Contributions to Marine Bionomics.

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II. The Function of Antero-lateral Denticulations of the Carapace in Sand-burrowing Crabs.

THE antero-lateral margins of the carapace in many of the crabs of our own and of foreign coasts are beset with a row of teeth or spines, which vary in character and number in different species and genera. In the Oxyrhyncha (Spider-crabs) the whole surface of the carapace is generally studded with spines and stiff hairs of a peculiar character, but there is no general restriction of these processes of the carapace to the antero-lateral margins of the body. These crabs, moreover, do not adopt burrowing habits. Their armature of spines, tubercles, and hairs is employed, as is well known, for protective purposes: in some cases possibly as an actual defence against attack, in others (*i.e.*, *Eurynome aspera*) as a means of protective resemblance to their surroundings; but in the great majority as mere pegs and hooks for the fixation of foreign bodies, such as algæ, hydroids, polyzoa, and ascidians, for purposes of concealment and disguise.

In the Catometopa (Land-crabs, etc.) the carapace is usually smooth over its whole surface. These animals often burrow in sand, but for the most part their burrows are permanent subterranean tunnels and chambers.

In the Cyclometopa, however—the group which includes most of our commoner British crabs—the back of the carapace is generally smooth, while the antero-lateral margins are in most forms conspicuously serrated. Most of these animals inhabit sandy or gravelly areas, and show a marked propensity towards burrowing habits. Their burrows are never* permanent channels or tunnels in the sand, but are mere temporary excavations, the sand, mud, or gravel being in actual contact with their bodies when imbedded.

So far as I am aware no one has hitherto elucidated the remarkable constancy of antero-lateral serrations of the carapace in this group of crabs. I here present evidence which tends to show that the presence

* *Scylla serrata* of the Natal coast *appears* to be exceptional in this respect. (KRAUSS, *Die Südafricanischen Crustaceen*, 1843, p. 12.)

of conspicuous serrations on these margins of the carapace is functionally related to the exigencies of respiration when these animals are buried in sand.

The marginal teeth are perhaps best developed and most conspicuous in crabs of the family Portunidæ (Swimming-crabs). As M. Alphonse Milne-Edwards has remarked: "Je ne connais aucun Portunien où le bord latéro-antérieur de la carapace soit entier ou armé d'épines arrondies ou de tubercules obtus." (1860, p. 202.)

In *Bathynectes longipes* there are five sharp-pointed teeth on each of the antero-lateral borders. These teeth increase in size regularly from before backwards, and the posterior tooth is a particularly stout and sharp structure. This crab is almost invariably an inhabitant of sandy areas (*e.g.*, Mounts Bay in Cornwall); and the individual whose habits I am about to describe was also dredged upon a bottom of fine sand in the neighbourhood of the Eddystone.

In an aquarium containing sand the crab burrows into the sand just beneath the surface, leaving its eyes and the transverse slit-like aperture of the buccal frame exposed. The crab is actually imbedded up to the anterior edge of the external maxillipeds; but it pushes away the sand in front of it by means of these appendages, and when at rest maintains these appendages in a sloping posture, so that they act as a quadrangular sieve-like fence in front of the buccal area. This happens both in very fine siliceous sand and in fine shell sand. The crab was not seen at any time to go completely beneath the surface, though I do not mean to imply by this that the crab never buries itself entirely. This may or may not be the case. *Atelecyclus heterodon* is another sand-burrowing crab, whose habits I have studied for a much longer period; and this crab has very diversified habits. It may remain partially imbedded at the surface of the sand, with its eyes and a broad funnel formed by the second antennæ alone protruding, or it may disappear completely beneath the sand to a depth of several inches.

When the crab (*Bathynectes longipes*) is partially imbedded in the sand as above described, it may be noticed that the chelipeds are flexed and approximated to the under side of the antero-lateral regions of the carapace in an attitude precisely similar to that assumed by *Atelecyclus heterodon*, or the Oxystome crab *Matuta*, under the same conditions (1897). The position of the cheliped is such that the marginal teeth of the antero-lateral region of the carapace exactly overhang the slit-like orifice between the distal half of the cheliped (carpopodite and propodite) and the pterygostomial fold of the carapace. There is thus produced on each side of the crab, between cheliped and carapace, a channel similar to that which would be produced by the approximation in parallel planes of two flat plates. This channel communicates below with the afferent (inhalant) aperture of the branchial chamber, which is situated at the base of the cheliped, and opens above through the notches between the teeth of the antero-lateral margins of the carapace. Since the back of the crab is covered with sand, it will readily be understood from this description that the antero-lateral teeth act as a coarse sieve or grating placed over the orifice of this accessory channel, and that they prevent the accidental intrusion of sand-particles into the lumen of the channel, a function which it was easy to determine that they efficiently discharged.

The pair of accessory channels produced by the approximation of chelipeds to carapace I propose to term the "exostegal channels," owing to their situation on the external face of the branchiostegite. I show elsewhere (1897) that these channels probably represent in a generalised condition certain remarkable accessory afferent branchial canals of the Oxystome Brachyura, which attain their most specialised form and relations in *Ebalia* and other Leucosiidæ.

M. Alphonse Milne-Edwards (1860, p. 207) states that in the Portunidæ "les mains ne sont jamais conformées de facon à pouvoir s'appliquer exactement contre la région buccale, ainsi que cela se voit chez quelques autres Brachyures nageurs tels que les Calappes et les Matutes." This contrast is quite in accordance with my view, that the afferent channel of the Portunidæ represents a primitive and relatively unspecialised type, from which the highly elaborate canals of the Oxystomata have been derived.

That these accessory channels in the Portunidæ are functionally connected with the respiratory process, was demonstrated by me in the case of *Bathynectes longipes* in the following manner:—

When the crab was partially imbedded in sand with its face close to the front of a square glass aquarium, in the attitude already described, it could be seen that beneath the body of the crab was a shallow ventral water-chamber, free from sand. The crab was resting with its body in an approximately horizontal plane. Sand-particles were supported over the orifice of the exostegal channel by the sieve-like row of teeth along the antero-lateral margins. Some water, coloured black with Indian ink, was then added by means of a pipette to the water lying above the slit between cheliped and carapace. The coloured water was at once sucked downwards between the grains of sand into the exostegal channel in waves which apparently corresponded to blows of the scaphognathite, and after a few seconds emerged in a black stream out of the afferent orifice of the branchial chamber situated in front of the mouth. It was quite clear that the water passed downwards through the exostegal channel to the afferent aperture at the base of the cheliped, and that it entered the branchial chamber by this aperture.

Similar observations and experiments were made upon numerous specimens of *Atelecyclus heterodon*, a crab belonging to an altogether different family. In this crab the antero-lateral margins are provided with as many as nine teeth, but the function of the teeth was found to be essentially similar. Owing to the different form of the body, and the different shape of the cheliped in the two crabs, the orifice of the channel between cheliped and carapace is of greater relative extent in *Atelecyclus* than in *Bathynectes;* but the length of the denticulated margin of the carapace was found to correspond precisely with the extent of the inhalant gap in each case. The following conclusions may be drawn, therefore, from these observations:—

(1) Antero-lateral denticulations of the carapace in crabs may subserve a sieve-like function.

(2) The extent of the denticulated area corresponds with the extent of the inhalant gap between the carapace and the cheliped when the latter appendage is approximated to it in the flexed position.

It is also obvious that a new function must be ascribed to the chelipeds of sand-burrowing crabs provided with antero-lateral denticulations of the carapace. In such cases the chelipeds act as organs temporarily subservient to the respiratory process by providing a broad operculum to the exostegal channel. Attention may be recalled in this connection to the fact elucidated by Milne-Edwards in 1839, that in the Leucosiidæ the floor of the afferent branchial channel is also provided by one of the appendages, in this case by the external maxillipeds. The relations of the afferent channel in the Leucosiidæ to the external channel which I have now described in the Cyclometopa are discussed by me in the paper to which reference has already been made (1897).

The subservience of the chelipeds to the respiratory process enables me, moreover, to explain the function of a remarkable spine which in the Portunidæ is almost universally present on the inner margin of the distal extremity of the carpal joint (carpopodite or wrist) of the cheliped. This carpal spine, though usually strong and conspicuous, presents various minor modifications of form which are employed by systematists in the discrimination of different species.

The appearance of the spine in *Bathynectes longipes* is represented by Bell and Risso. When the cheliped is fully extended the carpal spine projects freely from its anterior margin; but when the propodite is flexed towards the proximal part of the cheliped, it is arrested at a certain angle with the carpopodite by the carpal spine in question. If now the arm (meropodite) of the cheliped be approximated to the carapace in the position requisite for the completion of the exostegal canal, it will be found that the angle at which the propodite has been arrested by the carpal spine is precisely the angle required for the proper apposition of cheliped to carapace in connection with the respiratory process. The carpal spine acts then as a stay or barrier to excessive flexion of the cheliped. Its function corresponds, therefore, in part to the function of such skeletal processes as the olecranon of the human ulna, which prevents excessive extension of the arm. Examination of a series of Portunids reveals that the variations in the form of the carpal spine in different species and genera are all functionally correlated with the different shapes and proportions of the carapace, and of the segments of the cheliped in the forms examined; the result in all cases being that the shape of the carpal spine is adapted to ensure the due amount of flexion of the cheliped for the completion of the respiratory channel between cheliped and carapace.

A similar function seems also to be discharged by the enlarged posterior spine of the antero-lateral margins in *Bathynectes longipes*, since the carpopodite presses upwards against it during flexion of the cheliped. An examination of preserved specimens of the Mediterranean *Lupa hastata*, and of the American *Callinectes sapidus*, in which the posterior spine is greatly elongated, seems to me to support this view, though I do not regard the evidence in this case as altogether unequivocal. A complete explanation of the enlargement of this posterior antero-lateral spine should also throw light on the great epibranchial spines of the Oxystome genus *Matuta*, and of the Lencosiid genera *Iphis* and *Ixa*. In the latter cases any relation between the development of the spines and the formation of an inhalant chamber between cheliped and carapace is precluded by the known course of the afferent current in a gutter running between the pterygostomial plate and the exopodite of the third maxilliped.

The phenomena presented by the respiratory processes of these sand-burrowing crabs throw light, as it seems to me, not only on the problem of the utility of a number of morphologically trivial, but systematically important features of Decapod Crustacea, but also on an altogether different problem, viz., the phylogeny of the Brachyura Oxystomata. Crabs of the latter group are all characterised by their sand-burrowing habits of life. Similarity of habits often induces homoplastic changes of form in types genetically distinct; but there are certain significant details of structure in the different Oxystome types which appear to me to be only explicable on the view that these crabs are descended from ancestors in which the form of the body closely resembled that of sand-burrowing Cyclometopa in being provided with antero-lateral serrated margins, and in which the chelipeds were employed for the production of an extensive inhalant channel, completely roofed over by the projecting teeth of the carapace. For a fuller discussion of this subject I must refer the reader to another paper to be published in the *Quarterly Journal of Microscopical Science* (1897).

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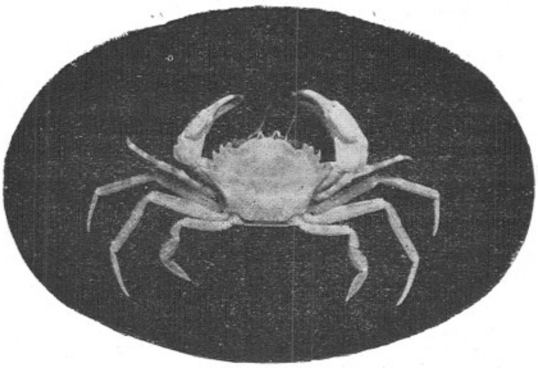

FIG. 1.

Fig. 1.—*Bathynectes longipes.* Dorsal view, showing the five teeth of the antero-lateral margins. The chelipeds are in a half-extended condition; their propodites (hands) are shown resting against the carpal spines. The specimen shows an abnormality in the union of the two anterior marginal teeth of the right side to form a single bifid tooth.

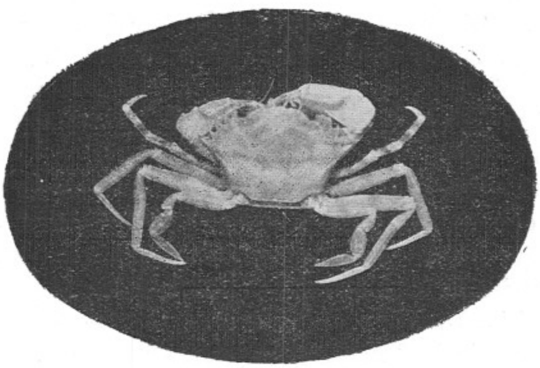

FIG. 2.

Fig. 2.—*Bathynectes longipes.* Dorsal view, showing the position of the chelipeds after flexion of the wrists (carpopodites) as well as of the hands. The left cheliped is in the attitude assumed by the crab when imbedded in sand; the antero-lateral teeth are seen to form a sieve above the orifice of the inhalant gap between cheliped and carapace. On the right side the arm (meropodite) of the cheliped does not rest in its proper position beneath the enlarged posterior marginal tooth; hence the inhalant gap is imperfectly formed, and its aperture is imperfectly covered by the marginal teeth.

III. The Systematic Features, Habits, and Respiratory Phenomena of Portumnus nasutus (Latreille).

The crab whose habits I now describe has not previously been recorded as an inhabitant of British seas. I found two specimens, both male, imbedded in a patch of coarse shell sand on the south side of Drake's Island at low water, spring tides: one on August 11th, 1896, and the other on the following day.

1. Nomenclature.

My first impression on noticing this remarkable little crab was that I had an abnormal specimen of a young *Carcinus maenas* before me; but the possibility of such a leap from the normal as the frontal area of this specimen would produce on a variation-chart was soon disposed of by Professor Weldon, and we identified the crab with the *Portunus biguttatus* of Risso (1816), now usually known under the name *Platyonichus nasutus* of Latreille (1825, p. 151; cf. also Milne-Edwards, 1834; Costa, 1853, p. 11; Carus, 1885).

The genus *Platyonichus* of Latreille (1818) was originally coextensive with the genus *Portumnus* of Leach (1815), Latreille having simply altered Leach's name owing to its similarity to the name *Portunus*, with which he feared it might be confused. Dana (1852), however, and Bell (1853), showed that the species included within the genus *Platyonichus* were separable into two well-marked groups, which were accordingly named by these writers *Platyonichus* and *Portumnus* respectively, the latter name being reapplied to the group which included Leach's type, viz., *Portumnus latipes*. It is to the latter group that *Platyonichus nasutus* belongs, so that I must refer to it for the future as *Portumnus nasutus*.

It is true that the earliest specific name applied to the present species is *biguttatus* of Risso (1816), the name *nasutus* of Latreille (1825) being nearly ten years later. Since, however, the species has been invariably referred to under Latreille's name, probably owing to the influence of Milne-Edwards' adoption of it, I submit that we have here an exceptional case which demands exceptional treatment. The rule of priority provides a decisive method of dealing with a confused and complicated synonymy; but its application in the present case could not be urged on such grounds, and would be distinctly inconvenient. I shall therefore adhere to the employment of Latreille's name *nasutus* in referring to the species under discussion. In the event, however, of possible differences being discovered between Mediterranean and Atlantic races of this species, I would point out that Risso's name was created for Mediterranean specimens, while Latreille's type came from the west coast of France.

2. Generic Characters.

The genus *Portumnus* takes its place together with *Carcinus, Platyonichus,* and *Polybius* in the Platyonichinæ, a sub-family of the Portunidæ distinguished from the Portuninæ by the absence of lateral ridges on the prælabial plate, and by the absence of a distinct accessory lobe to the endopodite of the first maxillipeds.

Portumnus is distinguished from *Platyonichus* by having the dactylus of the fifth thoracic leg of a slender lanceolate form, and the carapace not broader than long. In *Platyonichus* the dactylus is elliptical or broadly oval, and the carapace is broader than long. To these distinctions I may add that in *Platyonichus* the interorbital margin is at most tridentate or quadridentate, while in *Portumnus* the inner angle of the orbit contributes a distinct accessory tooth to the frontal margin, rendering this margin five-toothed, as in *Polybius Henslowii.*

3. Specific Characters.

The two species of the genus which alone are known to me are *P. latipes* (Pennant) and *P. nasutus.* A description of the former species may be found in Bell (1853) under the name *Portumnus variegatus.* The characteristic features of *P. nasutus* are as follows:—

Frontal area projecting in front of the orbits in the form of a conspicuous triangular lobe with gently undulate lateral margins.

The undulations mark the subdivision of the interorbital margin into five rounded lobules, which correspond to the five interorbital teeth of *P. latipes.* The interorbital lobe bends downwards in front.

The carapace is relatively broader than in *P. latipes,* so that the antero-lateral margins make a sharper angle with the median transverse axis.

The orbit shows two superior fissures and one inferior fissure (*pace* Latreille and H. Milne-Edwards, who mention only one superior fissure), while in *P. latipes* the orbit is stated to be either entire (Bell; Leach, 1815) or provided with a single fissure above (H. Milne-Edwards, 1834).

The basal joint of the second antenna is movable.

4. Colour.

The colour of the carapace of *Portumnus nasutus* is thus described by Risso (1816, p. 31)—"yellowish-white, adorned with two great spots of coral-red . . . The red spots are larger in the female than in the male." On account of the presence of these spots Risso named the species *Portunus biguttatus, portune à deux taches, portune bimaculé* (p. 25).

Costa, on the other hand (*Addizioni*, 1853, p. 11), describes the colour as "livid olive-brown tending towards purple; that of the feet and of the inferior face more pallid. In fresh specimens one may sometimes observe two rose-coloured spots in the middle of the carapace, which vanish after death."

Of my own specimens the larger one was of a uniform dull greenish yellow colour, the smaller one having the carapace and basal joints of the legs absolutely white, and the two terminal joints of the four posterior pairs of thoracic legs coloured pale brown and amethyst-violet. No reddish spots were visible in the living specimens. It is possible that these spots are only to be observed in the breeding season, and that they are due to the colour of the reproductive glands showing through the carapace. Such a phenomenon is at any rate described by Risso for *Bathynectes longipes*. He states (1816, pp. 30, 31): "La femelle, dans le temps des amours, est ornée de deux grandes taches d'un rouge foncé sur la partie antérieure du têt." The eggs of the latter species are described as "d'un rouge aurore," which would sufficiently account for the red colour of the ovarian regions before deposition of the ova; those of *P. nasutus* are described as "d'un jaune doré." Risso states that the eggs of *P. nasutus* are laid in May and August.

5. Sand-burrowing Habits.

The habits of *Portumnus nasutus* have hitherto been very imperfectly described. Risso (1816, pp. 25–31) states simply that at Nice the crab inhabits "la région des polypiers corticifères" (p. 25), or "la région des coraux" (p. 31). Latreille's specimen (1825, p. 151) was obtained by D'Orbigny on the coast of La Vendée, which probably implies a sandy habitat, especially as Latreille's specimens of "*Platyonichus variegatus*" (*Portumnus latipes*) were obtained by the same naturalist on the same coast (*Nouv. Dict. d'Hist. Nat.*, 1818), and the latter species is known to have sand-burrowing habits.

My own observations are, however, unequivocal. The specimens were found burrowing in coarse shelly gravel, and when the crabs were introduced into an aquarium containing a deep layer of the same gravel they were observed to burrow into it at once with extreme agility until their bodies were completely covered to a depth of an inch or more. The act of burrowing is effected by means of the hinder thoracic legs, as is usual among Portunids. The crabs can also burrow in fine siliceous sand.

When imbedded, *P. nasutus* seems always to adopt a nearly horizontal position—not the upright attitude exhibited by *Corystes cassivelaunus* (this Journal, 1896, p. 223). The anterior part of the body is, however, generally a little higher than the posterior.

6. Respiratory Currents.

Under these circumstances, *Portumnus nasutus* exhibits a reversed water-current through its branchial chamber, though this is much more difficult to demonstrate in the present species than in the case of *Corystes.* The method I adopted was as follows:—

The depth of gravel in the aquarium was so regulated that the crab could not burrow far beneath the surface. The fragments of sand and shell which lay upon the front of its carapace and upon its interorbital lobe were then gently removed, one by one, with a pair of fine forceps, until the aperture of the buccal frame was exposed. These proceedings were, however, incessantly watched by the crab, which, not unnaturally, did not hesitate to disturb my preparations whenever it conceived that there was due cause for alarm. I therefore took the precaution to leave some fragments of shell over its eyes, and thus did not seriously disturb its impression that it was safely ensconced. I eventually succeeded in getting the crab so suitably situated that, on the addition of a little black-coloured water by means of a pipette to the region in front of the crab's maxillipeds, I had the satisfaction of seeing the water sucked inwards on both sides, to reappear again in a pair of streams at the base of the chelipeds. The two exhalant streams rose above the surface of the sand in a pair of clouds, one on each side of the body. Suddenly, and without warning, the normal current was set up, and then the lateral clouds of inky water were rapidly sucked in again on each side, to re-emerge again a second or two afterwards in a continuous stream in front of the mouth. Without this kindly co-operation on the part of the crab it would have been difficult, if not impossible, to get so successful a demonstration of the reversal of the currents. One of the most interesting phenomena presented by this crab is indeed the frequency with which, when under observation, it will alternate the direction of the respiratory currents.* It may even suspend the respiratory currents altogether for long intervals; *e.g.*, for as long as fifty-five seconds. At such times there is absolutely no movement in the surrounding water.

7. Utility of Specific Characters.

The interorbital prolongation of the frontal area, which gives both its name and most peculiar feature to the species *Portumnus nasutus,* is

* Probably to eject distasteful particles. This is undoubtedly the explanation of similar phenomena in the case of *Corystes.* (See this Journal, vol. iv. 1896, p. 230.)

a feature usefully correlated with a habit of burrowing in coarse shelly gravel. It acts as an efficient buckler for the protection of the anterior sense-organs; but its unusual size and its downward bend seem to be more directly correlated with the reversal of the branchial currents, which I have shown to take place when the crab is imbedded. The advantage of reversal in the present case is a point to which I shall recur when dealing with the phenomenon in a more general manner; but, granted the reversal, the utility of the possession of a stout triangular shelf over the inhalant orifices is obvious after a study of the animal s habits and of the nature of the objects amid which the crab excavates its dwelling-place. In *Corystes,* which lives in fine sand, the inhalant antennal tube has been shown (1896) to subserve the double purpose of a supply pipe and a sieve. In *P. nasutus* a sieve is unnecessary so long as the crab inhabits coarse shell-gravel, the fragments of which are too large to enter the respiratory channels; and this appears to be the specific habit of the crab. But if the anterior inhalant apertures (during reversal) were altogether unprotected, the pointed fragments of shell might easily penetrate the inhalant orifices (during reversal), and so occlude their lumen. Such occlusion would prevent the crab from burrowing in the kind of material most suitable to its respiratory organisation, and thus expose the animal to increased risks of destruction by its ever-watchful enemies among fishes. The overhanging buckler provided by the prominent frontal lobe acts, however, as a very efficient means of supporting the shell-fragments well above the inhalant orifices—a function the existence of which I do not throw out as an academical suggestion, but the value of which I had frequent opportunities of observing and appreciating in my aquaria.

The interorbital lobe of *P. nasutus* is remarkably similar to the frontal protuberance of *Carcinus maenas* in the *Megalops* stage, which becomes reduced in later stages of development. Since I have found no indications of a reversal of the respiratory currents in the latter species, I am inclined to believe that the retention of this larval feature in *P. nasutus* is to be correlated with the reversal of the currents which occurs, as I have shown above, in this type; while its eventual loss in *Carcinus maenas* is to be indirectly attributed to the lack of any further use for it after the larval stages. The larval forms of *P. nasutus* are at present, however, unknown, and it is impossible to support this view with the necessary embryological facts.

The other specific characters of *P. nasutus* (viz., breadth of carapace, retention of two supra-orbital fissures, mobility of basal joint of second antenna) are not new features acquired within the history of the present species, but are merely heirlooms from Portunid ancestors of less specialised habits. It is not their presence in *P. nasutus* which is to be accounted for, but their absence in *Portumnus latipes*. The elucidation of those features will be attempted in a subsequent article dealing with the habits of the latter species.

In conclusion I may add that a good figure of *P. nasutus* is given in Costa's classical memoir on the fauna of the Bay of Naples (1853).

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