

A Revision of the Genus "*Portunus*" (A. Milne-Edwards, Bell, etc.).

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With 9 Figures in the Text.

I. INTRODUCTION.

It is to-day realised very generally that such superficial characters as colouration and ornament, though in many cases of value for approximate identification, may frequently be mere effects of environment, not attributable to actual genetic differences at all. The characters of the adult animal are seen to be a complex resultant of both genetic and environmental factors, and taxonomy, if it is to have a firm genetic basis, must take both of these influences into account. These considerations point to the need for a critical re-examination of many of the doubtful species and varieties with which zoology abounds, with the object of determining whether their distinguishing characters are sufficiently definite and numerous to admit of their being regarded as genetically distinct types.

The swimming crabs, "*Portunus*" *holsatus* and "*Portunus*" *mar-moreus*, are cases in point. Typical specimens are readily distinguishable by their colouring, but on the basis of the descriptions so far published it is understandable that considerable doubt has existed as to their complete distinctness. The majority of authors have considered them as very closely allied, and several, notably Stimpson (1869), A. Milne-Edwards and Bouvier (1899), and Bouvier (1922), have regarded them as identical. With the object of deciding the question finally, the present author therefore examined in detail large numbers of both fresh and preserved specimens of both species, and found as a result a number of definitely diagnostic characters clearly separating the two forms. These characters and others were found to be of value in considering the relationships of all the species of the genus, and to justify a short paper on the subject, especially as no detailed revision of the genus had appeared since A. Milne-Edwards' monograph on the Portunidæ (1861, a).

In considering the relationships of the species the probable degree of genetic complexity of a character has been borne in mind in estimating its morphological value. Much more genetic work in all groups requires, of course, to be done, before this criterion can be used in any exact sense, but it was felt that some such conception will ultimately be of importance in taxonomic work, and that even to-day it is not without value as a guiding principle. Further examples of its application in other groups could be given were space available.

It was found that the species arrange themselves fairly naturally in the phylogenetic scheme shown in Fig. 1. In view of the paucity of the

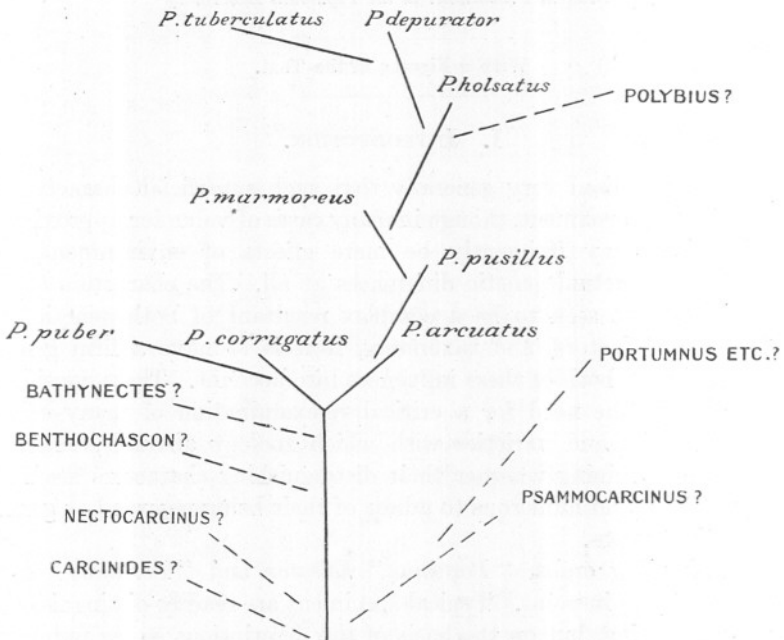


FIG. 1.—Tentative scheme of relationships of "Portunus" and its allies.

fossil evidence, this scheme is very tentative; but it was thought to be useful as a working hypothesis, and it is implicitly referred to in the discussions of specific characters. No attempt has been made to describe exhaustively those specific characters which have already received adequate attention in previous accounts, and the descriptive portion is to be regarded as, in the main, merely a guide to the figures. The latter have, with the exception of those of *P. tuberculatus*, been drawn from the mean of a large number of specimens, all of which approached the maximum size found in the species. The same precaution of using only full-sized individuals was employed in arriving at the statistical

data, so that errors arising from the heterogonic growth that Huxley (1927) has shown to exist in certain characters of various Brachyura might be avoided. The figures of the carapace are only outlines and follow at the postero-lateral corners the raised rim that is in most cases continuous round the carapace, rather than the less definite margin.

I wish to express my thanks to Dr. W. T. Calman for his kindness in permitting me to examine and revise the collection in the British Museum; to Dr. Mary Rathbun of the U.S. National Museum, for information on a number of points; and to Dr. Marie Lebour, for the use of unpublished data on the developmental forms.

II. THE SYNONYMY OF THE GENERIC NAME.

The generic name of the species included under the genus "*Portunus*" in the sense of Milne-Edwards and the vast majority of authors, presents a very tangled problem in nomenclature. The name *Portunus*, as originally published by Weber (1795) and used by Fabricius (1798), included practically all the members of the Portunidæ then known. In 1810 the genus was restricted by Latreille to those species which were later placed by Leach in his genera of *Portunus* and *Lupa*. Subsequent authors until 1897 have consistently followed Leach in considering the name *Portunus* to be applicable (with various further restrictions of minor importance) to the familiar forms with five teeth on each side, that are dealt with in this paper. Rathbun (1897) pointed out, however, that this usage was an infringement of the rule of specification of type. Latreille (1810) had mentioned a number of species as types of their respective genera, and had given *P. pelagicus* (L.) as that of *Portunus*. Subsequent restrictions have made this form, first *Lupa pelagica* of Leach, and, secondly, *Neptunus pelagicus* of de Haan. Provided, then, that Latreille intended by "type," "the type of the genus" rather than merely "an example of the genus," *Neptunus pelagicus* of de Haan, being synonymous with *Portunus pelagicus* of Latreille, becomes the type of *Portunus*. *Neptunus* de Haan therefore becomes *Portunus* Weber and Fabr., and the species included by the majority of authors under *Portunus* Weber and Fabr., are left without a generic name. Dr. Rathbun has since pointed out to me that actually Latreille appears to have designated the type of *Portunus* at a much earlier date. In "Additions" to Vol. 6, Hist. Nat. Crust. et Insectes, an. XI (1802-1803), p. 336, he says: "Portune réticulé; *portunus reticulatus*. Herbst a donné la figure de cette espèce, Pl. L; et nous l'avons fait copier, comme type du genre, Pl. XLIII, fig. 3, tome V. Nous l'avons oubliée en mentionnant les espèces:" etc. Herbst's *P. reticulatus* is a synonym of *Neptunus pelagicus* (L.). If these two cases are to be taken as constituting a specification of type, and if, in that

case, the rule is to be strictly enforced, a new name is required for the species of "*Portunus*" in the more usual sense. Rathbun has suggested *Liocarcinus* Stimps., 1869 (see below, Section XIV), as an available name.

Such is the history of the name *Portunus*. While it has to be admitted that Dr. Rathbun has made a strong case for her use of the name, there are certain considerations which have to be taken into account. In the first place it is still open to question whether Latreille used the word "type" in the modern sense, or whether he merely meant "example." So far as his 1810 list is concerned this seems very debatable, especially as in certain genera (e.g. *Maia*) he has there "specified" more than one type species. The same doubt applies to the earlier "specification." If Latreille had forgotten *P. reticulatus* in mentioning the other species in the main part of his work, it seems hardly likely that he would proceed to make it the type species in the modern sense. Two citations from a later work by Latreille give further support to this view. In "Cour d'entomologie" 1^{re} ann. 1831, p. 349, he says: "Ce genre est celui de portune ou d'étrille (*portunus*), de Fabricius, mais qu'on a maintenant réduit. Nos côtes offrent communément: 1. Le P. étrille (*puber*, Fab.) . . . 2. Le P. ridé (*corrugatus* Leach) . . . P. de Rondelet de M. Risso . . . Le P. de tranquebar (*tranquebaricus*) a neuf dents à chaque bord latéral." It is obvious from this that Latreille regards *P. puber* as the typical species of the genus since he uses the same common name for both. Furthermore, on p. 350 he mentions *Lupa pelagica*, accepting without any comment Leach's alteration of the generic name of what Dr. Rathbun regards as his type species.

There are other more practical objections to the proposed alteration of the general usage in this case. Firstly, while *Liocarcinus* is a valid name under the Code, there are logical objections to its use since it was originally used for two species of the genus as opposed to the rest. Secondly, the genera "*Neptunus*" and "*Portunus*" are large ones, and the confusion resulting from the change is consequently considerable. Thirdly, "*Neptunus*" contains a species, *N. tuberculatus* Stimps., which if spoken of as *Portunus tuberculatus* is liable to be confused with the totally different species, *P. tuberculatus* Roux. Finally, it may be urged that in the whole of the existing literature with the exception of Dr. Rathbun's papers and to my knowledge, three others, the names *Portunus* and *Neptunus* are used in A. Milne-Edwards' sense, although thirty years have elapsed since Dr. Rathbun published her amendment.

In spite of all this, however, it must be admitted that Dr. Rathbun is legally right under the Code, since in 1910 the International Commission, rightly or wrongly, gave an Opinion validating Latreille's 1810 types. This being the case, I cannot agree with those eminent carcinologists who have, in opposition to the Rules, continued to use the name *Portunus*

without qualification, for the species discussed in this paper. Such individual action is likely to make confusion worse confounded. I consider on the contrary that this is an instance in which an Opinion by the Commission suspending the Rule of specification of type in this case, and legalizing the almost universal usage of the names, is the only practical and permanent way out of the difficulty. A case is being placed before the Commission to this end, and in the meantime the name "*Portunus*" will be used in inverted commas in this paper.

III. *P. CORRUGATUS* (Penn.).

Cancer corrugatus. Pennant, 1777; Herbst, 1783.

Portunus corrugatus. Leach, 1814, 1816; H. Milne-Edwards, 1834; Bell, 1853; A. Milne-Edwards, 1861, etc.

Portunus puber. Blainville.

Portunus strigilis. Stimpson, 1858.

Liocarcinus strigilis. Rathbun, 1902.

Portunus subcorrugatus. A. Milne-Edwards, 1861.

Portunus carcinoides. Kinahan, 1857.

Liocarcinus corrugatus. Rathbun, 1902.

Portunus Leachii. ? Risso, 1826.

The *carapace* (B. Fig. 2) is slightly convex and rather contracted posteriorly. Nineteen males had a mean value for $\frac{\text{breadth}}{\text{length}}$ of 1.29, and thirteen females a mean value of 1.27. (In this and subsequent statements as to the proportions of the carapace, by "breadth" is meant the distance between the tips of the posterior antero-lateral teeth, and by "length" the distance between the anterior side of the posterior rim of the carapace and the tip of the median frontal tooth or lobe. In *P. puber*, where there is no median tooth, the tips of the two inner frontal teeth formed the anterior limit.) The species varies within wide limits in regard to this character, all variations from females with value 1.24 to a male with the value 1.35 having been found. The *front* is divided into three crenulated lobes, and is moderately advanced. The *antero-lateral teeth* are strong, pointed, and sub-equal. The first two teeth show slight traces of the grouping seen in *P. arcuatus*. The *orbits* have a somewhat sinuate ventral margin (G), this term being understood to include in this and subsequent descriptions the whole ventral side of the orbits shown in the figures. The *epistome* (D) is considerably extended laterally in the majority of specimens, but is a rather variable character in this species. The *merus of the third maxillipeds* (F) is rather short, with its inner margin obliquely truncate. The slight notch seen in ventral view at the antero-lateral corner is due to an in-turning of the edge at this point to

meet the edge of the opposite face over the next joint, whose base is thus enclosed between the two faces of the merus. The *carpus of the chelipeds* (H) is somewhat rectangular, and in common with most of the surfaces of this form is considerably crenulated. A group of tubercles on the outer margin below the equally tuberculate antero-external corner form together a sort of blunt tooth. The chelæ are bluntly carinate, and are slightly unequal, the right being usually the larger. In the *last pair of thoracic limbs* (A) the dactylus is lanceolate, with a mean value for $\frac{\text{length}}{\text{breadth}}$ of about 2.35. The propodus is short and rounded. Both joints have a well-marked ribbing. The *abdomen of the male* (C) shows a very abrupt narrowing at the penultimate joint, and its proximal joints are very broad. The sutures between the 3rd, 4th, and 5th joints, are obscure. The tip of the *1st abdominal appendage* in the male (E) is bent almost at right angles. The *colour* is usually a uniform light red-brown, sometimes rather darker. The *surface* of the carapace is covered with transverse rows of crenulations, each row being set with a fringe of hairs. The regions are rather indistinct.

P. corrugatus is moderately common on shelly gravel at Plymouth.

IV. P. PUBER (Linn.).

Cancer puber. Linnæus, 1758.

Portunus puber. Fabricius, 1798; Leach, 1816; H. Milne-Edwards, 1834; Bell, 1853, etc.

Cancer velutinus. Pennant, 1777.

The *carapace* is broad and flattened, and very little contracted posteriorly. The mean value for $\frac{\text{breadth}}{\text{length}}$ in sixteen individuals measured was 1.36. There was no significant difference in this character between the males and the females measured. The *frontal teeth* are usually from eight to ten in number, and are frequently asymmetrical as in the figure. On each side of the middle line is a large tooth, which in some specimens appears to be made up of a number of crenulations. Occasionally these two inner teeth are fused. Beyond this tooth on each side are two or three small spike-like teeth. External to these is a large crenulated tooth whose outer edge slopes down towards the orbit. In the 5th and subsequent juvenile stages the two inner teeth are represented by crenulated lobes with only a slight depression between them (Fig. 3, juv.), and in

FIG. 2.—*Portunus corrugatus*.—A, left propodus and dactylus of last pair of thoracic limbs. B, outline of carapace. C, male abdomen. D, epistome. E, tip of left first abdominal appendage of male. F, ventral view of merus of right third maxilliped. G, ventral view of sub-orbital margin. H, carpus of right cheliped.

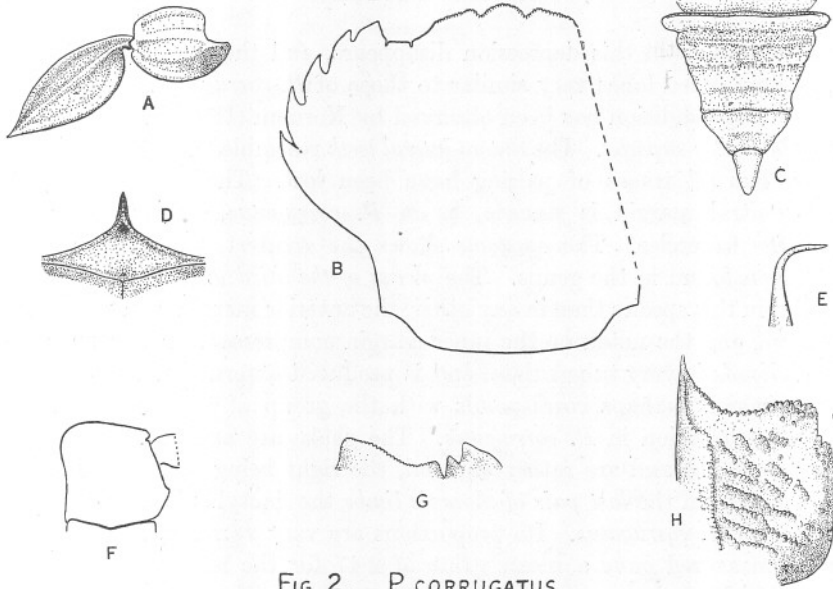


FIG. 2. — *P. CORRUGATUS*.

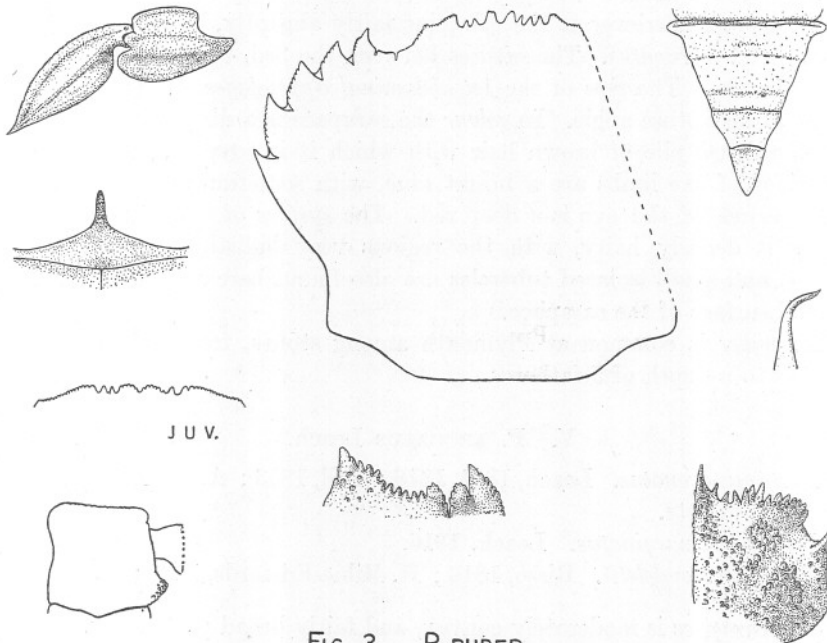


FIG. 3. — *P. PUBER*.

Juv., front of juvenile.

earlier stages still this depression disappears, and the front consists of three crenulated lobes very similar to those of *P. corrugatus*. A similar three-lobed condition has been observed by Norman (1891) in the young of *Bathynectes superba*. The *antero-lateral teeth* resemble those of *P. corrugatus*, but all traces of pairing have been lost. The *orbits* are large. The ventral margin is sinuate, as in *P. corrugatus*, but is bordered by large tubercles. The *epistome* shows the greatest degree of lateral extension found in the genus. The *merus of the third maxillipeds* is also shorter in this species than in any other, the anterior margin being slightly concave, and the notch on the inner margin compressed. The *carpus of the chelipeds* is very tuberculate, and is produced externally into a sharp tooth, which perhaps corresponds with the group of tubercles seen in the same position in *P. corrugatus*. The chelæ are armed with tuberculated carinæ and are rather unequal, the right being more frequently the larger. In the *last pair of thoracic limbs* the dactylus is very similar to that of *P. corrugatus*. Its proportions are very variable, but sixteen males measured gave a mean value of 2.47 for the ratio of length to breadth, the values ranging from 2.37 to 2.60. The propodus has a prominent distally-projecting lobe on its posterior side, rather resembling that of *P. holsatus*. Both joints are even more strongly ribbed than in *P. corrugatus*. The *abdomen of the male* is moderately broad proximally, and becomes narrower at the 6th joint fairly abruptly, but much less so than in *P. corrugatus*. The sutures between the 3rd, 4th, and 5th joints, are obscure. The tips of the *1st abdominal appendages* of the male are bent at an obtuse angle. In *colour* the carapace is a dirty brown, owing to the dense pile of brown hair with which it is covered. The naked portions of the limbs are a bright blue, with sometimes specks of red. The cornea of the eye is a deep red. The *surface* of almost the whole body is densely hairy, with the regions very indistinct. Crenulated ridges and small isolated tubercles are also found here and there on the dorsal surface of the carapace.

P. puber is common at Plymouth among stones, from between tide marks to a depth of 5 fathoms.

V. *P. ARCUATUS* Leach.

Portunus arcuatus. Leach, 1814, 1816; Bell, 1853; A. Milne-Edwards, 1861, etc.

Portunus emarginatus. Leach, 1816.

Portunus Rondeletii. Risso, 1816; H. Milne-Edwards, 1834; A. Costa.

The *carapace* is moderately convex, and fairly broad posteriorly. The mean value for $\frac{\text{breadth}}{\text{length}}$ of thirty-two specimens of both sexes was 1.27.

In the specimens measured there was no significant difference between the sexes in this respect. The *front* is entire, though there are three faint undulations on its edge reminiscent of *P. corrugatus*, and these undulations are more marked in juveniles. It is fringed with a sparse row of hairs. The *antero-lateral teeth* show a marked grouping into pairs, the 1st and 2nd and the 3rd and 4th being associated. The 2nd and the 4th are considerably reduced, the 4th sometimes almost obsolete. The 5th is very strongly developed, suggesting comparison with *Bathynectes longipes*. The *orbits* are in dorsal view very like those of *P. corrugatus*. The ventral margin is, however, more rounded and concave. The *epistome* is intermediate in lateral extension between that of *P. corrugatus* and that of *P. puber*. The *merus of the third maxillipeds* is rather more obliquely truncated than in *P. corrugatus* and the region in front of the notch on the inner edge is more extended. The *carpus of the chelipeds* is longer, smoother, and more rectangular than in *P. corrugatus*, and is without the cluster of tubercles seen on the outer margin in that species. The *chelæ* are nearly smooth, somewhat stout and rather unequal, the right being usually the larger. In the *last thoracic limbs* the dactylus is very slender, the mean proportion of length to breadth being about 3.1. The *propodus* is longer than in *P. corrugatus*, and in general rather nearer to the probable primitive type. The ribbing of both joints is less distinct than in *P. corrugatus*. The *abdomen of the male* differs strikingly from that of *P. corrugatus*, having its sides almost straight. The sutures between the 3rd, 4th, and 5th joints, are obscure. The tips of the *1st abdominal appendages* of the male are bent at an obtuse angle. The *colour* is dark brown, the limbs being generally rather lighter than the carapace. The *surface* of the carapace is covered with minute transverse rows of crenulations, resembling on a smaller scale those of *P. corrugatus*, but less continuous and without hairs. The regions are rather indistinct.

I have not taken Leach's "*P. emarginatus*." This form differs from *P. arcuatus* only in the concave character of the front, and is certainly no more than a variety of that species, though a remarkable one. It appears to be extremely rare since Leach only saw one specimen—that in the British Museum—and Bell found none among some hundreds of *P. arcuatus* examined.

P. arcuatus is moderately common at Plymouth on coarse shelly gravel.

VI. *P. PUSILLUS* Leach.

Portunus pusillus. Leach, 1814, 1816; Bell, 1853; A. Milne-Edwards, 1861, etc.

Portunus pusillus. H. Milne-Edwards, 1834; Lucas, 1840.

Portunus maculatus. Risso, 1826; Roux, 1828.

Liocarcinus pusillus. Rathbun, 1900.

The *carapace* is fairly convex, and is not greatly narrowed posteriorly. Its proportions vary enormously. Of twenty-six female specimens measured the mean value for $\frac{\text{breadth}}{\text{length}}$ was 1.20, the limiting values being 1.17 and 1.24. Thirteen males had a mean value of 1.215. This number included one exceptional specimen with the very low value of 1.06. Several such abnormally long specimens are in the British Museum collection, one of them actually being longer than broad. $\left(\frac{\text{Breadth}}{\text{Length}} = .95\right)$

In other characters such specimens appear to be quite normal. The *front* is greatly advanced as a broad shelf between the orbits, and is divided into three lobes, of which the median is the more advanced. The greatly produced front is by far the most striking character of the species. The *antero-lateral teeth* show the same kind of paired arrangement as was seen in *P. arcuatus*, but the size differences are less marked. The first four teeth are rather blunt, and the fifth spiniform and curved somewhat upwards. The *orbits* are modified dorsally by the forward extension of the front. The ventral margin is very similar to that of *P. arcuatus*, but, taken as a whole, rather shallower. The *epistome* is less extended laterally than in *P. arcuatus*. The *merus of the third maxillipeds* shows a further increase in the size of the anterior extension, and is still more oblique than in the last species. The *carpus of the chelipeds* is very similar in general shape to that of *P. corrugatus*, but agrees with that of *P. arcuatus* in being without a tooth of any sort on its external margin. The *chelæ* are in most specimens practically smooth, but slight *carinæ* may occasionally be present. The right is more usually slightly the larger. In the *last thoracic limbs* the *dactylus* is broader than in *P. arcuatus*, and less acutely lanceolate, the mean proportion of length to breadth being about 2.4. The median rib is almost obsolete, but traces of it are visible if the joint is held up to the light. The *propodus* resembles that of *P. arcuatus* in general form, but the ribbing is much less distinct than in that species. The *abdomen of the male* differs little from that of *P. arcuatus* in shape, but is rather narrower proximally, and the sutures between the 3rd, 4th, and 5th joints, are even more obscure. The tips of the *1st abdominal appendages* of the male are similar to those of *P. arcuatus*. The *colour* varies enormously, from a yellow variegated with red-brown, both on the *carapace* and the *limbs*, to a uniform dark brown on the *carapace*, with the *limbs* variegated in shades of lighter brown. The *surface* of the *carapace* is also variable, being sometimes quite smooth, and in other specimens coarsely and irregularly granulated. The regions vary greatly in degree of distinctness.

P. pusillus is fairly common at Plymouth on shelly gravel.

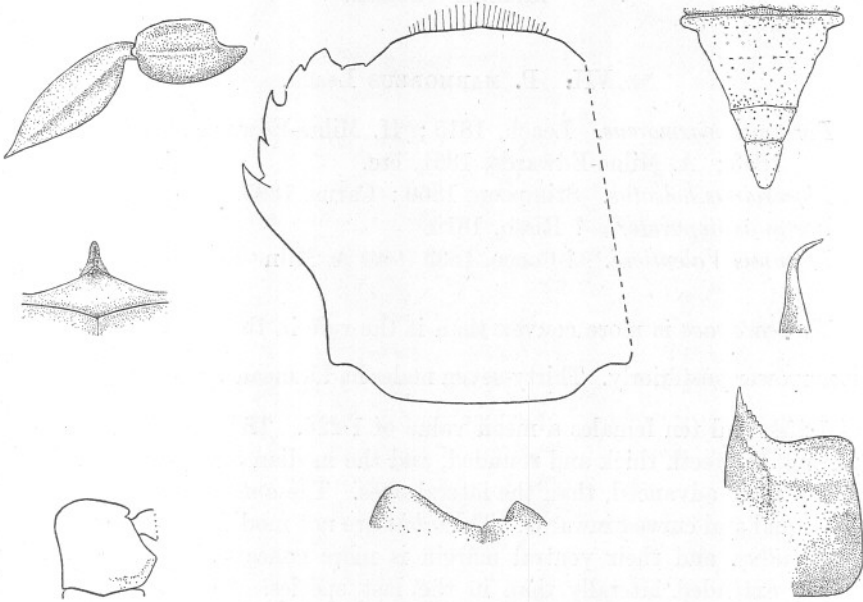


FIG. 4 — P. ARCUATUS.

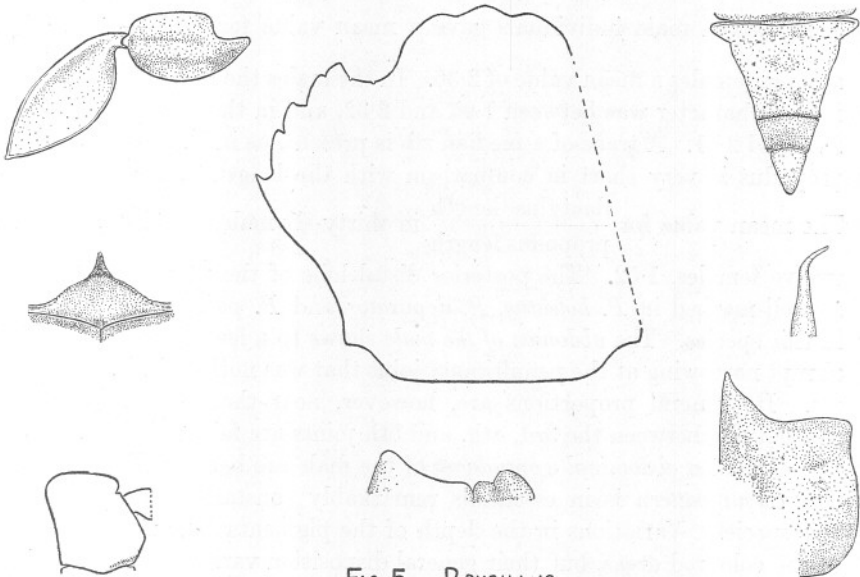


FIG. 5 — P. PUSILLUS.

For description see Fig. 2.

VII: *P. MARMOREUS* Leach.

Portunus marmoreus. Leach, 1815; H. Milne-Edwards, 1834; Bell, 1853; A. Milne-Edwards, 1861, etc.

Liocarcinus holsatus. Stimpson, 1869; Carus, 1885.

Portunus depurator. ? Risso, 1816.

Portunus Valentieni. ? Cocco, 1833 (*teste* A. Milne-Edwards).

The *carapace* is more convex than is the rule in the last species, and is narrower posteriorly. Thirty-seven males had a mean value for $\frac{\text{breadth}}{\text{length}}$ of 1.254, and ten females a mean value of 1.224. The *front* is not projecting, the teeth thick and rounded, and the median one less advanced, or not more advanced, than the lateral ones. The *antero-lateral teeth* are sub-equal and curved inwards. The *orbits* are not modified dorsally as in *P. pusillus*, and their ventral margin is more concave. The *epistome* is less extended laterally than in the last species. The *merus of the third maxillipeds* is considerably longer, particularly in its anterior extension. The carpus of the chelipeds is more rounded, and the large tooth at the internal angle more produced than in *P. pusillus*. The carinæ of the chelæ are indistinct. The right chela is usually slightly the larger. In the *last thoracic limbs* the dactylus is rather broader than in *P. pusillus*. Thirty-seven male individuals gave a mean value for $\frac{\text{length}}{\text{breadth}}$ of 2.12, and ten females a mean value of 2.36. In the males the range of variation in this character was between 1.95 and 2.32, and in the females between 2.27 and 2.51. A trace of a median rib is present, as in *P. pusillus*. The propodus is very short in comparison with the length of the dactylus. The mean value for $\frac{\text{dactylus length}}{\text{propodus length}}$ in thirty-six males was 1.47, and in twelve females, 1.52. The posterior distal lobe of the propodus, that is so well marked in *P. holsatus*, *P. depurator* and *P. puber*, is very slight in this species. The *abdomen of the male* shows to a less extent the same abrupt narrowing at the penultimate joint that was noticed in *P. corrugatus*. Its general proportions are, however, near those of *P. pusillus*. The sutures between the 3rd, 4th, and 5th joints are fairly distinct. The tips of the *1st abdominal appendages* of the male are bent at right angles. The *colour-pattern* is in essentials remarkably constant and regular in this species. Variations in the depth of the pigmentation affect the size of the coloured areas, but their general disposition varies very little. In the matter of colour the present species is more nearly approached by *P. depurator* than by *P. holsatus*. In the former species all variations

pusillus

exist from the typical whole-coloured forms to specimens which exhibit a colour-pattern closely resembling in a simplified form that of *P. marmoreus*. The *surface* of the carapace is very smooth, and the regions indistinct.

I have taken three abnormal examples of this species. One of these, a male, differs from the typical form only in that it is completely whole-coloured, like *P. holsatus*. Another, a female, approaches *P. holsatus* to some extent in the ventral margins of the orbits, in the frontal teeth, and in the possession of two small teeth on the outer margin of the carpus of the chelipeds. In other respects it is normal. The third differs from the type only in being whole-coloured over most of the carapace, but marbled quite typically on the antero-lateral teeth and legs.

P. marmoreus is moderately common on fine sand at Plymouth, and is found with *P. holsatus*, sometimes in the same haul. Its distribution in Great Britain appears, however, to be more local and southerly than that of *P. holsatus*, although it has been recorded by T. Scott (1888) as occurring occasionally as far north as the Firth of Forth.

VIII. *P. HOLSATUS* Fabr.

Portunus holsatus. Fabricius, 1798; H. Milne-Edwards, 1834; Bell, 1853; A. Milne-Edwards, 1861, etc.

Cancer depurator. Pennant, 1777.

Portunus lividus. Leach, 1814, 1816; Thompson, 1843.

Liocarcinus holsatus. Stimpson, 1869.

Portunus dubius. Rathke, (*teste* Heller).

Portunus Valentieni. ? Cocco, 1833, (*teste* Carus).

The *carapace* is less convex than in the previous species, and is considerably narrowed posteriorly. Forty-four males gave a mean value for $\frac{\text{breadth}}{\text{length}}$ of 1.30, and twelve females a mean value of 1.28, these differences from *P. marmoreus* being found highly significant by the χ^2 method. The *frontal teeth* are angular, and the median tooth the most advanced. The *antero-lateral teeth* are sinuate or flattened externally, sharply pointed and somewhat thin. The *orbits* are small relative to the breadth of the carapace. In ventral view the sub-orbital margin appears as a symmetrical curve, or even, in some cases, is more concave internally. This point of difference from *P. marmoreus*, though very striking in actual specimens, is difficult to bring out completely in any figure. In comparing the two figures in regard to this character, the ventral fissure should be ignored and the curves treated as if continuous. It is a case in which the presentation of structural details diverts attention from the general form, which is, in this instance, of greater diagnostic value. The *epistome* is almost rhomboidal in shape, showing the least degree of lateral extension to be found

in the genus, though a closely comparable condition is seen in *Polybius*. The *merus of the third maxillipeds* differs very little from that of the last species, but the anterior margin is usually more flattened. The *carpus of the chelipeds* differs strikingly from that of *P. marmoreus*. It is considerably more rectangular in shape, and possesses on its outer margin two well-marked teeth. Of these, the posterior is acute, and forms the termination of a sharp carina bounding the postero-external margin of the joint. The anterior tooth is more rounded, and in young specimens is sometimes nearly obsolete. The antero-external corner of the joint is more produced than in *P. marmoreus*, and may almost be said to constitute a third rounded tooth. The chelæ are fairly sharply carinated and are slightly unequal, the right being usually the larger. In the *last pair of thoracic limbs* the dactylus is broader than in the last species, but not rounded at the end as has been stated by some authors.

Forty-three males gave a mean value for $\frac{\text{length}}{\text{breadth}}$ of 1.95, and twelve

females a mean value of 1.99, the differences from *P. marmoreus* being found highly significant when tested by the χ^2 method.

Traces of a median rib are present, as in *P. marmoreus*. The propodus differs noticeably in shape from that of the last species, and is longer in proportion to the dactylus, the mean value for $\frac{\text{dactylus length}}{\text{propodus length}}$ in forty-four males examined being 1.34, and in nine females 1.37, differences from *P. marmoreus* which again were shown to be highly significant by the χ^2 method. The posterior margin of the propodus is extended distally in adult specimens into a rounded lobe, as in *P. puber*.* The *abdomen of the male* agrees with that of *P. marmoreus* in becoming abruptly narrower at the penultimate joint, but is proximally considerably broader in the adult than in that species, and the sutures between the 3rd, 4th, and 5th joints, are more clearly marked. The tips of the *1st abdominal appendages* of the male are bent at a right angle, as in *P. marmoreus*, but the bent portion is rather longer. The *colour* is usually a brownish grey with a tinge of green and with a row of lighter-coloured spots following the cervical groove on each side and curving backwards to the postero-lateral margins. In *P. marmoreus* these spots are present, but are obscured by the rest of the colour-pattern. The *surface* of the carapace is typically almost smooth with the regions indistinct, but specimens are occasionally taken which possess to a greater or less degree the coarse irregular

* Since this was written the *merus* of this pair of legs has been found to be a further difference between *P. holsatus* and *P. marmoreus*. In *P. holsatus* the mean value in twenty-two male individuals for $\frac{\text{merus length penultimate limbs}}{\text{merus length last limbs}}$ was 1.97, with a range from 1.87 to 2.15. In *P. marmoreus* the value for twenty-two males was 1.52 with a range from 1.45 to 1.60.

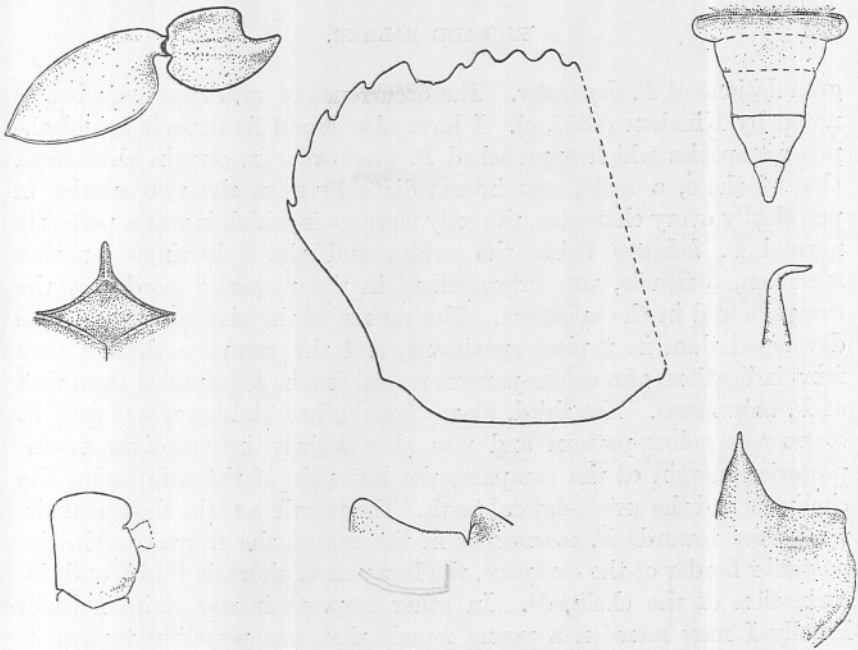


FIG. 6. — P. MARMOREUS.

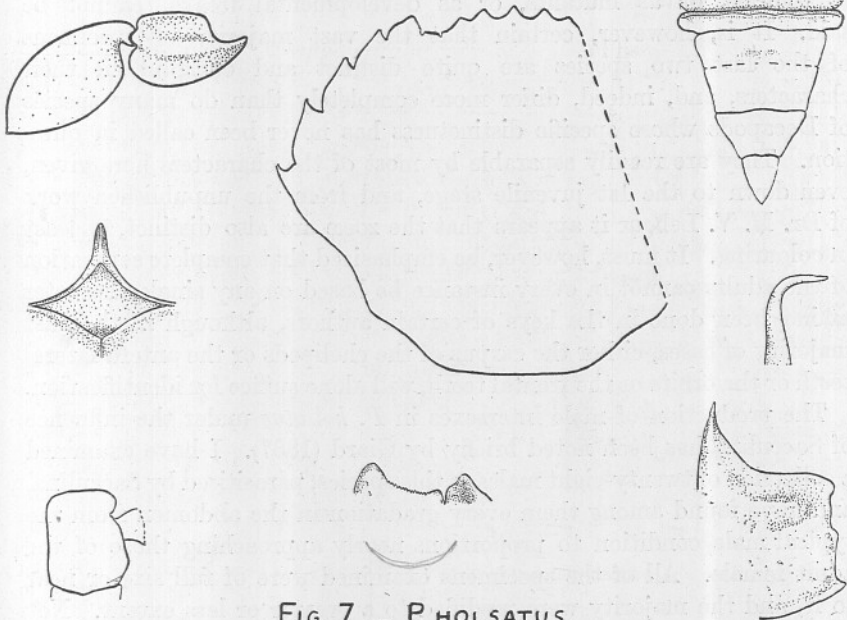


FIG. 7 — P. HOLSATUS.

For description see Fig. 2.

granulations of *P. depurator*. The occurrence of such specimens is also noted by Kinahan (1857, c). I have also found five specimens of the present species which approached *P. marmoreus* in certain characters. One of these, a male, was intermediate between the two species in practically every character, the only features in which it was a perfectly normal *P. holsatus* being the orbits and the colouring. Another specimen, a female, was intermediate in the posterior border of the carapace and in the epistome. The carinæ of the chelæ were less well developed than in typical specimens, and the carapace showed very faint indications of a colour-pattern resembling in a simplified form that of *P. marmoreus*. The third, also a female, had similar traces of a *P. marmoreus* colour-pattern and was also slightly intermediate in the posterior margin of the carapace, the last pair of thoracic limbs, the chelipeds and the antero-lateral teeth. The fourth, a male, showed slight tendencies towards *P. marmoreus* in the orbits, the frontal teeth, the posterior border of the carapace, the last pair of thoracic limbs, and the carination of the chelipeds. In other respects it was quite normal. Finally I may mention a young female that was perfectly typical in every respect except that it had a fairly well-developed colour-pattern of the *P. marmoreus* type.

Whether such atypical specimens as the above are to be considered as hybrids, or as mutants, or as developmental freaks, cannot be said. It is, however, certain that the vast majority of specimens of the last two species are quite distinct and constant in their characters, and, indeed, differ more completely than do many species of Decapods whose specific distinctness has never been called in question. They are readily separable by most of the characters here given, even down to the 1st juvenile stage, and from the unpublished work of Dr. M. V. Lebour it appears that the zoeæ are also distinct, at least in colouring. It must, however, be emphasized that complete separation of the adults cannot in every instance be based on any single character as has been done in the keys of certain authors, although in the vast majority of cases, either the carpus of the chelipeds or the antero-lateral teeth or the orbits or the frontal teeth, will alone suffice for identification.

The production of male intersexes in *P. holsatus* under the influence of *Sacculina* has been noted briefly by Giard (1887). I have examined a collection of twenty-eight males of this species, parasitised by *Sacculina*, and have found among them every gradation in the abdomen from the typical male condition to proportions nearly approaching those of the adult female. All of the specimens examined were of full size or near to it, and the majority were modified to a greater or less extent. Not only were the proportions of the abdomen affected, but the sutures between the 3rd, 4th, and 5th segments were distinct as in female

specimens. The abdominal appendages appeared to be normal. Thirteen parasitised females showed no signs of sexual abnormality. Six parasitised males of *P. marmoreus* were examined, but appeared to be unmodified. It might not be out of place to suggest in this connection that new light might be thrown on the physiology of the production of such intersexes in Brachyura, if the abnormal condition of the abdomen were treated as a problem in heterogonic growth.

P. holsatus is moderately common in small numbers at Plymouth, being occasionally taken on fine sand with *P. marmoreus*.

IX. *P. DEPURATOR* (Linn.).

Cancer depurator. Linnæus, 1758.

Cancer depurator (var.). Pennant, 1777.

Portunus depurator: Fabricius, 1798; Leach, 1814, 1816; Bell, 1853; A. Milne-Edwards, 1861, etc.

Portunus plicatus. Risso, 1816; Roux, 1828; H. Milne-Edwards, 1834; Lucas, 1849.

Portunus vernalis. ? Risso, (teste Carus).

The *carapace* is broad and flattened and little contracted posteriorly. The mean value for $\frac{\text{breadth}}{\text{length}}$ in one hundred individuals (fifty males and fifty females) was 1.33,* with a standard error of .0023. There is no significant difference between the males and females in this character. The *frontal teeth* are sharp, the median one being the narrowest and most advanced. The outer teeth differ from those of *P. holsatus* in having their external edge convex. The *antero-lateral teeth* are sharp, somewhat flattened externally, and in general rather intermediate in form between those of *P. holsatus* and *P. marmoreus*. The *orbits* are large and shallow. In ventral view the sub-orbital margin is sinuate and advanced, almost completely covering the eyes when the latter are retracted. The *epistome* is rather broader in proportion than that of *P. holsatus*. The *merus of the third maxillipeds* is rather longer than in *P. holsatus*, and is somewhat oblique. The *carpus of the chelipeds* closely resembles that of *P. holsatus*. In this case, however, the anterior of the two teeth of the outer margin is the more pronounced. The *chelæ* are more sharply carinated than in *P. holsatus*, and are rather unequal, the right being usually the larger. In the *last pair of thoracic limbs* the dactylus is somewhat more rectangular

* Warren (1896) obtained a rather lower figure, through using slightly different criteria of "length." He found no significant change in this value with absolute size. From other carapace measurements he reached the interesting conclusion that the correlation between the two sides of the body is greater in *P. depurator* than in *Carcinoides mœnas*, and that this greater symmetry is probably connected with the swimming habit of the former.

than in the last species. The mean value for $\frac{\text{length}}{\text{breadth}}$ of the dactylus in fifty males was 1.8682 with a probable error of .01063, and in fifty females 1.9348 with a probable error of .01225. Using the χ^2 method, it was shown that the difference obtained between the male and female frequency curves for this character was a significant one, the male dactylus being on the average rather broader than the female dactylus. There are indications that this is so in other species of "Portunus," but sufficient data have not been obtained to decide the matter finally. In all cases the figures of this and other characters have been drawn from male specimens. The posterior lobe of the propodus is greatly produced distally as a rectangular expansion. The median rib of the dactylus is faintly suggested in *P. holsatus*. The abdomen of the male differs sharply from that of *P. holsatus* and *P. corrugatus*, and to a lesser extent from the other species discussed above, in that its shape is regularly triangular without any abrupt narrowing at the 6th joint. The sutures between the 3rd, 4th, and 5th joints, are rather obscure. The 1st abdominal appendages of the male are bent nearly at right-angles. The colour is usually a uniform red-brown, or occasionally dark brown, especially in juveniles. In some cases, however, the frontal region is sharply marked off in a lighter colour, and all stages exist from this condition to a pattern closely resembling in a less complex form that of *P. marmoreus*. A very constant character is the violet coloration of the tips of the swimming dactylus. The surface of the carapace is irregularly covered with coarse rows of crenulations, and is moderately hairy. The regions are rather indistinct.

P. depurator is abundant, and generally distributed at Plymouth at a depth of 3-30 fathoms.

X. *P. TUBERCULATUS* ROUX.

Portunus tuberculatus. Roux, 1828; A. Milne-Edwards, 1861, etc.

Portunus macropipus. Prestandrea, 1833.

Portunus pustulatus. Norman, 1861.

Ellipticodactylus rugosus. Doflein, 1904.

The carapace is flattened and very broad, its breadth being, however, accentuated by the length of the last antero-lateral tooth. $\frac{\text{Breadth}}{\text{Length}}$

is normally about 1.6, but some specimens in the British Museum are considerably less broad. The carapace is fairly broad posteriorly. The frontal teeth differ hardly at all from those of *P. depurator*. The antero-lateral teeth are sharp and pronounced, the last one in particular being

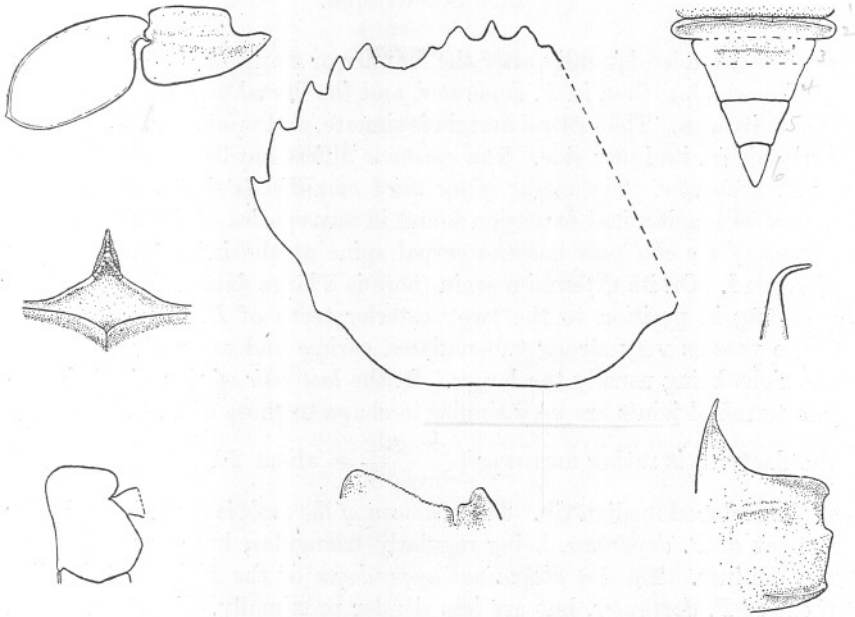


FIG. 8. — P. DEPURATOR.

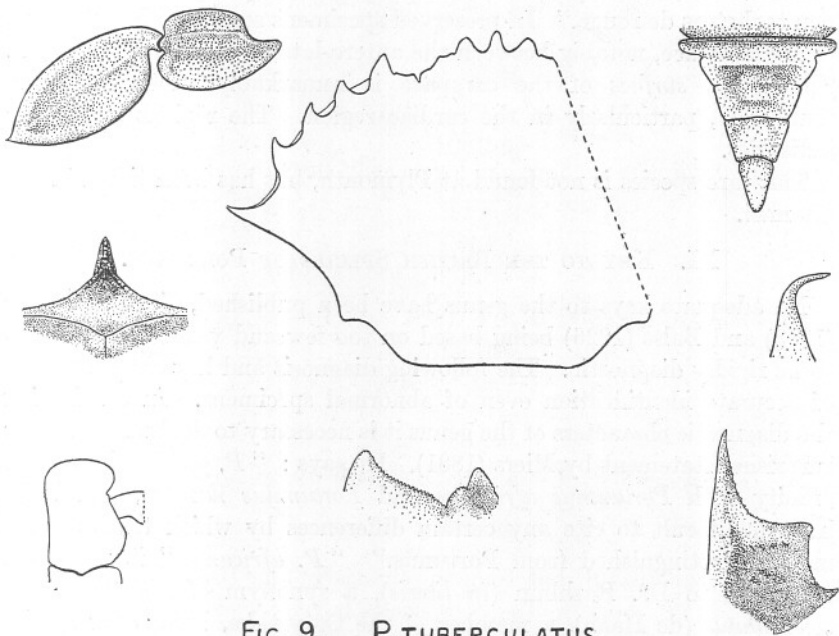


FIG. 9. — P. TUBERCULATUS.

For description see Fig. 2.

greatly extended laterally after the manner of many *Lupinæ*. The *orbits* are less shallow than in *P. depurator*, and the dorsal and ventral fissures are more open. The ventral margin is sinuate, and produced considerably forwards on its inner side. The *epistome* differs hardly at all from that of *P. depurator*. The *merus of the third maxillipeds* shows the greatest degree of longitudinal extension found in any species of the genus. The *carpus of the chelipeds* has the carpal spine at the inner angle greatly elongated. On its external margin there is a large flattened tooth corresponding in position to the two posterior teeth of *P. depurator*. The *chelæ* possess very strong tuberculated carinæ and are rather unequal, the right being usually the larger. In the *last pair of thoracic limbs* the two terminal joints are very similar in shape to those of *P. holsatus*, but the *dactylus* is rather narrower ($\frac{\text{length}}{\text{breadth}} = \text{about } 2.1$) and possesses a well-developed median rib. The *abdomen of the male* is essentially similar to that of *P. depurator*, being regularly triangular, but the sutures are less distinct. The *1st abdominal appendages* of the male are also like those of *P. depurator*, but are less slender proximally. I have not seen living specimens, nor ones in which the *colour* has been perfectly retained after death. A. Milne-Edwards (1861a) states, however, that the colour is "d'un roux jaunâtre, avec les pinces un peu plus claires et un peu tachetées de rouge." In preserved specimens some polished portions of the carapace, notably between the antero-lateral teeth, are iridescent. The whole *surface* of the carapace is remarkably tuberculate and sculptured, particularly in the cardiac region. The regions are rather indistinct.

This rare species is not found at Plymouth, but has been taken in the Channel.

XI. KEY TO THE BRITISH SPECIES OF PORTUNUS.

No adequate keys to the genus have been published, those of Heller (1863) and Balss (1926) being based on too few and variable characters to be rigidly diagnostic. The following diagnosis and key should permit of accurate identification even of abnormal specimens. In considering the diagnostic characters of the genus it is necessary to deal with a rather surprising statement by Miers (1881). He says: "*P. pusillus* has much affinity with *Portumnus africanus* and *Portumnus nasutus*, and it is, indeed, difficult to cite any certain differences by which these species may be distinguished from *Portunus*." "*P. africanus*" is probably, according to Dr. Rathbun (*in literis*), a synonym of *Nautilocorystes octodentatus* (de Haan), a member of the *Corystidæ*, but so far as the species of *Portumnus*, *Ovalipes*, and *Xaiva* are concerned, I consider they are very sharply distinct from "*Portunus*." The orbits, the eyes,

the male abdomen, and the merus of the third maxillipeds may be mentioned as specially important characters in this connection. There is, in fact, such a degree of fundamental agreement in these characters in the three genera mentioned, as distinct from Portunus and its allies, that I cannot agree with the separation of Ovalipes (type *O. ocellatus* (Herbst)) and Portumnus in different sub-families in Alcock's classification (1899b). I agree also with Balss (1921) and others in considering the characters separating Portumnus and Xaiva to be too small to admit of a generic separation. It will be noticed that Bathynectes has only been separated from Portunus in the following diagnosis by the character of the front. It is, indeed, difficult to find any character of importance in which this genus can be said to be sharply distinct from Portunus and the wisdom of placing it in a separate genus seems, therefore, very questionable.

DEFINITION OF PORTUNUS.

Portunidæ in which : (1) The carapace is typically of moderate breadth with five antero-lateral teeth on each side. (2) The front is typically with three teeth or lobes or with eight to ten teeth, or entire ; never with four lobes. (3) The median suture of the sternum occupies only the last two thoracic segments. (4) The palatal crests are present and well defined. (5) The inner infra-orbital angle is never fused with the inner supra-orbital angle. (6) The eye-stalks are short and narrower than the eyes. (7) The basal joint of the external antenna is usually narrow and fused to the front. (8) The last pair of thoracic limbs are modified for swimming ; other pairs normal.

KEY TO THE SPECIES.

- 1. { Front with 8-10 teeth ; (carapace broad and densely hairy) *P. puber.*
- { Front with 3 teeth or lobes, or entire 2
- 2. { Front entire, ciliated ; (swimming dactylus very narrow with distinct median rib, antero-lateral teeth very unequal) *P. arcuatus.*
- { Front with 3 teeth or lobes 3
- 3. { Front with 3 lobes, the median being the most advanced ; (swimming dactylus acutely lanceolate) 4
- { Front with 3 teeth 5
- 4. { Front much advanced ; swimming dactylus without distinct median rib ; male abdomen not abruptly narrowed at the 6th joint ; carapace almost hairless and usually smooth *P. pusillus.*
- { Front not much advanced, crenulated, swimming dactylus with strong median rib ; male abdomen very abruptly narrowed at the 6th joint, carapace hairy and transversely crenulated *P. corrugatus.*
- 5. { Posterior antero-lateral tooth greatly extended laterally ; (carapace flattened, at least half as broad again as long, and very coarsely tuberculate ; carpus of chelipeds with one large tooth on the postero-external margin) *P. tuberculatus.*
- { Posterior antero-lateral tooth not greatly extended 6

6. { Carapace broad, flattened, and coarsely tuberculate; swimming propodus with large rectangular, distally-projecting lobe; male abdomen regularly triangular; (carpus of chelipeds with 2 teeth on the postero-external margin; frontal teeth acute) *P. depurator.*
 These characters not combined 7
7. { Frontal teeth acute, the median the most advanced; antero-lateral teeth externally sinuate or flattened; carpus of the chelipeds with 2 teeth on the postero-external margin; orbits small and with their ventral margin forming a symmetrical curve; chelæ sharply carinate; merus of penultimate pair of thoracic limbs twice as long as that of the last pair; colour brownish grey with a tinge of green *P. holsatus.*
 Frontal teeth rounded, the median typically the least advanced; antero-lateral teeth externally convex; carpus of chelipeds un-toothed on its postero-external margin; orbits large, with their ventral margin most concave externally; carinæ of chelæ obsolete; merus of penultimate pair of thoracic limbs only half as long again as that of the last pair; colour marbled in various shades of brown *P. marmoreus.*

XII. DOUBTFUL, NON-BRITISH AND FOSSIL SPECIES OF *Portunus*.

P. parvulus Parisi.

This species has been described by Parisi (1915) from the Bay of Naples, but has not been figured. His description is as follows (translation) :—

“ This species has close affinities with *P. pusillus* Leach, from which it is distinguished by the following characters: (1) The carapace is proportionately broader and the regions more distinct. (2) Of the five teeth of the antero-lateral margin, the 1st or extra-orbital is not lobiform, but triangular and similar to the rest; the 2nd and 4th teeth are small and the 5th spiniform; (in some examples the 3rd tooth has the point acute as in the 5th). (3) The chelipeds have the carpus rugose and are furnished at the antero-internal angle with a robust acuminate spine, and at the antero-external angle with a small spiniform tubercle. The propodus has two carinæ on its superior margin, and another one, less marked, on its external face. (4) The first three walking-legs increase gradually in length from the 1st to the 3rd. (5) Between the basal joint of the external antenna and the sub-orbital margin there is a well-marked hiatus, represented in *P. pusillus* only by a simple fissure. The colour is very varied: generally greenish brown and reddish brown predominate, with lighter spots and bands.”

Dr. Parisi has very kindly sent me two specimens of this form for examination. After careful comparison of these specimens with a long series of *P. pusillus*, I am somewhat doubtful as to the specific distinctness of the two forms. The great degree of variation in the proportions of the carapace of *P. pusillus*, which I have mentioned above, makes this

character of doubtful value for the separation of *P. parvulus*. The degree of distinctness of the regions of the carapace is also a variable character, though I have seen no specimens of *P. pusillus* from Plymouth that approach the condition seen in Parisi's form. I have specimens of *P. pusillus* which approach *P. parvulus* very closely in the antero-lateral teeth and this character is also, therefore, of doubtful value. One specimen of *P. pusillus* that I have taken agrees with *P. parvulus* in the carpus of the chelipeds, and to a less extent in all the other characters that he mentions. Dr. Parisi considers it, however, to be nearer to *P. pusillus*. Most of the Plymouth specimens of *P. pusillus* that I have examined hardly differ from *P. parvulus* in the walking-legs. Finally, while in most examples of *P. pusillus* the fissure between the sub-orbital margin and the base of the external antennæ is narrow, I have met with a number of specimens showing the well-marked hiatus found in *P. parvulus*. Since Dr. Parisi has no doubt based his species on a large number of living specimens, I hesitate to question its distinctness. It seems to me, however, from the two specimens I have seen, that the characters in which it differs from *P. pusillus* are of varietal rather than specific value, and that a fuller redescription of the form is required.*

P. subcorrugatus A. M-E. and *P. strigilis* Stimps.

P. subcorrugatus is described by A. Milne-Edwards (1861, a) from the Red Sea, and is, according to him, probably conspecific with de Haan's *P. corrugatus* from Japan and Savigny's "*P. Rondeletii*" from Egypt. The specimen from Naples in the British Museum agrees with Milne-Edwards' figure in that the front is only faintly trilobed, though in the text Milne-Edwards contradicts himself on this point. The carapace is also less strongly corrugated than in *P. corrugatus*. *P. strigilis* was described by Stimpson (1858) from a single specimen .28" long taken off the south of Japan. In his description it differs from *P. corrugatus* only in that the front is "indistincte trilobata," and in that it possesses a small spine on the propodus of the chelipeds above the base of the dactylus, whereas in *P. corrugatus* the spine is long and placed rather further back. As, however, he does not mention *P. corrugatus* in his description, it is possible that this last character is not intended to be distinctive. Rathbun (1902) has since described under the name of *Liocarcinus strigilis* (Stimps.) a form from Japan. She states, however, that in contradistinction to *P. corrugatus*, *L. strigilis* has "the median tooth of the front more triangular, its sides at right-angles to each other,

* Since this was written I have received a letter from Dr. Parisi, in which he says: "I find that your observations are very accurate, and it is possible that my species is only a 'variety' or 'form' of *P. pusillus*."

tip acute." This account of the front differs, therefore, inexplicably from Stimpson's original description. She also states that *L. strigilis* is longer and narrower than *P. corrugatus*, the value for $\frac{\text{length}}{\text{breadth}}$ of the carapace in the former species being .85--.87. In view of the contradiction that exists between the two accounts of this species it is impossible to say anything definite as to its validity. It is, however, of interest to note that Rathbun gives *P. corrugatus* of de Haan as a synonym of *L. strigilis*. And since Milne-Edwards regarded *P. corrugatus* of de Haan as synonymous with his *P. subcorrugatus*, it seems probable, as Miers considers (1879), that *P. subcorrugatus* and *L. strigilis* are identical. Whether, further, they are only to be regarded as local varieties of *P. corrugatus* can only be decided by future investigations.*

P. barbarus Lucas.

This name was applied by Lucas (1849) to a form which he says is widely distributed and very abundant on the coasts of Oran and Algeria. It is described as being intermediate between *P. marmoreus* and *P. depurator*, differing from the former "par la carapace qui est plus bombée, dont la partie postérieure est moins rétrécie, et surtout par la granulation assez forte dont elle est entièrement parsemée, ainsi que par les poils courts et peu serrés que l'on aperçoit parmi cette granulation," and from the latter "par le front, qui n'est pas relevé, et par la carapace qui n'est pas ridée." The colour is said to be bottle green. The figure given, though very beautiful, is admittedly inaccurate in showing four frontal teeth instead of three, a fact which leads one to doubt its reliability in other respects. A. Milne-Edwards regards this as a variety of *P. marmoreus*. It has not been since described.

Ellipticodactylus rugosus Doflein.

This form was described by Doflein (1904) on the basis of two specimens from the Congo region. Doflein suggests affinities with *Lupocyclus* and *Ovalipes*, and does not mention *P. tuberculatus*, with which, however, his species is undoubtedly conspecific, as Balss (1921) has pointed out. Going by Doflein's figures his specimens were rather less broad, and with the last antero-lateral tooth less produced than in typical specimens of *P. tuberculatus*; but all gradations exist in this character in the examples

* Dr. Rathbun has since written me: "I have re-examined the *strigilis* and *corrugatus* specimens together with more recent accessions and think you are right to combine the species and also *subcorrugatus*, on account of variation. There is, however, something odd about the Japanese specimens—more elongate and more deeply areolate."

of that species at the British Museum, and it is therefore doubtful whether Doflein's specimens are even varietally distinct.

P. carcinoides Kinahan.

Kinahan (1857, b) describes this species as follows: "Carapace smooth, without raised ridges, regions marked out by rounded prominences only, sparsely hirsute. Front *three-lobed*, middle lobe largest, *edges of lobes entire*. Antero-lateral margin of carapace five-toothed. First pair of legs equal, surface nearly smooth, hirsute; two flattened triangular teeth at anterior superior angles of wrist; hand with two well-marked carinæ on the upper sides, *the inner terminating in a very minute, obtuse tubercle*. Upper edges of second, third, and fourth pair of legs very sparsely hirsute; fourth joint broadly keeled above; fifth and sixth acutely keeled; sixth joint slender, styliform; terminal joint of posterior pair of legs narrowly lanceolate, with a raised central line, hairy on the edges." The species is based on three young specimens. Kinahan states that it is "easily mistaken for young of *Carcinus mænas*," and A. Milne-Edwards (who seems, however, only to have seen the figure (1857, a) and not the description) considered it to be this species. From Kinahan's figure it appears more probable, however, that it is the young of *P. corrugatus*, and this apparently was the view taken by Miers (1886) since he cites *P. carcinoides* as a synonym of *P. corrugatus*. It has not been recorded since as a distinct species.

P. guadulpensis H. de Sauss.

This species, described by de Saussure (1858) from Guadeloupe, is defined by A. Milne-Edwards as follows: "Carapace bombée et longue, régions à peine indiquées. Bords latéro-antérieurs découpés chacun en cinq épines aiguës. Front à cinq dents, dont les deux externes rudimentaires, les trois autres également avancées, la médiane aiguë, les mitoyennes plus arrondies. Bras court et lisse. Avant bras armé d'une seule épine à son angle antéro-interne. Mains fortement carénées portant une petite épine au-dessus de la base du pouce. Pattes suivantes grêles." Milne-Edwards includes the internal angles of the orbits among the frontal teeth, so that this species is not to be taken to differ from most members of the genus in this respect. From the above description it does not appear to approach closely any known member of the genus, and may be a distinct species. It has not, to my knowledge, been since recorded.

P. Brouweri Van Straelen.

This name has been given by Van Straelen (1924) to a fossil impression of the carapace of a crab found in the Lower Miocene of Celebes. The

carapace is half as broad again as long and somewhat hexagonal, with six antero-lateral teeth, including the extra-orbital, on each side, and four acute frontal teeth. From the figure given, this crab is, in the present author's opinion, much more closely allied to *Charybdis* de Haan (= *Goniosoma* A.M.-E.) than to "Portunus."

XIII. DISTRIBUTION.

No attempt will be made in this section to include every locality from which the species have been recorded, but merely to indicate the present state of knowledge regarding their general distribution. In certain cases (e.g. Heller) the authority given is not the original recorder of the species at the locality, but a later compiler of a list of localities such as this.

P. corrugatus.—British Isles, France, Belgium, Mediterranean, Adriatic, Canary Is. (Heller, 1863); Scotland to Cape Verde, Azores, and Canaries (Bouvier, 1922); Oran (Lucas, 1849); Red Sea (A. Milne-Edwards, 1861); Senegambia (Miers, 1881); Senegambia to Sierra Leone (Balss, 1922); Japan (Miers, 1879); Victoria, Australia (Miers, 1886); New Zealand (Borradaile, 1916).

P. puber.—British Isles, N. France, Belgium, Mediterranean (Heller, 1863); Holland (Balss, 1926); North Sea and Mediterranean (Bouvier, 1922); Adriatic (Parisi, 1915).

P. arcuatus.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Adriatic (Heller, 1863); Holland (Balss, 1926); West Indies (Neumann, 1878) (?); Black Sea (Blohm, 1915); Algeria, Oran (Lucas, 1849).

P. pusillus.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Adriatic (Heller, 1863); Senegambia (Miers, 1881); Senegambia to Sierra Leone (Balss, 1922).

P. marmoreus.—British Isles, France, Belgium, Mediterranean (Heller, 1863); Portugal (Blohm, 1915); Azores (A. Milne-Edwards and Bouvier, 1899).

P. holsatus.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Canary Is., Black Sea (Heller, 1863); Portugal (Blohm, 1915); Holland, Denmark (Balss, 1926); Iceland, Farøes (Hansen, 1908).

P. depurator.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Adriatic (Heller, 1863); Scandinavia to Mediterranean (Bouvier, 1922); Algeria, Oran (Lucas, 1849).

P. tuberculatus.—Mediterranean (Heller, 1863); rare from Shetlands to Azores and Mediterranean (Bouvier, 1922); Adriatic (Parisi, 1915); mouth of Congo (Doflein, 1904).

XIV. RELATIONSHIPS.

Apart from the somewhat crude and inaccurate divisions of Leach, the only attempt at a sub-generic classification of "Portunus" is due to Stimpson (1869). This author went, indeed, beyond a mere sub-generic division. He proposed to divide the genus generically into *Portunus*, including "*P. puber*, *corrugatus* etc.", and *Liocarcinus* "for *P. holsatus* and its allies." Except for the fact that he regards *P. marmoreus* as identical with *P. holsatus*, he gives no indication regarding which genus the other species belong to. In addition to this, the characters upon which he bases his generic division are all of them ones which vary either within the species or continuously throughout the genus. For instance, he states that the basal joint of the second antenna is slightly movable in *P. holsatus*. The examination of living specimens (which were not available to Stimpson) shows that this character varies within the species, probably in relation to the length of time since the last moult. It is in any case a negligible character, easily affected by developmental conditions. He also mentions the median rib of the swimming dactylus in *P. puber* and *P. corrugatus* as a generic character. It has been shown above that this character varies continuously throughout the genus, and the same is true of the other characters that he cites. Some species, such as *P. depurator* and *P. tuberculatus*, could not be placed in either of his genera since they exhibit characters of both.

In discarding Stimpson's genera, it may be said further, that until new evidence is available there appears to be no justification for a generic or sub-generic division of any kind. The most widely different species are linked together by intermediate forms, a fact which has been sufficiently brought out in the description of the species. The order of relationship suggested in Fig. 1 (p. 878) is fairly strongly supported by the characters discussed. More room for debate exists regarding the precise *direction* in which the series is to be read, and there is little indication within the genus upon this point. A consideration of allied genera suggests, however, the use of the scheme shown in Fig. 1 as a working hypothesis. The adaptation to a swimming habit which exists in the majority of the Portunidae is undoubtedly a secondary one, and in the absence of contrary evidence those forms have to be regarded as the most primitive which approach most nearly the non-pelagic Cancroid type. We have, therefore, to seek links between the more typical Portunidae and the other Cancroid families. One such link is provided by Carcinides Rathb. (*Carcinus* of Leach, of which the common shore-crab, *C. maenas*, is the only living representative), or its ancestors. This form is spoken of by Alcock (1899, b) as linking the Portunidae with the Cancridae, and it is actually included by Ortmann (1899) in the latter group. Its

almost world-wide distribution lends further colour to the view that it is to be considered as a primitive form. Among the species of "Portunus," *P. corrugatus* and *P. arcuatus* approach more nearly to this primitive form than do any other members of the genus. Another stage in the progress towards a pelagic habit is, perhaps, represented by *Nectocarcinus*. This form, though specialised in many respects, is nevertheless intermediate in a number of features, between Carcinides and "Portunus." In certain characters, particularly in the species *N. integrifrons*, it has distinct affinities with *P. corrugatus* and *P. arcuatus*, and the fact that it has only four antero-lateral teeth is, no doubt, secondary since the large flat first tooth probably corresponds to the first two teeth of other forms, and since a tendency towards the suppression of the second tooth has already been noted in *P. arcuatus*. (Alcock (1899, b) considers *Nectocarcinus* to form a link with the Xanthidæ. In this case the Portunidæ are diphyletic, and should be split up.) The fossil, *Portunites* (A. Milne-Edwards, 1861, b), found in the London clay, so far as it is known, appears to be intermediate in some respects between Carcinides and *P. arcuatus*, and certainly has much less affinity with forms at the other end of the series. The genus *Banthochascon* may, perhaps, represent another link in the chain. While its nearest affinities are probably with *Bathynectes*, as Alcock (1899, a) has suggested, it is reminiscent in some features, of *Nectocarcinus* and Carcinides. Finally, *Bathynectes* may be mentioned as a form which, though considerably specialised in certain characters, notably in the lateral extension of the carapace and legs and in the four frontal teeth of the adult, is in other characters closely similar, in some features to *P. corrugatus*, and in others to *P. arcuatus*. It will be seen, therefore, that it is possible tentatively to trace a progression of forms from Carcinides to "Portunus," and that this chain links up most closely with the species, *P. arcuatus* and *P. corrugatus*. The most significant feature of this evolutionary sequence is the gradual increase in the degree of adaption for swimming, found in the last pair of thoracic limbs. The modification of this pair of appendages is not confined to the last two joints, but affects the proximal joints also, notably the merus. In the Cancridæ and Xanthidæ this joint hardly differs from that of the penultimate pair of thoracic limbs. In *Carcinus* it is somewhat specialized, and this process can be traced through the series mentioned above, to "Portunus." In this genus the species *P. arcuatus* and *P. corrugatus* show the least degree of modification of the merus, while the greatest specialization is seen in *P. holsatus* and *P. depurator*, both strong swimmers. *Polybius* has carried the process even further than in these two species, the merus being practically as broad as it is long. I have no suggestions to make as to the origin of the other sub-families of the Portunidæ, except to point out that the fossil

Psammocarcinus (Miocene), forms a possible link between Carcinides on the one hand and Portumnus and its allies on the other.

It will be seen, therefore, from the above discussion of allied genera, that the evidence points, on the whole, to *P. corrugatus* and *P. arcuatus* as being the nearest species to the primitive ancestor of the genus. This view is also supported to some extent by the early juvenile stages, most of which have been investigated by Dr. M. V. Lebour. All of the forms studied, including even *P. depurator* and *P. holsatus*, show to a greater or less degree the partial suppression of the second and fourth antero-lateral teeth which has been noted in the adult of *P. arcuatus*. The same fact has been observed by Milne-Edwards and Bouvier (1899) in the young of *Bathynectes*. The swimming dactylus in the young stages of all species is of the narrowly lanceolate, acutely pointed type. Again, *P. corrugatus* has a world-wide distribution, and *P. arcuatus* is said by Neumann to have been found in the West Indies, whereas the other species with the exception of *P. pusillus* and *P. tuberculatus*, described from Senegambia and the Congo region respectively, are confined to Europe, or the Mediterranean coast of Africa.

Assuming that the ancestral "Portunus" lay somewhere between *P. corrugatus* and *P. arcuatus* in its characters, no further comment need be made on the evolutionary tendencies within this genus, which have been sufficiently brought out in the descriptive text. Some consideration must, however, be given to the position of *Polybius henslowi*. This form has been widely separated from "Portunus" by some authors following H. Milne-Edwards (1834), and considered to be nearer to Portumnus, and its allies, *Ovalipes* Rathb. and *Xaiva* MacLeay. This grouping appears to be based almost exclusively on a supposed similarity in the external antennæ. The literature on this point is confused and contradictory, and no attempt will be made to follow its intricacies. It may, however, be mentioned that H. and A. Milne-Edwards regard the basal joint in *Polybius* as slender and movable, and that Ortmann (1899) mentions the second joint as being cylindrical—in both cases in contradistinction to "Portunus." After examining in detail a large number of specimens I can find no basis for a division on this character. The basal joint in *Polybius* is almost indistinguishable from that of *P. holsatus*, and is slightly movable or completely fused, in different specimens, as in that species. The second joint does not differ from that of "Portunus." Borradaile (1900) groups *Polybius* and Carcinides in the same sub-family entirely on the grounds that the basal joint of the external antenna is slender as opposed to that of "Portunus" and its allies, whereas actually in Carcinides the basal joint is broader than in any species of "Portunus" except *P. puber*. There appears to be no reason, therefore, for grouping *Polybius* with Portumnus and its allies

on these grounds, and, in fact, the genera differ most markedly, notably in the eyes, the orbits, the male abdomen, and the merus of the third maxillipeds. On the other hand, *Polybius* shows very close affinities with *P. holsatus* in a number of characters, particularly in the ventral margin of the orbits, the epistome, the carpus of the chelipeds, the antero-lateral teeth, and the last pair of thoracic limbs. The merus of the third maxillipeds is also of the elongated type, and the first abdominal appendages of the male and the male abdomen are almost identical with those of *P. holsatus*. For these reasons *Polybius* is regarded provisionally, in Fig. 1, as fairly closely allied to *P. holsatus*, but as very greatly specialised in adaptation to a semi-pelagic existence.

XV. SUMMARY.

1. The characters of the species of "*Portunus*" are redescribed in detail and comparatively.
2. On the basis of the characters studied an attempt is made to determine the relationships of the constituent species, both within the genus and with allied genera, *P. corrugatus* and *P. arcuatus*, being regarded as the more primitive forms.
3. *P. marmoreus* and *P. holsatus* are separated by a large number of characters.
4. The status of various foreign, fossil and doubtful species is discussed.
5. An account is given of the present state of knowledge regarding the distribution of the species.
6. The synonymy of the generic name is considered at length.

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