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In addition to forming an integral portion of the plankton of both fresh and salt water, copepods have also been found in several unique situations. Some species inhabit damp moss in the Black Forest of Germany and other European woodlands long distances from any body of water. Other species live within the branchial chambers of land crabs, which enter the ocean only during their spawning season, once a year. Copepods have also been found in the rain water which accumulates inside the cup formed by the tightly sheathed leaves of certain epiphytic Bromeliads saddled on the limbs of tropical trees far away from the water. But these are simply distribution freaks, likely to occur in any animal or plant group, and confined to so few species as to be worthy only of passing notice.

There has recently been discovered, however, a new copepod habitat of vastly more importance and claiming as its tenants a sufficient number of genera and species to constitute an important group. According to their habits and mode of life, copepods have hitherto been divided into three well-known groups: free-swimmers, commensals, and parasites. The dwellers in this new environment will constitute a fourth group, which may be designated as terraqueous copepods because they actually live in both water and sand or mud. Brief mention has already been made[1] of this group, and the name benthonic was suggested for them. But that term has already come into general use to designate the fauna and flora of the sea bottom as opposed to the plankton. Certain of the free-swimming copepods live close to the bottom and move about in the water or among the vegetation above the bottom. They are the forms which should be designated as benthonic, whereas these terraqueous copepods actually penetrate the sand or mud, and hence can never be captured by towing. They are not free-swimmers, therefore, and are neither commensal nor parasitic in their habits, but must form a new group.

The discovery of these sand and mud dwellers was first made by the late Dr. N. A. Cobb, government specialist on nematodes. While

[1] U. S. Nat. Mus. Bull. 158, p. 6, 1932.

washing out some of his nematodes from the sand of the bathing beach at Woods Hole, he found copepods among them. Further examination revealed that the sand of that beach and other beaches along Cape Cod and on the neighboring islands was fairly teeming with copepods. Many more could be washed out of the sand than could be obtained by towing along the shore.

During the following summer the same was found to be true of the sand beaches around Mount Desert Island on the Maine coast. And since every sand beach yielded its quota of copepods, the search was extended to the mud flats, the mussel beds, and the tide pools—in fact, to all kinds of localities where the beach was not composed of solid rock. Let it be remembered that the exceptional tides (12 to 16 feet) of the region lay bare immense areas of shore at low water. Every locality examined yielded at least one or more copepod species, usually more, and a few localities as many as 20 or 25. In the mussel beds they were found in the sand or mud beneath the upper layer of living mussels; in areas covered with seaweed they were in the soil beneath the plants; in the tide pools they were washed out of the sand or mud covering the bottom of the pool.

These copepods not only live in the sand and mud while it is covered by the tide, but remain there after the tide has ebbed and left the beach uncovered. As some of them are found as far up on the beach as the average high water mark, the time during which their habitat is covered by the ocean water is very much shorter than the interval during which it is left uncovered. And yet such conditions do not seem to be at all disadvantageous, to say nothing of being inimical. Sand that had remained uncovered at least 10 hours and had become rather warm in the hot sunlight, yielded living and active copepods when washed out in the laboratory.

Nor are the copepods confined to the beach between tide marks, but are found everywhere in the sand and mud constantly beneath the water down to moderate depths. Portions of the sea bottom brought up on the flukes of anchors or in a dredge usually yield some copepods on being washed out and strained. Many such species have been obtained in dredging and have been described and figured by various authors without the knowledge that they were really sand dwellers. It is of course impossible to tell whether a dredged specimen comes from above or beneath the surface of the ocean bottom. The descriptions and figures, however, show just such modifications in size, shape, and structure as appear in these sand dwellers.

Upon reflection it will appear that two conditions are requisite in order to induce the copepods to penetrate the sand or mud and remain

there for any length of time. There must be plenty of food and the environment must be such as to allow the copepods more or less freedom of locomotion. The former is readily explained by the presence in the sand or mud of such organisms, especially diatoms, as ordinarily serve for copepod food. This would constitute a sort of cold storage supply amongst which the copepods could browse with much less danger from outside interference. But can the copepods move about in the sand or mud with anything like freedom of locomotion? Consider the sand first.

What is commonly designated as sand may be derived from several sources, and its constituent grains may vary greatly in size, with considerable resultant differences in the sand itself. If derived from the geologic weathering and erosion of crystalline rocks, the sand is made up very largely of rounded grains of quartz. Such is the sand of Cape Cod and the Maine coast, and it cannot be compressed sufficiently to obliterate or even greatly diminish the interstices between the grains. These open spaces make an ideal forage ground for copepods small enough to move about within them, and there is little danger of being crushed. Such sand always contains copepods even on exposed beaches like those of the south shore of Marthas Vineyard, where a heavy surf breaks almost continuously. Such sand also frequently collects in the tide pools along the Maine coast and often contains a good assortment of copepods. One pool at Sea Wall on Mount Desert Island, about the size of a small room, yielded more than 20 copepod species, including calanids, harpactids, and cyclopids.

If the sand is largely made up of broken shells, as it often is in the Tropics, its grains are not spherical but more or less flattened, and when the flattened surfaces come together, which is the usual tendency, the interstices are entirely obliterated. Any minute organism that tried to live in such sand would be in constant danger of being crushed. This kind of a sand beach never contains copepods, and the bathing beach on the eastern shore of Mount Desert Island just south of Bar Harbor is an excellent example. Two-thirds of the sand of that beach is broken shells, and it is the only sand beach examined on the island that yielded no copepods.

A third source of sand is coral disintegration, and this is the prevalent kind of sand beach everywhere in the Tropics. The coral rock is so soft that the resultant grains tend to become extremely small and to vary considerably in size. Here again the interstices between the grains can be practically obliterated by pressure, and if any are left they become so small and irregular as to be uninhabitable. Only rarely

and in exceptional localities would any copepods be found in this sort of sand.

In view of these considerations the final answer to the question whether copepods can move about freely in sand is in the affirmative if it is quartz sand, and in the negative if it is shell or coral sand. The fact also that both the shell and the coral sand are calcareous may have some influence upon the copepods.

As to the mud, its composition is also the most important factor in determining whether it is to be inhabited or not. If it is dense clay there will be no chance of finding copepods within it, and on the other hand if it be sandy the probability of its being inhabited by copepods will become greater as the percentage of sand it contains increases. The upper layers of ordinary mud are more or less flocculent, that is they are made up of small flattened flakes or floccules. These are to a certain extent buoyant in water and are so irregular in form that they do not pack together closely but leave sufficient open spaces for the copepods to move about freely. Many of the floccules are also so small and light that they can be easily pushed aside by the copepods during their progress, and so soft that contact with them is not likely to be at all harmful. Consequently, in the mud there is not the same restriction in size that prevails in the sand, and the larger copepods can move about as freely as the smaller ones, possibly with even greater facility.

Such a life as this, moving about all the time within the confines of the sand and mud, is just as different from that of the typical free-swimming forms that frequent the open water as are the lives of the commensal and parasitic copepods. The investigations carried on in these last two groups have already revealed numerous modifications resulting from their habits and mode of life. It is reasonable to suppose that these terraqueous copepods would also exhibit modifications similar in their interpretation but differing in their details, and such we find to be the case.

The first of these modifications is shown in the restricted size of the fully developed adult. In the other groups we find great variations in size up to 200 mm in a few parasitic forms. Here there is great uniformity in size, from a minimum of a quarter of a millimeter to a maximum of half a millimeter in the sand dwellers, and a maximum of slightly more than a millimeter in the mud dwellers.

A second modification is one of shape; it is evident that a linear form will have greater freedom of motion under the restrictions of the sand and mud than a rotund or corpulent form. The terraqueous copepods all exhibit a more or less pronounced slenderness, the length

being many times the width of the body. The accompanying figures of four different genera of sand-dwelling copepods show their typical linear form, which is admirably suited to their mode of life (figs. 1 and 2).

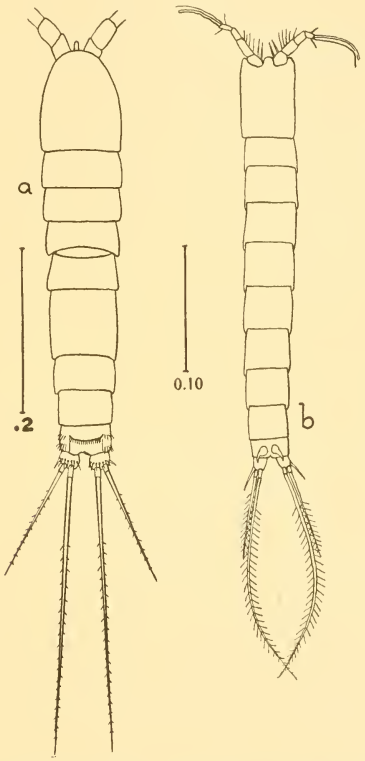

FIG. 1.—*a*, dorsal view of a female *Nitocra chelifer*, a sand dweller; *b*, dorsal view of a male *Arenosetella spinicauda*, a sand dweller.

A third modification results in increased flexibility; mere slenderness of body would contribute but little to freedom of motion unless accompanied by flexibility. In the jointed body of the ordinary copepod only one of the articulations is really movable, all the others being more or less rigid and incapable of motion. In these copepods there

is much freedom of motion in every one of the articulations, and the body can be flexed considerably upward or downward, to the right or to the left, as may be necessary. This increased flexibility enables the copepod to realize fully all the advantages of its modified size and shape. If one of these copepods is put in an aquarium with sand

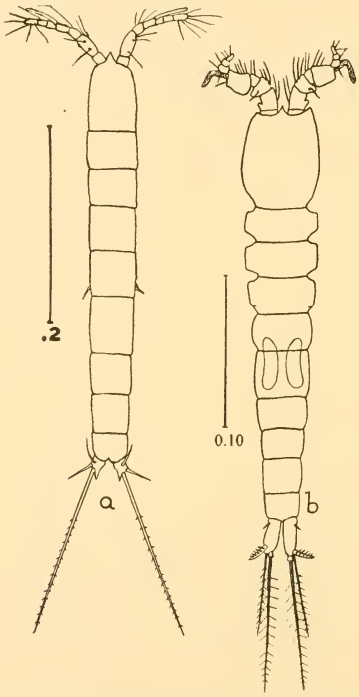

FIG. 2.—*a*, dorsal view of a female *Paraleptastacus brevicaudatus*, a sand dweller; *b*, dorsal view of a male *Emertonia gracilis*, a sand dweller.

at the bottom, it quickly buries itself in the sand, and during the process gives abundant evidence of its great flexibility.

Another useful modification is an increase in tactile equipment and sensibility. These terraqueous copepods are compelled to move about more or less in the dark, where their eyesight can be of little use for guidance. At the same time the space within which they move is so

restricted that the demand for some sort of guidance is greatly enhanced and becomes imperative. This demand is met by a greatly increased tactile sensibility in the first antennae, which here become " feelers " in the fullest sense of the term. The normal copepod usu-

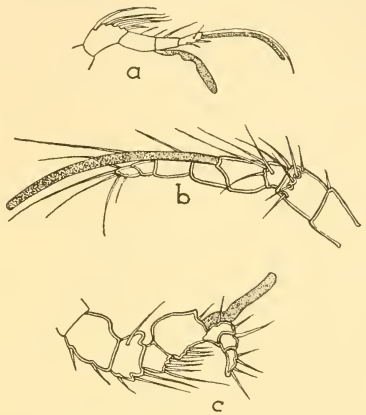

FIG. 3.—*a*, first antenna of a male *Arenosetella spinicauda*, with two large aesthetasks; *b*, first antenna of a male *Nitocra chelifer*, with a single long and stout aesthetask; *c*, first antenna of a male *Emertonia gracilis*, with a single enlarged aesthetask.

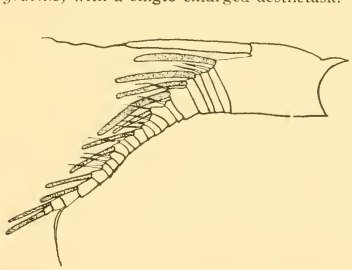

FIG. 4.—First antenna of *Arenocalanus tumidus*, female, a new genus of sand-dwelling calanids, showing an exceptional increase in the number of aesthetasks.

ally carries a single sensory club or aesthetask on each of the first antennae. In these terraqueous copepods the size and length of the aesthetasks may be considerably increased, as happens more often in the males (fig. 3). In the females either the number of aesthetasks is multiplied as in figure 4, or they are supplemented by thick finger-

like processes, carrying along one or both sides a row of coarse spines as in figure 5. There are sometimes six or eight such processes on each antenna, projecting in all directions and giving the appendage a decidely bizarre appearance. Nothing of this sort has ever been reported upon free-swimming copepods, and hence it may be regarded as a special modification for a special mode of life. Furthermore, the first antennae are short and curve around the front of the head in such a way as to offer least resistance to forward progress. At the same time

FIG. 5.—*c*, first antenna of a female *Rathbunula curticauda*, a sand dweller; *d*, first antenna of a female *Echinocornus pectinatus*, a sand dweller.

the frontal margin is thereby furnished with a highly sensitive armature admirably suited for guidance.

Of course these copepods cannot indulge in free-swimming, since there is no room for it within the sand and mud, and the copepods come out into the open water very seldom, if at all. We therefore find, as would be expected considerable modification of the swimming legs in some of the species. The long plumose setae, so useful in swimming, partially or wholly disappear and are replaced by stout spines. In figure 6 all the first four pairs of legs are modified in this way, and it is quite evident that they are thus made more serviceable

for crawling about in sand and mud. There is also sometimes a reduction in the number and size of the endopod segments until in a few species the entire endopod is reduced to a mere knob, of no use except to show that the leg is still biramose.

Another modification is concerned with the external ovisacs, which in the free-swimming copepods hang loosely from the genital segment and often diverge considerably from the body. The eggs themselves are of moderate size and fairly numerous, and may be carried in one or two ovisacs, or even extruded singly into the water without being carried at all. In the parasitic copepods a large number of eggs seems to be the primal requisite. When the eggs are arranged in a single

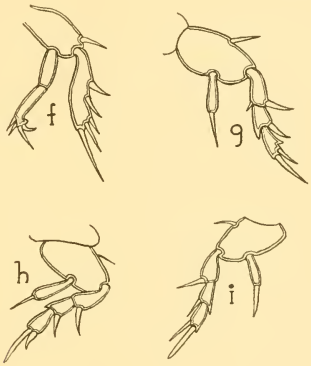

FIG. 6.—*f* to *i*, first, second, third and fourth leg of *Emertonia gracilis*, showing substitution of spines for plumose setae.

row, as in the Caligidae, the increase in number is obtained by lengthening the ovisacs, which sometimes become several times as long as the entire body. When the eggs are multiseriate, the diameter of the ovisac is increased and the size of the egg is at the same time diminished. As a result, the number of eggs in some copepods parasitic upon deep-sea fish may reach 10,000 or more in each ovisac. In the commensal copepods there are often no ovisacs, the eggs being gathered into a brood sack situated in the dorsal portion of the thorax.

In contrast with these three groups, the ovisacs of the terraqueous copepods are nearly always flattened and closely appressed to the surface of the genital segment and abdomen. Sometimes the fifth legs are enlarged and modified to cover the anterior ends of the ovisacs and thus partially protect them. The number of eggs is reduced, and

at the same time the size is increased, so that each ovisac contains very few eggs, in some instances only two as shown in figure 7, an harpactid, or a few more as in figure 8, a cyclopid.

In addition to the modifications in structure exhibited by these sand and mud dwellers, there are also such differences in habits and mode of life as would be expected from their habitat. Free-swimming copepods maintain nearly perpetual motion; as they are heavier than water,

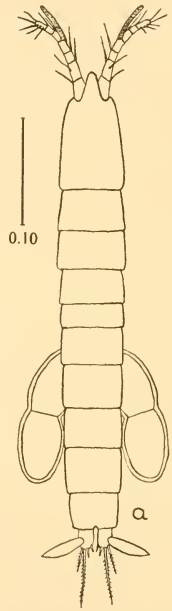

FIG. 7.—Dorsal view of female *Goffinella stylifer*, a sand dweller, showing the peculiar ovisacs and large eggs.

this is necessary to keep them suspended and prevent their sinking to the bottom. When they wish to rest, some species are able to suspend themselves from the surface film of the water, but all the others must find some support. For those that live near the bottom, the vegetation and the debris that collects on the bottom afford the requisite support, but it is quite different with those that live in the open ocean. For them, unless there happens to be something floating to which they can cling, it becomes the simple problem of sink or swim.

A great deal of motion and very little rest therefore constitutes the essential mode of life of a free-swimmer.

The great majority of the parasitic copepods, when once they are securely fastened to their hosts, do not move at all but may be, and usually are, carried long distances by their hosts. In early life all these parasitic forms are free-swimmers during their nauplius, metanauplius, and often their copepodid stages. And of course during those periods they must maintain a great deal of motion and enjoy but

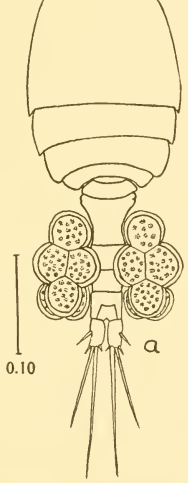

FIG. 8.—Dorsal view of female *Cyclopina agilis*, a dweller in sandy mud, with large eggs closely appressed to the body.

little rest. But in adult life this is exactly reversed even for such species as continue to practice more or less the free-swimming of early life. They may leave their hosts and move about freely in the water, but this is not continued for any length of time, and they quickly return to their hosts.

The commensal copepods spend their entire lives inside the body of their hosts, and hence they never swim freely except in so far as it is possible within such narrow confines. A great deal of rest and very little motion, therefore, are the characteristics of their mode of life.

These terraqueous copepods form a new group intermediate between the others and differing from them in many ways. There is no necessity for swimming in order to prevent them from sinking, and wherever they may stop when moving about will provide a convenient resting place. Their chief concern is to obtain an adequate food supply, and in doing this they scurry about freely in the sand or mud. They have much more freedom of motion than the commensal forms but not nearly as much as the free-swimmers; they may well be called free-movers but scarcely free-swimmers. In all probability their time is much more evenly divided between motion and rest than it is in the other groups.

Again, the free-swimmers, in consequence of their protracted movements, cover a considerable area and may even be carried long distances by currents or drifts. In this way they are widely distributed, and it is not uncommon to find some of the species in nearly every ocean on the globe. The same thing is true of the parasitic copepods, for here the females, and often both sexes, are carried about by the hosts, and if the latter are fish or other animals capable of extended migration, the parasites are thereby widely scattered.

On the contrary, most commensal copepods live within ascidians, holothurians, tunicates, and similar animals, which move about but little if at all. And since the movements of the copepod adults are also restricted, the species have only a limited distribution. Their chance for dissemination lies in the escape of the larvae from their host and the ability to swim about during their development stages.

Similarly, in these terraqueous copepods the distance covered by the locomotion of the adults is so limited that the distribution of the species is seriously handicapped. The presence of a given species in the sand or mud of one beach is no indication that it will be found in neighboring beaches. We may go farther and say that the component parts of the same beach are very likely to yield different species of copepods. In short, isolation is as much an accompaniment of dwelling in the sand or mud as is wide distribution a result of swimming freely in the open ocean.

A final consideration is concerned with reproduction and is also intimately associated with distribution. Among the free-swimmers the female carries her eggs about with her in external ovisacs or extrudes them singly at intervals into the water. In the former case the eggs are kept together until they hatch, in the latter case they are widely scattered, since the female is constantly moving about while extruding them. Similarly, when the eggs in the ovisac hatch, the nauplii do not all emerge at the same time, but there is a considerable interval between

the bursting of the first and the last egg shell. Here also the female copepod is moving about constantly while the nauplii are emerging, so that the latter are just as widely separated as when the eggs were deposited singly. Such a scattering of the larvae must contribute greatly to a wide distribution of the species, but we are chiefly concerned here with the separation of parent and offspring. It is quite evident that among these free-swimmers no inference of relationship can be drawn from a mere association of adults and larvae.

In the commensal copepods, on the contrary, every step in the process of reproduction from the preliminary mating to the final moult into the adult form takes place within the body of the host. If there were a single male and female at the outset it would be fairly certain that all the larvae were their offspring, and we would have a genuine copepod family from a genetical point of view. Relationship can be argued here from association of adults and larvae and might possibly continue through more than one generation.

The terraqueous copepods appear to occupy an intermediate position between the two extremes just noted. Compared with the free-swimmers they move about very little, compared with the commensals they have greater freedom of locomotion. It is highly probable, however, that the area covered by a female during the hatching of her eggs is very limited. As a result the emerging nauplii are not far removed from their parent and may be more or less closely associated with one another. The relationship of adults and larvae found together is not at all impossible, but neither is it as probable as among the commensal copepods.

The considerations here discussed show very clearly that these terraqueous copepods constitute a fourth group fully as well defined as either of the three already accepted. And they open up to the investigator an entirely new field of research along several interesting lines. Not only will a comparatively large number of the specimens obtained in the sand and mud prove to be new species and genera, but also they will exhibit some remarkable adaptations to their environment. The habitat is entirely new and one of the last to be suspected as a resort for copepods, and the mode of life is unique and entirely unlike that of other copepods. Such a combination ought to prove genuinely attractive and, supplemented by the abundant supply of working material, ought to yield important results.