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LIV.—Notes and Observations on the Distribution of the Larvæ of Marine Animals

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surface, not present in front of the eyes, on the limbs, rump, or tail. Under surface and inner aspect of limbs dull whitish, not sharply defined, the greyish bases of the hairs showing through; throat more yellow; scrotum brown. Ears of fair size, rounded, hairy, dark brown. Hands and feet dark brown, rather darker than the olivaceous arms and legs; hallux present; sole-pads transversely striated. Tail evenly well haired, blackish, a line along the middle of the lower surface paler brown.

Skull thickly built, of normal proportions, not so short-muzzled as is described in *D. albopunctatus*. Nasals anteriorly slightly opened out and separated in the middle line, their most anterior points lateral instead of mesial; posterior expansion present as usual. Supraorbital edges rounded, postorbital processes well developed. Palatal foramina short, ending opposite the anterior part of the canines. Bullæ high and conical. Teeth as usual, the upper premolars oval in section, without diastemata. Molars decidedly larger than in *D. albopunctatus*.

Dimensions of the type (measured in skin):—

Head and body 350 mm.; tail 285; hind foot (s. u.) 53; ear 30.

Skull: basal length 65·6; greatest breadth 42; nasals, length 25, breadth anteriorly 6·5, at middle 5·5, posteriorly 10·5; interorbital breadth 15·8; intertemporal breadth 9·6; palate length 36·5, breadth between outer corners of m^3 23; palatal foramen 4·2; combined length of three anterior molariform teeth 13·6; breadth of last molar 5·6.

This *Dasyure*, the representative in British New Guinea of the *D. albopunctatus* of N.W. New Guinea, is readily distinguishable from that animal by its much greater size, as may be seen by a comparison of the dimensions here given with those of *D. albopunctatus* published in the 'Catalogue of Marsupials.'

Perameles Cockerelli, Rams.

♂, ♀, 0, 6.

LIV.—*Notes and Observations on the Distribution of the Larvæ of Marine Animals* *. By J. STANLEY GARDINER, M.A.

IN considering the distribution of larvæ our object is to ascertain how far the pelagic or planktonic larvæ of marine animals

* This paper was read at a meeting of the 'Challenger' Society in June last, and is now published by request of several of its members.

are of importance in distributing species and genera from shore to shore, from one littoral zone to another. It may, perhaps, clear the ground if I suggest, in the first place, that we confine our attention to such animals as belong to the *benthos*, the sedentary, creeping, and burrowing fauna of the bottom. Here we can deal for the most part with well-defined groups, all of true benthos forms, any extensive wandering of the species or genera of which must be due to the distribution of their pelagic larvæ, direct migration of the adults of littoral forms across or beneath the deep-sea being quite exceptional.

It appears to me that it would be a profitable and perfectly legitimate question to consider what would be the fauna of a bank or the littoral zone of an island upheaved halfway between Land's End and Bermuda after 100 or 1000 years! We should want to know accurately a great number of factors to answer such a question. First, we make inquiry as to what currents would lave our bank and what would be the temperature of the water around it at each and every season of the year. In the case cited, the only current of importance would be the Gulf Stream, and it would be an easy matter to ascertain or calculate the temperatures. We then carefully examine the topography of the ocean-basin and the surrounding coasts to see from whence it could with such currents become populated. If our bank arises, as it would, from 2000 fathoms and there are no shoals of less than 1000 or, possibly, 500 fathoms, our task would be simplified, and we would at once commence an examination into the littoral fauna of the Bermuda reefs and slopes. If, however, we found, as is quite possible, ridges or isolated banks arising to a less depth from the surface—I should suppose the vertical distribution of the littoral fauna to continue down to about 250 fathoms, the approximate depth to which light in the tropics appears to penetrate the sea-water—our task would be complicated by an almost complete absence of knowledge of the vertical range of most of the benthos animals; and in view of its extraordinary range as found by the 'Siboga' Expedition it is a factor which could not be neglected by us.

The subject, however, of our main inquiry would be the extent to which the benthos animals of Bermuda produce definite pelagic larvæ and the distances to which these could be carried by the currents. In the course of centuries a few of the animals would doubtless be conveyed over to our bank by means of floating timber or pumice or the feet of birds, much beloved of writers on distribution; but after full consideration we would be inclined to reject these sources as of small account. Our research, in truth, resolves itself into a

simple question, before which all others are of little moment : How many days can the various larvæ of the benthos animals live in the plankton ?

To this question we may seek an answer by two means. First, we might take the faunas of a series of coral or recent volcanic islands, and compare them with the faunas of the nearest land-masses, or, better, of such land-masses as are swept beforehand by the currents which reach their shores. We may thus compare the littoral fauna of Bermuda with that of the Tortugas or Bahamas, or even the West Indies in general. We shall get certain positive results of utility, but those really valuable for our purpose should be negative. Certain littoral animals, and even groups of animals, will not be found. We say that their larvæ have not been able to live long enough to reach Bermuda ! But is the temperature suitable ? Surely Bermuda is mainly corallaginous, while the West Indies are largely volcanic, and in any case the bottom deposits of the latter are rich in silica ! The West Indies are continental and have, as compared with Bermuda, a far richer food-supply ! In effect the environment of the two localities is absolutely different, and our inquiry at first sight seems futile.

Perhaps the case of Bermuda and the West Indies is an extreme instance, where the conditions are widely diverse, but yet in respect to any islands or groups of islands in the Pacific the same arguments could be put forward, and in no instance that I am at present aware of could be properly confuted as regards banks more than 100 miles apart. Let not this, however, nor any other method of inquiry be despised ! It is capable of results of some considerable value. Has our shore or that of Norway, of France, or of Spain, any of the characteristic animals of the West-Indian littoral fauna ? In this instance a thousand conditions porchance are different ; but why does the Indo-Pacific fauna reach to the Sandwich group, the Marquesas, and the Paumotus, and yet fetch no part of the American shore ? The method may, indeed, give us differential results as we travel eastward in the Pacific Ocean or compare the faunas of the Azores, the Canary or Cape Verd groups with those of the nearest West-Indian banks. Some West-Indian genera, families, and even groups, maybe, are absent from the Western-Atlantic banks ; other families are present, but their genera are different ; yet in others we may find the same genera but the species are different ; and, lastly, in still others the species are identical.

The critics of our views on distribution will, perhaps, and
Ann. & Mag. N. Hist. Ser. 7. Vol. xiv.

do, use the argument that identical species in the above and many other distant localities are cases of parallel or even convergent evolution if they cannot raise ridges to span the intervening gaps sufficient to permit of the migration over of the species, so as to allow intercrossing to take place. We ourselves—I have done so—use that argument; but we ought first to exhaust every possibility, in the absence of direct observations of such evolution, to avoid getting into such a strait. At most, by our faunas we get the possible range of distribution of the larvæ, but what we want in the first place to know is their regular and average range. If we find different species of the same genera or different varieties of the same species of animals on the Ceylon and Maldive slopes, we may infer that the larvæ of these genera and species seldom interchange, and we may deduce from the known currents of the region the length of time for which the larvæ can—or rather do—continue to live as such. Although I consider that for the due progress of any science we must have a certain amount of speculation, yet it seems to me that this method is rather fatuous in the absence of any direct evidence of the length of time to which any of the larvæ can live in the open ocean.

Our second method is the direct study of the length of life of larvæ as such. In considering it I divide the larvæ for convenience under three heads—the crustacean, the trochosphere and its derivatives and allies, and the planula and its allies. I deliberately omit certain larvæ, partly because they are unimportant, or I have not found any observations to aid me, or they have not come under my notice in the plankton with which I have had to deal. The most important of those thus omitted is the ascidian tadpole, in respect of which I have no direct observations, never having found it more than twenty-four hours (measuring the current in time) from land, though one is compelled to suppose from its structure, so efficient for pelagic life, that it can be carried for many days and considerable distances. In any case the distribution of the Tunicata is so little known that it is of no aid, but I have not heard of any occurrence that would give it a life of more than five or six days. I mention it, however, because it has saved me from one error, which I nearly committed rather extensively, but which suggests a method that may yet yield valuable results. Certain acinetid and vorticellid Protozoa commonly settle on tunicate and other larvæ. They branch dichotomously, and, according to some observations of my own at Naples in 1895, they divide and hence branch dichotomously each night, the observations

being continued to the seventh and eighth branchings, 128 and 256 heads, on the seventh and eighth successive nights. Here we have an apparently ready means of determining the age of the larvæ on which the Protozoa may be settled, but one which fails absolutely, since I have, on some specimens of the ascidian tadpole 20 hours old which Prof. Herdman has been kind enough to allow me to examine, found colonies of such animals with 8 and 16 heads, 3 and 4 branchings.

Crustacean larvæ may be soon disposed of. I have kept zoœas unchanged for 12 days. I have found them and also a few nauplii right to the west of Minikoi in the south-west monsoon, not conceivably less than 25 to 30 days old, unless there be shoals that we know not of or unless they belong to adults which live below 1000 fathoms—an unlikely supposition. I have caught them on the east of Male in the Maldives (lat. $4^{\circ} 12' N.$), and fancy from the currents that they must have come rather from the Nicobars or the East Indies than from Ceylon. We secured some to the south of Funafuti, scarcely less than twenty days from the Phoenix and Samoan groups, and my observations show that they made nought of the journey of 250 to 300 miles from Fiji to Rotuma, at least twelve days. Here is positive evidence enough, and one is inclined to conclude that wherever any bank may appear in the Indo-Pacific or Atlantic Oceans it should be speedily provided with a fauna of such Crustacea as possess free-swimming larvæ of the zoœan and more developed types*.

The trochosphere is in its typical forms the larva of the Polychæta, the Echiuroidea, and the Mollusca, modified but yet quite distinct in the Echinoderms, *Phoronis*, and the Enteropneusta, and also, though still more changed, of the Nemertean and the Sipunculoidea. In its Echinoderm and Enteropneustan forms it differs for different species almost as much as do the adults, and so, perhaps, any direct research on the subject may be expected to yield in these groups the most definite results. According to Mortensen, in his "Plankton-Expedition" report, these (Echinoderm) larvæ would appear to be seldom found in the high-sea plankton—that of the open ocean. The inference would be that their period of life is, under normal circumstances, only of a few days' duration. As in the Sargasso Sea were found bipinnaria, auricularia, and ophiopluteus larvæ at least 800 miles from the nearest bank, and as it is in the highest degree improbable

* I have not found it possible to distinguish between the nauplius larvæ of pelagic and littoral forms.

that they belong to adults living in the deep sea, Mortensen's conclusion would point to there being a bank in the Sargasso Sea or to the adults living in the floating weed. So certain, too, are the students of the Enteropneusta of the limited distribution of their larvæ that, if there is one species of that group in a locality, they unhesitatingly refer to it any *Tornaria* that may be found in the same locality, even a single specimen, and describe it as its larva.

At the present day the keeping and rearing for experimental purposes of Echinoderm larvæ is a regular business and one of which I had some experience in 1895-96. Now those larvæ which have been worked at do not feed for 3 to 4 days after they have definitely assumed the larval condition, and they finally metamorphose after 20 to 40 days*. Any deduction from these facts must be in absolute disagreement with Mortensen's results; but possibly in the sea the period of Echinoderm larvæ before metamorphosing is quicker. However, one must conclude that they may at times be drifted for 20, 40, or some even 60 days at the mercy of the currents. Nevertheless I only found in the localities cited above larvæ of Echinoderms off Rotuma, 4 plutei, 1 bipinnaria, and 1 brachiolaria, each from a different sample of plankton. I may parenthetically remark that my observations at Naples showed that the more food given to these and all larvæ the quicker they grow and metamorphose, other conditions being the same. All the Echinoderm larvæ float in the tanks near the surface of the water so long as they are healthy and the water be undisturbed, while the typical trochospheres sink down to varying depths, some of the largest and really healthiest ones almost lying on the bottom both by night and day. To summarize and to conclude, it would appear to me that no results in distribution can be expected, so far as the Indo-Pacific is concerned, from Echinoderms—and probably also from Enteropneusts—other than the Crinoids, the motile condition of the larvæ of which would seem to be scarcely longer than that of the planulæ to be mentioned later.

The typical trochospheres, both Molluscan and Annelid, are more difficult to keep in tanks than the Echinoderm larvæ.

* Mr. L. Doncaster has given me the following data:—

		Fertilized.	Metamorphosed.
34 days.	<i>Strongylocentrotus</i> ♂ × ♀	May 14.	June 17.
32 "	<i>Echinus</i> ♂ × ♀	June 23.	July 25.
38 "	<i>Echinus</i> ♀ × <i>Strongylocentrotus</i> ♂.	March 5.	April 12.
27 "	" "	May 16.	June 11.
27 "	" "	June 14.	July 11.

Generally my stock died off in 4 or 5 days, an occurrence ascribed at the time to wrong and insufficient food, &c. Unfortunately I could not carry the experiments very far; but the larvæ of one molluscan, given to me by Signor Lo Bianco, began to show decided changes to veligers after their third night as trochospheres, i. e. 70 to 80 hours; but this, I fancy, is altogether exceptional. At the previously cited localities I found no such larvæ (nor veligers), though they were numerous and increasingly common as one beat up for the last 150 miles from Rotuma to Fiji. I obtained, however, off Rotuma a number of specimens of what appeared to be a Sipunculid larva, and which must have come from Fiji or from deep-sea parentage.

I now come to the planula-group of larvæ, a group to which the young of most Cœlenterates belong, as well as certain sponges, Turbellaria, &c. My observations in the tropics were carried out mainly in connexion with the distribution of Cœlenterates, and particularly of corals. The difficulties on account of size and delicacy are much greater when one sets out to examine a group of larvæ such as these; yet I convinced myself that the nets &c. were suitable, and I found at Minikoi practically no difference in depth either by night or day. Actinian larvæ, according to my observations at the latter locality, at Rotuma, and at Funafuti, live for seven or eight days as such, but on the fifth day the planulæ of several species of corals had settled in the jars kept for the purpose. In none of the localities cited above from which I took plankton did I find any planulæ, nor, indeed, did I obtain any at a greater distance than 50 miles away from the nearest reef. In fact, my observations lead me to conclude that in no case could they be directly carried from Ceylon to the Maldives, though it is conceivable that these larvæ might be swept from reef to reef *viâ* the various Laccadive banks, and so reach that group.

I fear, however, that in the present state of our knowledge any consideration of larval distribution is premature and must be inconclusive. I start, perhaps, with a fallacy in assuming that the deep-sea fauna on our ocean routes does not send up larvæ to the surface-waters, though the general tendency of its forms appears to me to be to give up larval development or to reduce it as much as possible. I leave out of account the effect on the different forms of the various predatory animals of the plankton, well knowing that my limited observations may be invalidated by the larvæ having been preyed on by some particular form abundant at the time. I know that my observations are not sufficiently numerous to

be free from error, and, furthermore, I am quite aware that one should consider species and genera rather than groups. *But yet I venture with due respect to direct attention to the subject in the hope that zoologists who are dealing with plankton will not confine their attention merely to the adult groups of the same, but will, in addition, arrange for the examination of the larvæ therein in view of the distribution of the different groups of littoral animals.*

Considering each side of the question, remembering in particular the faunas of oceanic banks, so far as we know them, I venture to suggest that there are no banks to which an abundant variety of Crustacean larvæ cannot pass, that the maximum regular passage for Echinoderm (not Crinoid) and Enteropneust larvæ is about twenty days, while for Sipunculids, Annelids, Mollusca, and Crinoidea it is progressively less, the series passing on to Müller's larva, found in the Turbellaria, and ending with regular planulæ not as a rule exceeding more than four or five days of oceanic life, and probably in many forms averaging much less.

Take the Chagos Archipelago as a case in point. Crustacean larvæ should reach it freely from the Seychelles or Africa and Australia, and the Crustacean faunas of the three localities should be approximately the same for all forms of the group possessing larval development. Many of the Echinoderms and Enteropneusta should be common to the Seychelles and Western Australian, but the Chagos forms might reasonably be expected to show some small variations from their possibly parent stocks on either side. These differences should be progressively more important in Sipunculids, Chaetopods, and Echiuroids, while the corals and Turbellaria should have no more resemblance to those of the Australian than to those of the African shore, and should for the most part, indeed, have begun to take on forms which are distinct varieties or subspecies of those found in the Seychelles.

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LV.—*The Butterflies of the Group Callidryades and their Seasonal Phases.* By ARTHUR G. BUTLER, Ph.D., F.L.S., F.Z.S., &c.

BETWEEN the years 1897 and 1899 I revised a number of genera of Pieridine Butterflies in the pages of the 'Annals,' and indicated their seasonal phases; but I unaccountably