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On the Coral-Gall Prawn
Paratypton.

BY

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XI. On the Coral-Gall Prawn *Paratypton*.

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(Communicated by W. M. Tattersall, D.Sc.)

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There is no task more fascinating to the naturalist than breaking up a block of some branching coral, such as *Pocillopora* or *Madrepora*, and dislodging from among its boughs the various animals that shelter there; nor of all these latter is there any more interesting than the crab *Hapalocarcinus*, which gives rise to the well-known galls that Semper described in his "Animal Life." This organism has recently been very thoroughly investigated by Potts.¹ He has shown how the female settles in the fork of a young branch while she is still very small and immature; how by her gill-stream she directs the growth of the coral so as to mould it around her into a gall, which eventually closes, leaving only a row of little openings through which the stream flows in and out; how meanwhile she is undergoing the changes by which she reaches the adult condition, with a large, soft-bordered abdomen enclosing as in a pouch below the cephalothorax the limbs which bear the eggs; how midway in this development she is visited by the male, which is free-living and smaller than his mate was even at her first settling; how she feeds on the minute organisms (nannoplankton) brought to her by the stream of water which she draws through the gall; how her mouth-parts are modified in correspondence with this, the slender endopodites of the maxillipeds of the first pair and the exopodites of the second and first having long fringes, presumably for gathering the food much as does the China Crab *Porcellana*, and the inner mouth-parts being greatly reduced in the absence of the need for much mastication; and how, finally, she would appear to lay, after one impregnation,

1. Carnegie Institute, Washington, 1915, 212.

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successive broods of eggs, setting free typical crab larvæ of the first zoæa stage, which must pass to the exterior through the outlets of the gall.

Hitherto it has been supposed that all the coral galls were formed by *Hapalocarcinus*. Now, however, Potts has made an interesting discovery which shows that for some a prawn is

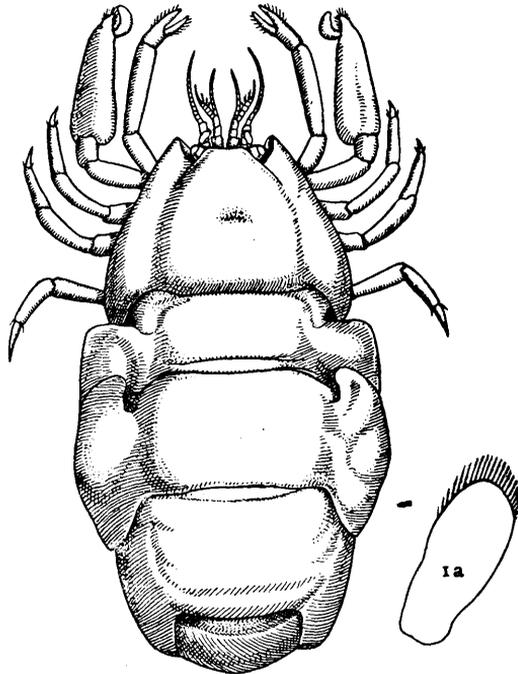


Fig. 1.

Fig. 1. *Paratypton siebenrocki*, Balss, 1914.

Fig. 1a, Antennal scale, more highly magnified.

responsible. The prawn was already known, having been described by Balss in 1914,² under the name of *Paratypton siebenrocki*, but Balss was not aware of its gall-raising habits. Mr. Potts has kindly placed in my hands his single specimen, which is a female. A male was with her, but was unfortunately

2. *Zool. Anz.*, 45, 83.

not preserved. They were taken from a large robustly-branched coral of the genus *Acropora* (= *Madrepora*) which was growing at a depth of one or two fathoms in the harbour of Pago Pago, American Samoa. *Hapalocarcinus* has been taken on various corals, but it is not yet recorded from *Acropora*. Details of the structure and mode of formation of the gall are not available, but it was unlike that of *Hapalocarcinus*, though the prawns were well enclosed. It did not project, but was hollowed into the coral.

The body of the female has the heavy, clumsy, and simplified aspect which is commonly presented by members of an active group of animals that have taken to a sedentary life, and are therefore able to further reproduction by sacrificing that elegance which is the result of adaptation to acute perception and swift movement. In this respect, and indeed to some extent in the main outlines of its build, it resembles *Hapalocarcinus*, though, since its anatomy is that of a prawn, the details that make up its habit of body are naturally different from those of the crab, and recall rather the extreme members of the series of similar adaptations which is found in the Pontiine prawns.³ Among these, indeed, it shows a considerable likeness to *Conchodytes*, which lives within the shells of bivalve molluscs, though this prawn is less degenerate than *Paratypton*. The back is broad, but its breadth is largely due to spreading branchiostegites and abdominal pleura. Between the branchiostegites the cephalothorax is rather compressed and narrows gently forwards. It is altogether without rostrum, the front being almost straight, and, in Balss' specimen, though not in mine, exposing in a dorsal view the convex middle region of the eye segment. The anterior edge of the branchiostegite projects forward beyond the median region of the carapace and bears no spines or angles whatever. The abdominal pleura, particularly the first four, are very large and, arching, enclose on the under side of the body a great brood-pouch in which lie the abdominal limbs. The last pair of limbs, with the telson, complete the pouch wall. The abdominal segments are altogether without spines or angles save that the hinder angles of the sixth segment project sharply. The cuticle of the body is everywhere very thin and perfectly smooth.

3. A group of prawns treated by some authors as a sub-family of the Palæmonidæ, and by others as a separate but closely related family. Many of its members are commensal, or at least associated, with sessile or sub-sessile organisms.

In life the animal is colourless and almost transparent. As might be expected, the *sensory appendages* are not well developed. The eyestalks are short and broad, and the eyes small and pale. The antennule is of the normal Palæmonid type, but short and stout, with sub-equal flagella, no longer than the stalk, of which the outer, though thickened as usual in its basal half, is not cleft. The stylocerite is blunt, but the outer distal angle of the first joint is sharply produced. The statocyst appears well developed. The antenna has a stalk not quite as long as that of the antennule with a flagellum about twice as long as the antennular flagella,⁴ and a small, sub-oval, fringed scale, which barely reaches the end of the stalk.

In considering the *mouth-parts* of the animal, one is drawn inevitably into speculation as to its food and mode of feeding. *Hapalocarcinus*, as has been said, feeds on the nannoplankton, and it is natural to suppose that *Paratypton* does the same, in which case we should expect to find its mouth-parts modified in the same way as those of the gall crab. It will be convenient to study these parts in order from behind forwards.

The third maxilliped has neither exopodite nor epipodite. For the rest, it is very suggestive of those of certain Pontoniinae. In it as in them, by fusion of propodite and dactylopodite, and again of basipodite, ischiopodite, and meropodite, the limb becomes four-jointed. The second joint is long and broad; the distal two considerably narrower. All these joints are fringed with bristles, but those are not exceptionally long or numerous. The long joint has a concave inner edge, and is not flat but somewhat warped. The result of this disposition is that even the broadest of the third maxillipeds of such prawns do not close the mouth-area below as do those of the crabs, but wall it in at the sides, leaving underneath it an opening, partly fenced by bristles. The second maxilliped is also without epipodite or exopodite. In other respects it is that of the Palæmonidæ and relative families. The organ, formed by the last two joints, for gathering in the food and passing it to the deeper-lying jaws is rather shorter than usual, and the limb a good deal resembles that of *Phyllognathia* (Gnathophyllidæ). The first maxilliped is quite of the type which is normal in the same group of families. Its epipodite is distinctly lobed and its exopodite truncated and somewhat more hairy than usual.

4. Balss says it is scarcely longer. Possibly he was describing a specimen in which it was broken.

The maxilla is unlike that of the Palæmonidæ in lacking both the cleft lobes. In this respect it recalls the Anchistioididæ and the Crangonoida. The maxillule has both laciniaë a good deal drawn out. According to Balss, they are united for some distance at the base. Unfortunately, one of the pair removed from my specimen was accidentally destroyed, and in the other the inner lacinia is missing. The very strong spines which are usually borne at the end of the outer lacinia are in *Paratypton* reduced to short, conical vestiges, which in the middle of the row almost disappear. In the endopodite, the end lobe is reduced to a low, rounded prominence, and the lobe proximal to it, which is usually curved to hook round the edge of the metastoma, is long and conical, and ends in a very strong spine, like that which in Palæmonidæ usually tips the endopodite of the first maxilliped. The lower lip (metastoma) is much like that of the Palæmonidæ, but its cleft is partly closed and converted into a gutter, which runs between two fleshy pilasters, and leads to a notch of the edge of the organ, at the sides of which the pilasters end in knobs. The mandibles are placed in a mouth-chamber like that which I have described for the Palæmonidæ, bounded behind by the metastoma, in front by the labrum, and at the sides by the bases of the mandibles. They have no palp. Their form is on the whole that of the Palæmonidæ, but they show two remarkable features. The molar process is reduced to a conical spike, the end of which, however, is truncated and bears on its edge one large tooth and a row of smaller ones. This apparatus differs a little on the two mandibles. The slenderness of the molar process is a little reminiscent of the Gnathophyllidæ. The incisor process ends in what seems at first a plain edge like that of *Hapalocarcinus*, but is in reality very finely toothed, the notches between the minute, sharp teeth running for a short distance over the surface of the process as parallel furrows separated by ridges continuous with the teeth. At one end of edge is a stouter tooth. The whole has the appearance, not of having arisen by a multiplication of the coarse teeth which are usual on the end of the incisor process, but of being an organ *sui generis*. The labrum is of the usual Palæmonid form.

It will be seen that the mouth-parts of *Paratypton* present no very abnormal feature. Their general aspect is that of the same organs of the Palæmonidæ, and in particular the third maxilliped recalls the Pontoniinæ; but certain features are reminiscent of the Gnathophyllidæ and Anchistioididæ. There

is nothing which strongly suggests a diet of plankton. Certainly there is no conspicuous apparatus for gathering it, though possibly both here and in some Pontoniinæ the broad third maxilliped may be of use by forming a wall to the mouth region and thus enabling finely divided food to be kept under control. The peculiarities of the maxillules are probably connected with those of the metastoma, but what their effect may be it is impossible to say. The most striking features are those of the mandible, and here there is probably a definite adaptation to some specific food. But there is nothing to show that that is plankton. For information on this point we must wait till further knowledge of the habits of the prawns, and of the structure of their galls, shall have been gained. There are several possibilities. The openings of the galls are probably small, but we are quite in the dark on this point, and it may be that the prawn receives relatively large morsels of food through the agency of its stream. Or, it may be that the animal feeds, as *Hapalocarcinus* was formerly supposed to feed, on the fleshy parts of the coral, which in that case must regenerate rapidly. Or, again, it may be that *Paratypton* has some means, not obvious when it is not feeding, of gathering the nannoplankton. Possibly it may live, as certainly does the crab *Melia* which carries anemones in its chelæ, by stealing food caught by the polyps. If this be accompanied by mucus, the surprisingly normal character of the mouth-parts of the prawn could be accounted for in the same way as that of the same organs in *Pinotheres*, commensal with bivalve molluscs, and probably also of those Pontoniinæ which have a like habitat. In these organisms the food is not in fact finely divided, but consists of the strings of mucus with entangled food which the host is forming for its own nourishment.

The *legs* are rather short and stout, with rounded joints, which have no spines or sharp angles, and for the greater part of their length bear sparsely a few short hairs, though at the ends of the propodites these structures are longer and more numerous. This reduction of the hairs of the legs, many of which are undoubtedly tactile, is a part of the degeneration of the sensory apparatus in sedentary Crustacea; and, taken in connection with the clumsiness of the movements of such animals when they are removed from their hiding-places, lends support to Doflein's suggestion that it is a function of the tactile hairs of Crustacea to enable their possessor to co-ordinate the movements of its limbs. They would naturally

be retained at the end of the leg, since that is still in constant contact with external objects. The first pair of legs is of the form which that limb has in the Palæmonidæ generally, and its hairy chela is no doubt used in the ordinary way for cleaning the body and limbs. The second pair are equal and alike. Their chelæ are somewhat reminiscent of the large chela of an Alphæid. They have a very large, oblong "hand," compressed in the near half, but a little widened and oddly depressed at the base of the fingers, which are short. The moveable finger is a very clumsy, blunt hook, biting along and across a still smaller fixed finger, which is shaped like the prow of a boat, with sharp edges and point, and bears a number of soft hairs on its sides. What use the animal can make of these rather remarkable organs it would be unprofitable to attempt to guess. The walking legs end in small, simple, sharp-pointed, curved dactylopodites. As usual, they differ somewhat in their proportions, the hinder pair being the most slender.

The *gill-formula* is that of *Conchodytes*—a row of five pleurobranches above the legs of each side—though a few minute folds in the position of the pleurobranch of the third maxilliped probably represent that gill. Thus here, as in the Pontoniinæ, a reduction of the gill apparatus accompanies a sedentary life. The *abdominal limbs* of the first five pairs are large, and are borne each at the end of a ridge which runs outwards across the underside of the pleuron. The basipodite is long and flat, and in the fifth pair, which is shorter than those before it, is widened, and probably strengthens the hinder part of the brood-pouch. In the first pair the endopodite is very small; in the others endopodite and exopodite are sub-equal, pointed, fringed plates. An *appendix interna*, with the hooked spines well developed, is borne on the endopodite in the second to fifth pairs, as in Palæmonidæ and Gnathophyllidæ. It seems probable that these broad and well-formed limbs serve, not only to carry the eggs, but also to maintain, or from time to time to reinforce, the current in the gill; as in a resting *Leander* they are used to renew the water below the body. The uropods are well-developed and resemble those of the Pontoniinæ.

I am unfortunately compelled by an accident, which cost me the loss of the telson of my specimen as well as of one of its maxillules, to describe this organ from memory, aided by some rough notes and an even rougher sketch. It is broad and sub-triangular with convex sides and rounded end. The

most conspicuous structures on its edge are some half-dozen strong, unfeathered bristles on each side, around the end. At the end stand also on each side two short, conical spines, the outer pair rather larger than the inner. At some distance forward on each side, a similar spine, of about the same size as the inner pair at the end, stands in a notch. There are no spines on the dorsal surface. The whole structure is very unlike the telsons of the Pontoniinae, but rather suggestive of those of the Anchistioididae. The length of the specimen is about 20 mm.

The foregoing description relates solely to the female. It is highly desirable that we should know how the male differs from her. Mr. Potts informs me that he is not much smaller. Since Balss, who had males, did not describe this sex, we may infer that the differences between the two are not greater than those which exist, for instance, between the sexes in *Conchodytes*. It would seem that, as in various other sedentary Crustacea, they associate in pairs, but it would be interesting to have further particulars of the partnership. At what stage is the female when the male joins her, and how long does he live with her? What influence has he upon the formation of the gall, and is he alive when it closes? Does impregnation take place more than once? These and other such questions remain to be answered. In any case, it is pretty clear that the female is immured for life. Mr. Potts informs me that the female he sent me lived for two or three days in sea-water and was quite healthy when he killed it. In freedom it was very slow-moving and clumsy.

Balss' specimens came from Kosseir on the Red Sea, and from Jaluit. They appear to belong to the same species as mine, the only differences that I can discover being that in the length of the antennal flagella, mentioned in a footnote above, and the exposure of the eye segment in dorsal view. In view of the facts of the distribution of Decapod crustaceans in the Indo-Pacific, it is probable that the animal exists throughout that area. It seems to be much rarer than *Hapalocarcinus*, but this is very likely due to some difference in habitat which causes it to be less often found. It was certainly not contained in any of a number of galls that I opened in the island of Minikoi, in the Indian Ocean.

It will be seen that there are many unsolved problems relating to the bionomics of *Paratypton*. To these may be added that of its affinities. Not unnaturally, in view of its habits and many of its features, Balss placed it among the

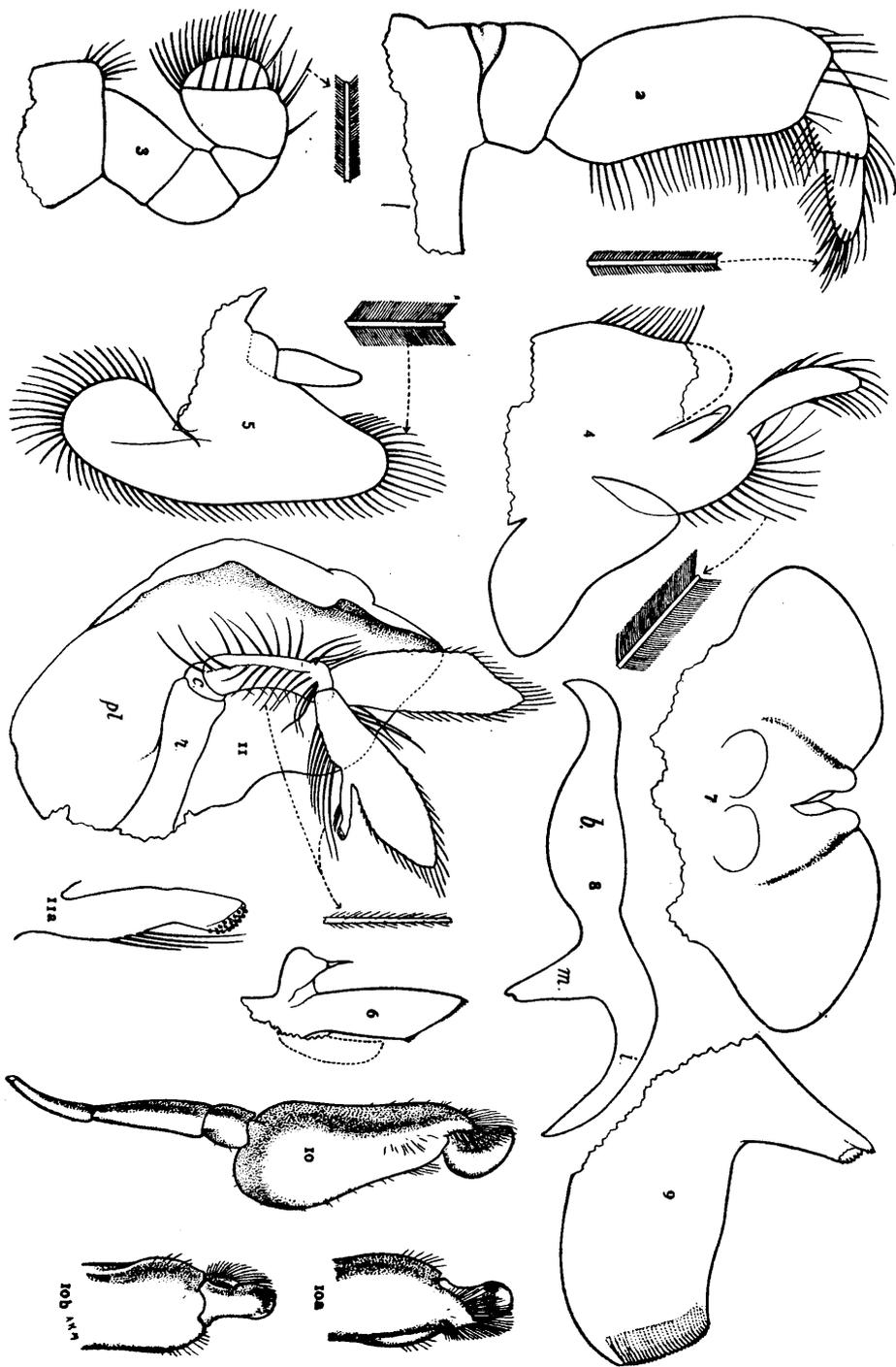
Pontoniinæ. I am, however, inclined to dissent from this conclusion. It is unlike the Pontoniinæ prawns in several features. Foremost of these is its telson, which has quite a different facies. To that may be added certain features of the mouth-parts which, as I have shown, are in some respects unlike those of the Pontoniinæ and suggest affinities with some of the families which connect the Palæmonidæ with the Crangonidæ. The uncleft outer flagellum of the antennule is also a point of difference from the Palæmonidæ, but this might quite well be due to retrogression connected with a sheltered life, and is approached in some Pontoniinæ. The inflated carapace a little suggests that of the Hippolytid *Pterocaris*, but this likeness is belied by the whole of the rest of the anatomy.

Taking the evidence as a whole, I am inclined to place *Paratypton* near the point to which the Palæmonidæ, Anchistioididæ, and Gnathophyllidæ converge, but I think that it would at present be rash to attempt to define its position more precisely than this.

The problem is complicated by the fact that the structure of the prawn is obviously greatly modified by its unusual mode of life. This is of course conspicuously true of its habit of body. Others of its features, such as those of the mouth-parts and chelæ, do not differ from those of free-living forms more than the latter differ among themselves, and it is at present impossible to say how far, if at all, their peculiarities are connected with the habit of living in a coral-gall.

Figs. 2—11a.

- Fig. 2.* *P. siebenrocki*, third maxilliped.
Fig. 3. " , second maxilliped.
Fig. 4. " , first maxilliped.
Fig. 5. " , maxilla.
Fig. 6. " , maxillule.
Fig. 7. " , metastoma.
Fig. 8. " , mandible.
 b, base; *i*, incisor process; *m*, molar process.
Fig. 9. *P. siebenrocki*, end of mandible, more highly magnified.
Fig. 10. " , great cheliped.
Fig. 10a. " , end of chela, from below.
Fig. 10b. " , " " " " above.
Fig. 11. *P. siebenrocki*, second abdominal pleuron, with limb.
 c, coxopodite; *pl.* pleuron; *r*, ridge, to which limb is attached.
Fig. 11a. Appendix interna, more highly magnified.



Figs. 2-11a.