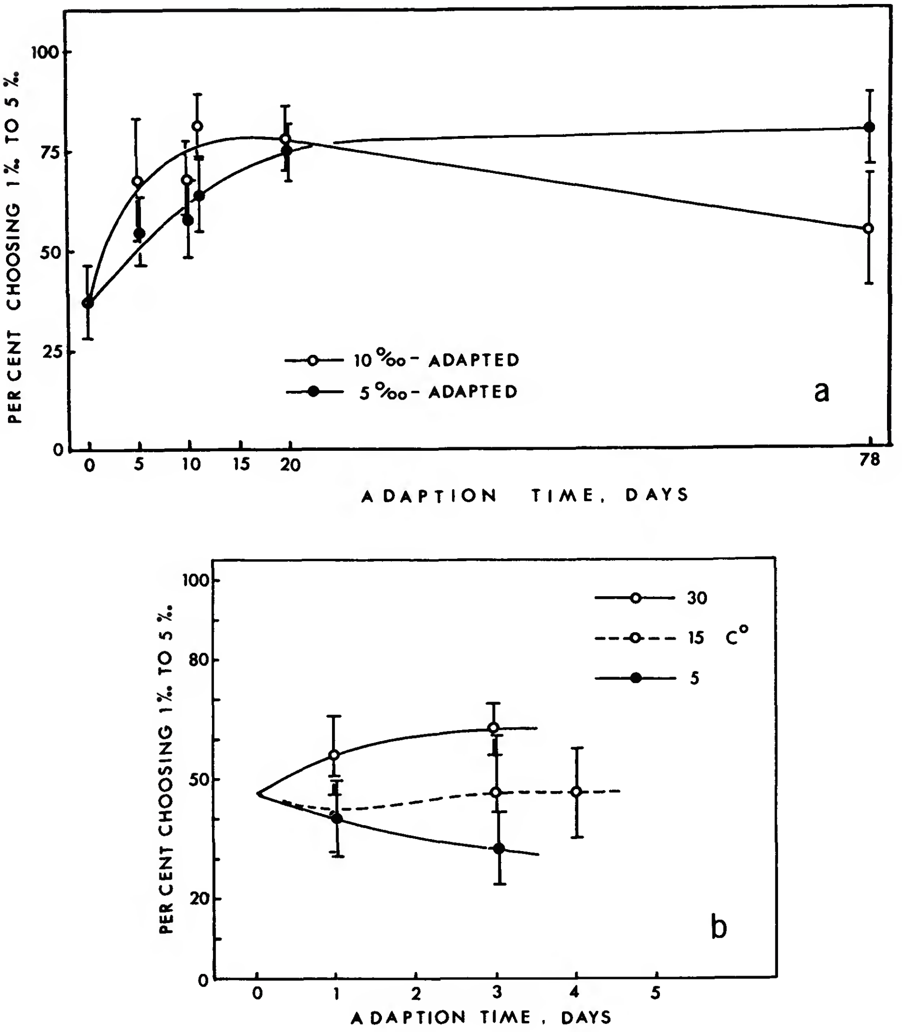

FIGURE 1.—Successive displacement of salinity preference of the enchytraeid *Marionina southerni*: *a*, from 7 ppt after adaption to different salinities at 15° C; *b*, after adaption to different temperatures in 6.5 ppt. Vertical bars indicate 95 percent confidence intervals.

Literature Cited

Amoureux, L.

1963. Étude des teneurs en oxygène dans les eaux interstitielles de l'Aber de Roscoff. *Cahiers de Biologie Marine*, 4:22–32.

1966. Étude bionomique et écologique de quelques Annélides Polychètes des sables intertideaux des côtes ouest de la France. *Archives de Zoologie Expérimentale et Générale*, 107:1–218.

Angelier, E.

1953. Recherches écologiques et biogéographiques sur la faune des sables submergés. *Archives de Zoologie Expérimentale et Générale*, 90:37–161.

Ax, P.

1954. Die Turbellarienfauna des Küstengrundwassers am Finnischen Meerbusen. *Acta Zoologica Fennica*, 81:1–54.

1966. Die Bedeutung der interstitiellen Sandfauna für allgemeine Probleme der Systematik, Ökologie und Biologie. *Veröffentlichungen des Instituts für Meersforschung in Bremerhaven*, Sonderband 2: 15–65.

Ax, P., and R. Ax

1960. Experimentelle Untersuchungen über die Saltzgehaltstoleranz von Ciliaten aus dem Brackwasser und Süsswasser. *Biologisches Zentralblatt,* 79:7–31.

Barnett, P. R. O.

1968. Distribution and Ecology of Harpacticoid Copepods of an Intertidal Mudflat. *Internationale Revue der gesamten Hydrobiologie,* 53:177–209.

Blanc-Vernet, L.

1958. Les milieux sédimentaires littoreaux de la Provence occidentale (côte rocheuse). Relations entre la microfaune et la granulometrie du sédiment. *Bulletin de l'Institut Océanographique, Monaco,* 1112:1–45.

Boaden, P. J. S.

1962. Colonization of Graded Sand by an Interstitial Fauna. *Cahiers de Biologie Marine,* 3:245–248.

1963. Behaviour and Distribution of the Archiannelid *Trilobodrilus heideri. Journal of the Marine Biological Association of the United Kingdom,* 43: 239–250.

1968. Water Movement—A Dominant Factor in Interstitial Ecology. *Sarsia,* 34:125–136.

Boaden, P. J. S., and D. G. Erwin

In press. *Turbanelle hyalina* versus *Protodrilus symbioticus:* A Study in Interstitial Ecology. Proceedings of the Third European Marine Biology Symposium. *Vie et Milieu,* supplement 20.

Brafield, A. E.

1964. The Oxygen Content of Interstitial Water in Sandy Shores. *Journal of Animal Ecology,* 33:97–116.

1965. Quelques facteurs affectant la teneur en oxygène des eaux interstitielles littorales. *Vie et Milieu,* 16:889–897.

Brenowitz, A. H.

In press. Ecology of the Interstitial Fauna on Selected Long Island Beaches. Proceedings of the Third European Marine Biology Symposium. *Vie et Milieu,* supplement 20.

Brinck, P.; E. Dahl; and W. Wieser

1955. On the Littoral Subsoil Fauna of the Simrishman Beach in Eastern Scania. *Kungliga Fysiografiska Sällskapets i Lund Förhandlingar,* 25:109–129.

Bruce, J. R.

1928. Physical Factors on the Sandy Beach. Part 1. Tidal, Climatic, and Edaphic. *Journal of the Marine Biological Association of the United Kingdom,* 15:535–552.

Callame, B.

1963. Le milieu interstitiel dans les sédiments sableaux intercotidaux. *Bulletin de l'Institut Océanographique, Monaco,* 60(1271):5–30.

Davant, P., and B. Salvat

1961. Recherches écologiques sur la macrofaune intercotidale du bassin d'Arcachon. I. Le milieu physique. *Vie et Milieu,* 12:405–471.

Delamare Deboutteville, C.

1960. *Biologie des eaux souterraines littorales et continentales.* 740 pages. Paris; Hermann.

Emery, K. O., and J. F. Foster

1948. Water Tables in Marine Beaches. *Journal of Marine Research,* 7:644–654.

Enckell, P. H.

1968. Oxygen Availability and Microdistribution of Interstitial Mesofauna in Swedish Fresh-Water Sandy Beaches. *Oikos,* 19:271–291.

Fenchel, T.

1968. The Ecology of Marine Microbenthos. II. The Food of Marine Benthic Ciliates. *Ophelia,* 5:73–121.

1969. The Ecology of Marine Microbenthos. IV. Structure and Function of the Benthic Ecosystem, Its Chemical and Physical Factors and the Microfauna Communities with Special Reference to the Ciliated Protozoa. *Ophelia,* 6:1–182.

Fenchel, T., and B. O. Jansson

1966. On the Vertical Distributon of the Microfauna in the Sediments of a Brackish-Water Beach. *Ophelia,* 3:161–177.

Fenchel, T.; B. O. Jansson; and W. von Thun

1967. Vertical and Horizontal Distribution of the Metazoan Microfauna and of some Physical Factors in a Sandy Beach in the Northern Part of the Øresund. *Ophelia,* 4:227–243.

Fraser, H. J.

1935. Experimental Study of the Porosity and Permeability of Clastic Sediments. *Journal of Geology,* 43:910–1010.

Ganapati, P. N., and G. C. Rao

1962. Ecology of the Interstitial Fauna Inhabiting the Sandy Beaches of Waltair Coast. *Journal of the Marine Biological Association of India,* 4:44–57.

Gerlach, S. A

1954. Das Supralitoral der sandigen Meeresküsten als Lebensraum einer Mikrofauna. *Kieler Meeresforschungen,* 10:121–129.

Govindankutty, A. G., and N. B. Nair

1966. Preliminary Observations on the Interstitial Fauna of South-West Coast of India. *Hydrobiologia,* 28: 101–122.

Graton, L. C., and H. J. Fraser

1935. Systematic Packing of Spheres—with Particular Relation to Porosity and Permeability. *Journal of Geology,* 43:785–909.

Gray, J. S.

1965. The Behaviour of *Protodrilus symbioticus* (Giard) in Temperature Gradients. *Journal of Animal Ecology,* 34:455–461.

1966a. Selection of Sands by *Protodrilus symbioticus* (Giard). *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:105–116.

1966b. The Response of *Protodrilus symbioticus* (Giard) (Archiannelida) to Light. *Journal of Animal Ecology,* 35:55–64.

1966c. Factors Controlling the Localizations of Populations of *Protodrilus symbioticus* (Giard). *Journal of Animal Ecology,* 35:435–442.

1966d. The Attractive Factor of Intertidal Sands to *Protodrilus symbioticus*. *Journal of the Marine Biological Association of the United Kingdom,* 46:627–645.

1967a. Substrate Selection by the Archiannelid *Protodrilus rubropharyngeus*. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 15:253–269.

1967b. Substrate Selection by the Archiannelid *Protodrilus hypoleucus* Armenante. *Journal of Experimental Marine Biology and Ecology,* 1:47–54.

1968. An Experimental Approach to the Ecology of the Harpacticoid *Leptastacus constrictus* Lang. *Journal of Experimental Marine Biology and Ecology,* 2:278–292.

Haarløv, N.

1959. The Diameters of Cavities (>0.1 mm) in the Soil and the Area of Their Surrounding Walls, Seen in Relation to the Micro-Arthropods Present. *Proceedings of the XVth International Congress of Zoology,* section 4, pages 360–363.

Haarløv, N., and T. Weis-Fogh

1953. A Microscopical Technique for Studying the Undisturbed Texture of Soils. *Oikos,* 4:44–57.

Husmann, S.

1968. Langsamfilter als Biotopmodelle der experimentalökologischen Grundwasserforschung. *Gewässer und Abwässer,* 46:20–49.

Jägersten, G.

1940. Die Abhängigkeit der Metamorphose vom Substrat des Biotops bei *Protodrilus*. *Arkiv för Zoologi,* 32(17):1–12.

Jansson, B. O.

1962. Salinity Resistance and Salinity Preference of Two Oligochaetes, *Aktedrilus monospermatecus* Knöllner and *Marionina preclitellochaeta* n. sp. from the Interstitial Fauna of Marine Sandy Beaches. *Oikos,* 13:293–305.

1966a. Microdistribution of Factors and Fauna in Marine Sandy Beaches. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sondeband 2:77–86.

1966b. On the Ecology of *Derocheilocaris remanei* Delamare and Chappius (Crustacea, Mystacocarida). *Vie et Milieu,* 17:143–186.

1967a. The Significance of Grain Size and Pore Water Content for the Interstitial Fauna of Sandy Beaches. *Oikos,* 18:311–322.

1967b. The Importance of Tolerance and Preference Experiments for the Interpretation of Mesopsammon Field Distributions. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 15:41–58.

1967c. The Availability of Oxygen for the Interstitial Fauna of Sandy Beaches. *Journal of Experimental Marine Biology and Ecology,* 1:123–143.

1967d. Diurnal and Annual Variations of Temperature and Salinity of Interstitial Water in Sandy Beaches. *Ophelia,* 4:173–201.

1968. Quantitative and Experimental Studies of the Interstitial Fauna in Four Swedish Sandy Beaches. *Ophelia,* 5:1–71.

Johnson, R. G.

1965. Temperature Variation in the Infaunal Environment of a Sand Flat. *Limnology and Oceanography,* 10:114–120.

1967. Salinity of Interstitial Water in a Sandy Beach. *Limnology and Oceanography,* 12:1–7.

Kinne, O.

1963. The Effects of Temperature and Salinity on Marine and Brackish Water Animals. I. Temperature. *Oceanography and Marine Biology, Annual Review,* 1:301–340.

1964a. The Effects of Temperature and Salinity on Marine and Brackish Water Animals. II. Salinity and Temperature Salinity Combinations. *Oceanography and Marine Biology, Annual Review,* 2:281–339.

1964b. Non-Genetic Adaptation to Temperature and Salinity. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 9:433–458.

1964c. Physiologische und ökologische Aspekte des Lebens in Ästuarien. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 11:131–156.

1966. Physiological Aspects of Animal Life in Estuaries with Special Reference to Salinity. *Netherlands Journal of Sea Research,* 3:222–244.

Kühl, H.

1964. Über die Schwankungen der abiotischen Faktoren in der Elbmündung bei Cuxhaven. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 10:202–216.

Lasserre, P.

1966. Oligochètes marins des côtes de France. I. Bassin d'Arcachon: Systématique. *Cahiers de Biologie Marine,* 7:295–317.

1967. Oligochètes marins des côtes de France. II. Roscoff, Penpoull, Étangs saumâtres de Concarneau: Systématique, Écologie. *Cahiers de Biologie Marine,* 8:273–293.

In press. Données ecophysiologiques sur la repartition d'oligochètes meiobenthiques. Proceedings of the Third European Marine Biology Symposium. *Vie et Milieu,* supplement 20.

Linke, O.

1937. Die Biota des Jadebusenwattes. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 1:301–348.

McIntyre, A. D.; A. L. S. Munro; and J. H. Steele

1970. Energy Flow in a Sand Ecosystem. In J. H. Steele, editor, *Marine Food Chains,* pages 19–31. Edinburgh: Oliver and Boyd.

McIntyre, R. J.

1963. The Supralittoral Fringe of New Zealand Beaches. *Transactions of the Royal Society of New Zealand,* 1:89–103.

Meadows, P. S., and J. G. Anderson

1966. Micro-Organisms Attached to Marine and Freshwater Sand Grains. *Nature,* 212:1059–1060.

1968. Micro-Organisms Attached to Marine Sand Grains. *Journal of the Marine Biological Association of the United Kingdom,* 48:161–175.

Morgans, J. F. C.

1956. Notes on the Analysis of Shallow-Water Soft Substrata. *Journal of Animal Ecology,* 25:367–387.

Münch, H. D., and H. G. Petzold

1956. Zur Fauna des Küstengrundwassers der Insel Hiddensee. I. Chemischphysikalische Verhältnisse und ihr Einfluss auf die Grundwasserfauna. *Wissenschaftliche Zeitschrift der Ernest Moritz Arndt-Universität Greifswald, Matematisch-naturwissenschaftliche Reihe,* 5:413–429.

Neel, J. K.

1948. A Limnological Investigation of the Psammon in Douglas Lake, Michigan, with Especial Reference to Shoal and Shoreline Dynamics. *Transactions of the American Microscopical Society,* 67:1–53.

Noodt, W.

1957. Zur Ökologie der Harpacticoidea (Crust. Cop.) des Eulitorals der deutschen Meeresküste und der angrenzenden Brackgewässer. *Zeitschrift für Morphologie und Ökologie der Tiere,* 46:149–242.

Pennak, R. W.

1940. Ecology of the Microscopic Metazoa Inhabiting the Sandy Beaches of some Wisconsin Lakes. *Ecological Monographs,* 10:537–615.

1942. Ecology of some Copepods Inhabiting Intertidal Beaches near Woods Hole, Massachusetts. *Ecology,* 23:446–456.

1951. Comparative Ecology of the Interstitial Fauna of Fresh-Water and Marine Beaches. *Année Biologique,* 27:449–480.

Perkins, E. J.

1958. The Food Relationships of the Microbenthos, with Particular Reference to That Found at Whitstable, Kent. *Annals and Magazine of Natural History,* series 3, 1:64–77.

Platt, R. B., and J. Griffiths

1965. Environmental Measurement and Interpretation. 235 pages. New York: Reinhold.

Prenant, M.

1960. Études écologiques sur les sables intercôtideaux. I. Questions de méthode granulometrique. Application à trois anses de la baie de Quiberon. *Cahiers de Biologie Marine,* 1:295–340.

1962. Fauna des plages marines et granulometrie des sediments. *Bulletin de la Societe Zoologique de France,* 84:412–424.

Reid, D. M.

1930. Salinity Interchange Between Sea-Water in Sand and Overflowing Fresh-Water at Low Tide. *Journal of the Marine Biological Association of the United Kingdom,* 16:609–614.

Remane, A.

1933. Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. *Wissenschaftliche Meeresuntersuchungen,* 21:161–221.

1952. Die Besiedelung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. *Zoologischer Anzeiger,* Supplementband 16:327–359.

1958. Ökologie des Brackwassers. *Die Binnengewässer,* 22:1–216.

Remane, A., and E. Schulz

1934. Das Küstengrundwasser als Lebensraum. *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein,* 20:399–408.

Renaud-Debyser, J.

1959. Contribution à l'étude de la fauna interstitielle du Bassin d'Arcachon. *Proceedings of the XVth International Congress of Zoology,* section 4, pages 323–326.

1963. Recherches écologiques sur la faune interstitielle des sables. (Bassin d'Arcachon, Ile de Bimini, Bahamas). *Vie et Milieu,* supplement, 15:1–157.

Renaud-Debyser, J., and B. Salvat

1963. Élements de prospérité des biotopes des sédiments meubles intertidaux et écologie de leurs populations en microfaune et macrofaune. *Vie et Milieu,* 14:463–550.

Reuter, M.

1961. Untersuchungen über Rassenbildung bei *Gyratrix hermaphroditus* (Turbellaria Neorhabdocoela). *Acta Zoologica Fennica,* 100:1–32.

Round, F. E.

1965. The Epipsammon; A Relatively Unknown Freshwater Algal Association. *British Phycological Bulletin,* 2:456–462.

Rullier, F.

1957. Teneur en air et en eau interstitiels des sables marins et son influence sur les conditions d'habitat. *Comptes Rendus de l'Académie des Sciences,* series D, 245:936–938.

Ruttner-Kolisko, A.

1953. Psammonstudien. I. Das Psammon des Torneträsk in Schwedisch-Lappland. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse,* 162:129–161.

1954. Psammonstudien. II. Das Psammon des Erken in Mittelschweden. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse,* 163:301–324.

1961. Biotop und Biozönose des Sandufers einiger österreichischer Flüsse. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie,* 14:362–368.

1962. Porenraum und kapillare Wasserströmung im Limnopsammal, ein Beispiel für die Bedeutung verlangsamter Strömung. *Schweizerische Zeitschrift für Hydrologie,* 24:444–458.

Salvat, B.

1964. Les conditions hydrodynamiques interstitielles des sédiments meubles intertidaux et la répartition verticale de la faune endogée. *Comptes Rendus de l'Académie des Sciences,* series D., 259:1576–1579.

1967. La macrofaune carcinologique endogée des sédiments meubles intertideaux (Tanaidacés, Isopodes et Amphipodes), éthologie, bionomie, et cycle biologique. *Mémoires du Muséum National d'Historie Naturelle,* series A, 45:1–275.

Salvini Plawen, L.

1966. Zur Kenntnis der Cnidaria des nordadriatischen Mesopsammon. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:165–186.

Scheltema, R. S.

1961. Metamorphosis of the Veliger Larvae of *Nassarius obsoletus* (Gastropoda) in Response to Bottom Sediment. *Biological Bulletin,* 120:92–109.

Schmidt, P.

1968. Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrand der Nordseeinsel Sylt. I. Faktorengefüge und biologische Gliederung des Lebensraumes. *Internationale Revue der gesamten Hydrobiologie,* 53:723–779.

1969. Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrand der Nordsee-Insel Sylt. II. Quantitative Verteilung und Populationsdynamik einzelner Arten. *Internationale Revue der gesamten Hydrobiologie,* 54: 95–174.

Schmidt, P., and W. Westheide

In press. Verteilung von Mikrofauna und Mikroflora in einem Strand der Nordsee-Insel Sylt. Proceedings of the Third European Marine Biology Symposium. *Vie et Milieu,* supplement 20.

Schrom, H.

1966. Verteilung einiger Gastrotrichen im oberen Eulitoral eines nordadriatischen Sandstrandes. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:95–103.

Soika, A. G.

1955. Studi di ecologia e di biogeografia. XIII. Ricerche sull'ecologia e sul popolamento della zona intercotidale delle spiagge di sabbia fina. *Bollettino del Museo Civico di Storia Naturale di Venezia,* 8:1–151.

Sourie, R.

1957. Étude écologiques des plages de la côte sénégalaise aux environs de Dakar. (Macrofaune). *Annales de l'École Supérieure des Sciences, Dakar,* 3:1–110.

Sterrer, W.

1965. Zur Ökologie der Turbellarien eines südfinnischen Sandstrandes. *Botanica Gothoburgensia,* 3:211–219.

Stowell, F. P.

1927. The Adsorption of Ions from Sea-Water by Sand. *Journal of the Marine Biological Association of the United Kingdom,* 14:955–966.

Sutcliff, W. H.; E. R. Baylor; and D. W. Menzel

1963. Sea Surface Chemistry and Langmuir Circulation. *Deep-Sea Research,* 10:233–243.

Swedmark, B.

1955. Recherches sur la morphologie, le développement et la biologie de *Psammodrilus balanoglossoides,* Polychète sédentaire de la microfauna des sables. *Archives de Zoologie Expérimentale et Générale,* 92:141–220.

1964. The Interstitial Fauna of Marine Sand. *Biological Reviews,* 39:1–42.

Tilzer, M.

1968. Zur Ökologie und Besiedlung des hochalpinen hyporheischen Interstitials im Arlberggebiet (Österreich). *Archiv für Hydrobiologie,* 3:253–308.

von Uuxküll, J.

1956. Streifzüge durch die Umwelten von Tieren und Menschen. 181 pages. Hamburg: Romoholt.

Wallace, H. R.

1958. Movement of Eelworms. I. The Influence of Pore Size and Moisture Content of the Soil on the Migration of Larvae of the Beet Eelworm, *Heterodera schachtii* Schmidt. *Annals of Applied Biology,* 46:74–85.

1959. The Movement of Eelworms in Water Films. *Annals of Applied Biology,* 47:366–370.

Wells, J. B. J., and M. E. Clark

1965. The Interstitial Crustacea of Two Beaches in Portugal. *Revista Biologia,* 5:87–108.

Westheide, W.

1968. Zur quantitativen Verteilung von Bakterien und Hefen in einem Gezeitenstrand der Nordseeküste. *Marine Biology,* 1(4):336–347.

Wieser, W.

1959. The Effect of Grain Size on the Distribution of Small Invertebrates Inhabiting the Beaches of Puget Sound. *Limnology and Oceanography,* 4:181–194.

Wilson, D. P.

1955. The Role of Micro-Organisms in the Settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biological Association of the United Kingdom,* 34: 531–543.

Wiszniewski, J.

1934. Recherches écologiques sur le psammon et spécialement sur les Rotifères psammiques. *Archiwum Hydrobiologji i Rybactwa,* 8:149–272.

1947. Remarques relatives aux recherches récentes sur le psammon d'eau douce. *Archiwum Hydrobiologji i Rybactwa,* 13:7–36.

de Zio, S.

1964. Distribuzione dei Tardigradi in spiagge pugliesi. *Annuario dell' Istituto e Museo di Zoologia dell' Universita di Napoli,* 16(4):1–8.

de Zio, S., and P. Grimaldi

1964. Analisi comparativa del mesopsammon di due spiagge pugliesi in rapporto ad alcuni fattori ecologici. *Archivio Botanico e Biogeografico Italiano,* 40:357–367.

1966. Ecological Aspects of Tardigrada Distribution in South Adriatic Beaches. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:87–94.

Zobell, C. E., and D. Q. Anderson

1936. Observations on the Multiplication of Bacteria in Different Volumes of Stored Sea Water and the Influence on Oxygen Tension and Solid Surfaces. *Biological Bulletin,* 71:324–342.

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Ecology of Intertidal Meiobenthos

ABSTRACT

Environmental factors including sediment, water saturation, temperature, salinity, oxygen, organic detritus, and microflora are reviewed in terms of their influence on intertidal meiofaunal populations.

As a comparatively young area of study most research on meiobenthos has remained taxonomic and descriptive. While the list of known intertidal meiofauna includes representatives of nearly every phylum of invertebrates, few investigators have attempted thorough ecological studies in this area. Within the last decade portions of four review articles have summarized available ecological information (Delamare Deboutteville, 1960; Swedmark, 1964; Jansson, 1968b; McIntyre, 1969).

Using these basic references and additional citations, the general aspects of intertidal meiofaunal populations are reviewed here, with consideration given to important intertidal parameters along with an estimate of their influence on the distribution of meiofauna. Any review of beach ecology must include also the valuable material compiled by Jansson (1962, 1966, 1967a–d, 1968a,b) Fenchel (1967, 1968) and Fenchel and Jansson (1966) on littoral beaches in the atidal Baltic Sea.

Meiofaunal Populations

Accurate quantitative information on meiofauna is difficult to obtain; therefore, literature in this area is limited. In coarse sandy tidal beaches, interstitial fauna occupy an area from low to high tide and from the sand surface to depths of several meters (Delamare Deboutteville, 1960; Renaud-Debyser, 1963). In fine sandy beaches, meiofauna generally is restricted to the upper 5 cm of sand (Perkins, 1958), while in mud flats it is concentrated in the top centimeter of sediment (Rees, 1940; Barnett, 1968). In standardizing records of intertidal meiofaunal abundance, McIntyre's (1969) data suggest a decrease in meiofaunal abundance from coarse intertidal sediments, where diversity of taxa is maximal, toward finer sand sediments. Nevertheless, maximal meiofaunal density is reached in very fine sediments of mud flats, although here diversity of taxonomic groups probably is lowest. Ganapati and Rao (1962) described a relationship between density and size wherein small forms exist in large numbers but large forms tend to be more scarce.

Sediment

Intertidal environments supporting interstitial meiobenthos include particulate sediments ranging from large-diameter shell-gravel to fine particles of clay and silt on mud flats. Characteristics of sedimentary particles determine the dimensions and extent of the interstitial labyrinth of capillary spaces and its penetrability by water burrowing meiofauna, and especially those forms of meiofauna that are too small to move particles of sediment and so are restricted to the interstitial spaces (Callame, 1963; Graton and Fraser, 1935; Rees, 1940; Ruttner-Kolisko, 1961). While surveys of particle-size composition by weight contribute meaningfully, particularly in studying homogeneous, fine sediments (Prenant, 1960), several investigators have observed that more emphasis must be placed on measuring spaces between particles in coarser intertidal areas (Enckell, 1968; Jansson, 1967b). Perhaps recently developed techniques for measuring spaces directly will prove valuable in as-

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sessing this parameter (Haarløv and Weis-Fogh, 1953; and the paper by R. Williams in these proceedings).

The sorting (or degree of heterogeneity of particle sizes), the tightness of sediment packing, and the shape of individual grains determine interstitial porosity, which comprises 36 to 44 percent of most beach sand samples (Ruttner-Kolisko, 1961, 1962). Grain size, sorting, tightness of packing, and shape of particles are factors in controlling porosity and permeability of sediment to water (Graton and Fraser, 1935; Ruttner-Kolisko, 1961; Salvat, 1967). These sedimentary characteristics reflect the availability of interstitial space both for meiofauna and environmental parameters. Salvat (1967) distinguished four zones along the surface of beaches with medium-fine sand which differ in interstitial hydrodynamic characteristics. The zone of dry sand is reached only by extremely high tides. The zone of retention is reached by all high tides but loses much of its pore water at tidal emersion. A zone of resurgence is the site of intense circulation of interstitial water at both rising and falling tide and a zone of saturation lies below the area drained by low tide. Salvat correlated distributions of several macrofaunal forms with this environmental zonation.

Physical dimensions of the capillary network influence interstitial animals and environmental parameters. As Jansson (1967b) pointed out, aquatic intertidal meiofauna occupy only that portion of an interstitial space which contains pore water. At low tidal drainage, this may take the form of water films surrounding individual sediment particles (Pennak, 1951). Living in this unusual environment, interstitial meiofauna has evolved, in remarkably convergent directions, a series of morphological adaptations (Delamare Deboutteville, 1960; Remane, 1952; Swedmark, 1964). These include small body size, elongation, flattening, fragility, adhesive organs, reduced number of eggs, and direct larval development.

For interstitial meiofauna, which pass through sediment spaces without moving the particles themselves, dimensions of interstitial pores may be limiting, especially when the proportion of fine grain-size materials is great (Renaud-Debyser and Salvat, 1963). Morphological adaptations and locomotor activity in several groups of meiofauna have been linked to specific ranges of sediment size (Gray, 1968; Swedmark, 1964). Wieser (1959) suggested that sand less than 200 μ in diameter may be a "critical grain size," preventing establishment of abundant interstitial meiofauna. Jansson (1967b), for one, suggested that smaller grain sizes often are indirectly important by diminishing water flow and consequently changing oxygen and food availability.

Tidal movements of seawater and local topography are important determinants of sedimentary characteristics and distribution. Through tidal wave activity, sediment particles of greatest diameter accumulate near the low-tide region (Barnett, 1968; Ganapati and Rao, 1962; Pennak, 1951; Rees, 1940). Generally, exposure to heavy surf produces either steep beaches of large particle size or more gently sloping beaches of fine sand, depending upon surrounding geoogical conditions. Usually moderate wave activity is associated with medium-to-coarse sandy beaches. Gentle water movements frequently produce broad flats of fine sediment.

Water Saturation

The chemical composition of intertidal interstitial water is determined by tidal seawater and limited quantities of fresh water from precipitation, runoff, and groundwater seepage. Superficial areas also lose water through evaporation during low tidal exposure (Bruce, 1928a,b; Gerlach, 1954; Johnson, 1965). The slope, porosity, and grain size of the sediment; tidal movements of seawater; distance from the water line; duration of low tidal exposure; and the strength of preipitation and/or evaporation all determine the specific amount of water present in intertidal sediments (Bruce, 1928a,b; Callame, 1963; Gerlach, 1954; Graton and Fraser, 1935; Jansson, 1967a; Johnson, 1965; Rees, 1940; Rullier, 1957). Capillary forces, which vary with grain size and sorting, are important in retaining water in pore spaces not exposed to broad tidal-water movements (Ruttner-Kolisko, 1962).

Restriction of water flow through the interstitial network is determined by the permeability of the sediment (Brafield, 1964; Emery and Foster, 1948). Ruttner-Kolisko (1962) and Brafield (1964) related diminished water circulation directly to an increasing proportion of particles less than 250 μ in diameter. Fine sediments lose little more than superficial water during low tide and interstitial water tends to stagnate in capillary spaces (Callame, 1963). While coarser sediments undergo extensive drainage at low tide (to a depth of 1 m or more in some cases, Renaud-Debyser, 1963), movements of water within the beach still are restricted to some degree and lag behind movements of the adjacent seawater for periods of several hours (Emery and Foster, 1948; Renaud-Debyser, 1963; Salvat, 1967).

Intertidal meiofauna is least abundant in sediments always saturated with water or in nearly dry layers (Ganapati and Rao, 1962). Usually meiofauna is limited to sediments containing more than 10 percent of their saturation water (de Zio, 1965; Enckell, 1968; Pennak, 1951). Water content apparently constitutes an important environmental determinant of littoral meiofaunal distributions (Jansson, 1967b, 1968a).

Temperature

The temperature of intertidal sediments is regulated by more-general factors such as seasonal and climatic weather conditions and time of day. These in turn are frequently modified by more-specific and local factors such as slope of the beach, moisture held in sedimentary spaces, the temperature of both air and seawater, and the insulation of the sediment (Bruce, 1928a,b; Pennak, 1942; Jansson, 1967c; Johnson, 1965; Salvat, 1967).

Temperatures naturally are highest during summer in superficial layers of sediment, which may undergo abrupt changes accompanying inundation by flooding tide (Bruce, 1928a,b; Jansson, 1967c; Johnson, 1965; Linke, 1939; Salvat, 1967). Generally a gradient of declining temperature forms with increasing depth in intertidal sediment (Bruce, 1928a,b; Jansson, 1967c), although this gradient may become reversed at night (Ganapati and Rao, 1962), during winter (Jansson, 1967c), and at flood tide (Salvat, 1967). While the severity of these gradients varies seasonally and by geographic location, little change in temperature occurs below about 20 cm depth (Bruce, 1928a; Jansson, 1967c). While Ganapati and Rao (1962) feel that most interstitial animals cannot tolerate broad changes in temperature, several intertidal meiofaunal animals survive exposure to extremely low temperatures (Gray, 1965; Jansson, 1968a; Moore, 1931). Renaud-Debyser (1963) demonstrated seasonal changes in overall distribution of meiofauna which live deeper in sand in winter, avoiding extremes in both temperature and salinity. Johnson (1965) suggests that animals living in the upper centimeter of fine sandy beaches are exposed to daily temperature ranges up to three times that experienced by subtidal individuals, while those living at 10 cm or deeper experience temperatures comparable to those in subtidal environments. Some meiofauna from mud flats are restricted in movements to the uppermost layers of sediment and, therefore, must endure the full range of environmental variation (Barnett, 1968; Rees, 1940). In this case, physiological resistance must be an important determinant of field distribution.

Salinity

In tidal beaches, seawater conditions dominate the chemistry of interstitial water. Except in areas of unusually concentrated precipitation, interstitial salinity remains approximately comparable to that of the seawater (Ganapati and Rao, 1962; Johnson, 1967), in a few cases slightly higher (Fenchel and Jansson, 1966; Ganapati and Rao, 1962), and in most other cases somewhat lower (Jansson, 1967c; Kühl and Mann, 1966; Renaud-Debyser, 1963; Salvat, 1967). Generally, gradients of decreasing salinity exist horizontally between the seawater and shoreward areas where terrestrial sources of fresh water may be important (Jansson, 1967c), and between the sedimentary surface where evaporation increases salinity (Gerlach, 1954; Johnson, 1967) and dilution by groundwater at greater depths (Jansson, 1967c). Gradients in salinity may be steep and variable in tidal areas (Jansson, 1967c) but are less so on tidal beaches where flooding and draining seawater prevents accumulation of fresh water (Linke, 1939; Reid, 1930). Variations in salinity are greatest high on sandy beaches and lowest towards the sublittoral (Johnson, 1967). However, less porous intertidal habitats, such as mud flats, are subject to more drastic variations of superficial salinity—the salinity increasing with evaporation and decreasing during precipitation (Barnett, 1968; Capstick, 1957).

At least under local extremes, salinity has an important influence on microfauna and meiofauna. Anderson and Meadows (1969) found that fresh water or rainwater removed some of the microbial flora from sand grains, thereby removing important food materials for meiofauna. Govindankutty and Nair (1966) and Ganapati and Rao (1962) recorded severe reductions in meiofaunal abundance during reduced salinity accompanying monsoon periods of heavy rain. In addition, meiofauna apparently seek deeper levels in the sediment in the presence of lowered salinity (Govindankutty and Nair, 1966; Jansson, 1968a). In fine sediments where mobility is restricted to superficial regions, Barnett (1968) observed that all but a few harpacticoids remained within 0.5 cm of surface of the mud flat despite exposure to heavy rains which drasticially reduced the salinity of interstitial water. Boaden (1963) studied the effect of lowered salinity on normal orientations of an archiannelid to water current. He demonstrated that a balance between variable responses to salinity changes and to current flow can maintain a population of motile animals within a restricted intertidal zone.

Oxygen

In an oversimplified sense, oxygen is present within interstitial spaces in decreasing abundance from the water's edge toward the shore and from the sand surface toward greater depth (Jansson, 1967d; Pennak, 1951). However, patterns are frequently irregular and difficult to distinguish (Jansson, 1967d). In some cases, increased oxygen levels are associated with groundwater flow (Jansson, 1966, 1967d).

The abundance of oxygen within a beach is related to the permeability of sediments to water (Brafield, 1964). In beaches containing large quantities of clay, silt, or organic debris (Jansson, 1967d; Rullier, 1957), in beaches of very fine-grain sand (Brafield, 1964; Ruttner-Kolisko, 1961), or where ice-cover prevents exposure to air and waves (Jansson, 1967d), a black layer of ferrous and hydrogen sulfides forms close to the sedimentary surface and often indicates the depth at which anaerobic conditions prevail (Bruce, 1928b; Gordon, 1960).

Replenishment of oxygen depends largely upon circulating water during the rising tide (Brafield, 1964; Gordon, 1960), on out-flow of groundwater (Jansson, 1966, 1967d), and on wave activity (Gordon, 1960; Jansson, 1967d). In field studies, Ruttner-Kolisko (1962) and Brafield (1964) related increased abundance of oxygen to increased water movements, and recently Enckell (1968) quantified this effect in laboratory studies of freshwater movement.

In several cases, meiofaunal distributions were shown to be limited by lack of oxygen (Jansson, 1968a, for a review). Animals living at depths greater than 10 cm in fine intertidal sediments must be capable of surviving extended periods of anaerobiasis (Fenchel, 1967; Fenchel and Jansson, 1966; Gordon, 1960; Pamatmat, 1968; Riedl, 1969; Wieser and Kanwisher, 1961). Fenchel (1967) observed that ciliate Protoza dominate in anaerobic conditions where most Metazoa did not survive. Nevertheless, some meiofaunal Metazoa, apparently living anaerobically, are found at depths well below the "black layer" (Wieser and Kanwisher, 1961).

In intertidal areas of larger sediment size, the oxygen content is often low but is seldom zero (Ganapati and Rao, 1962; Jansson, 1967d; Renaud-Debyser, 1963). Renewal of interstitial water during tidal ebb and flow is important to the maintaining of oxygen abundance in intertidal beaches (Gordon, 1960; Pennak, 1951). Some meiofauna living in beaches of coarser grain showed a clear preference for areas of increased oxygen abundance (Gray, 1966b, 1967a; Jansson, 1967a,d).

Acidity-Alkalinity

Several investigators have studied the pH of interstitial water and reported readings similar to those from adjacent seawater (Bruce, 1928b; Ganapati and Rao, 1962; Renaud-Debyser, 1963; Salvat, 1967). Apparently variations in pH are not great, and the interstitial water in most marine beaches is only slightly more acid than the sea. Bruce (1928b) observed that pH changes are moderated by an alkali-reserve buffering effect of calcareous material in the sand.

Organic Detritus

Generally, organic detritus is available in small quantities in sandy beaches (Ganapati and Rao, 1962; Renaud-Debyser, 1963; Salvat, 1967) but is more abundant in fine intertidal sediments (Meadows and Anderson, 1966). Accumulation of debris in an intertidal area depends upon wave exposure, water currents, slope of the beach, coarseness of the sand, and the amount of vegetation in nearby areas (Dahl, 1953). The importance of this material to intertidal organisms is physical, chemical, and biological. In contrast to relatively even gradients in most intertidal parameters, distribution of decaying organic matter tends to be patchy (Jansson, 1968a). As small particulate material, debris accumulates and clogs pore spaces, sometimes limiting interstitial spaces severely, changing their penetrability and capacity for water retention (Jansson, 1967b; Pennak, 1942). In addition, this material contributes to the formation of a ferrous sulfide layer in the sand and, through by-product of its degradation, to the general chemistry of interstitial water (Bruce, 1928a,b). Finally, organic detritus has been considered an important source of food in intertidal communities (Dahl, 1953; Perkins, 1958; Remane, 1952; Renaud-Debyser and Salvat, 1963). Abundant intertidal meiofauna usually is associated with an intermediate abundance of organic material—not in beaches thoroughly cleaned by waves, nor in sediments clogged by debris (Pennak, 1942; Renaud-Debyser and Salvat, 1963).

Intertidal food materials include organic detritus, algae living on grains of sand or washed in from near-shore water, bacteria, and the meiofauna themselves. As Jansson (1968a) suggested, the range of materials generally termed "detritus" is broad in composition. Studies of microfauna and microflora of marine intertidal sediments have demonstrated a great diversity and abundance of organisms in this material (Anderson and Meadows, 1969; Meadows and Anderson, 1966, 1968; Steele and Baird, 1968). In addition, careful determinations of food chosen by meiofauna indicate that "detritus feeders" may be highly selective in the portions of detritus they choose (Fenchel, 1968; Thane-Fenchel, 1968).

Microflora

While heavy surf limits their distribution to low tidal regions on exposed beaches (Steele and Baird, 1968), microalgae are extremely abundant in flats of fine particle size. Steele and Baird (1968) predicted that in situ productivity of intertidal areas should increase with decreased wave exposure. Pamatmat (1968) conducted a study of community metabolism in an intertidal sand flat. He found that microflora provided most of the primary productivity (about 200 to 300 liters of oxygen/m^2/year) of the area. He estimated that community respiration was 140 to 226 liters of oxygen/m^2/year. Although seasonal and tidal fluctuations in both of these measurements make studies of this sort still more complex, he found that the portion of community respiration produced by the complex of bacteria-microfauna-meiofauna was greater than that contributed by the macrofauna.

Studies of bacterial distribution in intertidal areas should be valuable in interpreting distributions and ecology of meiofauna browsing on films of bacteria (Anderson and Meadows, 1969; Meadows and Anderson, 1966, 1968; Westheide, 1968). Several taxa have shown attraction to sediments possessing films of organic materials (Gray, 1966a,b, 1967a,1968; Jägersten, 1940; Wilson, 1955). In some cases, the attractiveness is specific for particular groups of bacteria or to by-products of their presence in the recent past (Gray, 1967a,b, 1968). Bacterial abundance apparently is greatest in areas of low wave exposure (Anderson and Meadows, 1969). In medium-coarse sands maximal densities occurred near the sand surface in low and high tidal regions (Westheide, 1968). Presumably microbial flora is extremely rich in flats of sand and mud (Zobell, 1946).

Information presently available on the ecology of intertidal sand areas includes general characterizations of the substratum and chemical analyses of seawater and groundwater, mostly from low-tide measurements. While much more of this kind of data are needed, future studies must also include analyses of conditions through tidal, daily, and seasonal changes in order for us to visualize the dynamics of the environment. In addition we must design equipment and techniques for studying environmental parameters in "microhabitat" dimensions of water films surrounding grains of sand.

Literature Cited

Anderson, J. G., and P. S. Meadows.

1969. Bacteria on Intertidal Sand Grains. *Hydrobiologia,* 33:33-46.

Barnett, P. R. O.

1968. Distribution and Ecology of Harpacticoid Copepods of an Intertidal Mudflat. *Internationale Revue der gesamten Hydrobiologie,* 53:177-209.

Boaden, P. J. S.

1963. Behaviour and Distribution of the Archiannelid *Trilobodrilus heideri. Journal of the Marine Biological Association of the United Kingdom,* 43:239-250.

Brafield, A. E.

1964. The Oxygen Content of Interstitial Water in Sandy Shores. *Journal of Animal Ecology,* 33:97-116.

Bruce, J. R.

1928a. Physical Factors on the Sandy Beach. Part I. Tidal, Climatic and Edaphic. Part II. Chemical Changes. *Journal of the Marine Biological Association of the United Kingdom,* 15:535–552.

1928b. Physical Factors on the Sandy Beach. Part II. Chemical Changes—Carbon Dioxide Concentration and Sulphides. *Jorunal of the Marine Biological Association of the United Kingdom,* 15:553–565.

Callame, B.

1963. Le milieu interstitiel dans les sédiments sableaux intercotidaux. *Bulletin de l'Institut Océanographique, Monaco,* 60(1271):1–32.

Capstick, C. K.

1957. The Salinity Characteristics of the Middle and Upper Reaches of the River Blyth Estuary. *Journal of Animal Ecology,* 26:295–315.

Dahl, E.

1953. Some Aspects of the Ecology and Zonation of the Fauna on Sandy Beaches. *Oikos,* 4:1–27.

Delamare Deboutteville, C.

1960. *Biologie des eaux souterraines littorales et continentales.* 740 pages. Paris: Hermann.

Emery, K. O., and J. F. Foster.

1948. Water Tables in Marine Beaches. *Journal of Marine Research,* 7:644–654.

Enckell, P. H.

1968. Oxygen Availability and Microdistribution of Interstitial Mesofauna in Swedish Fresh-Water Sandy Beaches. *Oikos,* 19:271–291.

Fenchel, T.

1967. The Ecology of Marine Microbenthos. I. The Quantitative Importance of Ciliates as Compared with Metazoans in Various Types of Sediment. *Ophelia,* 4:121–137.

1968. The Ecology of Marine Microbenthos. II. The Food of Marine Benthic Ciliates. *Ophelia,* 5:73–121.

Fenchel, T., and B. O. Jansson.

1966. On the Vertical Distribution of the Microfauna in the Sediments of a Brackish-Water Beach. *Ophelia,* 3:161–177.

Ganapati, P. N., and G. C. Rao.

1962. Ecology of the Interstitial Fauna Inhabiting the Sandy Beaches of Waltair Coast. *Journal of the Marine Biological Association of India,* 4:44–57.

Gerlach, S. A.

1954. Das Supralitoral der sandigen Meeresküsten als Lebensraum einer Mikrofauna. *Kieler Meeresforschungen,* 10:121–129.

Gordon, M. S.

1960. Anaerobiosis in Marine Sandy Beaches. *Science,* 132:616–617.

Govindankutty, A. G., and N. B. Nair.

1966. Preliminary Observations on the Interstitial Fauna of South-West Coast of India. *Hydrobiologia,* 28:101–122.

Graton, L. C., and H. J. Fraser

1935. Systematic Packing of Spheres—with Particular Relation to Porosity and Permeability. *Journal of Geology,* 43:785–909.

Gray, J. S.

1965. The Behaviour of *Protodrilus symbioticus* (Giard) in Temperature Gradients. *Journal of Animal Ecology,* 34:445–461.

1966a. The Attractive Factor of Intertidal Sands to *Protodrilus symbioticus. Journal of the Marine Biological Association of the United Kingdom,* 46:627–645.

1966b. Factors Controlling the Localizations of Populations of *Protodrilus symbioticus* Giard. *Journal of Animal Ecology,* 35:435–442.

1967a. Substrate Selection by the Archiannelid *Protodrilus rubropharyngeus. Helgoländer wissenschaftliche Meeresuntersuchungen,* 15:253–269.

1967b. Substrate Selection by the Archiannelid *Protodrilus hypoleucus* Armenante. *Journal of Experimental Marine Biology and Ecology,* 1:47–54.

1968. An Experimental Approach to the Ecology of the Harpacticid *Leptastacus constrictus* Lang. *Journal of Experimental Marine Biology and Ecology,* 2:278–292.

Haarløv, N., and T. Weis-Fogh

1953. A Microscopical Technique for Studying the Undisturbed Texture of Soils. *Oikos,* 4:44–57.

Jägersten, G.

1940. Die Abhängigkeit der Metamorphose vom Substrat des Biotops bei *Protodrilus. Arkiv för Zoologi,* 32 (17) :1–12.

Jansson, B. O.

1962. Salinity Resistance and Salinity Preference of Two Oligochaetes, *Aktedrilus monospermatecus* Knöllner and *Marionina preclitellochaeta* n. sp. from the Interstitial Fauna of Marine Sandy Beaches. *Oikos,* 13:293–305.

1966. On the Ecology of *Derocheilocaris remanei* Delamare and Chappius (Crustacea, Mystacocarida). *Vie et Milieu,* 17:143–186.

1967a. The Importance of Tolerance and Preference Experiments for the Interpretation of Mesopsammon Field Distributions. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 15:41–58.

1967b. The Significance of Grain Size and Pore Water Content for the Interstitial Fauna of Sandy Beaches. *Oikos*, 18:311–322.

1967c. Diurnal and Annual Variations of Temperature and Salinity of Interstitial Water in Sandy Beaches. *Ophelia*, 4:173–201.

1967d. The Availability of Oxygen for the Interstitial Fauna of Sandy Beaches. *Journal of Experimental Marine Biology and Ecology*, 1:123–143.

1968a. Quantitative and Experimental Studies of the Interstitial Fauna in Four Swedish Sandy Beaches. *Ophelia*, 5:1–71.

1968b. Studies on the Ecology of the Interstitial Fauna of Marine Sandy Beaches. Thesis, University of Stockholm, pages 1–16.

Johnson, R. G.

1965. Temperature Variation in the Infaunal Environment of a Sand Flat. *Limnology and Oceanography*, 10:114–120.

1967. Salinity of Interstitial Water in a Sandy Beach. *Limnology and Oceanography*, 12:1–7.

Kühl, H., and H. Mann

1966. Änderungen im Chemismus des Interstitialwassers am Strand von Cuxhaven während einer Tide. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 13:238–245.

Linke, O.

1939. Die Biota des Jadebusewattes. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 1:301–348.

McIntyre, A. D.

1969. Ecology of Marine Meiobenthos. *Biological Reviews*, 44:245–290.

Meadows, P. S., and J. G. Anderson

1966. Micro-Organisms Attached to Marine and Freshwater Sand Grains. *Nature*, 212:1059–1060.

1968. Micro-Organisms Attached to Marine Sand Grains. *Journal of the Marine Biological Association of the United Kingdom*, 48:161–175.

Moore, H. B.

1931. The Muds of the Clyde Sea Area. III. Chemical and Physical Conditions; Rate and Nature of Sedimentation; and Fauna. *Journal of the Marine Biological Association of the United Kingdom*, 17:325–358.

Pamatmat, M. M.

1968. Ecology and Metabolism of a Benthic Community on an Intertidal Sandflat. *Internationale Revue der gesamten Hydrobiologie*, 53:211–298.

Pennak, R. W.

1942. Ecology of some Copepods Inhabiting Intertidal Beaches near Woods Hole, Massachusetts. *Ecology*, 23:446–456.

1951. Comparative Ecology of the Interstitial Fauna of Fresh-Water and Marine Beaches. *Année Biologique*, 27:449–480.

Perkins, E. J.

1958. The Food Relationships of the Microbenthos, with Particular Reference to that Found at Whitstable, Kent. *Annals and Magazine of Natural History*, series 13, 1:64–77.

Prenant, M.

1960. Études écologiques sur les sables intercotidaux. I. Questions de méthode granulométrique. Application à trois anses à de la Baie de Quiberon. *Cahiers de Biologie Marine*, 1:295–340.

Rees, C. B.

1940. A Preliminary Study of the Ecology of a Mud-Flat. *Journal of the Marine Biological Association of the United Kingdom*, 24:185–199.

Reid, D. M.

1930. Salinity Interchange between Sea-Water in Sand and Overflowing Fresh-Water at Low Tide. *Journal of the Marine Biological Association of the United Kingdom*, 16:609–614.

Remane, A.

1952. Die Besiedelung des Sandbodens im Meere und die Beduntung der Lebensformtypen für die Ökologie. *Zoologischer Anzeiger*, Supplementband 16:327–359.

Renaud-Debyser, J.

1963. Recherches écologiques sur la faune interstitielle des sables. (Bassin d'Arcachon, Île de Bimini, Bahamas). *Vie et Milieu*, supplement 15:1–157.

Renaud-Debyser, J., and B. Salvat

1963. Éléments de prospérité des biotopes des sediments meubles intertideaux et écologie de leurs populations en microfaune et macrofaune. *Vie et Milieu*, 14:463–550.

Riedl, R.

1969. Gnathostomulida from America. *Science*, 163:445–452.

Rullier, F.

1957. Teneur en air et en eau interstitiels des sables marins et son influence sur les conditions d'habitat. *Comptes Rendus de l'Academie des Sciences*, series D, 245:936–938.

Ruttner-Kolisko, A.

1961. Biotop und Biozönose des Sandufers einiger österreichischer Flüsse. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 14:362–368.

1962. Porenraum und kapillare Wasserströmung im Limnopsammal, ein Beispiel für die Bedeutung verlangsamter Strömung. *Schweizerische Zeitschrift für Hydrologie*, 24:444–458.

Salvat, B.

1967. La macrofaune carcinologique endogée des sédiments meubles intertideaux (Tanaidacés, Isopodes et Amphipodes), éthologie, bionomie et cycle biologique. *Mémoires du Muséum Nationale d'Histoire Naturelle*, 45:1–275.

Steele, J. H., and J. E. Baird

1968. Production Ecology of a Sandy Beach. *Limnology and Oceanography*, 13:14–25.

Swedmark, B.

1964. The Interstitial Fauna of Marine Sand. *Biological Reviews*, 39:1–42.

Thane-Fenchel, A.
1968. Distribution and Ecology of Non-Planktonic Brackish-Water Rotifers from Scandinavian Waters. *Ophelia,* 5:273–297.

Westheide, W.
1968. Zur quantitative Verteilung von Bakterien und Hefen in einem Gezeitenstrand der Nordseeküste. *Marine Biology.* 1:336–347.

Wieser, W.
1959. The Effect of Grain Size on the Distribution of Small Invertebrates Inhabiting the Beaches of Puget Sound. *Limnology and Oceanography,* 4:181–194.

Wieser, W., and J. Kanwisher
1961. Ecological and Physiological Studies on Marine Nematodes from a Small Salt Marsh Near Woods Hole, Massachusetts. *Limnology and Oceanography,* 6:262–270.

Wilson, D. P.
1955. The Role of Micro-Organisms in the Settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biological Association of the United Kingdom,* 34:531–543.

de Zio, S.
1965. Distribuzione del mesopsammon in rapporto alla distanza della linea di riva e distanza da un corso di aqua salmastra. *Bollettino di Zoologia,* 32:525–537.

Zobell, C. E.
1946. *Marine Microbiology.* 240 pages. Waltham, Massachusetts: Chronica Botanica.

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Observations on the Status of Subtidal Meiofauna Research

ABSTRACT

The regional distribution, vertical distribution, seasonal fluctuations, and composition of populations of subtidal meiofauna and the effects of sampling techniques on estimates of subtidal meiofauna are reviewed. It is concluded that geographic and depth sampling must be extended, seasonal changes in meiofauna must be studied in more detail, and sampling techniques must be refined.

In recent years the increase of interest in meiofauna has produced an expanding volume of literature on many aspects of this field. However, because of the obvious advantages of sampling close to laboratory facilities, and of easier accessibility, much of the work has been concerned with beaches, tidal or atidal. Further, there has been a marked concentration on sandy areas, so that the interstitial fauna has received greater attention than those forms which crawl on the surface (epipelic) or burrow into the sediment (endopelic). A comprehensive review has recently appeared (McIntyre, 1969) but the availability of new data and the desire to highlight the subtidal situation make it useful to reconsider this aspect. The present paper brings together published data on quantitative aspects of marine meiofauna populations and their ecology from sediments below the low-water mark of spring tides. There are only 20 relevant papers, all published within the last 38 years, and these are summarized in Table 1.

Regional Distribution

For the continental shelf it is convenient to divide the data according to three habitats—sea-grass, sand, and mud—and we may consider first the regional coverage of the information. The sea-grass communities are found in shallow coastal waters, and most of the sampling has been done at less than 1 m depth. Work in Japan (Kikuchi, 1966) is based on only a few samples from beds of *Zostera marina* Linné, but in Danish waters studies have been much more extensive (Muus, 1967), and other macrophytes (*Ruppia maritima* Linné and *Chaetomorpha linum* (Müller)) were present as well as *Zostera* Linné in the sampling area. In America, work at Miami dealt with the nematodes only of a *Thalassia testudinum* Koenig and Sims community, and Tietjen (1969) made a detailed investigation of meiofauna populations in *Zostera* areas of two New England estuaries. Data are available also on *Spartina alterniflora* Loiseleur from flats on the American east coast at Massachusetts and Georgia (Wieser and Kanwisher, 1961; Teal and Wieser, 1966), and although these refer to intertidal areas they have been included in Table 1 for comparison.

On sandy grounds of the subtidal shelf, there is information from ten investigations. From tideless areas, Purasjoki (1947) in the Gulf of Finland, and Fenchel and Jansson (1966) in the Baltic worked at low salinities of 3 to 7 ppt, while Bregnballe (1961) and Muus (1967) sampled the Kattegat in salinities ranging from 5 to 18 ppt. In the North Sea, sand in fully saline conditions was examined off the Danish coast by Smidt (1951). In warmer waters, observations are available from off Banyuls in France (Guille and Soyer, 1968) and from calcareous sand on the shelf inshore at Ber-

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muda (Coull, 1968). Farther north, on the American coast, Wieser (1960) provided data from Buzzards Bay in Massachusetts while nearby, on the shelf, Wigley and McIntyre (1964) sampled stations at several depths. Finally, Tietjen (1969) studied two sandy stations (median grain sizes 210 μ and 440 μ) in two New England estuaries.

For subtidal mud on the shelf, eleven areas have been examined. The studies of Purasjoki (1947) in Finland and Muus (1967) in the Kattegat, already referred to for sand, were extended into muddy grounds, while additional information for the Baltic region is available from Krogh and Spärck (1936) from the Øresund. Round the British Isles, Mare (1942) worked in the English Channel, Moore (1931) in the Clyde, and McIntyre (1964) in the sea lochs of the Scottish west coast as well as in the North Sea off the east coast. Bougis (1946, 1950) and Guille and Soyer (1968) sampled mud off the Mediterranean coast of France, and some of the investigations already referred to for sand off New England (Wieser, 1960; Wigley and McIntyre, 1964) and off Bermuda (Coull, 1968) also dealt with muddy grounds.

Beyond the continental shelf, little quantitative information is available. Wigley and McIntyre (1964) described two samples from silt-clay and fine sand on the slope off New England, and from the abyssal regions Thiel (1966) gave a preliminary account of work done in the Indian Ocean.

TABLE 1.—*Summary of Subtidal Meiofauna Data.*

Habitat	Reference		Water depth	Region	Season	Dominant group and its mean density (individuals per 10 cm²)		Total meiofauna mean per 10 cm²
Sea-Grass	Kikuchi	(1966)	< 5 m	Japan	August	Nematoda	534	670
	Muus	(1967)	< 1 m	Baltic	May–July	Nematoda	430	643
	Hopper & Meyers	(1967)	< 1 m	USA (Miami)	All Year	Nematoda	796	——
	Tietjen	(1969)	1 m	USA (New England)	All Year	Nematoda	2,030	2,369
	Wieser & Kanwisher	(1961)	Intertidal	USA (New England)	Nov. & June	Nematoda	1,870	——
	Teal & Wieser	(1966)	Intertidal	USA (Georgia)	March	Nematoda	12,400	——
Sand	Purasjoki	(1947)	15–40 m	Gulf of Finland	January	Nematoda	2	5
	Fenchel & Jansson	(1966)	< 0.5 m	Baltic	July–Aug.	Rotifera	97	376
	Bregnballe	(1961)	< 1.5 m	Baltic	June	Nematoda	789	——
	Muus	(1967)	< 1.0 m	Baltic	Apr.–July	Nematoda	658	968
	Smidt	(1951)	2–3 m	North Sea	All Year	Nematoda	132	——
	Guille & Soyer	(1968)	15–91 m	Mediterranean	———	Nematoda	121	202
	Coull	(1968)	3–13 m	Bermuda	All Year	Nematoda	423	580
	Wieser	(1960)	12–30 m	USA (New England)	July–Aug.	Nematoda	364	375
	Wigley & McIntyre	(1964)	40–58 m	USA (New England)	June	Nematoda	553	663
	Tietjen	(1969)	1 m	USA (New England)	All Year	Nematoda	2,132	2,626
Mud	Muus	(1967)	< 1 m	Baltic	Mar.–June	Nematoda	220	365
	Krogh & Spärck	(1935)	5–54 m	Baltic	Aug.–Jan.	Nematoda	53	88
	Purasjoki	(1947)	9–55 m	Gulf of Finland	January	Nematoda	23	41
	Wieser	(1960)	18 m	USA (New England)	July–Sept.	Nematoda	798	838
	Bougis	(1946/50)	30 m	Mediterranean	Mar.–May	Nematoda	614	818
	Guille & Soyer	(1968)	30–85 m	Mediterranean	———	Nematoda	79	150
	Mare	(1942)	45 m	English Channel	Mar.–May	Nematoda	83	145
	Moore	(1931)	24–166 m	Scotland (Clyde)	Single season	Nematoda	193	237
	McIntyre	(1964)	146 m	North Sea (northern)	All Year	Nematoda	1,845	1,959
	McIntyre	(1964)	101 m	Scotland (west coast)	All Year	Nematoda	853	1,008
	Wigley & McIntyre	(1964)	69–179 m	USA (New England)	June	Nematoda	355	395
	Wigley & McIntyre	(1964)	366–567 m	USA (New England)	June	Nematoda	114	122
	Thiel	(1966)	1000–5000 m	Indian Ocean	———	Nematoda	56	79
	Coull	(1968)	27 m	Bermuda (Devils Hole)	All Year	Nematoda	38	40

This summary draws attention to the restricted global coverage of the data from subtidal zones. A high proportion of the samples were taken in the waters of northwestern Europe, and there is clearly great scope for extension of comparable work into other regions. Sufficient information has not yet accumulated to permit detailed comparisons to be made of populations on a regional basis.

Depth

As indicated above, the depth coverage also is severely restricted. Most of the samples were taken in water of only a few meters depth, and samples from over 50 m are available from a very small number of cores.

Vertical Distribution

Similar restrictions apply to our knowledge of the vertical distribution of organisms in the sediment because of the difficulty of obtaining long-undisturbed cores from subtidal grounds. In most of the surveys referred to in Table 1, sampling was confined to the top 4 to 6 cm of deposit. On muddy grounds, a high proportion of the fauna is confined to these surface layers, but this is not so for all animal groups in sand. Tietjen (1969) used cores of 5 cm and showed that harpacticoids, ostracods, and polychaetes were greatly reduced or absent at the 4 to 5 cm level but substantial numbers of nematodes were still present. McIntyre (unpublished) examined cores 23 cm long collected in Scotland by divers from a sandy ground (median grain size 200 μ) at 1 to 8 m depth, where he found mainly nematodes, but he also found several other groups down to the deepest section of the cores. Numbers were much reduced below 16 cm, but strongly bimodal vertical distributions have been recorded from intertidal areas, and a similar picture may be found in some subtidal areas when suitable sampling devices are developed.

Seasonal Fluctuations

Details of seasonal fluctuations also are sparse Only five of the investigations listed in Table 1 give data collected throughout a full year, and most refer to a single season or even to a once-only sampling; consequently, knowledge of overall changes in subtidal populations is limited.

Workers from shallow Danish waters agree that nematodes are at a minimum in winter months and that there are marked seasonal fluctuations in harpacticoids—apparently associated with reproduction—while ostracod populations, by comparison, are much more stable throughout the year. At Bermuda, Coull (1968) noted distinct seasonal patterns, with the lowest values for total populations occurring in winter and the highest in late spring, although nematodes often reached highest numbers in winter at the time of lowest temperatures. Coull was able to show that seasonal fluctuations in density were related not only to the reproductive activity of the animals, stimulated apparently by temperature increase, but also to regular physical events which caused changes in the sediments. For example, at one site harpacticoids declined when the well-sorted, coarse-grained sediments characteristic of summer months received a considerable input of silt-clay material as a result of winter hydrographic conditions. Such regular annual fluctuations may have habitat changes on a larger scale superimposed on them. Hopper and Meyers (1967), for example, showed how gradual deterioration of the plants in a seagrass bed could complicate the interpretation of seasonal changes. A further difficulty in this respect is that in many investigations meiofauna species are not identified but are lumped together in the presentation to give total counts for major taxonomic groups. Because of the ecological diversification which exists within such groups, greater taxonomic discrimination would undoubtedly help in the interpretation of seasonal patterns. Thus Tietjen (1969), by dividing the nematodes he studied into feeding types, found significant peaks in epigrowth feeders in spring and summer, after which there was a rapid decline, apparently associated with changes in the microflora. Peaks were less obvious in other feeding types, but deposit feeders tended to peak in the fall, winter, and early spring when epigrowth feeders were least abundant.

Marked seasonal fluctuations might not be expected in deep water where conditions are much more uniform. McIntyre (1964) could not detect significant differences due to season in meiofauna populations at about 100 m off the Scottish coast. Matthews (1964), working on benthic copepods of deep Norwegian fjords, also found no great seasonal changes, but he did observe that the copepods were most abundant when the plankton of the upper waters was in decline, suggesting a scavenging role for these benthic forms.

Composition of the Populations

It is clear from the surveys shown in the table that nematodes are overwhelmingly the dominat group numerically, often making up over 90 percent of the metazoan fauna. Occasionally in single samples, or on a particular ground, copepods are more abundant than nematodes, but in general they are a poor second in the subtidal zone. Other groups, such as ostracods in shallow brackish water, have only occasionally been recorded as quantitatively important.

Some of the earlier surveys produced very low counts of population density, but the more refined techniques of recent years have resulted in total meiofauna counts from single subtidal samples ranging from 95 to 1,269 individuals per 10 cm^2 for sand, and 177 to 3,163 per 10 cm^2 for mud. While it is probably true that nematodes are the most important group numerically, it may well be that their importance has been exaggerated because of the comparative ease with which they can be preserved and counted. Unfortunately, it often is necessary to work on preserved samples for subtidal studies, so recognition of soft-bodied taxa is difficult. Knowledge of such groups as Turbellaria and Gastrotricha, which has advanced so much recently in intertidal areas, depends on examination of live material, and it is probable that such groups will be found in greater numbers when suitable techniques can be applied to subtidal deposits.

Effects of Sampling Techniques

As suggested above, the sorting and processing techniques used may affect the relative quantitative picture of the meiofauna. The methods used in collecting the original sample may be of even greater importance. Three main techniques were used in the surveys listed in this review. In very shallow water, samples were collected by hand in core tubes or small containers; second, some form of gravity corer was used; and third, subsamples were taken from a grab. Of the three methods, there is no doubt that the diver-collected core is the most satisfactory. On sandy ground, where there may be marked substrate differences within short distances, the diver can note the exact situation from which the sample is taken, whether from a crest or a trough in ripple areas, for example, and whether the spot is representative of a wider area. Further, the diver usually is able to collect a core of the desired length and bring it to the surface more or less intact—a useful achievement on a sandy ground.

Muddy grounds may seem to present less of a problem since they often are more uniform and frequently yield an apparently intact sample in a gravity corer. It is known, however, that the flocculent surface layer is easily washed aside by the downwash of a sampler. Work presently in progress by the Aberdeen Marine Laboratory in a Scottish sea loch at 25 m has shown that when using an open core tube of just over 2 cm internal diameter it is extremely difficult for a diver to collect a vertical core which includes the intact surface layer. Even a tube of over 4 cm diameter caused some washing aside of the flocculent material in spite of the most gentle insertion into the deposit. It was only when tubes of a much larger size—almost 10 cm diameter—were used that the divers felt confident of obtaining a completely intact surface layer. It seems unlikely that any existing instrument could compete with this method of collection. Our present procedure is to collect an intact sample in a wide tube and slowly siphon off all but the last 1 cm of supernatant water. It then is possible to subsample with narrow tubes without disturbing the surface. Comparative counts are now being made on samples taken by this method and from a free fall corer, and initial results indicate that the diver-collected core gives a significantly higher estimate of fauna for the upper layer. This procedure eliminates error from another source—core shortening. On the ground referred to above, divers observed that pushing a 2-cm tube into the mud beyond 6 to 8 cm caused shortening of the core, so, in long samples, the validity of the vertical layering was in doubt. By subsampling from a large core in the laboratory, this could be allowed for, but with a remote gravity corer, shortening of the sample could take place without this being obvious to the operator.

It would seem, then, that the best subtidal meiofauna samples are those collected by hand by diving—an activity restricted to about 30 m. At greater depths, remote core devices must be used, or subsamples taken from a grab. For remote coring it must be accepted that there will be some loss of surface material, and shortening of the core during penetration may produce distortion of the layers. For grab sampling, care must be taken to use only those hauls which produce comparatively undisturbed sediment surfaces.

Conclusions

It is clear that information on the subtidal meiobenthos is very sparse indeed. We require a great extension of sampling, both geographically and depth-wise, and we also need detailed work throughout the year to define seasonal changes. Even sampling methods are by no means satisfactory except in shallow water where SCUBA can be used. Because of all these deficiencies, ecological knowledge for the subtidal region, either from the autecological or the synecological aspect, is almost nonexistent.

Literature Cited

Bougis, P.

1946. Analyse quantitative de la micro-faune d'une vase marine à Banyuls. *Comptes Rendus de l'Academie des Sciences,* 222:1122–1124.

1950. Méthode pour l'étude quantitative de la microfaune des fonds marins (Meiobenthos). *Vie et Milieu,* 1:23–37.

Bregnballe, F.

1961. Plaice and Flounders as Consumers of the Microscopic Bottom Fauna. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser,* 3 (6) :133–182.

Coull, B. C.

1968. Shallow Water Meiobenthos of the Bermuda Platform. Unpublished Ph.D. dissertation, Lehigh University.

Fenchel, T., and B.-O. Jansson

1966. On the Vertical Distribution of the Microfauna in the Sediments of a Brackish-Water Beach. *Ophelia,* 3:161–177.

Guille, A., and J. Soyer

1968. La Faune benthique des substrats meubles de Banyuls-sur-Mer. Premières Données qualitatives et quantitatives. *Vie et Milieu,* 19:323–360.

Hopper, B. E., and S. P. Meyers

1967. Population Studies on Benthic Nematodes within a Subtropical Seagrass Community. *Marine Biology,* 1 (2) :85–96.

Kikuchi, T.

1966. An Ecological Study on Animal Communities of the *Zostera marina* Belt in Tomioka Bay, Amakusa, Kyushu. *Publications from the Amakusa Marine Biological Laboratory, Kyushu University,* 1 (1) :1–106.

Krogh, A., and R. Spärck

1936. On a New Bottom-Sampler for Investigation of the Micro Fauna of the Sea Bottom with Remarks on the Quantity and Significance of the Bottom Micro Fauna. *Kongelige Danske Videnskabernes Selskabs Skrifter, Biologiska Skrifter,* 13(4):1–12.

McIntyre, A. D.

1964. Meiobenthos of Sub-Littoral Muds. *Journal of the Marine Biological Association of the United Kingdom,* 44 (3) :665–674.

1969. Ecology of Marine Meiobenthos. *Biological Reviews,* 44:245–290.

Mare, M. F.

1942. A Study of a Marine Benthic Community with Special Reference to the Micro-Organisms. *Journal of the Marine Biological Association of the United Kingdom,* 25(3):517–554.

Matthews, J. B. L.

1964. On the Biology of Some Bottom-Living Copepods (Aetideidae and Phaennidae) from Western Norway. *Sarsia,* 16:1–46.

Moore, H. B.

1931. The Muds of the Clyde Sea Area. III. Chemical and Physical Conditions; Rate and Nature of Sedimentation; and Fauna. *Journal of the Marine Biological Association of the United Kingdom,* 17(2):325–358.

Muus, B. J.

1967. The Fauna of Danish Estuaries and Lagoons. Distribution and Ecology of Dominating Species in the Shallow Reaches of the Mesohaline Zone. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser,* 5(1):1–316.

Purasjoki, K. J.

1947. Quantitative Untersuchung über die Mikrofauna des Meeresbodens in der Umgebung der Zoologischen Station Tvärminne an der Südküste Finnlands. *Societas Scientiarum Fennica, Commentationes Biologicae,* 9(14):1–24.

Smidt, E. L. B.

1951. Animal Production in the Danish Waddensea. *Meddelelser fra Kommissionen for Danmarks Fiskeri-og Havundersøgelser, Series Fiskeri,* 11(6):1–151.

Teal, J. M., and W. Wieser
1966. The Distribution and Ecology of Nematodes in a Georgia Salt Marsh. *Limnology and Oceanography,* 11(2):217–222.

Thiel, H.
1966. Quantitative Untersuchungen über die Meiofauna von Tiefseeboden. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:131–147.

Tietjen, J. H.
1969. The Ecology of Shallow Water Meiofauna in Two New England Estuaries. *Oecologia,* 2(3):251–291.

Wieser, W.
1960. Benthic Studies in Buzzards Bay. II. The Meiofauna. *Limnology and Oceanography,* 5(2):121–137.

Wieser, W., and J. Kanwisher
1961. Ecological and Physiological Studies on Marine Nematodes from a Small Salt Marsh near Woods Hole, Massachusetts. *Limnology and Oceanography,* 6(3)262–270.

Wigley, R. L., and A. D. McIntyre
1964. Some Quantitative Comparisons of Offshore Meiobenthos and Macrobenthos South of Martha's Vineyard. *Limnology and Oceanography,* 9(4):485–493.

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Ecology of Subtidal Meiobenthos

ABSTRACT

The difficulties of conducting synecological studies of meiobenthos are discussed. Studies on the benthic population dynamics and biomass, with emphasis on meiobenthos that have been conducted in the Black Sea by Romanian investigators, are reviewed. The importance of meiobenthos in the economy of the sea is emphasized.

The fact is well known that in the last few years the tiny world of bottom marine organisms has drawn the attention of more and more research workers. Studies undertaken so far have revealed not merely the qualitative and quantitative richness of microbenthos but also the great importance of the latter in sea-economy. Many of the difficulties that occur during microbenthic ecological investigations have been recorded. The most difficult problem in microbenthic synecological studies is the necessity for a great number of specialists to work as a team for the various groups of organisms (Ciliata, Nematoda, Tardigrada, Harpacticoida, Ostracoda, Foraminifera, Diatomea, etc.).

Microbenthos is defined in this paper according to the following scheme proposed at the seminar on the "Quantitative Methods for Benthos Studies and Dimensional Scale of the Benthos" held at Marseilles in November, 1963:

Macrobenthos	Megistobenthos	
	Megabenthos	2 mm
Microbenthos	Mixobenthos	
	Meiobenthos	1 mm
	Nanobenthos	0.1 mm
	Hypobenthos	0.01 mm

Thus, the usage of the term microbenthos appears wider and slightly more imprecise than that of meiobenthos, which is fairly restricted and generally agrees with the opinions of different authors. It is, nevertheless, very difficult to find a precise basis for defining the size categories of benthos (McIntyre, 1969).

Other difficult problems in the study of subtidal benthos reside in the complexity of abiotic and biotic conditions of the shallow-water subtidal zone. A specific bathymetrical delimitation of intertidal zone is necessary. The scheme proposed by Pérès and Picard (1959) with regard to the range of benthal formations includes the subtidal zone infralittoral (in French terminology) as follows:

> L'étage infralittoral est limité vers le haut par le niveau à partir duquel les peuplements sont toujours, ou à peu près toujours immergés (toute émersion prologée entraînant la mort des espèces constituant le peuplement). Sa limite inférieure est celle qui est compatible avec la vie des Phanérogames marines ou des Algues photophiles. Le classement des algues en photophiles et sciaphiles est résolu par l'étude des passages lateraux par rapport aux Phanérogames marines prises comme base de référence.

The environmental factors of the shallow-water zone 20 to 30 m deep are in a state of perpetual instability. Environmental dynamism is quite amplified in estuarine regions. In shallow-water zones, topographical, geological, climatological, hydrological, hydrochemical, and even anthropological factors permanently interact and constantly change, and their actions upon marine organisms are complex and multilateral. Thus, as many environmental factors as possible should be recorded when studying the ecology of benthos.

As an example, wind, a complex meteorological factor, acts in many ways. It produces gales resulting in waves, forming currents, changing sea level, moving and replacing water masses, etc. Waves and currents, in turn, act directly or indirectly upon

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living organisms—such as displacing organisms from the substratum, moving them, or destroying them. Bottom topography may be modified, sediments moved and redeposited, sediment structure modified, and suspensions raised into the water mass thereby fertilizing it. By moving water masses, winds thus modify saline and thermic regimes, water transparency, and color. Thus, within a few hours, organisms of shallow zones can be exposed to waters of diverse properties and qualitatively to new environmental conditions (Gomoiu, 1968). This example, with its several aspects, illustrates the necessity of recording as many environmental factors as possible to obtain as complete an image as possible of the environment in which the organisms live.

In interpreting data and establishing causal connections, the complex action of environmental factors on the organism should be considered. Present-day tendencies of establishing connections between single environmental factors and the evolution of organisms should be avoided. Encountered are studies of the distribution of organisms or other aspects of their biology based on a single factor such as substratum, on organic substances, or other elements. Such relations undoubtedly are important, but they are insufficient. The parallel study of the action of different factors upon organisms, followed by studies of their combined influence which results in a complex physioecological study, will yield the clue to causalities and may explain the dynamics of benthal populations (Gomoiu, 1966).

Two difficult problems arise in a complex ecological study of meiobenthos: the collection of material and its processing and sorting. Various authors point out that small core tubes are convenient for collecting meiofauna. Core tubes are satisfactory under certain conditions, especially when one station and several samples are to be collected. How many depends on the distribution of organisms as determined by a preliminary study. The distribution of organisms is not uniform, most organisms having a patchy distribution. Thus, a very large number of small samples will be necessary from one station for statistical treatment of the material.

The collection of larger samples from greater areas, though necessitating more labor for processing (although subsamples may be taken for individual analysis), will yield better results as far as real meiobenthos abundance is concerned and perhaps will provide better correlation with the abundance of macrobenthos. It is up to each investigator to analyze his collecting and processing methods. Before starting a complex study on a large zone it is necessary to undertake a preliminary investigation in order to determine the most adequate methods.

Another widely discussed but unsolved problem which deserves particular attention is that of expressing biomass. Biomass has been expressed in various ways, including wet weight, dry weight, weight of ash, etc. Thus, it is very difficult to make comparisons and to realize the richness of meiobenthos from one zone to another. The author considers that the expression of meiobenthos biomass in wet weight, though apparently somewhat difficult, is the most adequate. The very etymology of the word "biomass" indicates that it must be considered as the weight of living matter. Meiobenthos enters the food chain in its natural, wet weight. Fish reserves are assessed and fishing or certain problems connected with their biology are expressed by wet weight. When biomasses are indicated in any form, conversion modalities should be specified or conversion tables given. Both biomasses and densities should be related to area dimensions which can easily be related to a square meter.

Romanian studies of bottom population dynamics in the Black Sea over the last ten years are characterized by a simultaneous approach to both macrobenthos and microbenthos. The importance of microbenthos has been shown many times in Romanian works (Bacescu, 1961, 1963, 1966).

A brief systematic survey of recent studies of Romanian Black Sea waters revealed over 160 microzoobenthonic and 210 microphytobenthonic species. Many of these are new species, not only for the Black Sea but to science. Thus, of 20 nematodes found, 3 were new to science; of 35 ostracodes, 8 were new species; of 6 oligochaetes, 2 were new; of 40 harpacticoids, 12 were described for the first time. All of these species were studied qualitatively, quantitatively, and seasonally (Bacescu, Dumitrescu, Manea, Por, and Mayer, 1957; Bacescu, Dumitrescu, Marcus, Paladian, and Mayer, 1963; Bacescu, Gomoiu, Bodeanu, Petran, Müller, and Stanescu, 1965; Bacescu, Gomoiu, Bodeanu, Petran, Müller, and Manea, 1965; Bacescu, Gomoiu, Bodeanu, Petran, Müller, and Chirila, 1967; Gomoiu and Müller, 1962).

Over 100 animal species were identified on the quartzose-micoceous fine-sand bottoms, a holocoenose characterized by the presence of the small bivalve *Corbula* Bruquière. Among these species more than 40 are typically psammothalassobiontic, i.e., living in sand and exhibiting special adaptations to life in sandy environments; the rest are more or less psammoxenic. Typical species include the harpacticoids *Ectinosoma intermedia* Nicholls, *Canuella perplexa* Scott, and *Canuella furcigera* Sars, the ostracode *Pontocythere bacescoi* (Caraion), the cumaceans *Pseudocuma longicornis maeotica* Bacescu and *Iphinoe maeotica* (Sov.) Bacescu, the amphipods *Bathyporeia guilliamsoniana* (Bate) and *Perioculodes longimanus* Bate, and various species of Archiannelida and Polychaeta including *Spio filicornis* O. F. Müller, *Nerine cirratulus* (Della Chaje), *Nephtyes* Cuvier, and *Glycera* Savigny. Some meiobenthic species are so numerous and so typical that they can be defined as well as the mollusc subcoenotic units. Thus, we can recognize the following subcoenoses: *Corbula-Chione-Harpacticus flexus, Corbula-Canuella, Corbula-Streblus,* etc.

The dominant meiobenthic organisms exhibiting the highest diffusion index in the sandy *Corbula* coenose include *Streblus* Fischer and *Ammovertellina* Cushman, 100 percent; *Canuella perplexa* and *Spio filicornis,* over 90 percent; *Ectinosoma* Boeck, *Microarthridion littorale* Poppe, and *Harpacticus flexus* Brady and Robertson, over 70 percent; *Ameira* Boeck, *Acartia* Dana, and *Parathalestris* Brady and Robertson, nearly 65 percent; *Leptinogaster histrio* (Pelseneer), *Pontocythere* Dobowsky, and *Asellopis* Brady and Robertson, nearly 60 percent.

On the littoral stony bottoms of the Romanian Black Sea, nearly 100 zoobenthonic species were identified, of which 73 belong to meiobenthos. Some meiobenthonic species are new to science (*Tegastes elenae* Marcus, *Mesochra pontica* Marcus, *Centroderes spinosus agigensis* Bacescu), many are new to the Pontic basin (*Amphiascella subdebilis* (Willey), *Psylocamptus minutus* Sars, *Tricoma nematoides* (Greeff), *Halichoanolaimus* DeMan), and many others are new to the Romanian fauna.

Beyond subtidal boundaries and toward the deeper water of the Romanian Black Sea coast there is a gradual disappearance of macrobenthic forms to a depth of 180 m. Only dwarfed specimens of *Terebellides stroemi* Sars can be found below 180 m, together with another few meiobenthonic species including species of *Lagena* Walker and Jacobs and a few nematodes of the genus *Sabatiera* deRouville which occur to a depth of 220 m. A new coenose was established in the Black Sea periazoic zone on the basis of the presence of certain meiobenthonic taxa dominated by the foraminiferan *Lagena,* the hydrozoan *Bougainvillea* Forbes, and the nematode *Spirina parazitifera.*

An analysis by groups of the main meiobenthic organisms of Romanian Black Sea littoral reveals the following. In terms of density, Foraminifera represent one of the main constituents of sediments and of the benthos of sandy zones, usually numerically exceeding the rest of the organisms. Of more than 50 species quantitatively reported from the Black Sea, the most abundant are *Ammonia becarri* (Linné) and *Ammovertellina prima* (Suley.), particularly in sandy bottoms, and species of *Lagena, Pyrgo* Defrance, and *Quinqueloculina* d'Orbigny in silty bottoms. Sometimes the Foraminifera from sand are so numerous that they give the sediment the appearance of a "pure culture." Cases in which the density of these Protozoa exceeds 4.5 million specimens/m^2 (= 215 g/m^2) are fairly common. Thus, Foraminifera constitute a fairly abundant and permanent source of food not merely for the small psammophagous organisms (the gastropod *Retusa* Brown for instance; Bacescu and Caraion, 1956) but also for some fishes which appear to select Foraminifera from the sand with great facility. There is no doubt that the nutritional value of Foraminifera is not of the same importance as that of copepodes, nematodes, or of many other meiobenthonic organisms as fish food, but they are at least equal and in proportion to that of molluscs.

Worm groups, including numerous meiobenthic forms, are well represented in all biotopes. The nematodes, including over 150 species in the Black Sea, are numerically dominant among the worms. The psammobionts, species living on or in sand, though small (mostly under 1 mm) and weighing between 0.003 and 0.0047 mg each, have an important role in the biocenose due to their ubiquitous nature (100 percent diffusion index) and the fact that their densities may easily exceed 250,000 specimens/m². The mesopsammic or interstitial worm fauna is dominated by *Enoplus littoralis* Filipjev, *Epsilonema* Steiner, *Sabatieria,* and others. Although the densities of nematodes are very high, their biomasses are small and their trophic importance is far from negligible. Nematodes represent the food of microphagous young fishes during this most critical period.

As nematodes are dominant in terms of density, the polychaetes are dominant in terms of biomass and contribute considerably to raising the general trophic value of biocenoses. Of the nearly 200 polychaete species in the Black Sea, the great majority are microbenthic, while the others have meiobenthic juvenile stages. In sand zones, the density of *Spio filicornis, Micronephtys stammeri* (Augener), and *Nephtys cirrosa* Ehler. determines the general abundance of polychaetes, which sometimes exceeds 10,000 specimens/m². Among petricolous species, *Grubea clavata* (Claparède) is found in densities of over 10,000 specimens/m², *Exagone gemmifera* Pagenstecher 50,000 specimens/m², and *Fabricia sabella* (Ehrenberg) 74,000 specimens/m².

Oligochaetes also play an important role in benthic economy. The 35 species known to occur in the Black Sea include *Peloscolex svirenkoi* (Jarus) and *Peloscolex euxinicus* Hrabe which may reach densities of 2,500 specimens/m². *Tubifex euxinicus* Hrabe, which is at the limit of microbenthos in size, reaches densities of 15,000 specimens/m².

Turbellaria are less abundant and their densities vary greatly. As many as 140 specimens have been recorded from 1 cm³ of sand. The Kinorhyncha are fairly abundant. In the more muddy zones the most abundant is *Echinoderes dujardini* Claparède, followed by *Pycnophies ponticus* (Reinhard) and *Pycnophies kielensis* (Zelinka). From more than 600 quantitative meiobenthos samples of the Romanian littoral, the highest density of kinorhynchs was 7,980 specimens/m². Among typical psammobiontic nemertines are the meiobenthic species *Arenonemertes microps* Friedrich, *Prostomatella arenicola* Friedrich, *Amphiporus* Ehrenberg, and *Pontolineus arenarius* G. I. Müller. These are, however, only of minor importance in terms of density and biomass in the economy of the cenoses. Although the other worms (Gastrotricha, 23 species; Rotifera, 11 species) have likewise been studied from the systematic point of view, they are not presently included in synecological studies.

Next to the worms, the crustaceans represent the group with the most numerous meiobenthic representatives. Crustaceans also are of high trophic value and of considerable importance in benthic economy. Among crustaceans, the major meiobenthic forms with respect to density and biomass are the copepods. Most species of this group are represented by harpacticoids, with the following species in the sand zones: *Canuella perplexa, Canuella furcigera, Ectionosoma elongatum* Sars, *Nannopus palustris* Brady, *Parathalestris harpacticoides* (Claus), *Harpacticus flexus, Ameira parvula* (Claus), *Microarthridion littorale, Asellopsis sarmatica* Jakubisiak, *Enchydrosoma longifurcatum* Brady, and *Stenhelia palustris* Brady. These species often are found in densities of the order of 150,000 to 170,000 specimens/m² depending on depth and season. *Microarthridion littorale* is the most abundant.

The ostracodes are represented in the Black Sea by nearly 50 species, and they have two typical psammobiontic representatives: *Cyprideis littoralis* Brady, occurring in the more freshwater zones, and *Pontocythere bacescoi,* a more halophilous and stenotopous species strictly limited to the *Corbula* cenose. The density of ostracodes generally is small, seldom exceeding a few hundred specimens/m².

Cumaceans and mysids are meiobenthic forms of a relatively small abundance, rarely reaching 5,000 specimens/m². Among the species living on sandy bottoms are *Iphinoe maeotica* Bacescu, *Pseudocuma ciliata* Sars, *Cumopsis goodsiri* (van Beneden), *Bodotria arenosa mediterranea* Stener, *Paramysis* Czerniavsky, and *Gastrosacus* Meyer.

The 107 species of amphipods are of particular importance in the Black Sea. Some species, including *Talorchestia* Dana, *Orchestia* Leach, and *Pontogammarus* Sowinsky, are dominant in certain biocenoses. They have large biomasses and, based on size, they are situated at the upper limit of meiobenthos. Restricted to the biocenose of fine sands with *Corbula* are *Bathyporeia guilliamsoniana* and *Perioculodes longimanus,* which are characteristically interstitial in the intertidal. Other species, including *Ampelisca diadema* (Costa), *Nototropis guttatus* (Costa), *Gammareus carinatus* Rathke, *Cardiophilus baeri* Sars, and *Corophium* Latrielle are either cenophilous, i.e., accidental occurrences, or originate from neighboring biotopes.

Psammobiontic isopodes (*Euridice pontica* Czerniavsky and *Euridice dollfusi marisnigri* Bacescu), inhabiting the upper intertidal and the wave-breaking zone, do not play an important role in benthic economy but do exhibit interesting adaptive characters.

In the Black Sea, only the most important groups with meiobenthic representatives that can be studied quantitatively from a single sample have been mentioned. There is no doubt that the list of Pontic basin meiobenthos is fairly long. Benthic ciliates alone total nearly 280 species and their contribution is far from negligible. This review emphasizes the contribution and role of meiobenthic elements, especially of the psammobiontic ones, in the framework of the bottom fauna rather than showing the relationship between organisms and environmental conditions which have been amply expounded in various Romanian ecological works (Bacescu, Dumitrescu, Manea, Por, and Mayer, 1957; Bacescu, Gomoiu, Bodeanu, Petran, Müller, and Stanescu, 1965; Bacescu, Gomoiu, Bodeanu, Petran, Müller, and Manea, 1965; Bacescu, Gomoiu, Bodeanu, Petran, Müller, and Chirila, 1967; Gomoiu, 1966, 1968, 1969; Gomoiu and Müller, 1962).

Another problem in meiobenthic ecology which will be emphasized is that of microphytobenthos. Among sources of food for benthos—other than animal and vegetable, organic debris, dead and dying animals, suspended plankton and organic detritus—algal microflora represent a highly importance source. Literature on the microflora of silty and rocky bottoms is rather abundant but studies of sandy bottoms are only beginning. Bodeanu has found in the last few years a varied and rich flora of psammophilous diatoms (Bodeanu, 1964, 1968).

Over 210 microbenthic diatoms species have been identified in the fine, quartziferous sand zone of the Romanian littoral. Most of these forms, represented by Pennata, are mobile, noncolonial diatoms and are adapted to the very harsh conditions of the sand biotope. Many of these are smaller than 20 μ. Not only are the psammobiontic microphytobenthos interesting from a qualitative point of view but the quantitative values recorded are quite striking.

The average size of sand grains on sandy bottoms is 90 μ at a depth of 8 to 16 m. Here, environmental conditions are rather constant as compared to those in shallower depth, and diatom concentrations of 85,600 cells/cm^2 (or 856,000,000 cells/m^2) have been recorded. These records are far higher than the number of planktonic microphyta in a cubic meter! In the Romanian littoral, the variable quantities of psammobiontic microphytobenthos have an average of about 72,000,000 cells/m^2 and 253 mg/m^2 (Bodeanu, 1968). In spite of these variations, the benthic microflora is still the only autotrophic photosynthesizing element that increases the primary trophic level, being the main supplier of psammobiontic microfauna food. Thus, the microphytobenthos is an important trophic element on the sea bottom, being a source of nutrition for many benthophagic animals, viz. filter feeding or actively "grazing" molluscs, ciliates, copepods, ostracodes, and certain fishes (juveniles of *Pleuronectres flesus* Linné, *Mugil* Linné, and, presumably, *Pomatoschistus microps* Kessler, *Callionymus belenus* Risso, *Blennus* Walbaum, etc.). The significance of the microphytobenthos in the nutrition of molluscs has been demonstrated (Bodeanu and Gomoiu, 1964). Analysis of the diet of ten mollusc species, mostly psammobiontic, yielded 92 microphytic species of which 75 species are exclusively benthic.

Thus, we see the great importance of meiobenthos in the economy of the sea. It is vitally necessary to analyze in detail the complex ecology of meiobenthos, as shown above, as well as all possible abiotic and biotic environmental factors.

Literature Cited

Bacescu, M.

1961. Cercetări fizico-chimice şi biologice româneşti la Marea Neagră, efectuate în perioada 1954-1959. *Hidrobiologia*, 3:17–46.

1963. Contribution a la biocoenologie de la Mer Noire. L'Étage périazoique et le faciès dreissenifère, leurs caractéristiques. *Rapports et Proces-Verbaux des Réunions, Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 17:107–122.

1966. Cercetări românesti privind microbentosul Mării Negre. *Studii si Cercetari de Biologie,* seria Zoologie, 18(5):415–423.

Bacescu, M., and F. E. Caraion

1956. Animale mîncătoare de Foraminifere. *Comunicările Academiei Republicii Populare Române,* 6(4):551–553.

Bacescu, M.; H. Dumitrescu; V. Manea; F. Por; and R. Mayer

1957. Les sables à *Corbulomya (Aloidis) maeotica* Mil.—base trophique de premier ordre pour les poissons de la Mer Noire. I. Aspect hivernal de la biocénose. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa,"* 1:305–374.

Bacescu, M.; E. Dumistrescu; A. Marcus; G. Paladian; and R. Mayer

1963. Données quantitatives sur la faune pétricole de la Mer Noire à Agigea (secteur Roumain), dan les conditions spéciales de l'année 1961. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa,"* 4:131–155.

Bacescu, M.; M. T. Gomoiu; N. Bodeanu; A. Petran; G. Müller; and S. Stanescu

1965. Recherches écologiques sur les fonds sablonneux de la Mer Noire (Côte Roumaine). *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa,"* 5:33–81.

Bacescu, M.; M. T. Gomoiu; N. Bodeanu; A. Petran; G. Müller; and V. Manea

1965. Studii asupra variaţiei vieţii marine în zona litorală nisipoasă la nord de Constanţa. *Ecologie Marină,* 1:7–138.

Bacescu, M.; M. T. Gomoiu; N. Bodeanu; A. Petran; G. I. Müller; şi V. Chirila.

1967. Dinamica populaţiilor animale şi vegetale din zona nisipurilor fine de la nord de Constanţa în conditiile anilor 1962–1965. *Ecologie Marină,* 2:7–167.

Bodenau, N.

1964. Contribution à l'étude quantitative du microphytobenthos du littoral roumain de la Mer Noire. *Revue Roumaine de Biologie,* series Zoologie, 9(6):435–445.

1968. Recherches sur le microphytobenthos du littoral roumain de la Mer Noire. *Rapports et Proces-Verbaux des Reunions, Commission Internationale pour l'Exploration Scientifique de la Mer Méditérranée,* 19:205-207.

Bodeanu, N., and M. T. Gomoiu.

1964. Données sur l'importance des microphytes dans la nourriture des Mollusques. *Revue Roumaine de Biologie,* series Zoologie, 9:211–220.

Gomoiu, M. T.

1966. Écodynamique du bivalve *Aloidis (Corbulomya) maeotica* Mil. de la Mer Noire. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa,"* 6:39–56.

1968. On the Effects of Water Motion on Marine Organisms in the Mesolittoral and Infralittoral Zones of the Rumanian Shore of the Black Sea. *Sarsia,* 34:95–108.

1969. Studiul sedimentelor nisipoase de la litoralul românesc al Mării Negre. *Ecologie Marină,* 3:227–325.

Gomoiu, M. T., and G. I. Müller

1962. Studies Concerning the Benthic Association Dominated by *Barnea candida* in the Black Sea. *Revue de Biologie, Académie de la République Populaire Roumaine,* 7:255-271.

McIntyre, A. D.

1969. Ecology of Marine Meiobenthos. *Biological Reviews,* 44:245-290.

Pérès, J. M., and J. Picard

1959. On the Vertical Distribution of Benthic Communities. *Preprints of the First International Oceanographic Congress, New York,* pages 349–350.

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Ecological Studies on Freshwater Meiobenthon in Layers of Sand and Gravel

ABSTRACT

The sand and gravel sediments of freshwater streams contain a rich meiofauna. The biotopes are considered as biozones of the groundwater ecosystem. The ecological relationships of the interstitial meiofauna to groundwater biotopes are discussed.

Investigation of interstitial water in benthal[1] layers of sand and gravel shows that the microcaverns in such subtrates can be typical biotopes of a rich freshwater meiofauna. Benthal biocoenoses of this sort can consist of freshwater organisms of the following taxa: Hydrozoa, Turbellaria, Nematoda, Oligochaeta, Cladocera, Harpacticoida, Cyclopoida, Syncarida, Amphipoda, Halacaridae, Hydrachnellae, and young larvae of insects. The biotopes of such benthal interstitial fauna are to be considered as biozones of the ecosytem "groundwater" (stygocoen). This concept is indicated by Thienemann (1925) in his definition of the term "ground water": "By ground water we mean all water under the surface of earth and circulating in the outermost crust of the earth." In this sense, water in interstitial benthal regions may be considered as a part of the groundwater. Moreover, Thienemann mentioned in this definition that groundwater can be in contact with surface water in the beds of rivers and lakes.

Nearly 20 years after the publication of the cited definition Chappuis (1942) discovered biocoenoses of stygobiont, stygophile, and stygoxene freshwater organisms living together in interstitial waters of sandy and gravelly riverbeds. His discovery (see also Chappuis 1944) and the investigations of other authors (Karaman, 1935; Angelier, 1953; Ruttner-Kolisko, 1953, 1954, 1956; Viets, 1955, 1959; Husmann, 1956; Motaş, 1958, 1962; Orghidan, 1959; Meštrov, 1960; Ponyi, 1960; Schwoerbel, 1961a,b, 1964, 1967; Picard, 1962; Štěrba, 1965; Bou and Rouch, 1967; Gourbault and Leisher-Moutoué, 1967; Rouch, 1968; Tilzer, 1968) have added new points of view in regard to benthal productivity, especially in sandy and gravelly riverbeds.

The stygophile meiofauna elements of such ecosystems have otherwise generally been found as sporadic individuals in deposits of mud and detritus or in moss (Dittmar, 1955; Illies, 1952). Apart from these investigations, most researchers have dealt particularly with the macrobenthon.

The investigations of interstitial benthal meiofauna, however, show that the interstitial waters of sandy and gravelly beds of streams are by far the princpal biotopes of these freshwater meio-organisms and also show the highest productivity in these ecosystems (Schwoerbel, 1967).

As mentioned, the biotopes of these benthal-mixed biocoenoses of stygobiont, stygophile, and stygoxene interstitial freshwater organisms are to be regarded as a part of the ecosytem "groundwater." This also seems to correspond to the similar biotopes of lakes (Noodt, 1952, 1954, 1955; Pen-

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[1] Terms ending in "al" describe a biotope, those ending in "on" describe a biocoenose, and those ending with "coen" describe the complete ecosystem.

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nak, 1939, 1940, 1951; Ruttner-Kolisko, 1953, 1954, 1956; Husmann, 1969).

The position of those benthal-mixed biocoenoses within the various communities of subterranean freshwater organisms may be determined by many-sided ecological investigations of groundwater fauna.

Investigations of the subterranean freshwater fauna in sandy and gravelly riverbeds as well as in wells, springs, and caves of a geomorphologically heterogeneous region in the Weser-System (Germany) produced the first information about the ecological relations of interstitial benthal to other groundwater biotopes (Husmann, 1956).

The clearly proved dependence of stygobiont groundwater organisms on the structure of the subterranean biotopes show that interstitial waters in sand and gravel were the main biotopes of nearly all the stygobionts caught. Continuous intersitial biotopes in layers of sand and gravel can reach from terraces and valley floors into sandy and gravelly riverbeds. Therefore, in such underground regions there are no ecological limits conditioned by substratum for interstitial groundwater organisms. Because of underground conditions of this sort, it is understandable that most of the stygobionts living in the interstitial underground water of terraces and valley floors also could be caught in interstitial waters of sandy and gravelly riverbeds (Figure 1).

Those stygobionts which are ubiquitous in waters of sand and gravel may, as already mentioned, form mixed biocoenoses with elements of the surface or epigean freshwater fauna.

The existence of two very different interstitial biozones results from the following underground ecological conditions: (a) subterranean, interstitial biotopes situated far from rivers and, moreover, extremely isolated from coenological influences of surface waters; and (b) benthal biotopes in layers of sand and gravel in riverbeds with coenological influences of the interstitial groundwater biocoenoses of the neighboring valley floor, and with immigration of organisms living in the connected surface water.

By and large, the first biozone is colonized by stygobionts, here and there united with extreme stygophile species that live there only sporadically. This stygozone, which is extremely isolated against coenological influences of surface-water biocoenoses, is to be regarded as the kernel zone of the ecosytem "stygocoen." It can be characterized by the designation "eustygocoen."

Because benthal biotopes in sand and gravel are biozones with coenological influences from groundwater and surface water, they can be characterized by demonstrable terms. Accordingly, the interstitial benthal ecozone of mountain streams was named "rhithrostygocoen" in reference to the surface-water ecosytem "rhithrocoen" (Illies, 1961; Husmann, 1970) and the groundwater ecosytem "stygocoen." In this way the interstitial stygozone of rivers (ecosystem "potamocoen") and of lakes (ecosystem "eulimnocoen") have been characterized as "potamostygocoen" and "eulimnostygocoen" (Husmann, 1970).

The colonization of intersitial biotopes in sand and gravel by elements of the freshwater intersitial fauna is dependent on the size of the interstitial spaces, which, in turn, depends on the grain size. The nature of substrate is to be seen, therefore, as the most important factor for the characterization of our interstitial biotopes.

The components of sand, gravel, and shingle are classified by geologists as "Psammite" (diameter, 2 to 0.02 mm) and as "Psephite" (diameter, 2 mm). Biotopes in psammite are named "mesopsammal" (Remane, 1940), those in psephite are called "mesopsephal" (Husmann, 1966). The biocoenoses living in these biotopes are "mesopsammon" and "mesopsephon."

Sandy and gravelly biotopes of intersitial ecozones and the biocoenoses living in them are marked more clearly with regard to the nature of substrate; for example, "eustygopsammal" (mesopsammal of eustygocoen) and "potamostygopsammon" (mesopsammon of ecosytem potamostygocoen). See Figures 2, 3.

The ecological system of benthal and eustygal interstitial freshwater biocoenoses given here may be completed by characterizing two other biotopes of benthal interstitial biocoenoses. One of these is to be found in sandy and gravelly deposits in the outflows of springs called "krenostygopsammal" and "krenostygopsephal," respectively. The other is the interstitial benthal of streams in caves called "troglostygopsammal" and "troglostygopsephal" (Figure 4).

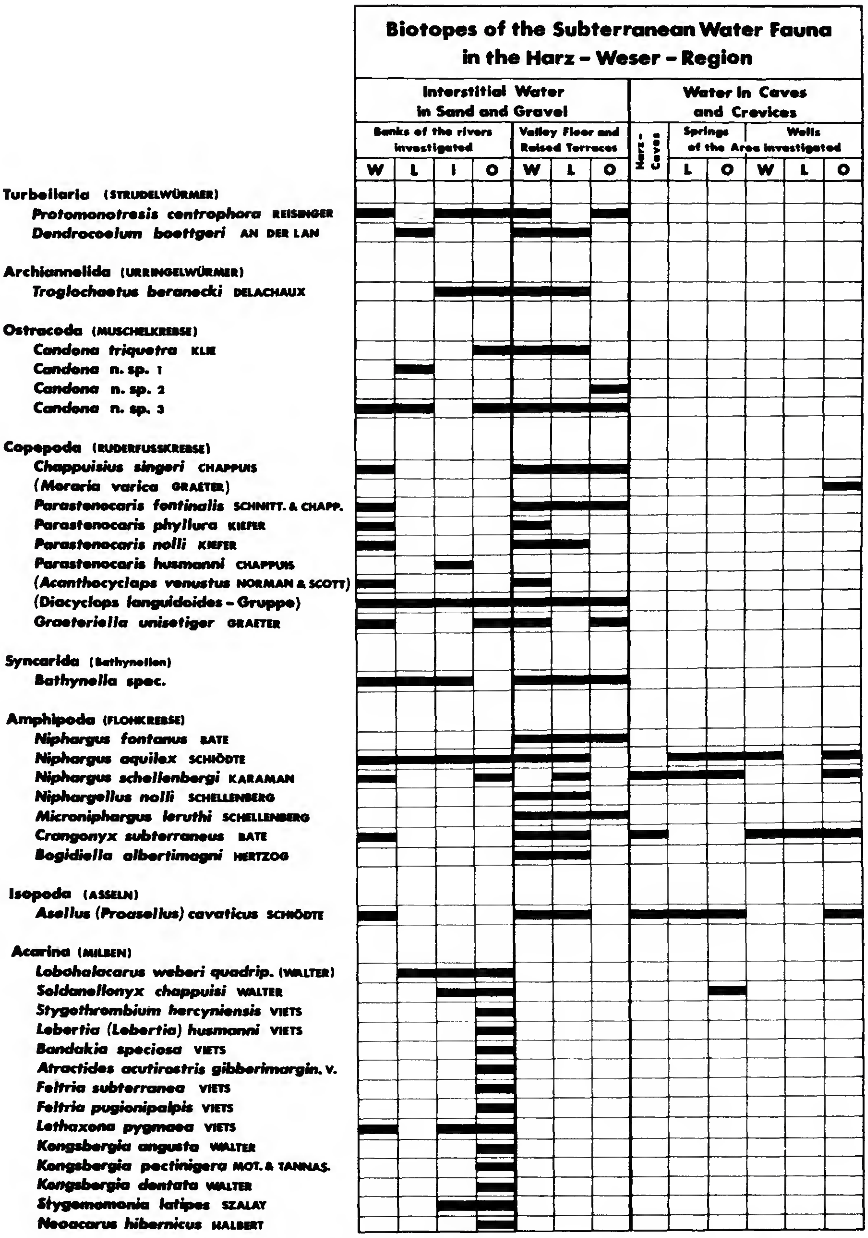

FIGURE 1.—The ecological distribution of stygobiont groundwater organisms in various valleys of the Weser-system (W, Weser; L, Leine; I, Innerste; O, Oker) and in caves of the Harz Mountains.

The limnobenthal interstitial-mixed biocoenoses "rhithrostygon," "potamostygon," and "eulimnostygon" cannot be separated from the coenologically isolated biocoenoses "eustygopsammon" and "eustygopsephon" (Figure 4) by clear ecological limits. On the contrary, there are between them biozones of ecological indistinctness which correspond to the zones of ecological "Unschärfe" of Schwabe and

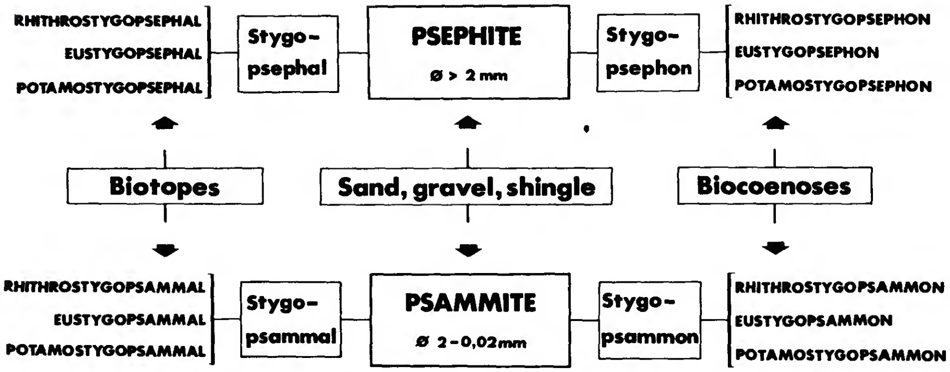

FIGURE 2.—Biotopes and biocoenoses of groundwater organisms in sand, gravel, and shingle of the following ecosystems: rhithrocoen (mountain streams, I, O, as in Figure 1); potamocoen (rivers in lowlands, W, L, as in Figure 1); and eustygocoen (underground of valley floors and raised terraces without coenological influences out of surface waters; see Figure 1).

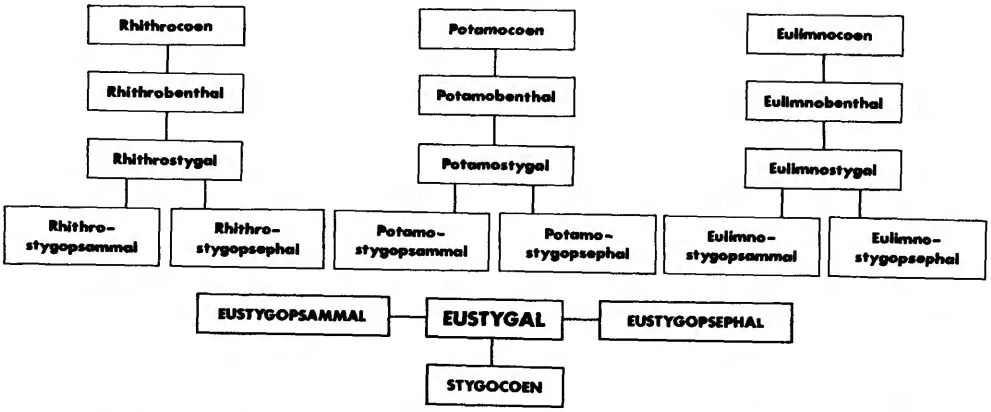

FIGURE 3.—The ecological system of groundwater biotopes in layers of psephites and psammites of benthal and eustygal underground regions.

Klinge (1960). The ecological indistinctness mentioned in such intermediary biozones is characterized by a diminution of stygophile freshwater organisms in proportion to the distance from benthal biotopes of the interstitial-mixed biocoenoses. With the increase in distance from the benthal interstitial biocoenoses there is an increase in the number of stygobionts until the coenological state of "eustygocoen" is reached (Figures 3, 4).

The variety of coenological conditions, depending on the distance from eustygon or from benthostygon, demonstrates the impossibility of integrating the biocoenoses of such intermediary biozones in a typological system. It is only possible to mark (as we have done) on both sides of these indefinite ecological border zones the clearly definable kernel regions "eustygocoen," respectively "rhithrostygal," "potamostygal," and "eulimnostygal" (Figure 3).

The mesopsammal and mesopsephal biotopes are found in deposits of varying size in the benthal and eustygal regions. Compared to the mesopsephal, the mesopsammal is found much more in nature. Apart from homogeneous deposits of sand in beaches of lakes or in banks of rivers, mesopsammal biotopes often fill the interstices in gravel and in coarse-grained rubble forming an interpsephite mesopsammal biotope. In this way the extent of

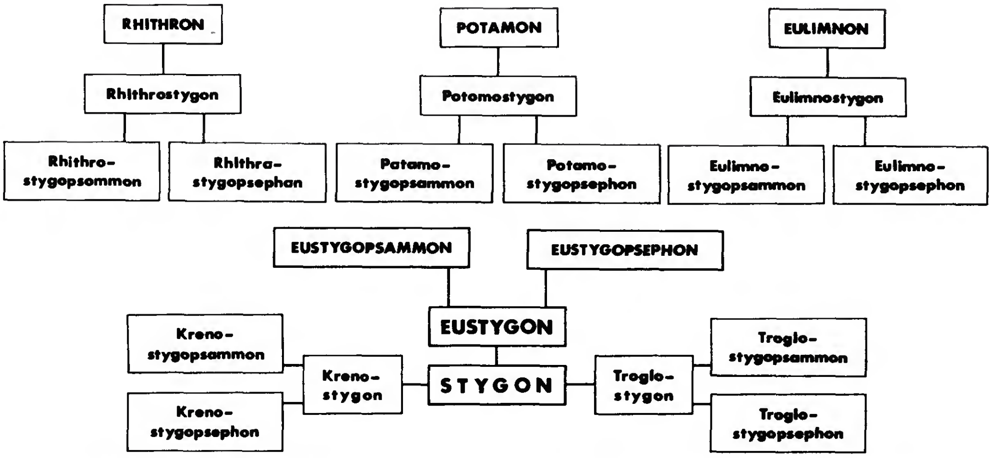

FIGURE 4.—The ecological system of groundwater biocoenoses in layers of psephites and psammites of eustygal and benthal underground regions including the groundwater fauna in caves (troglostygon) and springs (krenostygon).

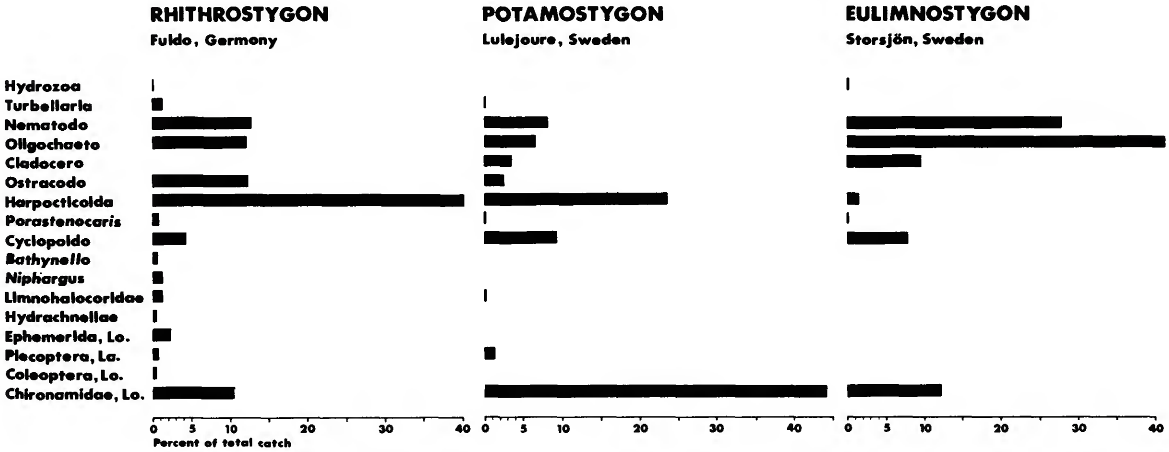

FIGURE 5.—The percentage quota of biomass from interstitial biocoenoses of sandy and gravelly benthal biotopes of a mountain stream (rhithrostygon; Fulda), of a lowland river (potamostygon; Lulejaure) and of a lake (eulimnostygon; Storsjön).

mesopsephal biotopes in mixed deposits of sand and gravel is greatly reduced. Consequently, most interstitial organisms in all the mentioned biotopes are recruited from elements of freshwater meiofauna (see Figure 1).

In benthal-mixed biocoenoses, Nematoda, Oligochaeta, Harpacticoida, and Cyclopoida comprise the most important meio-elements of interstitial biocoenoses. This applies to interstitial biotopes in European as well as in tropical regions (Figures 5, 6). In temperate and tropical regions species of the family Bathynellidae and of the copepod genus *Parastenocaris* Kessler are the most characteristic elements of mesopsammal freshwater meiofauna. This is so in the eustygocoen as well as in the rhithro-, potamo- and eulimnocoen. In contrast with stygobionts of such a ubiquitous occurrence in interstitial waters, many Hydrachnellae species are found only in the benthal interstitial of rhithrostygocoen. The ecological findings of investiga-

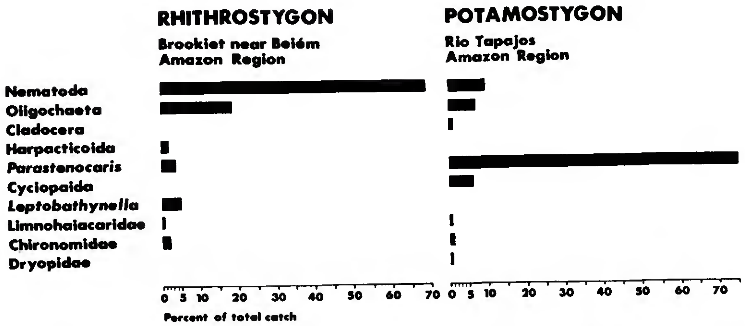

FIGURE 6.—The percentage quota of biomass from interstitial biocoenoses in tropical sandy and gravelly benthal biotopes of rhithrostygon (sampled by W. Sattler) and of potamostygon (sampled by H. Sioli).

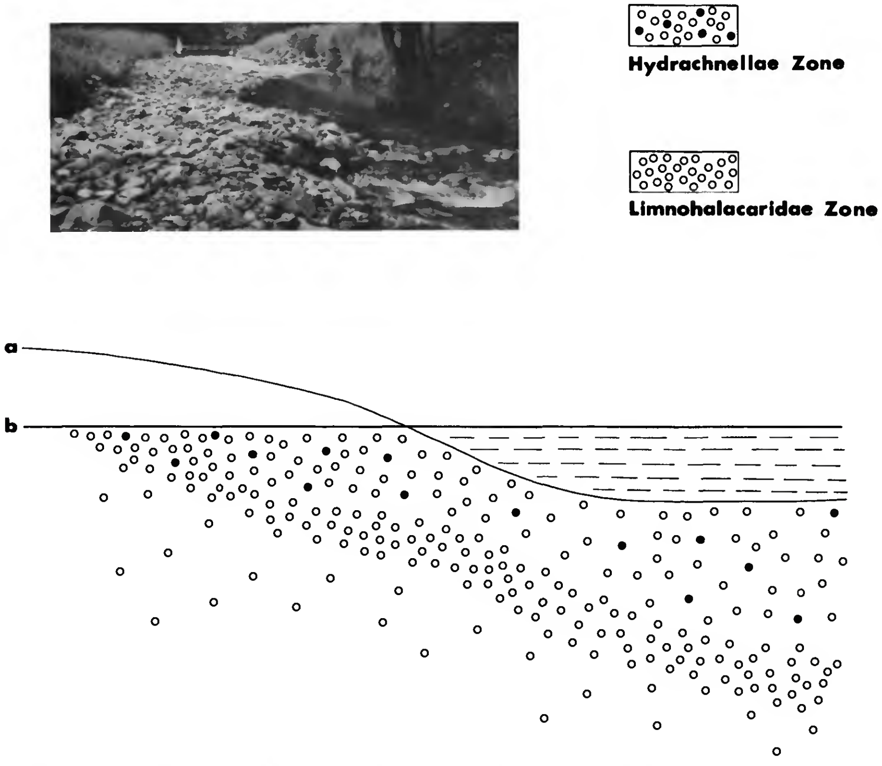

FIGURE 7.—The gravelly and sandy riverbed of the Oker mountain stream in the Harz Mountains with a schematic cross section of one riverside showing the distribution of Hydrachnellae and Limnohalacaridae in the interstices of substratum and, with this, the forming of the "Hydrachnellae Zone" and the "Limnohalacaridae Zone."

tions about the benthal interstitial fauna in rhithrostygocoen of European countries showed that coenobiont and coenophile Hydrachnellae are connected with Limnohalacaridae in their distribution in sandy and gravelly riverbeds. They can mark two biozones that are called the "Hydrachnellae zone" and the "Limnohalacaridae zone" (Husmann, 1966). See Figure 7. The biocoenoses of eustygo-

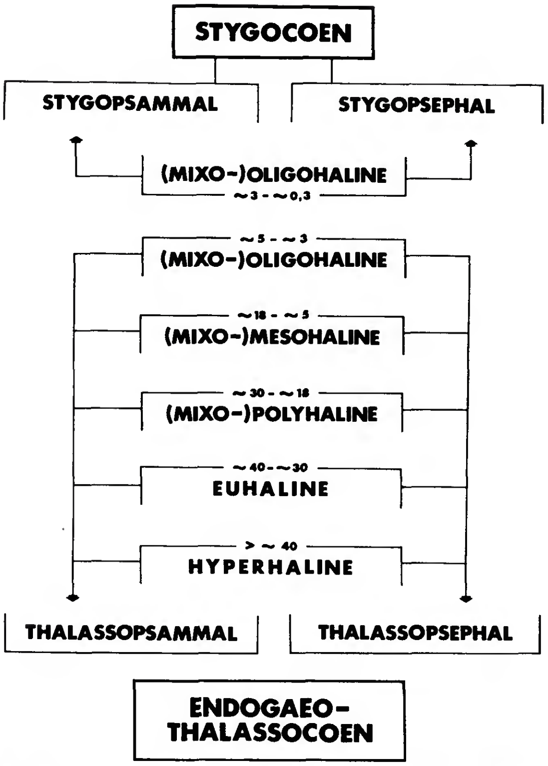

FIGURE 8.—Zones of halinity in the mesopsammal and mesopsephal passage between stygocoen and endogaeo-thalassocoen with marks of salinity (ppt).

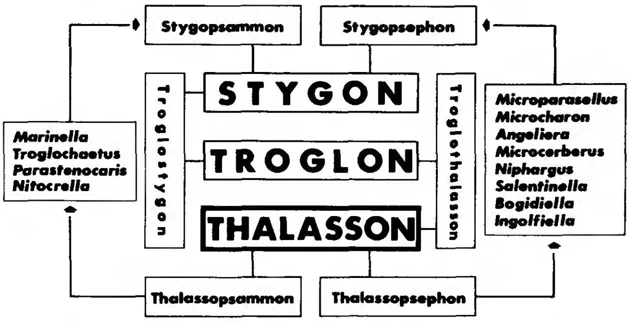

FIGURE 9.—Mesopsammal and mesopsephal stygo-organisms of marine origin and their distribution in subterranean freshwater biocoenoses.

coen may also be characterized by stygobionts, which are found only in these coenologically isolated regions (Figure 1).

As mentioned earlier, the interstial benthal biocoenoses rhithrostygon, potamostygon, and eulimnostygon exist in the ecological periphery of the interstitial groundwater eco-region, which is characterized by mixed biocoenoses of stygobiont, stygophile, and stygoxene freshwater meio-organisms.

The benthal coenoses rhithrostygon, potamostygon, and eulimnostygon are not the only mixed biocoenoses on the ecological periphery of the stygocoen. Coastal groundwater is another such mixed biocoenosis; it is composed of elements of stygon and those of the neighboring interstitial marine water.

The coastal groundwater biocoenosis is of special importance because the (mixo-) oligohaline thalassopsammal and thalassopsephal zones are to be regarded not only as zones of ecological contact between marine and limnic meiofauna (Figure 8) but also as palaeobiotopes of a number of stygobiont freshwater organisms which have immigrated into the benthal and eustygonal biotopes of the limnic groundwater fauna (Figure 9).

So, the ecological problems of the coastal groundwater form a meeting point for meiobenthologists of marine and freshwater ecology, and the many common problems (Husmann, 1967) may give rise to a cooperation of marine ecologists and limnologists.

Literature Cited

Angelier, E.
1953. Recherches écologiques et biogéographiques sur la faune des sables submergés. *Archives de Zoologie Expérimentale et Générale,* 90(2):37-161.

Bou, C., and R. Rouch
1967. Un nouveau champ de recherches sur la faune aquatique souterraine. *Comptes Rendus de l'Académie des Sciences,* series D, 265:369-370.

Chappuis, P. A.
1942. Eine neue Methode zur Untersuchung de Grundwasserfauna. *Acta Scientifica Mathematica et Naturalia Universitalis Francois-Joseph,* 6:1-7.
1944. Die Grundwasserfauna de Körös und des Szamos. *A Magyar Tudomanyos Akademia Kiadasa,* pages 1-42.

Dittmar, H.
1955. Ein Sauerlandbach. Untersuchungen an einem Wiseen-Mittelgebringsbach. *Archiv für Hydrobiologie,* 50:305-552.

Gourbault, N., and F. Lescher-Moutoué
1967. Sur la Faune hypogée peuplant le sous-écoulement d'une rivière de moyene altitude. *Comptes Rendus de l'Académie des Sciences,* series D, 265:1813-1816.

Husmann, S.
1956. Untersuchungen über die Grundwasserfauna zwischen Harz und Weser. *Archiv für Hydrobiologie,* 52:1-184.
1966. Versuch einer ökologischen Gliederung des interstitiellen Grundwassers in Lebensbereiche eigener Prägung. *Archiv für Hydrobiologie,* 62:231-268.
1967. Klassifizierung mariner, brackiger und limnischer Grundwasserbiotope. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 16:271-278.
1970. Weitere Vorschläge für eine Klassifizierung subterraner Biotope und Biocoenosen de Süsswasserfauna. *Internationale Revue de gesamten Hydrobiologie,* 55:115-129.

Illies, J.
1952. Die Mölle. Faunistisch-ökologiesche Untersuchungen in einem Forellenbach im Lipper Bergland. *Archiv für Hydrobiologie,* 46:424-612.
1961. *Die Lebensgemeinschaft des Bergbaches.* 106 pages. Leipzig: Willy Kolbe.

Karaman, S.
1935. Die Fauna der unterirdischen Gewässer Jugoslaviens. *Verhandlugen der Internationale Vereinigung für Theoretische und Angewandte Limnologie,* 7:46-73.

Kulhavý, V.
1961. Über das Vorkommen der west- und osteuropäischen Elemente in der Crustaceenfauna der böhmischen unterirdischen Gewässer. *Acta Societatis Zoological Bohemoslovenicate,* 25:297-301.

Meštrov, M.
1960. Faunistisch-ökologische und biozönologische Untersuchungen unterirdischer Gewässer des Savetales. *Biološki Glasnik,* 13:73-109.

Motaş, C.
1958. Freatobiologia, a noua ramura a Limnologiei. *Natura,* 10:95-105.
1962. Proédés de sondages phréatiques. Divisione du domaine souterrain. Classification écologique des animaux souterrains. Le psammon. *Acta Musei Macedonici Scientiarum Naturalium, Skoplje,* 8:135-173.

Noodt, W.
1952. Subterrane Copepoden aus Norddeutschland. *Zoologischer Anzeiger,* 148:331-341.
1954. Copepoda Harpacticoida aus dem limnischen Mesopsammal der Türkei. *Veröffentlichungen der Hydrobiologischen Naturwissenschaftlichen Fakultät der Universität Istanbul,* 2:27-40.
1955. Limnisch-subterrane Harpacticoiden (Crust. Cop.) aus Norditalien. *Zoologischer Anzeiger,* 154:78-85.

Orghidan, T.
1959. Ein neuer Lebensraum des unterirdischen Wassers: der hyporheische Biotop. *Archiv für Hydrobiologie,* 55:392-414.

Pennak, R. W.
1939. A New Copepod from the Sandy Beaches of a Wisconsin Lake. *Transactions of the American Microscopial Society,* 58:224-227.
1940. Ecology of the Microscopic Metazoa Inhabiting the Sandy Beaches of some Wisconsin Lakes. *Ecological Monographs,* 10:537-615.
1951. Comparative Ecology of the Interstitial Fauna of Fresh Water and Marine Beaches. *Annales de Biologie,* 27:449-480.

Picard, J. Y.
1962. Contribution à la connaissance de la faune psammique de Lorraine. *Vie et Milieu,* 13:471-505.

Ponyi, J.

1960. Über im interstitialen Wasser der sandigen und steinigen Ufer des Balaton lebende Krebse (Crustacea). *Annales de Biologie Tihany,* 27:85–92.

Riemann, F.

1966. Die interstitielle Fauna im Elbe-Aestuar. Verbreitung und Systematik. *Archiv für Hydrobiologie,* supplement, 31:1–279.

Remane, A.

1940. Einführung in die Zoologische Ökologie der Nord- und Ostsee. *Tierwelt der Nord- und Ostsee.* 238 pages.

Rouch, R.

1968. Contribution à la connaissance des Harpacticides hypogés (Crustacés-Copépodes). *Annales Spéléologie,* 23:5–167.

Ruttner-Kolisko, A.

1953. Psammostudien I. Das Psammon des Torneträsk in Schwedisch-Lappland. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse,* 162:129–161.

1954. Psammostudien II. Das Psammon des Erken in Mittelschweden. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse,* 163:301–324.

1956. Psammonstudien III. Das Psammon des Lago Maggiore in Oberitalien. *Memorie dell' Istituto Italiano Idrobiologia,* 9:365–402.

Schwabe, G. H., and H. Klinge

1960. Gewässer und Boden als Forschungsgegenstand. *Anales de Edafologia y Agrobiologia,* 19:519–568.

Schwoerbel, J.

1961a. Über die Lebensbedingungen und die Besiedlung des hyporheischen Lebensraumes. *Archiv für Hydrobiologie,* Supplementband 25:182–214.

1961b. Subterrane Wassermilben (Acari: Hydrachnellae, Porohalacaridae und Stygothrombiidae), ihre Ökologie und Bedeutung für die Abgrenzung eines aquatischen Lebensraumes zwischen Oberfläche und Grundwasser. *Archiv für Hydrobiologie,* Supplementband, 25:242–306.

1964. Die Bedeutung des Hyporheals für die benthische Lebensgemeinschaft der Fliessgewässer. *Verhandlungen der Internationale Vereinigung für Theroretische und Angewandte Limnologie,* 15:215–226.

1967. Das hyporheische Interstitial als Grenzbiotop zwischen oberirdischem und subterranem Ökosystem und seine Bedeutung für die Primär-Evolution von Kleinsthöhlenbewohnern. *Archiv für Hydrobiologie,* Supplementband 33:1–62.

Štěrba, O.

1965. Plazivsky (Copepoda, Harpacticoida) Moravy a Slovenska. *Acta Universitatis Palakianae Olomucensis,* 19: 203–313.

Thienemann, A.

1925. *Die Binnengewässer Mitteleuropas. Die Binnengewässer I.* 255 pages. Stuttgart: Schweizerbart.

Tilzer, M.

1968. Zur Ökologie und Besiedlung des hochalpinen hyporheischen Interstitials im Arlberggebiet (Österreich). *Archiv für Hydrobiologie,* 65:253–308.

Viets, K.

1955. In subterranen Gewässern Deutschlands lebende Wassermilben (Hydrachnellae, Porohalacaridae und Stygothrombiidae). *Archiv für Hydrobiologie,* 50: 33–63.

1959. Die aus dem Einzugsgebiet der Weser bekannten oberirdisch und unterirdisch lebenden Wassermilben. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* 6:303–513.

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On Changes of the Interstitial Water after Decomposition of Organic Matter

ABSTRACT

The production of NH_4^+, NO_2^-, and NO_3^- from decaying organic matter under laboratory conditions was investigated in a series of experiments utilizing various grain sizes of sediment. The relationship between the production of these compounds and various environmental parameters (pH, alkalinity, and oxygen) is noted and the relationship between the products of decay investigated and grain size is discussed.

It often has been reported in studies carried out on meiofauna that certain groups of organisms have disappeared when the same place was re-investigated at a later date. Investigations have shown that interstitial water does not necessarily have the same chemical composition as the surrounding water above the bottom—for example, the flotsam lying on the bottom had eutrophied the interstitial water. Initially, the oxygen content was reduced. Such changes in the environment can take place very rapidly. It may be that this condition could cause the disappearence of a population of a certain species (Kühl and Mann, 1966a,b).

Previously, the author found that in a large bed of *Mya arenaria* about 80 percent of the individuals had died in a short period of time. The excavated sediment had a strong odor of H_2S and a black color to a depth of 20 cm. The density of the *Mya* population was about 100 to 150 specimens/m^2 (Kühl, 1952). The question arose as to what would happen to the decomposition products of larger macro-organisms—such as molluscs, worms, etc.—that are produced in the sediment at a certain depth. Do such products come to the surface water; are they partially washed away; or do they remain in the sediment, and, if so, to what extent do they influence the surrounding interstitial water?

The experiments reported in this paper were a continuation of previous investigations on nitogen metabolism in aquaria (Kühl and Mann, 1956, 1961, 1962). The organic breakdown was not investigated during these experiments but has been studied by Hecht (1933) and Krause (1959, 1961). Only the final products of decay—including NH_4^+, NO_2^- and NO_3^-, which can be poisonous to organisms—water temperature, salinity, pH, alkalinity, and oxygen content were investigated. The methods used were the same as in the previous experiments (Kühl and Mann, 1956, 1961, 1962).

The experiments were conducted in unaerated, 5-liter aquaria. From 5 to 10 g of mussel flesh (*Mytilus* and *Mya*) was put into the sediment at a depth of 5 cm. Four different grain sizes were used —mud, sand, and two different coarse sands with broken shells (Figure 1). The sediment was washed and dried, but not ashed. A control experiment without flesh demonstrated the normal decomposition, of importance especially in the mud series. Further experiments were made in glass tubes with lengths of 30 and 55 cm and a diameter of 5.5 cm. The tubes had two and five lateral outlets. In this way the dispersal of the decomposition products could be determined.

In the first series of experiments (series 1), 5 g of *Mya* flesh were placed in three separate aquaria. In aquarium 1, the flesh was placed on the surface of the sediment; in aquarium 2, the flesh was placed

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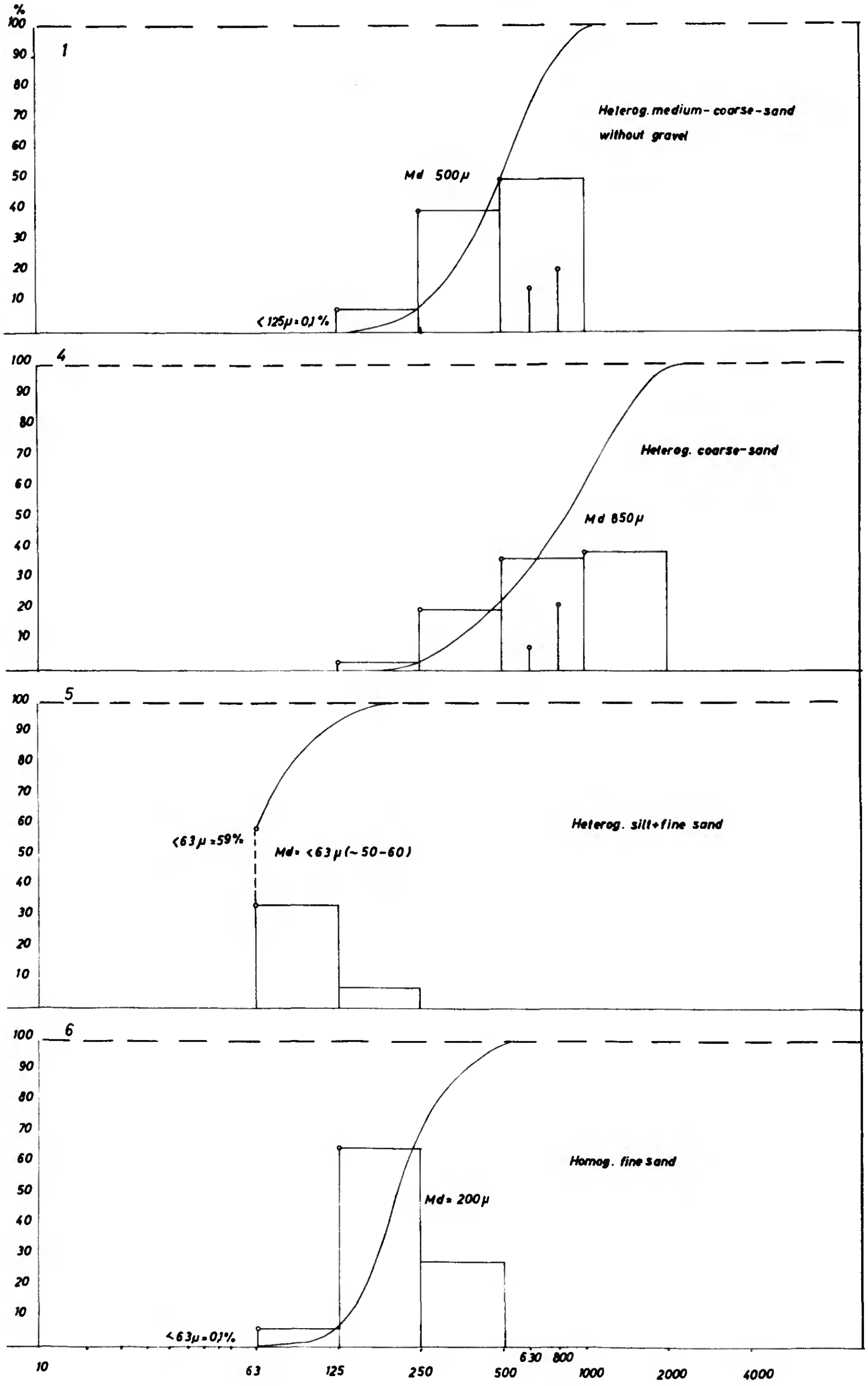

FIGURE 1.—Grain size of the bottom material used in experiment series 2–5.

into sandy mud sediment. Aquarium 3 served as a control, i.e., no *Mya* flesh was placed in the aquarium. This series was conducted from 13 May 1953 to 17 June 1953; the salinity was 22.43 ppt and the water temperature 16.5° to 22.8° C. The results of this series are shown in Figure 2. The ammoni-

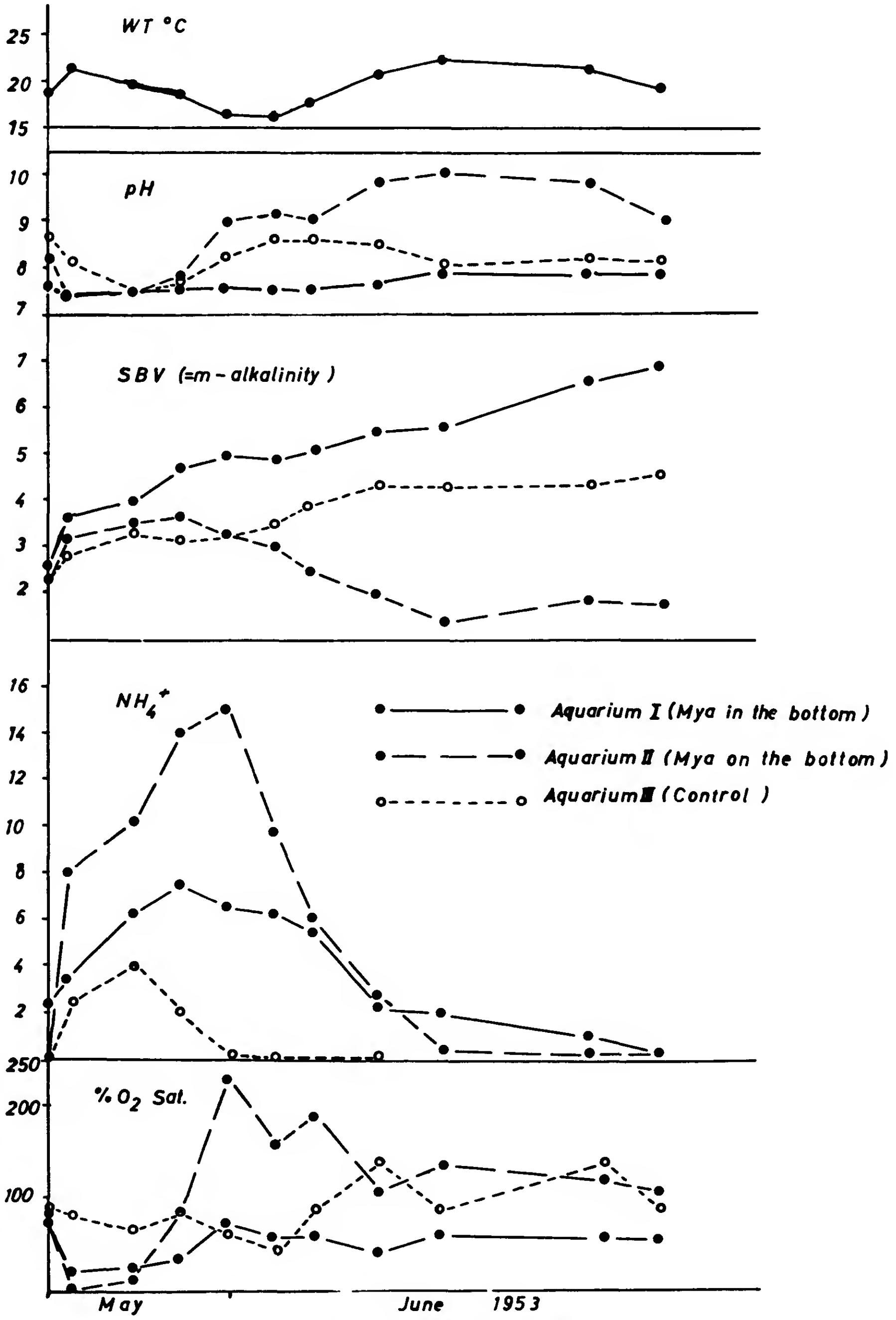

FIGURE 2.—Experiment series 1.

fication started immediately after beginning the experiment. In aquarium 1, the highest ammonia content, 15 mg/liter, was found after 19 days. In aquarium 2 there was decay in the sediment and NH_4^+ was found in the surrounding water but after 13 days the NH_4^+ content was only half that of aquarium 1. In aquarium 3, without additional organic matter, NH_4^+ appeared to be coming from the muddy sediment and the maximum of 4 mg/liter was found within 9 days.

Nitrite and NO_3^- were not detected before the end of the experiment in aquarium 1. In aquaria 2 and 3 quantities of these compounds were very low, a maximum of 0.8 mg NO_2^- and 0.4 mg NO_3^-. In aquarium 3 these compounds were detected at the beginning of the experiment and disappeared later.

The pH and alkalinity differed significantly in the three experiments. In aquarium 1 green algae began to grow on June 1. The pH increased rapidly, the alkalinity decreased, and the oxygen content reached very high values (238 percent oversaturation) as a result of assimilation. The pH and alkalinity cycles were more normal in aquaria 2 and 3; the alkalinity showed slightly more increase in aquarium 2 than in aquarium 3.

The loss of oxygen in aquaria 1 and 2 was very clear, with an increase beginning after one week. In aquarium 2 the oxygen content was not very high, about 50 percent of saturation.

The experiments of series 2 involved the use of two types of sediment of different grain size, one being coarse sand (500 μ) and the other coarse sand with some shell particles (850 μ). Four aquaria, with the following combinations, were used: aquarium 1, 5 g of *Mytilus* flesh placed within 500-μ sediment; aquarium 2, 5 g of *Mytilus* flesh placed on the surface of the 500-μ sediment; aquarium 3, control, only 500-μ sediment; and aquarium 4, 5 g of *Mytilus* flesh placed within 850-μ sediment. The experiment was conducted from 8 March 1968 to 22 April 1969; the salinity was 31.13 ppt and the water temperature was 19.6° to 22.6° C.

In aquarium 3, the control, no nitrification was observed during the experiment because the sandy bottom was without additional organic matter. The pH values were 8.0 to 8.1. Within 40 days the alkalinity increased from 2.5 to 2.9. The oxygen content varied between 89 and 140 percent of saturation. In aquarium 2, decomposition occurred on the surface of the sediment and ammonification started immediately; the maximum of 6.5 mg/liter NH_4^+ was reached after 14 days. After an additional 14 days the NH_4^+ disappeared (Figure 3). In aquarium 1 with mussel flesh in the sediment, ammonification was observed after 12 days, and the maximum (7 mg/liter) was reached a week later. Ammonification in aquarium 4, with coarse sandy sediment, started within 4 days from the beginning of the experiment. The amount of ammonification was higher than in aquaria 1 and 2. After the decrease of NH_4^+, the formation of NO_2^- and NO_3^- in aquarium 1 was less than in aquaria 2 and 4. The disappearance after a short time apparently was caused by the growth of a diatom layer on the bottom.

The changes in the oxygen content were very interesting. As expected, the oxygen content in aquarium 2 was reduced to a minimum after a short time. Fourteen days later, an increase began approaching 100 percent saturation. Similarly, but some days later, the oxygen in aquarium 4 diminished; on the other hand, the oxygen deficit was not so obvious in aquarium 1, with the decrease reaching only 70 percent of saturation. A second decrease of oxygen probably was caused by the oxidation of nitrogen compounds.

The experiments of series 3 were designed to compare decomposition of mussel flesh in four different sediments of different grain size. In aquarium 1, 5 g of mussel flesh was placed 5 cm deep in sand having a median diameter of 500 μ; in aquarium 4, the same, except for the sediment, which was coarse sand with a median diameter of 850 μ; in aquarium 5, the same, except with mud (median diameter, 50 to 60 μ); in aquarium 6, the sediment was fine sand (median diameter, 200 μ).

This series of experiments was conducted from 7 May 1968 to 21 June 1968; the salinity was 34.08 ppt and the water temperature 19.2° to 21.8° C. As seen in Figure 4, ammonification occurred in all aquaria. In the aquaria with sand—aquaria 1, 4, and 6—ammonification started after 14 days. The maximum value was between 2 and 3 mg/liter NH_4^+. This was contrary to the results in aquarium 5, with the mud layer. Ammonia appeared in the water 30 days later and very quickly reached a high

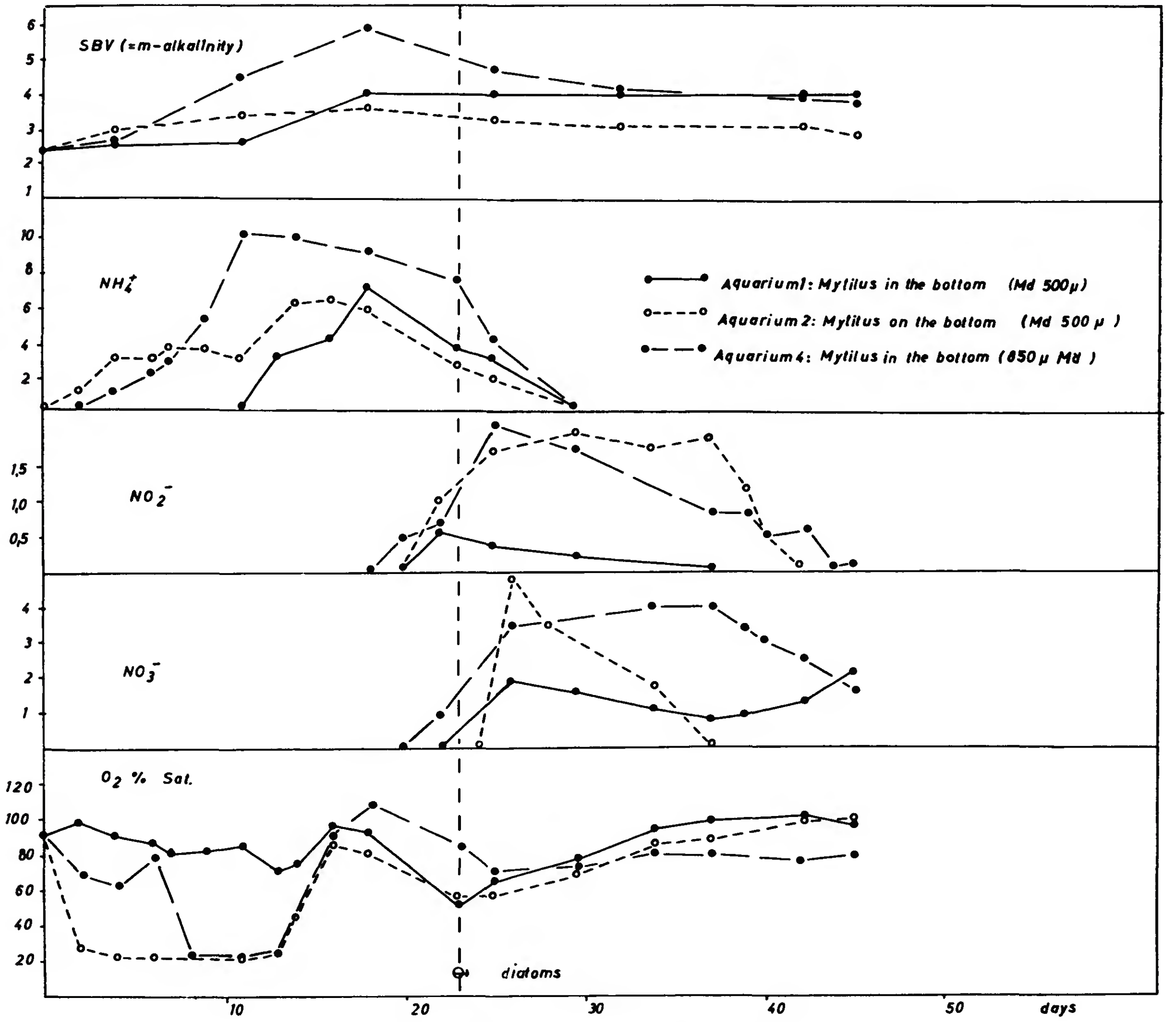

FIGURE 3.—Experiment series 2.

value of 18 mg/liter. In the control (mud) the ammonification began sooner and increased to a high amount (Figure 4). This apparently was caused by organic substances in the mud layer. The formation of NO_2^- and NO_3^- in aquarium 5 was higher than in the other aquaria. Nitrate was seen only for a short time, probably because diatoms grew on the bottom. The oxygen content decreased before the ammonification started in aquarium 5. The loss of oxygen was high; in the other aquaria the oxygen was reduced to 10 to 40 percent saturation.

In series 4, sand (median diameter, 500 µ) was placed in a glass tube that was 55 cm long and 5.5 cm in diameter and that had outlets at 10 cm intervals. Five grams of *Mytilus* flesh was placed at a depth of 18 cm between outlets 2 and 3 (Figure 5). This experiment was conducted from 25 April 1968 to 21 June 1968; the salinity was 31.5 ppt and the water temperature was 19.8° to 22.5° C. After three days the sediment surrounding the mussel flesh turned black. Within the next eight days the zone of reduction extended downward to the bottom of the tube, but not to the upper end at outlet 2. The ammonification was strongest at

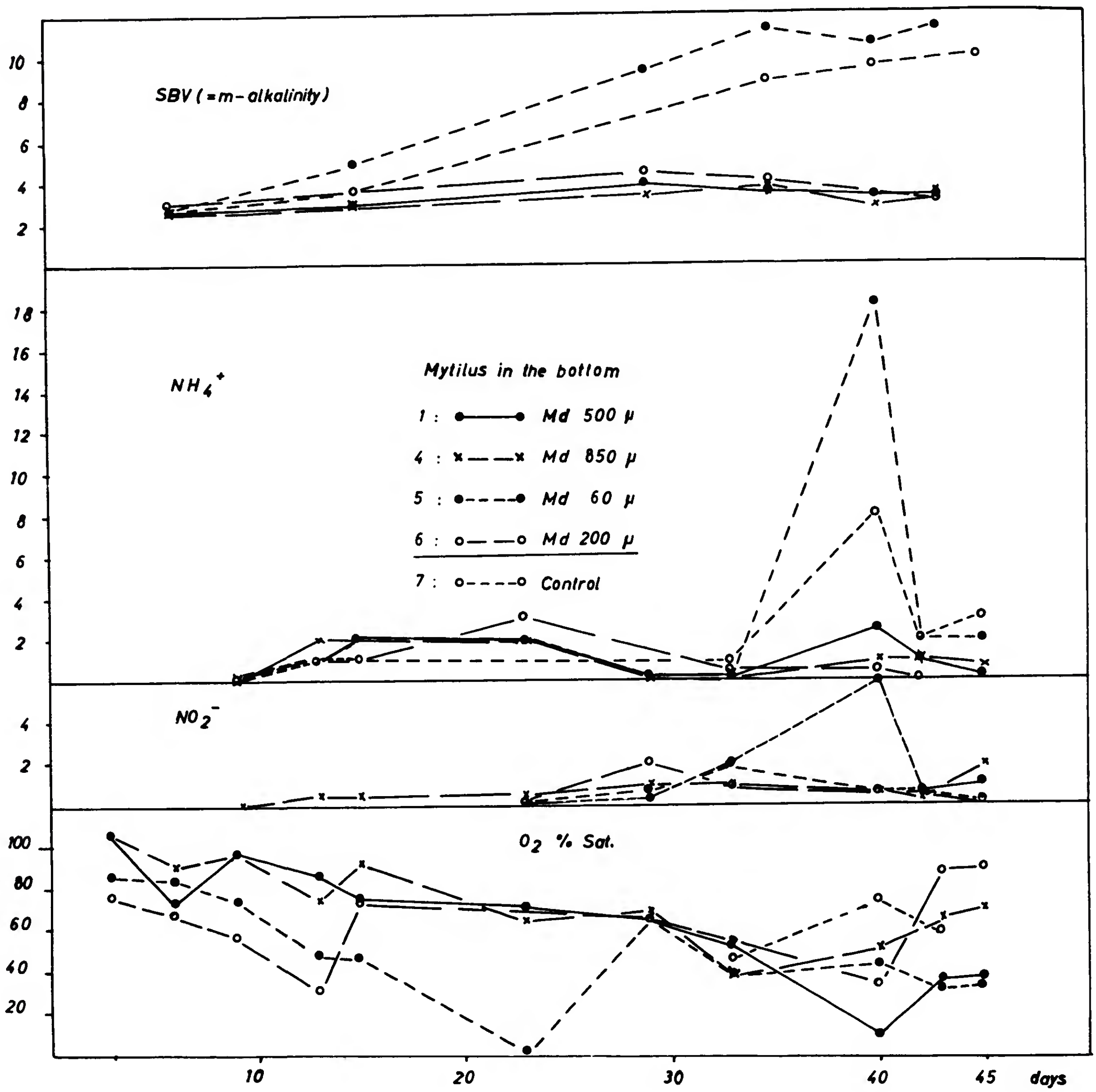

FIGURE 4.—Experiment series 3.

outlet 3 (Figure 5) and less at outlets 4 and 5. Above outlet 3, no NH_4^+ was observed. After 30 days NO_2^- appeared at outlet 2 above the decay (Figure 5).

Series 5 was a similar experiment, except that the glass tube was 30 cm long and 5.5 cm in diameter and had two outlets at a distance of 10 cm. The tube was filled with coarse sand mixed with broken shell (median diameter, 850 μ) and 5 g of *Mytilus* flesh was placed at a depth of 15 cm between outlets 1 and 2.

This experiment was conducted from 30 June 1968 to 29 August 1968; the salinity was 34.5 ppt and the water temperature was 21.3° to 23.0° C.

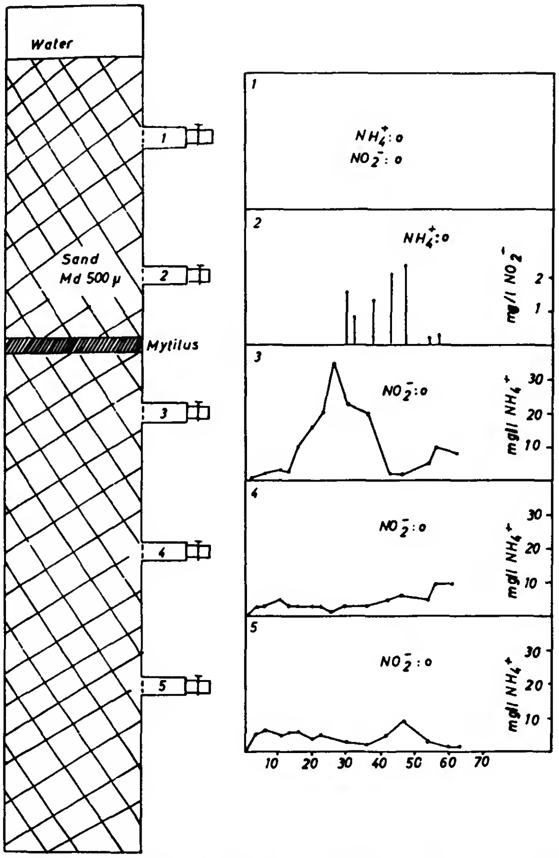

Figure 5.—Experiment series 4, decomposition of *Mytilus* flesh in a glass tube with five outlets in a sand (Md, 500 µ).

The results were very similar to those of series 4, with differences caused by the use of sediment of a different grain size. The black coloring below appeared sooner, reaching the lower end after 5 days, but the reduction zone extended above outlet 1. The oxidation zone was only some centimeters broad and the limit not sharp.

The formation of NH_4^+ was very intensive in the region of the mussel flesh. The maximum of 40 mg/liter was reached after ten days, and the decrease was very slow. Ammonification was observed at the upper outlet 1, the maximum being 12 mg/liter. Nitrite and NO_3^- appeared only at outlet 1, above the decomposition spot.

The decomposition of organic substances in the water column or in the bottom sediments is a complex interaction of abiotic and biotic factors. Likewise, nitrogen metabolism is of considerable complexity (Brand, Rakestraw, and Renn, 1937, 1939; Cooper, 1937; Postma, 1966; Ulken, 1963; Wuhrmann and Woker, 1948, 1953). Botan, Miller, and Kleerekooper (1960) report eleven reaction stages. In the experiments reported here, only NH_4^+ and the nitrification from NO_2^- to NO_3^- (series 2 and 3) were analyzed.

Ammonia compounds can split in the following manner: $NH_4^+ + OH^- \rightleftharpoons NH_3 + H_2O$, depending on water temperature and pH. It is NH_3 that is very poisonous to organisms. Several groups of bacteria participate in all the transformations of NH_4^+ to NO_3^- but with different requirements of oxygen. Nitrogen metabolism (denitrification) can be reversed, $NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+$ (Gessner, 1960; Green, 1968).

In previous experiments on nitrogen metabolism in aquaria (Kühl and Mann, 1956, 1961, 1962) it was found that ammonification proceeds rapidly through biological activity. In aerated water, with abundant oxygen, the decay is accelerated, the ammonification is abbreviated, and the formation of nitrite and nitrate increases. During this process, oxygen diminishes as a result of oxidations. The loss of oxygen by biological activity remains the same.

Nitrification is completed earlier in fresh water than in brackish water or seawater, but the quantity of nitrites and nitrates increase with increased salinity. If algae or other plants are present, the nitrate suddenly disappears.

The experiments on the decay of organic matter in bottom sediments indicate that the above processes are the same as in the water column but are modified by grain size, morphology of the grains, pore volume or actual water content of the pore space, rate of diffusion, and oxygen content. The products of decomposition can appear on the surface of the sediment and in the water column. The nitrates, or, in the case of denitrification, ammonia, can be an important factor in the formation of a layer of diatoms on the sediment.

Berner (1963) conducted experiments similar to those reported in this paper. Bick (1964) studied the production and toxicity of ammonia and other compounds. Fenchel (1969) has reviewed the complex interaction of nitrogen compounds and H_2S, including factors controlling the depth of the reduction layer and toxicity. Other published works concerning the nitrogen cycle, bacterial activity, ecology of meiofauna, etc., include Beyers (1965), Brafield (1965), Callame (1963, 1966), Dietrich, Höhnk, and Manzel (1965), Fenchel and Jansson (1966), Jansson (1966, 1968a,b, 1969), Mare (1942), Muus (1967), Rheinheimer (1959), Waksman, Hotchkiss, and Carly (1933), and Zobell (1946).

The complexity of the problem has been aptly stated by Jansson (1966): "In my opinion the only way to elucidate a habitat so well-known for its instability and changes is perhaps to put a great number of such snapshots together to get an entire slow motion 'film' of the processes."

The results of the experiments show that the decomposition products can reach the surface of the sediment after a certain time. This time depends on the grain size of the sediment. The grain size also is important for the extension of the reduction zone. In coarse sand it penetrates deeper and shallower. In a fine sediment, the decomposition products remain for longer periods in the deeper layers than in coarse sand or in sediment mixed with broken shells. The oxygen in the area of decomposition can be diminished to zero for a week or longer. In a well-aereated region the time is significantly reduced.

I am much indebted to Dr. Lüneburg of the Hydrographische Abteilung, Institut für Meeresforschung, Bremerhaven, for the determination of the grain size.

Literature Cited

Berner, R. A.
1963. Electrode Studies of Hydrogen Sulfide in Marine Sediments. *Geochemica et Cosmochimica Acta,* 27:563–575.
Beyers, R. J.
1965. The Pattern of Photosynthesis and Respiration in Laboratory Microecosystems. *Memoire dell' Istituto Italiano Idrobiologia,* supplement 18:61–74.
Bick, H.
1964. Die Sukzession der Organismen bei der Selbstreinigung von organisch verunreinigtem Wasser unter verschiedenen Milieubedingungen. *Min. ELF Land Nordrhein-Westfalen, Düsseldorf.* 139 pages.
Botan, E. A.; J. J. Miller; and H. Kleerekooper
1960. A Study of the Microbiological Decomposition of Nitrogenous Organic Matter in Freshwater. *Archiv für Hydrobiologie,* 56:334–354.
Brafield, A. E.
1965. Quelques Facteurs affectant le teneur en oxygène des eaux interstitielles littorales. *Vie et Milieu,* 16:889–897.
Brand, T.; N. W. Rakestraw; and C. N. Renn
1937. The Experimental Decomposition and Regeneration of Nitrogenous Matter in Seawater. *Biological Bulletin,* 72:165–175.
1939. Further Experiments on the Decomposition and Regeneration of Nitrogenous Matter in Seawater. *Biological Bulletin,* 77:285–296.
Callame, B.
1963. Le Milieu interstitiel dans les sédiments sableaux intercotidaux. *Bulletin de l'Institut Océanographique, Monaco,* 60 (1271) :1–32.
1966. Sur la Diffusion de l'oxygène a l'interieur des sediments marins. *Cahiers de la Station Océanographique, La Rochelle,* pages 1–14.
Cooper, L. H. N.
1937. The Nitrogen Cycle in the Sea. *Journal of the Marine Biological Association of the United Kingdom,* 22:183–204.
Dietrich, R.; W. Höhnk; and W. D. Manzel
1965. Studien zur Chemie organischer Bodenproben. III. Beziehengen zwischen physikalischen und chemischen Grüssen in den Böden der Nordsee und der Aussenweser. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* 9:242–278.
Fenchel, T.
1969. The Ecology of Marine Microbenthos. IV. Structure and Function of the Benthic Ecosystem, Its Chemical and Physical Factors and the Microfauna Communities with Special Reference to the Ciliated Protozoa. *Ophelia,* 6:1–182.
Fenchel, T., and B. O. Jansson
1966. On the Vertical Distribution of the Microfauna in the Sediments of a Brackish-Water Beach. *Ophelia,* 3:161–177.
Gessner, F.
1960. Die Leistungen des pflanzlichen Organismus. *Handbuch der Biologie,* 4:34–186.
Green, J.
1968. *The Biology of Estuarine Animals.* 401 pages. London: Sidgwick and Jackson.
Hecht, F.
1933. Der Verbleib der organischen Substanz der Tiere bei meerischer Einbettung. *Senckenbergiana,* 15 (3–4) :165–249.
Jansson, B. O.
1966. Microdistribution of Factors and Fauna in Marine Sandy Beaches. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:77–86.
1968a. Quantitative and Experimental Studies of the Interstitial Fauna in Four Swedish Sandy Beaches. *Ophelia,* 5:1–71.
1968b. Studies on the Ecology of the Interstitial Fauna of Marine Sandy Beaches. Thesis, University of Stockholm. 16 pages.

1969. Factors and Fauna of a Baltic Mud Bottom. *Limnologica,* 7:47–52.

Krause, H. R.

1959. Biochemische Untersuchungen über den postmortalen Abbau von totem Plankton unter aeroben und anaeroben Bedingungen. *Archiv für Hydrobiologie,* supplement 25:67–82.

1961. Einige Bemerkungen über den postmortalen Abbau von Süsswasser-Zooplankton unter Laboratoriums— und Freilandbedingungen. *Archiv für Hydrobiologie,* 57:539-543.

Kühl, H.

1952. Studien über die Klaffmuschel *Mya arenaria.* Die Myasiedlungen am Hakensand (Elbmündung). *Archiv für Fischereiwissenschaft,* 4:126–132.

Kühl, H., and H. Mann

1956. Unperiodische Aenderungen im Stoffhaushalt von Seewasser-aquarien. *Hydrobiologia,* 8:66-78.

1961. Vergleich des Stickstoffabbaus in See- und Süsswasser-aquarein. *Vie et Milieu,* 11:532-545.

1962. Modellversuche zum Steffhaushalt in Aquarien bei verschiedenem Salzgehalt. *Kieler Meeresforschungen,* 18:89-92.

1966a. Chemische Unterschungen am Sandstrand von Cuxhaven und Helgoland. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:67-76.

1966b. Aenderungen im Chemismus des Interstitialwassers am Strand von Cuxhaven während einer Tide. *Helgoländer wissenschaftlichen Meeresuntersuchungen,* 13:238-245.

Mare, M. F.

1942. A Study of a Marine Benthic Community with Special Reference to the Micro-Organisms. *Journal of the Marine Biological Association of the United Kingdom,* 25:517-554.

Muus, B.

1967. The Fauna of Danish Estuaries and Lagoons. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser,* 5:1–316.

Postma, H.

1966. The Cycle of Nitrogen in the Waddensea and Adjacent Areas. *Netherlands Journal of Sea Research,* 3:186–221.

Rheinheimer, G.

1959. Mikrobiologische Untersuchungen über den Stickstoffhaushalt der Elbe. *Archiv für Mikrobiologie,* 34:358–373.

Ulken, A.

1963. Die Herkunft des Nitrits in der Elbe. *Archiv für Hydrobiologie,* 59:486–501.

Waksman, S. A.; M. Hotchkiss; and C. Carly

1933. Marine Bacteria and Their Role in the Cycle of Life in the Sea. *Biological Bulletin,* 65:137–167.

Wuhrmann, K., and H. Woker

1948. Experimentelle Untersuchungen über die Ammoniak- und Blausäurevergiftung. *Schweizerische Zeitschrift für Hydrologie,* 11:210–244.

1953. Ueber die Giftwirkung von Ammoniak- und Zyanidlösungen mit verschiedener Sauerstoffspannung und Temperatur auf Fische. *Schweizerische Zeitschrift für Hydrologie,* 15:236–260.

Zobell, C. E.

1946. *Marine Microbiology.* 240 pages. Waltham, Massachusetts: Chronica Botanica.

SAMPLING FOR MEIOFAUNA

J. B. J. Wells

A Brief Review of Methods of Sampling the Meiobenthos

ABSTRACT

The requirements for a valid sample of meiobenthos are discussed and evaluated in terms of collecting by use of coring devices, grabs, and dredges. The advantages and disadvantages of specific collecting devices are discussed as to their efficiency in obtaining samples of meiobenthos.

To be of maximum value a sample of meiobenthos should provide a sufficient quantity of fauna to allow a reasonable estimate of population density to be made, should furnish information on the vertical zonation of the fauna and on the nature of the substratum, and should contain all elements of the fauna, from the smallest species to the largest.

Three basic types of equipment are used to take samples of meiofauna: coring devices, grabs, and dredges. The method to be used for any particular program depends to a large extent on the area of seabed being investigated—whether the littoral region or shallow-water or deep-water substrata.

Sampling in the littoral region is best done by hand with a coring device. Many workers use a simple tube of metal or plastic to take a vertical core, pushing it into the sand to the required depth, corking the upper end, and withdrawing it. It may be preferable to dig to the bottom of the tube and lift it bodily from the substratum. This method is simple and quick and satisfies all the requirements given above. However, if the sample is to be used to provide information on the vertical zonation of the fauna it should be removed from the tube and cut into sections of suitable length as soon as possible, to avoid errors due to migration of the animals. The method of removal of the core also is critical. Pushing out the core with the plunger disturbs the surface and probably will cause compression of the sample. If the substratum is sufficiently moist it is likely to slide out of the tube under its own weight when the cork is removed; sections can be cut from it as it does so. Jansson (1967) has developed a method which avoids compression of the core during removal from the tube and, at the same time, provides a series of vertical subsamples. The coring tube is composed of a series of rings of uniform height (1, 2, and 5 cm are the sizes most commonly used) which fit closely within an outer tube. The sampler is pushed into the deposit and a core obtained. The inner, sectional tube is pushed out by a plunger which bears on the rings and not on the sediment, thus avoiding compression. The rings are removed separately as they emerge.

Transparent plastic tubing is preferable to metal tubing as the core seems to slide better in this material, and, being transparent, calibration is easier. Compression of the deposit can occur during insertion of the sampler. With transparent tubing this can more easily be seen to be happening and precautions can be taken. Various sizes of tubing are used, but it seems that a cross-sectional area of about 10 cm² is the most satisfactory, giving a sample large enough to be meaningful but small enough to permit rapid sorting of the fauna that it contains.

In most cases sampling to a depth of 25 to 30 cm is adequate, as the majority of the animals live in this zone. However, on the upper shore of many beaches the permanent water table lies deeper than this, and for a complete profile of the vertical dis-

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tribution of the fauna samples must be taken to the level of the water table. This involves a multiple-layer technique in which the tube is pushed down to 25 to 30 cm, the sand dug away to the bottom of the tube, and another tube inserted at the point reached by the first one. This process is repeated until the water table is reached. This method undoubtedly involves inaccuracies at the point of changeover of tubes. A square-section demountable corer of the Renaud-Debyser type (Renaud-Debyser, 1957) obtains apparently undisturbed cores of up to 1 m in length, which may be sufficient for this purpose.

In the sublittoral, shorter cores usually suffice and simple hand-coring of the type described can be carried out by using SCUBA to a depth of about 50 m. Beyond this, limitations of SCUBA outweigh its advantages and for deeper water specialized gear worked from a vessel is required.

It is possible to use for the meiobenthos most of the quantitative gear devised for macrobenthos studies (Holme, 1964; Hopkins, 1964). However, since a small sample usually is adequate for meiobenthos studies the various coring devices offer practical advantages over the grabs and dredges. Also, coring is the only type of sampling that fully satisfies the requirements outlined at the beginning of this paper. In practical terms, corers have an advantage in their light weight and ease of handling—which means that they can be worked in more severe weather conditions than can most grabs or dredges—and also in the speed with which successive samples can be taken.

Much of the early work in this field (e.g., Mare, 1942) was done with lightweight gravity corers initially designed for sampling mud substrata (Moore and Neill, 1930; Krogh and Spärck, 1936). These samplers are generally quite adequate for the meiobenthos, as deep cores are not necessary, the major part of the fauna being restricted to the upper few centimeters of the substratum (Smidt, 1951; Muus, 1964). Such samplers have been used successfully by several workers, usually with some minor modifications to their basic design (Bougis, 1950; McIntyre, 1961, 1964). Even in their modified state, however, they are suitable only for softer substrata, penetration being poor in sand and the sample sometimes being lost in hauling. Penetration can be improved by increasing the weight of the sampler and retention of the sample by fitting a core retainer, but the conventional internal retainer is useless because it disturbs the surface of the sediment, the very region with most interest. Mills (1961) has designed an external core retainer for use with the heavy "geological" corers, but for the lightweight instruments the simple rubber-ball closing mechanism is more suitable. Fenchel (1967) has thus modified a Moore and Neill sampler, and Willimoës (1964) and Craib (1965) have designed specialized coring devices using this method, in which the lower end of the coring tube is closed by a rubber ball as it is withdrawn from the substratum. The area sampled by most of these devices is about 9 to 10 cm². In the Fenchel and Craib systems the ball-release mechanism is external to the tube and the only disturbance caused to the core sample is at its bottom edge. In the Willimoës sampler the ball is hauled up to close the bottom of the tube by means of a cord running through the tube. This method causes disturbance of the core, and although a quantitative sample may be obtainable it cannot be used to study vertical zonation of the fauna. Also, as the ball hangs free a small distance beneath the tube during lowering, it is likely that it will disturb the surface of the deposit as the sampler approaches the bottom.

In coarse sand and gravel these samplers are unsatisfactory on two counts. First, the corer may not penetrate the substratum as the particles may be too large, and, second, the tube may lose the deposit when it is being withdrawn. Under these conditions the Craib corer, with a tube diameter of 5.7 cm, is more efficient than the smaller machines.

Another approach to the problem of core retention is the use of a cutting knife, which swings round from the horizontal position, cutting through the substratum adjacent to the coring tube, to seat beneath the tube. This method is less efficient than the rubber-ball method as it does not achieve such a close seal, but it does allow the use of a large core tube. Samplers employing this principle have been designed by Reineck (1963) and Drzycimski (1967). Both of these samplers work well in a range of substrata from loose mud to hard sand but their efficiency in coarse sand and gravel is suspect. There are two versions of the Reineck sampler, one weighing 150 kg, the other 750 kg. Drzycimski's sampler, which weighs only 7.5

kg, samples an area of 82 cm^2 to a depth varying from 3 to 5 cm in clay to 15 to 20 cm in loose mud. It can be used from a small boat and may be a useful device for sampling in fairly shallow waters. The weight of the sampler is an important consideration. Heavier instruments are required for sand than for mud, and it may be necessary to adjust the weight according to the type of sediment under investigation.

Two major problems are involved in the use of coring devices—compression of the core in the tube as the sample is taken, and disturbance of the surface of the deposit by the instrument as a whole as it approaches the substrate and by the core tube as it penetrates. These problems are more acute for mud deposits than for sand, particularly where the surface is of loose, flocculent material. Observations by SCUBA divers have shown that these problems are common to all free-fall or gravity corers. In shallow waters, within the operational limits of SCUBA, hand sampling obviates this damage. Craib (1965) claims that his sampler, which is set down on the bottom before the coring tube is activated, takes an undisturbed sample. Evaluation of the degree of disturbance of samples taken without observation by a diver is difficult, as a sample may appear to be undisturbed when, in fact, it has lost the superficial flocculent layer.

An important, if temporary, part of the sublittoral meiobenthos is formed by the newly settled stages of macrobenthic species. Qualitative samples of these animals and of the larger, more mobile meiobenthic species can be taken with the sled samplers of Mortensen (1925) and Ockelmann (1964). Muus (1964) has pointed out the difficulties of quantitatively sampling this element of the fauna—which inhabits the surface layer of the substratum—with the various coring devices discussed above, and his "mouse trap" sampler and the much more complicated device of Corey and Craib (1966) are the only pieces of apparatus that can perform this task.

Grabs are not entirely satisfactory for meiobenthos work. In the best of them, water drains out through the jaws and along the seams between the halves of the bucket during hauling, almost certainly washing away the animals on or near the surface of the sample. Another disadvantage is the disturbance that they cause to the surface of the sediment as they approach it. This problem can be alleviated by fitting a gauze cover to the top of the bucket, as in the Smith-McIntyre grab (Smith and McIntyre, 1954). Grab hauls can be subsampled with short cores (Wigley and McIntyre, 1964). Thiel (1966) has devised a special subsampler for this purpose.

Dredges are semiquantitative at best, and they should be reserved for those occasions when it is impracticable to use other types of gear. In very deep waters, where the time taken to obtain a sample is considerable, a dredge has the very real advantage of providing a large sample. Of all the varied types only the anchor dredge (Forster, 1953) is suitable, as it retains the entire sample, but the depth of bite is unnecessarily deep. Sanders, Hessler, and Hampson (1965) designed a modified anchor dredge which takes a shallow slice of the subtratum and provides a large sample. This type of dredge probably is adequate for the meiobenthos, but Hessler and Sanders (1967) point out that the more mobile elements of the epibenthic macrobenthos probably are not taken. A more efficient sampler is the epibenthic sled of Hessler and Sanders (1967), but this instrument has had insufficient use, as yet, for a proper evaluation to be made. A similar instrument is the sled sampler of Riedl (1960) but, again, information on its use for meiobenthos is lacking.

Literature Cited

Bougis, P.
1950. Méthode pour l'étude quantitative de la microfaune des fonds marins (Meiobenthos). *Vie et Milieu,* 1:23–37.

Corey, S., and J. S. Craib
1966. A New Quantitative Bottom Sampler for Meiofauna. *Journal du Conseil,* 30:346–353.

Craib, J. S.
1965. A Sampler for Taking Short Undisturbed Marine Cores. *Journal du Conseil,* 30:34–39.

Drzycimski, I.
1967. Czerpacz Rurowy do Pobierania Prób Cennych. *Ekologia Polska,* series B, 13:273–275.

Fenchel, T.
1967. The Ecology of Marine Microbenthos. I. The Quantitative Importance of Ciliates as Compared with Metazoans in Various Types of Sediments. *Ophelia,* 4:121–137.

Forster, G. R.
1953. A New Dredge for Collecting Burrowing Animals.

Journal of the Marine Biological Association of the United Kingdom, 32:193–198.

Hessler, R. R., and H. L. Sanders
1967. Faunal Diversity in the Deep-Sea. *Deep-Sea Research,* 14:65–78.

Holme, N. A.
1964. Methods of Sampling the Benthos. *Advances in Marine Biology,* 2:171–260.

Hopkins, T. L.
1964. A Survey of Marine Bottom Samplers. *Progress in Oceanography,* 2:213–256.

Jansson, B. O.
1967. The Significance of Grain Size and Pore Water Content for the Interstitial Fauna of Sandy Beaches. *Oikos,* 18:311–322.

Krogh, A., and R. Spärck
1936. On a New Bottom Sampler for Investigation of the Micro Fauna of the Sea Bottom with Remarks on the Quantity and Significance of the Benthonic Micro Fauna. *Kongelige Danske Videnskabernes Selskabs Skrifter, Biologiska Skrifter,* 13:3–12.

McIntyre, A. D.
1961. Quantitative Differences in the Fauna of Boreal Mud Associations. *Journal of the Marine Biological Association of the United Kingdom,* 41:599–616.
1964. Meiobenthos of Sub-Littoral Muds. *Journal of the Marine Biological Association of the United Kingdom,* 44:665–674.

Mare, M. F.
1942. A Study of a Marine Benthic Community with Special Reference to Micro-Organisms. *Journal of the Marine Biological Association of the United Kingdom,* 25:517–554.

Mills, A. A.
1961. An External Core Retainer. *Deep-Sea Research,* 7:294–295.

Moore, H. B., and R. G. Neill
1930. An Instrument for Sampling Marine Muds. *Journal of the Marine Biological Association of the United Kingdom,* 16:589–594.

Mortensen, T.
1925. An Apparatus for Catching the Micro-Fauna of the Sea Bottom. *Videnskabelige Meddelelser fra Dansk Naturhistorik Forening i København,* 80: 445–451.

Muus, B.
1964. A New Quantitative Sampler for the Meiobenthos. *Ophelia,* 1:209–216.

Ockelmann, K. W.
1964. An Improved Detritus-Sledge for Collecting Meiobenthos. *Ophelia,* 1:217–222.

Reineck, H. E.
1963. Die Kastengreifer. *Natur und Museum,* 93:102–108.

Renaud-Debyser, J.
1957. Description d'un carottier adapté aux prélèvements des sables de plage. *Revue de l'Institut Français du Pétrole,* 12:501–502.

Riedl, R.
1960. Ein Kinemeter zur Beobachtung von Dredgen in beliebigen Tiefen. *Internationale Revue der gesamten Hydrobiologie,* 45:155–167.

Sanders, H. L.; R. R. Hessler; and G. R. Hampson
1965. An Introduction to the Study of Deep-Sea Benthic Faunal Assemblages along the Gay Head-Bermuda Transect. *Deep-Sea Research,* 12:845–868.

Smidt, E. L. B.
1951. Animal Production in the Danish Waddensea. *Meddelelser fra Kommissionen for Danmarks Fiskeri-og Havundersøgelser, Serie Fiskeri,* 11(6): 1–151.

Smith, W., and A. D. McIntyre
1954. A Spring-Loaded Bottom-Sampler. *Journal of the Marine Biological Association of the United Kingdom,* 33:257–264.

Thiel, H.
1966. Quantitative Untersuchungen über die Meiofauna von Tiefseeboden. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:131–147.

Wigley, R. L., and A. D. McIntyre
1964. Some Quantitative Comparisons of Offshore Meiobenthos and Macrobenthos South of Martha's Vineyard. *Limnology and Oceanography,* 9:485–493.

Willimoës, M.
1964. A Ball-Stoppered Quantitative Sampler for the Microbenthos. *Ophelia,* 1:235–240.

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Problems of Meiobenthic Sampling in the Deep Sea

ABSTRACT

The problems of sampling for deep-sea meiobenthos, including those of time and expense, density of meiobenthos, sampling devices, technical difficulties, and processing, are discussed. Recommendations are given for improvement of the knowledge of deep-sea meiobenthos.

As is already known, information on the deep-sea meiofauna is scant. Some descriptions of deep-sea species and depth records have appeared, but for groups other than the Foraminifera these, by and large, are negligible. The *Challenger* Reports are deficient in taxa usually regarded as meiofauna. Only the papers of Wigley and McIntyre (1964) and Thiel (1966) have dealt with meiofaunal assemblages as a whole. Essentially, the entire job is still before us, and, for that reason, a consideration of the problems one must face in attempting to investigate the deep-sea fauna is in order. The present discussion is based on the author's own experience in investigating the deep-sea macrofauna and the meiofaunal studies of others.

Basically, there are three general reasons why so little is known today about the deep-sea meiobenthos. Deep-sea research is expensive. The standing crop of life in the deep sea is very low. Available technology is not truly adequate.

The first point requires only a moment's attention. Deep-sea work needs large ships and at least some sophisticated equipment, and these require a great deal of money. Many governments, however, are releasing money for this type of work, so opportunities for the scientist are improving.

The individual investigator must realize that such work is very expensive also in terms of time. In deep-water work only a few samples can be taken per day, and the time required to sort through these samples in the laboratory can be enormous. A side effect of the great amount of time needed for each sample is that a sampling program involving many samples is not really practical. One must design the program very carefully so that a minimum of samples yields a maximum amount of information.

Nearly every study comparing abundance of animals in shallow and deep water has shown that the amount of life in deep water is as much as several orders of magnitude less than that occurring in shallow water. In the northwestern Atlantic, Sanders, Hessler, and Hampson (1965) demonstrated that the density of benthic macrofauna from the abyssal plain at 4,000 m to 5,000 m is 20 to 640 times less than on the continental shelf. In the northwestern Pacific, Soviet investigators have noted a difference of as much as four orders of magnitude. Wigley and McIntyre (1964), in one of the rare studies of open-ocean benthic meiofauna, documented a definite diminution of faunal density down to their deepest station at 500 m. Phleger (1964) found that the density of Foraminifera in the Gulf of California was an order of magnitude less at bathyal-abyssal depths than in shallow water.

This low density means that for unit effort numbers of individuals captured in the deep sea will be significantly lower. In general, it forces the investigator to base his conclusions on data which are less convincing than those which could be obtained in shallow water. This difficulty frequently faces the

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systematist, who commonly must deal with species represented by only one or two individuals.

In this problem, the meiobenthologist has an advantage over the student of macrofauna. Wieser (1960) speculated that meiofauna was about 100 times more abundant than macrofauna. Wigley and McIntyre (1964) found meiofauna to be 35 to 770 times more abundant than macrofauna, averaging 223 times. Thiel (1966) collected from 35 to 426 meiofaunal animals per 25 cm² in depths from 1,000 to 5,000 m. Thus, a sample too small to yield sufficient macrofauna may have an adequate amount of meiofauna; however, this advantage probably will profit only the nematologist. Nematodes dominate the meiofauna in deeper water (Wieser, 1960). They average 81.5 percent of the individuals in Thiel's samples and 84.3 percent of Wigley and McIntyre's. Students of other groups may require larger samples.

In the deep-sea benthos, yield has been increased by using a grab or corer that samples an area larger than that usually taken in shallow water or by using a trawl or dredge. The largest grab now used in deep-sea work is the Cambell grab (Hartman, 1955), which samples 0.55 m². The Soviet Okean grab (Vinogradova, 1962) samples 0.25 m². Menzies and Rowe (1968) have developed a promising method for taking 0.25-m² cores. The author has recently modified the Bouma-Marshall box corer (Bouma and Marshall, 1964) to take 0.25-m² samples. Most other grabs and corers have been smaller. Thiel (1966) found a Van Veen grab to be very effective, and Wigley and McIntyre (1964) used a Smith-McIntyre grab.

All grabs have the disadvantage of offering so much resistance to the water as they descend that a "bow wave" may form. This will blow away the light animals on the surface of the sediment before the sample is taken unless the grab is properly modified (Wigley, 1967) or unless great care is used in lowering the grab the final short distance.

When properly taken, grabs and large-area cores offer the substantial advantages of being quantitative and of being amenable to subsampling because they yield undisturbed pieces of the bottom. Wigley and McIntyre (1964) and Thiel (1966) subsampled their grabs, the former by taking 10-cm² cores from the sample and the latter by means of a 25-cm² "Meiostecher." Thiel also subdivided the subsample vertically and was able to demonstrate that the majority of organisms live in the surface centimeter.

Where larger numbers of organisms are desired, one must use a dredge or trawl. These yield enriched samples by skimming off only the rich, uppermost layer of the sediment and by allowing a portion of the sediment to pass through the mesh of the collecting net while retaining the organisms larger than the mesh opening. The best device of this sort being used in the deep sea today is the epibenthic sled designed at Woods Hole Oceanographic Institution (Hessler and Sanders, 1967). Such a device may yield thousands of individuals, and single species have been represented by hundreds of specimens. Unfortunately, such samples are not quantitative; also, the mesh of the collecting net is not small enough to retain meiofauna. Thus, unless there is still mud retained in the net when it reaches the surface, the meiofauna will have been washed from the sample.

Finally, in this enumeration of the difficulties in deep-sea studies is a consideration of our technical inadequacy. The proof of this deficiency is that in any deep-sea sampling program there is a depressingly high percentage of failures ranging from no samples at all to samples which clearly are not representative. Most investigators would be delighted if they were successful only half of the time. The high rate of failure can be attributed to three major factors.

First, benthic sampling in the deep sea requires good weather, and that condition is fulfilled with distressing infrequency.

Second, the remoteness of the bottom makes it difficult to know what the sampling device is doing. The importance of this factor cannot be overemphasized. The simplest consideration, such as whether the gear is on the bottom or still in the water column, is a major problem in the deep sea. A pinger on the wire (Thiel, 1966) used in conjunction with a PDR is an essential aid in helping to know when the sampler is on the bottom. A recording tensiometer is more difficult to interpret, but it can let one know when the gear is sampling and when it is caught on some obstacle.

Third, the great length of the water column through which the sample must travel before it reaches the ship exposes it to the gradual destruction of the winnowing process. Few sampling devices are watertight; and with grabs and dredges there usually is no attempt to have them so. From the moment the gear leaves the bottom, the current, gravity, ship's surge, and other physical forces will cause the sampler to leak. The success of shallow-water sampling is based on the fact that the duration of this leakage is relatively short, so that only a small portion of the sample is lost. In deep water, the same amount of leakage per unit time or distance can result in the complete loss of the sample by the time the sampling device reaches the ship. This is probably the single most important reason for failure in deep-sea sampling. Winnowing is especially difficult to prevent on dredges and trawls. This is a further reason for employing grab and core techniques.

Additional problems face those who prefer that their animals be alive for initial processing. Usually, deep-sea benthic organisms are dead by the time the investigator can isolate them. Temperature changes, particularly, and mechanical damage seem to be the most important factors. Mechanical damage is probably not a serious problem with individuals of most meiofaunal taxa because of their small size. Deep-sea animals are stenothermal because the stable cold water in which they live has not stimulated thermal adaptability. Except in winter at high latitudes, surface waters invariably are significantly warmer, and the resulting thermal change is immediately lethal. At low latitudes, when the sample consists of a large volume of sediment, the animals may still be alive when they reach the ship because the sediment acts as an insulator, but they die as soon as they are washed from the sediment by warm surface water.

There are three solutions to this problem: (1) using techniques that do not require the animals to be alive, (2) sampling only where and when the surface temperature is compatible with the organisms' tolerance, and (3) washing the samples with refrigerated seawater. Ideally, the third solution is the best, but it requires special washing techniques that use a minimum of seawater because most ships today are not capable of refrigerating the amount of water necessary in our present routine washing procedures. The bubbling technique of Higgins (1964) meets realistic requirements in that it employs only a small amount of water; but undoubtedly there are other methods that will work as well.

To aid in sorting preserved animals in the laboratory, it is useful to bulk-stain the concentrated sample with Rose Bengal. Thiel (1966) found that staining properties were improved by adding the stain to a dilute phenol solution.

The following recommendations are offered to those who wish to improve our knowledge of the deep-sea meiobenthos. Plan the sampling program with care to obtain maximum benefit from each sample. Take grab or large-diameter core samples. Use a pinger and tensiometer to monitor the sampling process. Make every effort to reduce the bow wave effect and winnowing of the sample. On deck, be content with dead animals or use a washing procedure that requires only a minimum amount of refrigerated seawater. Stain the concentrated sample with Rose Bengal before sorting. Finally, be emotionally prepared for a high percentage of unsuccessful samples. Gleaning facts from the deep sea is time-consuming, often discouraging work, but those who make the effort are finding a fertile field for new discoveries.

Literature Cited

Bouma, A. H., and N. F. Marshall
1964. A Method for Obtaining and Analysing Undisturbed Ocean Sediment Samples. *Marine Geology*, 2:81–99.

Hartman, O.
1955. Quantitative Survey of the Benthos of San Pedro Basin, Southern California. *Allan Hancock Pacific Expeditions*, 19:1–185.

Hessler, R. R., and H. L. Sanders
1967. Faunal Diversity in the Deep-Sea. *Deep-Sea Research*, 14:65–78.

Higgins, R. P.
1964. A Method for Meiobenthic Invertebrate Collection. *American Zoologist*, 4:291.

Menzies, R. J., and G. T. Rowe
1968. The LUBS, a Large Undisturbed Bottom Sampler. *Limnology and Oceanography*, 13:708–714.

Phleger, F. B.
1964. Patterns of Living Benthonic Foraminifera, Gulf of California. In Symposium on the Marine Geology of the Gulf of California, *Geological Society of America Memoir*, 3:377–394.

Sanders, H. L.; R. R. Hessler; and G. R. Hampson
1965. An Introduction to the Study of Deep-Sea Benthic

Faunal Assemblages along the Gay Head-Bermuda Transect. *Deep-Sea Research,* 12:845–867.

Thiel, H.
1966. Quantitative Untersuchungen über die Meiofauna von Tiefseeböden. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven,* Sonderband 2:131–147.

Vinogradova, N. G.
1962. Some Problems of the Study of Deep-Sea Bottom Fauna. *Journal of the Oceanographical Society of Japan, 20th Anniversary Volume,* pages 724–741.

Wieser, W.
1960. Populationsdichte und Vertikalverteilung der Meiofauna mariner Böden. *Internationale Revue der gesamten Hydrobiologie,* 45:487–492.

Wigley, R. L.
1967. Comparative Efficiencies of Van Veen and Smith-McIntyre Grab Samplers as Revealed by Motion Pictures. *Ecology,* 48:168–169.

Wigley, R. L., and A. D. McIntyre
1964. Some Quantitative Comparisons of Offshore Meiobenthos and Macrobenthos South of Martha's Vineyard. *Limnology and Oceanography,* 9:485–493.

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Sample Size and Sample Frequency in Relation to the Quantitative Sampling of Sand Meiofauna

ABSTRACT

A comparison is made of the efficiency of three different-size corers (3.15, 3.75, and 5.95 cm diameter) in sampling meiofauna of a sandy beach. The best results were obtained by using a corer of 3.75 cm in diameter. Frequencies of two, four, and eight samples per 0.25 m² were taken. Using the Index of Dispersion Test the precision of the estimate of the degree of contagious distribution increased with increasing sampling frequency. An analysis of variance showed that only at sampling frequencies of four and eight samples per 0.25 m² were there significant differences between areas of beach.

A number of new core-sampling devices recently have been described. The efficiency of these devices usually is assessed by the ease with which an undisturbed deep core is taken. Fundamental to the design of a suitable sampler for sediment-living meiofauna should be a consideration of the sampling efficiency of cores of different sizes. Sampling efficiency is held to mean the accuracy of the estimate of population density achieved by the corer.

With the sole exception of the paper by Vitiello (1968), no investigation has been made to determine the number of samples within a finite area of sediment needed to establish the distributional pattern of the meiofaunal elements. Many quantitative studies on meiofauna have merely quoted population densities per 50 ml, based on paired samples, or have even converted and extrapolated the data obtained to numbers per square meter of sand. In many cases, such generalizations of faunal densities are unjustified and grossly oversimplify meiofaunal distribution patterns.

Thus, an attempt has been made to establish the most suitable core size for sampling the meiofauna and the optimal frequency of sampling necessary to establish the spatial variability of the fauna. The present study relates only to one beach on the northeast coast of England; clearly, different beaches will need different sampling techniques. The study reported here was made very simple by intention, and was done as a preliminary to the author's comparative ecological studies of the meiofauna on a polluted beach and on an unpolluted beach. It is felt, however, that the problem highlighted here is one which has received too little attention. This paper, therefore, should be regarded merely as an indication of some factors to be considered when sampling the meiofauna quantitatively. The authoritative works of Cochran (1966), Greig-Smith (1964), Southwood (1966), and Williams (1964) treat this subject in greater detail.

Methods

A quadrat 0.25 m² was divided into sixteen equal squares. It was decided to test sampling frequencies of two samples/0.25 m², four samples/0.25 m², and eight samples/0.25 m². A series of eight random

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numbers was chosen, giving four pairs of two samples/0.25 m², two pairs of four samples/0.25 m², and one set of eight samples/0.25 m².

Three plastic corers, each 5 cm in height and having respective inner diameters of 5.95 cm, 3.75 cm, and 3.15 cm were used. Each corer was fitted into a wooden guide so that a similar spatial relationship of corers was followed in each sampling area. The assumption had to be made that faunal densities and distributional patterns were similar under each corer.

Two positions were selected on the beach at Robin Hood's Bay, England. Area 1 was at mean tide level and was an apparently uniform patch of bare sand. Area 2 was in a shallow pool within the sand beach at mean tide level. In each area the quadrat was thrown randomly onto the sand. The wooden guide containing the corers was placed on the sand and the three corers were pushed simultaneously into the substratum. Each core was removed carefully, and the sand contained therein was placed in separate containers. This process was repeated for the eight sampling stations within each 0.25 m² quadrat.

In the laboratory the samples of sand were placed in separate containers and an equal volume of 6 percent $MgCl_2$ was added. After allowing ten minutes for anaesthetization the sand was stirred vigorously and the supernatant liquid poured through a fine-mesh plankton net (60-μ diameter pores). The sand was washed and shaken viorously with three changes of seawater followed by one change of fresh water. The animals and a little sand present on the filter were washed off to a Petri dish and counted under a low-power binocular microscope.

The sand was further washed with a 10 percent solution of ethyl alcohol in distilled water and then with three washes of seawater. It was found that 60 to 70 percent of the animals were removed by the first treatment and a total of 90 to 95 percent extraction was achieved by the additional alcohol treatment. The extraction efficiency was checked by direct counts of the animals remaining in the sand residue after the $MgCl_2$ and alcohol treatments. The nematodes, in particular, were not removed by $MgCl_2$ treatment alone. Samples were stored at 6° C prior to counting.

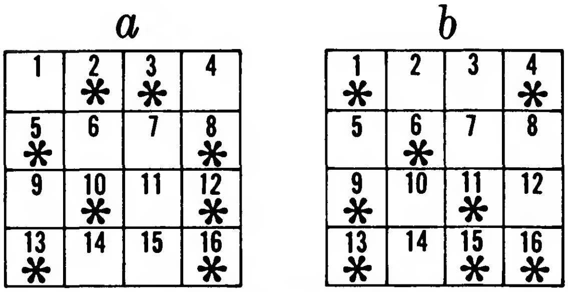

FIGURE 1.—Position of random stations (asterisks) taken from within a quadrat 0.25 m² at two separate areas of a sandy beach; *a*, open beach; *b*, pool. At each station three samples were taken simultaneously with cores having diameters of 5.95 cm, 3.75 cm, and 3.15 cm.

Results

Figure 1 shows the stations sampled within the two 0.25 m² areas investigated. Table 1 lists the combinations of stations used in the frequency analyses. Table 2 shows the numbers of animals found in area 1 (open beach) in the different cores and samples. Table 3 shows the same for area 2 (pool). Clearly, the population density is higher in the pool than on the open sand.

Comparison of Efficiency of Core Samples

The ratio of the volumes of the samplers from small, medium, and large was calculated to be 1 : 1.417 : 3.568. Thus, if the small sampler is as efficient as the other two samplers, one can simply multiply the mean number of animals found in the small core by the appropriate ratio to obtain an expected value for the other tubes, assuming similar distribution patterns of animals occur under each corer. If the observed value found for another core is greater than the value expected, then that corer gives a better sample when similar extraction methods are used. Conversely, if the observed value is less than the expected value, then the corer gives a poorer sample, with similar extraction methods.

Table 4 shows the results of this experiment for the total fauna found in areas 1 and 2. The medium-size corer contained more animals than expected, whereas the large corer contained fewer animals than expected. On the basis of these data the medium-size corer seems the most efficient.

TABLE 1.—*Combinations of samples used in comparing sampling frequencies of two, four, and eight/0.25m²*

Habitat	*2/0.25m²*	*4/0.25m²*	*8/0.25m²*
Area 1 (open beach)	12, 16 3, 2 13, 10 5, 8	12, 16, 3, 2 13, 10, 5, 8	12, 16, 3, 2, 13, 10, 5, 8
Area 2 (pool)	9, 15 1, 13 11, 16 4, 6	9, 15, 1, 13 11, 16, 4, 6	9, 15, 1, 13, 11, 16, 4, 6

It was thought, however, that this evaluation might hold true for some animal groups and not for others. For example, the Gastrotricha, being smaller than the Turbellaria, might be better sampled by a smaller corer. This, however, was found not to be the case.

Table 5 shows the expected and observed number of Turbellaria, Nematoda, and Gastrotricha when using the three corers. The medium corer produced observed/expected ratios in excess of unity in five of the six samples, whereas the larger corer produced only two of the six samples in excess of unity.

This evidence suggests that the smaller corer was

TABLE 2.—*Numbers of meiofauna in open sand (Area 1) taken simultaneously in cores of different sizes.*

Corer/Meiofauna	*Sample number*							
	2	3	5	8	10	12	13	16
LARGE CORER								
Turbellaria	24	31	14	22	17	10	30	22
Gastrotricha	3	9	3	6	2	0	1	1
Nematoda	23	21	61	59	18	31	37	27
Annelida	0	0	3	3	1	1	0	0
Mite	0	0	0	0	0	0	1	1
Amphipoda	0	1	0	0	0	0	1	0
Total	*50*	*62*	*81*	*90*	*38*	*42*	*70*	*51*
MEDIUM CORER								
Turbellaria	11	15	35	11	6	9	15	2
Gastrotricha	3	2	0	4	2	2	5	2
Nematoda	23	13	13	18	17	34	20	9
Annelida	0	0	0	1	1	0	0	0
Ostracoda	1	0	0	0	0	1	0	0
Amphipoda	1	0	0	2	0	0	1	1
Bivalve	1	0	0	0	0	0	0	0
Total	*40*	*30*	*48*	*36*	*26*	*46*	*41*	*14*
SMALL CORER								
Turbellaria	9	7	9	4	13	11	8	2
Gastrotricha	2	6	2	3	0	0	3	0
Nematoda	18	9	9	19	7	21	14	11
Annelida	1	0	0	1	0	0	0	0
Ostracoda	0	0	0	0	0	0	2	0
Amphipoda	1	0	0	0	0	2	0	1
Total	*31*	*22*	*20*	*27*	*20*	*34*	*27*	*14*

TABLE 3.—*Numbers of meiofauna in a pool (Area 2) taken simultaneously in cores of different sizes.*

Corer/Meiofauna	*Sample number*							
	1	4	6	9	11	13	15	16
LARGE CORER								
Turbellaria	78	90	58	96	102	77	58	84
Gastrotricha	35	28	75	23	34	36	18	13
Nematoda	25	28	46	35	37	67	26	22
Annelida	1	0	0	1	0	2	0	0
Amphipoda	0	0	0	0	0	0	2	0
Harpacticoida	0	0	0	0	0	1	1	0
Total	*139*	*146*	*179*	*155*	*173*	*183*	*105*	*119*
MEDIUM CORER								
Turbellaria	23	18	26	68	32	37	32	35
Gastrotricha	98	38	45	83	24	50	21	8
Nematoda	5	7	8	27	15	22	31	29
Annelida	0	1	0	0	0	0	0	0
Amphipoda	0	0	0	0	2	0	0	1
Harpacticoida	1	0	1	0	0	0	1	0
Total	*127*	*64*	*80*	*178*	*73*	*109*	*85*	*73*
SMALL CORER								
Turbellaria	14	12	24	21	25	23	14	13
Gastrotricha	53	30	71	23	12	54	7	1
Nematoda	13	11	7	7	6	7	13	4
Annelida	0	0	0	1	0	0	0	0
Amphipoda	0	0	0	0	0	0	1	1
Harpacticoida	0	1	0	0	0	0	0	0
Ostracoda	0	0	0	0	0	0	1	0
Total	*80*	*54*	*102*	*52*	*43*	*84*	*36*	*19*

sampling only part of clumps of animals, whereas the medium corer was sampling complete clumps. In support of this hypothesis the variance of samples taken with the small corer showed wider fluctuations than the variance of samples taken with either the medium corer or large corer. With the large corer the fauna may have been extracted less efficiently with the methods used, thus producing a lower observed number of animals than expected. Therefore, for the beach sampled and when using the extraction methods outlined, a corer 3.75 cm in diameter is the optimum size. It must be emphasized, however, that this size may not be appropriate for other areas or beaches (see McIntyre, in the present volume).

Number of Samples Per Unit Area

If beaches or areas of a beach are to be compared, then the variation in density of the meiofauna

TABLE 4.—*Mean numbers of animals taken simultaneously in cores of different sizes on open beach (Area 1) and in pool (Area 2).*

Habitat	*Small corer* (1.0)	*Medium corer* (1.417)			*Large corer* (3.568)		
		Expected	Observed	Obs./Exp.	Expected	Observed	Obs./Exp.
Area 1	24.37	34.54	34.87	1.01	86.97	60.50	0.69
Area 2	59.50	84.31	98.62	1.17	212.29	149.87	0.76

TABLE 5.—*Mean numbers of Turbellaria, Nematoda, and Gastrotricha taken in cores of different sizes on open beach (Area 1) and in pool (Area 2).*

Meiofauna	*Small corer*	*Medium corer*			*Large corer*		
		Expected	*Observed*	*Obs./Exp.*	*Expected*	*Observed*	*Obs./Exp.*
Turbellaria							
Area 1	7.87	11.16	13.00	1.16	28.10	21.25	0.76
Area 2	18.25	25.86	33.87	1.31	65.12	80.37	1.23
Nematoda							
Area 1	13.50	19.13	18.37	0.96	48.17	34.62	0.72
Area 2	8.50	12.04	18.00	1.49	30.33	35.75	1.18
Gastrotricha							
Area 1	2.00	2.83	2.50	1.13	7.14	3.12	0.44
Area 2	31.37	44.46	45.87	1.03	111.95	32.75	0.29

within a given area must be known. If too few samples are taken, the size of variations within a given area will in all probability be greater than any differences between areas.

Sampling frequencies of two, four, and eight samples were taken within 0.25 m^2 of the two areas investigated. The variance and mean were calculated for each sample at the different frequencies and at both areas. Using the Index of Dispersion (*I*), where $I = S^2(n\text{-}1)\overline{x}$ and where S^2 = variance, n = number of samples, and $\overline{x}$ = mean (Greig-Smith, 1964, p. 63), the pattern of contagious or noncontagious distribution could be assessed. The significance of the values of *I* was assessed by reference to the chi-square table (Fisher and Yates, 1963) for n-1 degrees of freedom. Deviation from random expectation towards a contagious distribution is significant if the values of *I* exceed $p = 0.05$. Table 6 shows the results of this analysis on the total fauna data. At a sample frequency of two samples per 0.25 m^2 only eight of twenty-four samples showed contagious distribution, whereas at a frequency of four samples per 0.25 m^2 seven of twelve showed contagious distribution, and at a frequency of eight samples per 0.25 m^2 five of six showed contagious distribution. In addition, the precision of the estimate of the degree of contagious distribution (lowering of the significance level to $p = 0.01$) increased with increasing sampling frequency.

Clearly, therefore, if beaches or areas of beaches are to be compared quantitatively in terms of total meiofauna (= biomass), a sampling frequency of

TABLE 6.—*Index of Dispersion (I) for total fauna data using different sampling frequencies.*

Corer/Area	*Sampling frequency*						
	2/0.25m²				*4/0.25m²*		*8/0.25m²*
LARGE CORER							
Area 1	0.44	0.64	4.74*	0.24	2.97	16.61†	35.17*
Area 2	4.81*	3.01	4.99*	1.67	16.39†	11.06*	32.73†
MEDIUM CORER							
Area 1	8.14†	0.71	1.98	0.86	13.04†	5.62	22.50*
Area 2	16.44†	0.69	0	0.89	28.07†	1.33	91.00†
SMALL CORER							
Area 1	4.17*	0.76	0.52	0.52	7.33	1.56	10.29
Area 2	1.45	0.05	4.64*	9.0†	18.81†	56.87†	87.12†

*p = 0.05; †p = 0.01

upwards of eight samples per 0.25 m^2 gives the greatest precision. For area 2 (Table 6) a sample frequency of four samples per 0.25 m^2 gave a reasonably accurate estimate of density, but this was not true for area 1.

This method of predicting the number of samples needed can be used for total fauna (= biomass) comparisons or in comparing numerically the major faunal elements. In another method used by macrofaunal workers the number of new species found in each successive sample are totalled. At first, each successive sample adds a large number to the cumulative species total. After a certain number of samples the number of new species added with each additional sample falls to almost zero. The number of samples needed to include 90 percent of the available species is taken as the sampling frequency needed. This method is unlikely to be applicable to meiofaunal sampling procedure unless one has access to a large number of systematists and technicians, as the number of species of meiofauna present in one sediment sample are very large.

Comparison of Two Areas of Beach

The variance of the samples taken was found to be proportional to the mean; therefore, the raw data was transformed to $\log_n$ in order to stabilize the variance. (Williams, 1964, and Southwood, 1966, have extensive reviews of transformation procedure.) Analyses of variance were conducted on the transformed data obtained by the medium corer at the three sampling frequencies used. Table 7 shows the results of these analyses. At a sampling frequency of two samples per 0.25 m^2 the F ratio was insignificant. However, at sample frequencies of both four and eight samples per 0.25 m^2 the F ratio was significant at $p = 0.01$ (i.e., the between-area variation was greater than the within-area variation). The areas, therefore, were significantly different from each other in terms of total fauna.

Significance of Results

For the sand sampled in this investigation (for both areas 75 percent of the grains were in the range 125 to 250 μ diameter) and for the animals found (size range 1 to 15 mm), a corer 3.75 cm in diameter was found to be the most suitable with the extraction procedure used. McIntyre (in the present volume) has found that, for mud, a corer 10 cm in diameter is necessary to prevent loss of surface floc. Thus, sample size should vary according to the environmental and faunistic conditions being investigated.

The meiofauna in beaches or in areas of beaches often have been compared quantitatively by using a single pair of samples. The present study has shown that, for the meiofauna at the beach investi-

TABLE 7.—*Analysis of variance tables after transformation to $\log_n$ of the total fauna data obtained from the medium corer (see Tables 2, 3). Sample frequencies of two, four, and eight samples per 0.25m^2 are based on the random numbers shown in Figure 1.*

Samples per 0.25m^2	*Source of variation*	*Sum of squares*	*Degrees of freedom*	*Mean square*	*F ratio*
Two samples	Between areas	0.4764	1	0.4784	5.293
	Within areas	0.1801	2	0.0900	
	Total	*0.6565*	*3*		
Four samples	Between areas	0.7470	1	0.7470	21.34*
	Within areas	0.2099	6	0.0350	
	Total	*0.9569*	*7*		
Eight samples	Between areas	0.8265	1	0.8265	30.495*
	Within areas	0.3792	14	0.0271	
	Total	*1.2057*	*15*		

*Significant at less than $p = 0.01$.

gated, the variation within a single pair of samples was larger than the variation between areas of a beach. Upwards of four samples per 0.25 m^2 were found to be necessary to render the variation for the total meiofauna between areas of beach greater than that within an area. However, four samples per 0.25 m^2 did not give a reliable estimate of the dispersion pattern of the fauna in one of the two areas investigated. Upwards of eight samples per 0.25 m^2 were found necessary to encompass the variations in spatial distribution patterns in both areas.

Since truly quantitative sampling techniques are being established for the meiobenthos (see Hulings and Gray, 1971), sampling procedure should be given more attention. It must be reemphasized that this investigation was intentionally made simple. This paper is intended merely to focus more attention on this important subject, which has been neglected by meiofaunal workers.

Literature Cited

Cochran, W. G.
1966. *Sampling Techniques.* 413 pages. New York: John Wiley.

Fisher, R. A., and F. Yates
1963. *Statistical Tables for Biological, Agricultural and Medical Research.* 146 pages. Edinburgh: Oliver and Boyd.

Greig-Smith, P.
1964. *Quantitative Plant Ecology.* 256 pages. London: Butterworths.

Hulings, N. C., and J. S. Gray
1971. A Manual for the Study of Meiofauna. *Smithsonian Contributions to Zoology,* 78:1–83.

Southwood, T. R. E.
1966. *Ecological Methods.* 391 pages. London: Methuen.

Vitiello, P
1968. Variations de la densité du microbenthos sur une aire restreinte. *Recueil des Travaux de la Station Marine d'Endoume,* 43:261–270.

Williams, C. B.
1964. *Patterns in the Balance of Nature.* 324 pages. New York: Academic Press.

R. Williams

A Technique for Measuring the Interstitial Voids of a Sediment Based on Epoxy Resin Impregnation

ABSTRACT

A vacuum impregnation technique for sand and gravel sediments using unsaturated polyester and epoxy resins is described. Simple methods are given for the measurements of porosity and particle and void dimensions, from the thin sections obtained by the above method. The technique enables the interstitial fauna to be related directly to the dimensions of the interstices of sand and gravel sediments rather than to their grain size composition.

Many attempts have been made to relate animal types to the deposits in which they occur. The influence of the particle size composition of a beach on the distribution of certain organisms has been suggested by Davis (1925), Prenant (1932), Holme (1949), Jones (1950), Wieser (1956), and Ganapati and Rao (1962). Wieser (1959) illustrated a correlation between particle size and the interstitial fauna.

The aim of this investigation, which utilizes the impregnation technique, is to enable one to relate the faunal components directly to the dimensions of the interstices of sand and gravel sediments rather than to their grain size composition. Although the interstitial system is influenced by the size, shape, and spatial relationships of the grains of the deposit, it is the labyrinth of channels between the sand grains that forms the real habitat for the fauna. Because the limitations of the interstices constitute the actual barrier to the interstitial animals, the percentage of voids exceeding a certain dimension will probably determine the suitability of the habitat for a given species. If the percentage of the interstices exceeds a certain value the voids may form a system which will be continuous for colonization by the animal. A technique was devised so that the dimensions of this habitat, i.e., the voids of the sediment, could be measured and a comparison made to those of other sediments. It is based on an established method for the preparation of thin sections of soil. In this method an air-dried sample of soil is fully impregnated with a hard-setting liquid, and is cut, mounted, and ground to the point at which the structure may be recognized.

In the past, materials used as impregnants had limitations. Materials used prior to 1940 are summarized by Volk and Harper (1939), and the more advanced materials and techniques are reviewed by Jongerius and Heintzberger (1963). In recent years, Hagn (1953), Alexander and Jackson (1954), Altemüller (1956, 1962), and Wells (1962) have attained a high degree of success by using cold and thermosetting, unsaturated polyester and epoxy resins. Although these resins make the complete im-

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pregnation of gravel and sands relatively simple, the preparation of sections still requires specialized equipment.

Preparing Thin Sections

Undisturbed samples of the sediment are collected with the use of brass rectangular samplers with double sliding lids (10 by 5 by 2.5 cm). The sampler is pressed into the surface of the deposit and when the sediment around the sampler has been cut away the lower lid can be slid into place. The sampler then is marked appropriately with orientation, tidal height, and date. The brass samplers are allowed to drain, leaving the minimum amount of water in the sample, and then are air-dried and impregnated with resin. The crystallized salt in the dried sample does not hinder impregnation or lessen, to any extent, the quality of the finished slides. In fact, a small amount of salt tends to maintain the structure of the sediment in the dry state before the resin sets in place.

The resins used for impregnation are Crystic 28C (Alexander and Jackson, 1954) and Araldite MY750 (Wells, 1962). When using Araldite for impregnation the inner surface of the sampler should be treated with Araldite Release Agent QZ12 to aid the release from the sampler of the hardened impregnated sample. A fluorescent dye, Uvitex SWN, is mixed with the resin following a technique outlined by Werner (1962). Under ultraviolet light, this dye in the pore system fluoresces reddish pink; the quartz fraction, red, and the calcium carbonate, blue. This coloration greatly assists in the identification and measurement of the interstices.

The vacuum apparatus used for impregnation (Figure 1) is a modification of the method used by Wells (1962). This apparatus can be constructed easily by using "Quick-Fit" glassware. A number of samples located around the periphery of the desiccator can be impregnated in succession by rotating the upper part of the apparatus in its socket. Sufficient vacuum for complete impregnation of cohesionless sediments, sands and gravels possessing a single grain structure, can be obtained with the use of a water pump. Water vapor is prevented from entering the vacuum apparatus by a vessel containing calcium chloride or silica gel introduced into the vacuum line.

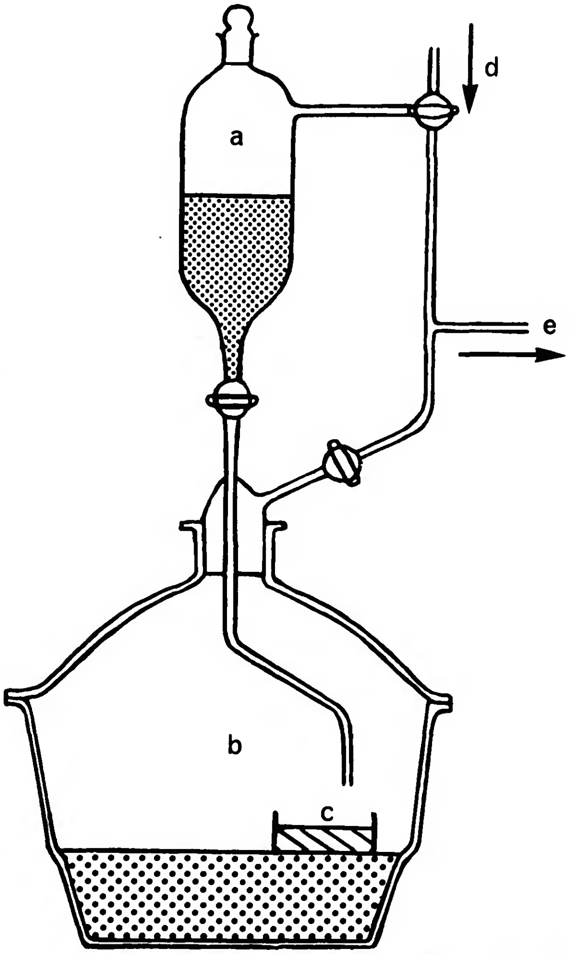

FIGURE 1.—Impregnation apparatus: *a*, vessel containing resin; *b*, desiccator containing anhydrous $CaCl_2$ and the sample (*c*) for impregnation; *d*, inlet for air into *a* and *b*; *e*, suction by water pump via a silica gel vessel inserted into the vacuum line.

Thin sections are prepared parallel to and at right angles to the surface of the deposit following the pattern outlined by Dalrymple (1957) and by Jongerius and Heintzberger (1963). For convenience, the hardened impregnated blocks of sediment (10 by 5 by 2.5 cm) are sawn into three blocks measuring 3 by 5 by 2.5 cm. Thin sections cut from these blocks are ground, polished, and mounted on slides. From each large block approximately three to six sections are cut vertically and six sections are cut horizontally to the original surface of the deposit. During grinding, the thicknesses of the sections on the slides are checked frequently by use of a polarizing microscope to observe the interference colors of the quartz grains. For sand deposits it is essential that mechanical grinding of the sections does not proceed beyond 50 μ because further grinding may crack the sand grains. The final thickness of the slides will vary with the different types of sediment and may vary with each sediment.

The ideal section thickness for measurement of the voids and particles is obtained when the maximum dimensions of the majority of particles still can be observed through the transparent embedding resin. Grinding is then finished by hand, using varying grades of carborundum powder. Sometimes, especially when the constituent grains are smooth, the samples need reimpregnation after grinding and polishing because the particles have been dislodged from the resin matrix. Coverslips are then placed over the thin sections, using Araldite AY103 as a mountant. When carrying out this procedure care must be exercised so that all the air bubbles are excluded. If not excluded the air bubbles show up clearly in transmitted light and interfere with the measurement of the sections. The slides are then set aside overnight for the mountant to cure, after which they are ready for microscopic examination.

Measuring Sections

Two different sets of measurements are obtained from the thin sections of sediment: one series for porosity determinations and the other for void and particle measurements.

The porosity measurements are taken when the microscope is focused on the surface plane of the sections. When the voids and particles are measured the complete thickness of the sections can be utilized. This is possible because the embedding resins are transparent and a three-dimensional view is obtained by the packing of the particles. Because the maximum dimensions of the particles are measured, there is no need to apply a conversion factor to the particle size data (Williams and Crisp, in preparation).

Measuring Porosity

Methods for the micromorphometric analysis of soil structure have been developed by Kubiena, Beckmann, and Geyger (1961, 1962, 1963), Jongerius (1963), Beckmann (1964), and Geyger (1962, 1964), but all of these methods require specialized equipment. One of the sophisticated techniques for measuring the porosity of photomicrographs utilizes the Zeiss Particle Size Analyser, which has 48 diameter classes (Jongerius, 1963). Its lower limit for measurement is 10 μ.

A similar but simpler method, developed by Rosiwal and adapted by Swanson and Peterson (1940), is used for the measurement of the percentage volume of pore space in thin sections of undisturbed soil. The microscope is focused on the surface of the section and measurements are taken in this plane only. The slide is traversed across a mechanical stage parallel to the direction of the graduated scale incorporated in the eyepiece, and the distance is measured between the intercepts made by each successive void and each successive particle (Figure 2). The traverses are repeated over the entire section following a grid system. The complete procedure is duplicated in a direction at right angles to the first series of measurements. Further measurements are made on the other sections horizontally cut from the three blocks. The total void measurement for the sample then is expressed as a percentage of the total measurement of void and solid. It has been assumed (Holmes 1930; Swanson and Peterson, 1940) that this value is equivalent to the porosity of the sediment defined as the fraction of the total volume occupied by the voids. An independent test, which

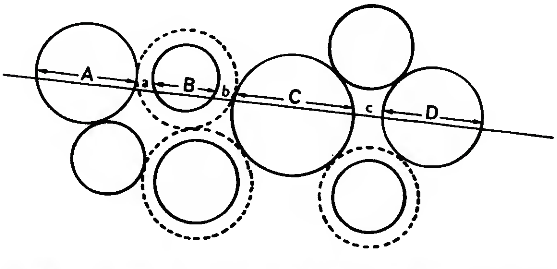

FIGURE 2.—Cross section of a model spherical system to illustrate the method of measuring porosity. Measurements are taken along the grid line. The solid outlines represent the plane in which the slide has been focused.

will be given in a later paper (Williams and Crisp, in preparation) has shown this assumption to be justified.

From Figure 2 an estimate of the porosity (P) is given by

$$P = \frac{a+b+c+d}{A+a+B+b+C+c+D+d}.$$

The technique may be used directly on the slides or it can be adapted for measurement of photographs taken from the slides by direct projection.

The views in Figure 3 are magnifications of small areas of sections of two shell gravels obtained by projection. Photographs obtained by this method are useful for making combination figures with accurate scale silhouettes of interstitial animals (Williams, 1969).

Sections of deposits from beaches having sand of small grain sizes are first projected to obtain a negative, which then is enlarged to give a positive at a magnification of about fifty times. Satisfactory photographs are not always obtained from sections of very fine sands because the thin sections of quartz transmit as much light as the voids, making the peripheries of the voids indistinct. In such cases the porosities are measured directly from the slides under ultraviolet light, which causes the voids to fluoresce characteristically.

Measuring Particles and Voids

Particle and void measurements are made only on the slides; however, instead of measuring intercepts, particles and voids are systematically located by utilizing a grid system. The grid is formed by traversing the mechanical stage of the microscope through a specified number of divisions between each series of measurements. The maximum dimensions in two directions at right angles of each particle and void so located are measured. The above method of measurement, utilizing the complete thickness of the section, is illustrated in Figure 4. The grain measurements are given by A_1A_2, B_1B_2, etc., and the void measurements by a_1a_2, b_1b_2, etc. The procedure is carried out for the sections which are taken parallel to and vertically to the surface of the deposit. The four sets of values thus obtained represent the maximum dimensions of the voids in three directions in the deposit, with a duplicate measurement of one of the directions parallel to the surface. From these measurements the possibility of directional orientation of the pores or the particles can be checked by analyzing the data statistically. The measurements of particle and void dimensions then can be plotted against a Log_{10} or Log_{-2} scale and the relevant statistical parameters, such as the mean, median, standard deviation, etc., can be obtained from the cumulative curves.

Conclusions

Although the method requires specialized cutting and grinding equipment, very reliable results can be obtained, even with little experience.

In recent years the development of water-soluble resins has made possible in situ impregnation of marine sediments. The development of this technique will overcome the use of the sampler for obtaining "undisturbed" samples and will eliminate a source of error and criticism of the method.

The accuracy of the technique was tested by impregnating various model systems of "Ballotini," which are uniform glass beads (Williams and Crisp, in preparation). Porosity, void, and particle measurements were made from the slides and excellent correlations were observed with results obtained from sieving and displacement methods for porosity estimates.

The resin impregnation method enables direct measurement and visual examination to be made of the interstitial habitat. The measurements of the interstices together with the other physical data from the sediment create a set of interwoven factors, the interplay of which will affect the distribution of the fauna. The information acquired from this technique is a further measurable character which will contribute towards a better understanding of this extremely complex biocoenosis.

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Figure 3.—Projections of thin sections of shell gravel. The angularity of the sediment is due to the plates of barnacle shells.

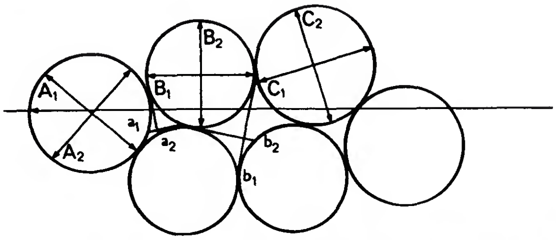

FIGURE 4.—Cross section of a model spherical system to illustrate the method of measuring voids and particles.

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Literature Cited

Alexander, F. E. S., and R. M. Jackson
1954. Examination of Soil Micro-Organisms in Their Natural Environment. *Nature,* 174:750–751.

Altemüller, H. J.
1956. Neue Möglichkeiten zur Herstellung von Bodendünnschliffen. *Zeitschrift für Pflanzenernährung, Düngung, Bodenkunde,* 72(117):56–62.
1962. Verbesserung der Einbettungs- und Schleiftechnik bei der Herstellung von Bodendünnschliffen mit VESTOPAL. *Zeitschrift für Pflanzenernährung, Düngung, Bodenkunde,* 99(144):164–177.

Beckmann, W.
1964. Zur Ermittlung des dreidimensionalen Aufbaues der Bodenstruktur mit Hilfe mikromorphometrischer Method. In A. Jongerius, editor, *Soil Micromorphology,* pages 429–444. Amsterdam: Elsevier.

Dalrymple, J. B.
1957. Preparation of Thin Sections of Soils. *Journal of Soil Science,* 8(1):161–165.

Davis, F. M.
1925. Quantitative Studies on the Fauna of the Sea Bottom. Part II. *Fishery Investigations, London,* 8(4):1–50.

Ganapati, P. N., and G. C. Rao
1962. Ecology of the Interstitial Fauna Inhabiting the Sandy Beaches of Waltair Coast. *Journal of the Marine Biological Association of India,* 4(1):44–57.

Geyger, E.
1962. Zur Methodik der mikromorphometrischen Bodenuntersuchung. *Zeitschrift für Pflanzenernährung, Düngun, Bodenkunde,* 99(144):118–129.
1964. Mikromorphometrische Untersuchungen über den Einfluss bestimmter Pflanzengemeinschaften auf die Strukturbildung im Boden. In A. Jongerius, editor, *Soil Micromorphology,* pages 445–457. Amsterdam: Elsevier.

Hagn, H.
1953. Polestar, ein Hilfsmittel für die Herstellung orientierter Dünnschliffe kleiner Objekt. *Mikrokosmos,* 43:68–72.

Holme, N. A.
1949. The Fauna of Sand and Mud Banks near the Mouth of the Exe Estuary. *Journal of the Marine Biological Association of the United Kingdom,* 28:189–237.

Holmes, A.
1930. *Petrographic Methods and Calculations.* New York: D. Van Nostrand.

Jones, N. S.
1950. Marine Bottom Communties. *Biological Reviews,* 25:283–313.

Jongerius, A.
1963. Optic-Volumetric Measurements on some Humus Forms. *Proceedings of a Colloquium on Soil Fauna, Soil Microflora and Their Relationships, Amsterdam,* pages 137–148.

Jongerius, A., and G. Heintzberger
1963. The Preparation of Mammoth-Sized Thin Sections. *Soil Survey Papers,* 1:1–37. Netherlands Soil Survey Institute, Wageningen.

Kubiena, W.; W. Beckmann; and E. Geyger
1961. Zur Methodik der photogrammetrischen Strukturanalyse des Bodens. *Zeitschrift für Pflanzenernahrung, Düngung, Bodenkunde,* 92(137):116–126.
1962. Zur Untersuchung der Feinstruktur von Bodenaggregaten mit Hilfe von Strukturphotogrammen. *Zeiss Mitteilungen,* 2(7):256–273.
1963. Mikromorphometrische Untersuchungen an Hohlräumen im Boden. *Anales de Edafologia y Agrobiologia,* 22(11–12):551–567.

Prenant, M.
1932. L'Analyse mécanique des sables littoraux et leurs qualités écologiques. *Archives de Zoologie Expérimentale et Générale,* 74:581–595.

Swanson, C. L. W., and J. B. Peterson
1940. Differences in the Microstructure of Profiles of the Marshall and Shelby Silt Loam. *Proceedings of the Soil Science Society of America,* 5:297–303.

Volk, G. W., and H. J. Harper
1939. A Revised Method for the Microscopic Examination of Natural Structure and Pore Space in Soils. *Journal of Soil Science,* 48:141–145.

Wells, C. B.
1962. Resin Impregnation of Soil Samples. *Nature,* 193:804.

Werner, J.
1962. Über die Herstellung fluoreszierender Bodenanschliffe. *Zeitschrift für Pflanzenernährung, Düngung, Bodenkunde,* 99(144):144–150.

Wieser, W.
1956. Factors Influencing the Choice of Substratum in *Cumella vulgaris* Hart (Crustacea, Cumacea). *Limnology and Oceanography,* 1(4):274–285.
1959. The Effect of Grain Size on the Distribution of Small Invertebrates Inhabiting the Beaches of Puget Sound. *Limnology and Oceanography,* 4(2):181–194.

Williams, R.
1969. Ecology of the Ostracoda from Selected Marine Intertidal Localities on the Coast of Anglesey. In J. W. Neale, editor, *The Taxonomy, Morphology and Ecology of Recent Ostracoda,* pages 299–329. Edinburgh: Oliver and Boyd.

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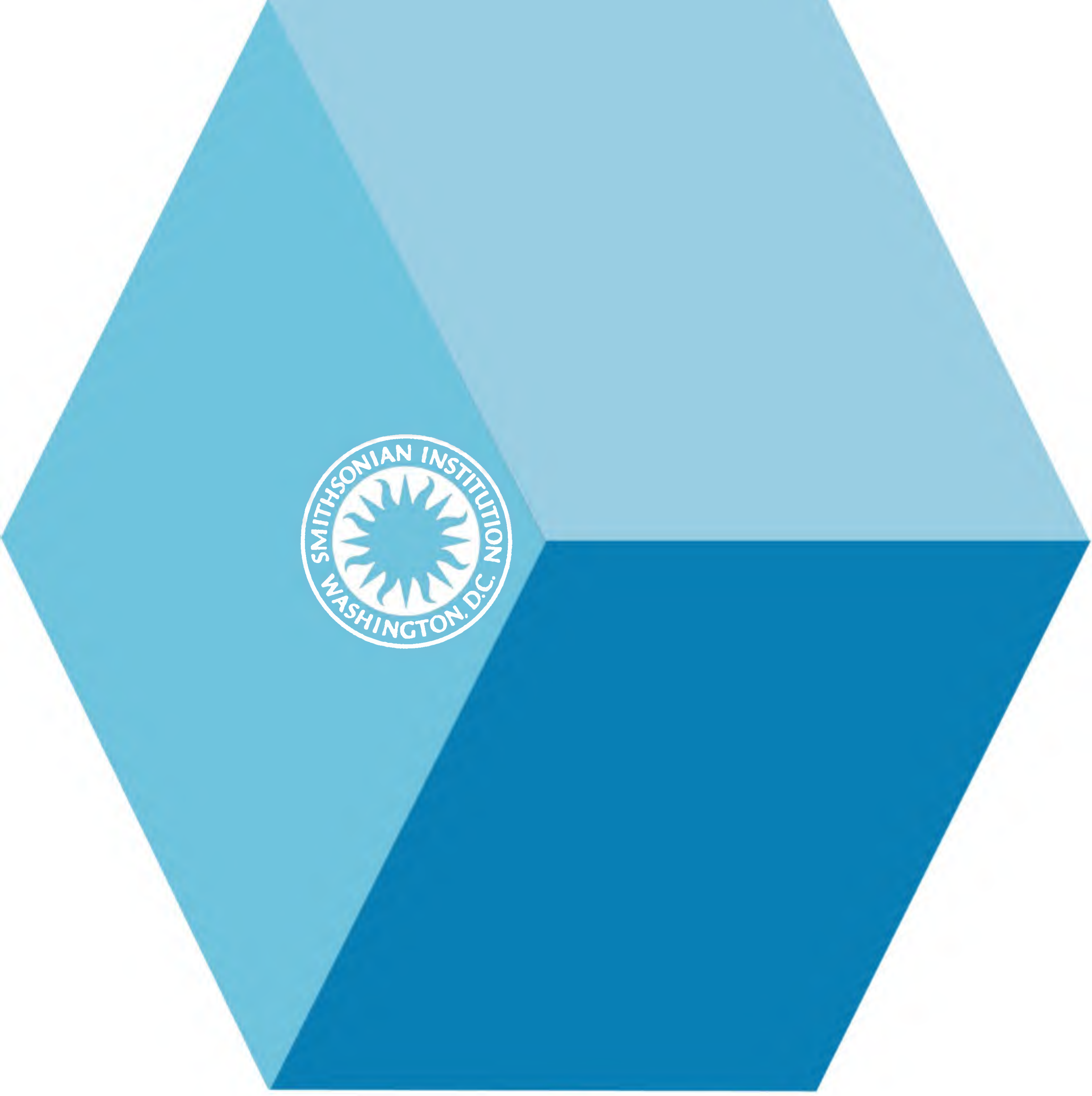
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