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BY

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(*Fellow, Dean and Lecturer of Selwyn College, Cambridge; Lecturer in Zoology in the University*).

WITH THIRTEEN FIGURES IN THE TEXT.

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THE "Terra Nova" Expedition captured off the northern end of New Zealand a berried female specimen* of *Porcellanopagurus*. Although four members of this genus have already been described,† our knowledge of the exceedingly interesting crustaceans which compose it is as yet very incomplete. The "Terra Nova" example (which I have provisionally referred to the type species *P. edwardsi*, Filhol) is in rather bad condition, all but the last pair of the legs being detached from the body, while the left cheliped and both legs of the fourth pair are missing. From this specimen, however, it is possible to gather certain facts which have not yet been stated, and to draw certain conclusions. The authorities of the Zoological Department of the British Museum have very kindly afforded me facilities for examining also two male specimens of *P. tridentatus*, Whitelegge, from the Kermadec Islands, and for comparing them with various other Paguridea. The following communication embodies the results of my observations upon this material.

Porcellanopagurus (Fig. 1) is one of the many attempts of Nature to evolve a crab. The material, in this instance, seems to have been an ordinary hermit-crab of the subfamily Eupagurinae, and the method followed was not only, as in other such cases, a broadening and depression of the cephalothorax, as though a weight had been placed upon it, together with reduction of the abdomen, but also a drawing out horizontally of the edges of that hard plate which roofs the forepart of the body of a hermit-crab. This plate is bounded at each side by the front part of the *linea anomurica*—the "line

* The specimen is mentioned on p. 97 of the systematic account of the Decapoda collected by the "Terra Nova" (Vol. III, No. 2).

† *P. edwardsi*, Filhol, 1885; *P. platei*, Lenz, 1902; *P. tridentatus*, Whitelegge, 1904; *P. japonicus*, Balss, 1914. The literature of the genus and its species is as follows: *Porcellanopagurus*, Filhol, Bull. Soc. Philomath. Paris (7), IX, p. 47 (1885); Miss. Ile Campbell, III, ii, p. 410 (1885). Thomson, Trans. N.Z. Inst., XXXI, p. 187 (1899). Alcock, Cat. Ind. Decap. Crust. II, i, pp. 27, 191 (1905). Chilton, Subant. Is. N.Z., XXVI, p. 610 (1909). Balss, Abh. K. Bayer. Ak. Wiss., math.-phys. Kl., Suppl. II, ix, p. 66 (1913). *P. edwardsi*, Filhol, Thomson, Alcock, Chilton, l.c. *P. platei*, Lenz, Zool. Jahrb. Syst., Suppl. V, p. 740 (1902). *P. tridentatus*, Whitelegge, Mem. Austral. Mus. IV, p. 180 (1904). Chilton, Trans. N.Z. Inst. XLIII, p. 552 (1911). *P. japonicus*, Balss, l.c. *P. edwardsi?*, Borradaile, "Terra Nova" Nat. Hist. Rep., Zool., III, No. 2, p. 97 (1916).

b" of Boas*—and extends backwards a little way beyond the cervical groove. In *Porcellanopagurus* (Fig. 5) its edges have grown out into a series of lobes, by which the spread of the back is increased. One of these lobes is a large, triangular rostrum, and there are on each side four others, which vary in size and shape according to the species. The rostrum bears a low median ridge. The first side-lobe stands at the angle of the carapace, above the antenna. The second has, in *P. edwardsi*, three cusps, of which the foremost is low and blunt, the middle long and sharp, and the hinder a mere knob. The third and fourth lobes, like the first, are simple. The fourth stands behind the

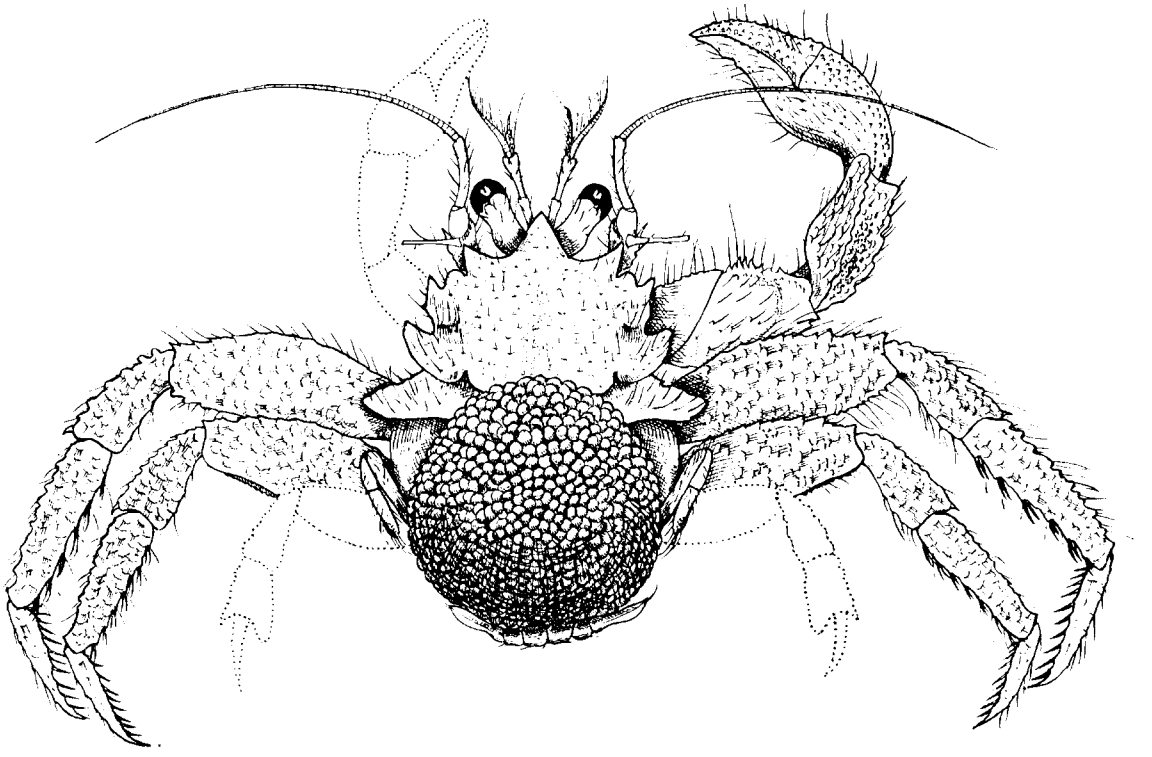


FIG. 1.—*Porcellanopagurus* sp., probably *P. edwardsi*, taken by the "Terra Nova" north of New Zealand: dorsal view of a berried female, × 3.

cervical groove on a fairly wide piece of hard cuticle, which in ordinary hermit-crabs is represented by a much narrower strip. Besides the ossicles of the fourth pair of lobes there is a little post-cervical calcification in the cardiac region. The cervical groove which separates this hinder series of small pieces from the main part of the back-plate is undoubtedly here, as in other hermit-crabs, the hinder of the two furrows to which that name has been applied,† the anterior cervical groove being absent in all Paguridea. The horizontal "line *d*" of Boas —the anterior part of the *linea thalassinica* —of which a trace exists in other Paguridae, in the form of a groove of varying depth

* K. Dansk Vidensk. Selsk. Skr. (6) I, p. iv.

† See Gardiner's "Fauna of the Maldives," Art. "On the Classification and Genealogy of the Reptant Decapods," vol. II, p. 690.

and length, is represented in *Porcellanopagurus* by a short, deep, forward branch from the cervical groove above the third lobe of each side, and perhaps by a faint forward continuation.

The substance of the dorsal plate, and of the armour of the first three pairs of legs, is very hard, porcellanous, and a little translucent, not at all like that of most hermit-crabs, but its surface is roughened by many short, transverse ridges, and somewhat sparsely covered with hairs, placed in little rows, each in front of one of the ridges, an arrangement which, developed in various degrees, is not uncommon in Eupagurinae. Below the projecting lobes of the back-plate, the sides of the cephalothorax (Fig. 2) are almost vertical, though rather low, and they and the hinder part of the thorax are soft, as in an ordinary hermit-crab. The post-cervical region is shorter and wider than in other Paguridae, and the concavity of its hinder edge is semicircular, not deep and narrow, as is usual in the family. In correspondence with this shortening of the region behind and above it, the hinder part of the *linea anomurica* is directed more downwards than usual. The "line *la*" of Boas branches as a **Y** at its upper end, the forward branch joining the *linea anomurica* opposite the cervical groove, the hinder branch behind the last side lobe.

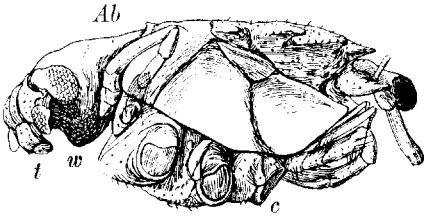


FIG. 2.—*Porcellanopagurus*: side view of the specimen shown in Fig. 1, × 3. *Ab*, Abdomen; *c*, base of cheliped; *s*, sixth abdominal tergum; *t*, telson; *w*, waist.

On the underside of the thorax (Fig. 3) the legs are set wider apart than in an ordinary hermit-crab, and the sternal series of plates is better developed, though in number and position its pieces faithfully resemble those of *Eupagurus*. The widely separated bases of the third maxillipeds are connected by a slender sternum, rather wider in the middle than at its ends. The two small sternal pieces on the segment of the chelipeds are fused, though their limits are still visible. They are not quite symmetrical, the left being rather more prominent than the right. The second pair of legs has a pair of large sternal plates. Behind them stands a transverse piece of good size, which appears to belong to the same segment as the two rather small ossicles at the bases of the third pair of legs. The sternum of the fourth pair of legs is a very narrow bar, placed more dorsally than that of *Eupagurus*, on the anterior wall of a deep furrow which separates from the cephalothorax a region consisting of the last thoracic segment together with the abdomen. On the hinder side of this furrow, thus seeming to belong to the abdomen, stands the sternum of the fifth pair of legs, which is also a very narrow bar. The oviducal opening is placed, not, as usual, on the ventral side of the coxopodite of the third leg, but on the hinder face of the joint, which is directed towards the furrow between the last

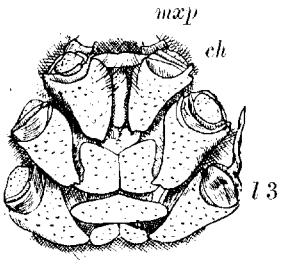


FIG. 3.—*Porcellanopagurus*: third to sixth thoracic sterna of the specimen shown in Fig. 1, × 3. *ch*, Cheliped; *l* 3, third leg; *mxp*, base of third maxilliped.

two thoracic segments, and is not covered by the sternum of the fourth pair of legs because the latter has receded to a more dorsal position than that which it usually occupies.

The condition of the abdomen in the living animal has, unfortunately, not been described. In spirit specimens (Figs. 2, 5, 13*a*) it forms a rounded sack, placed behind the cephalothorax. From the last thoracic segment it is separated by a groove, fairly deep on the ventral side, but little marked above. In front of that segment, however, there is a greater furrow, by which, as by a waist, the body is divided into two regions, one consisting of the major part of the cephalothorax, the other of the abdomen together with the last thoracic segment. The waist also is deepest on the ventral side. The abdomen is a good deal flattened above but bellies below. It is possible, though perhaps not likely, that its length is greater in living than in preserved specimens, in which case the true aspect of the animal might be considerably less crab-like than that under which it is at present known.

Where the thorax joins the abdomen there lies across the back a narrow transverse strip of hard cuticle (Fig. 13*a*), which has at least the appearance of being the tergite of the last thoracic somite. Its ends abut on a pair of oval plates of like substance, placed one above the base of each of the legs of the segment, and perhaps to be regarded as pleural structures. A similar arrangement is found in *Eupagurus*, where Boas* describes the transverse strip as part of the first abdominal tergite. That, however, it is not, either in *Eupagurus* or in *Porcellanopagurus*. It can hardly be a persistent thoracic tergite, since it is not found in lower Decapoda, and may perhaps be more correctly described as a structure *sui generis* than as a tergite at all; but in both genera it lies clearly in the thoracic region, and can be distinguished from the first abdominal tergite, which lies behind it, and from which is formed the opposite face of the thoraco-abdominal groove, along whose floor in *Eupagurus* there runs a fine, white, transverse line like a suture. The two tergal sclerites are, however, firmly united, and together provide a necessary strengthening of the back in the region of the attachment of the last pair of legs. The true tergite of the first abdominal segment has in *Porcellanopagurus* the form of a moderately broad transverse plate, lacking the median backward expansion which is found in *Eupagurus*. A pair of independent plates, of which the left bears a limb, stand in the female for the second tergite; a smaller plate bearing a limb is the remains of the third tergite, while at the base of the limb of the fourth segment there is barely a trace of such a thickening. The fifth segment is altogether soft. This arrangement is derived from that of *Eupagurus*† by the disappearance of the plate on the right hand side of the third and fourth segments, and of the whole tergite of the fifth. In the male (of *P. tridentatus*) there are no abdominal tergites, save a vestige on the first segment. But, although calcified remnants of the terga are

* *Loc. cit.*, p. 112.

† The shapes and sizes of the hard pieces of the abdomen vary a good deal from species to species in *Eupagurus*.

thus scanty, the segmentation of the abdomen is distinctly, though not strongly, marked by shallow grooves on the dorsal side, separating strips of slightly stouter cuticle on which stand the tergal pieces already described. The hinder edge of the fifth segment is sharply marked, and stands out as a half ring, under which the stout tergite of the sixth segment is telescoped for a short distance. This may also be seen

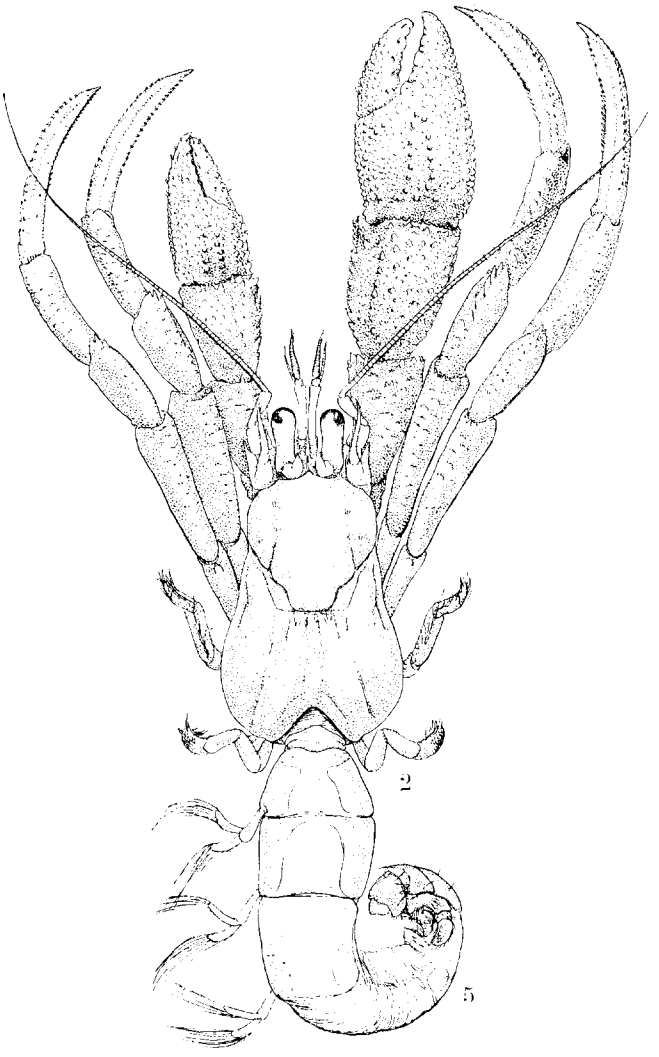


Fig. 4. *Eupagurus bernhardus*: dorsal view of a female specimen, nat. size. 2, 5, Second and fifth terga.

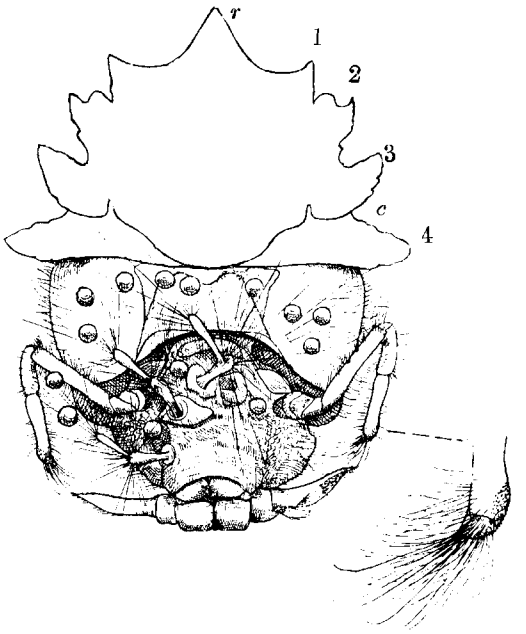


Fig. 5.—*Porcellanopagurus:* dorsal view of the specimen shown in Fig. 1, after removal of most of the eggs, × 4. The end of the fifth leg is also shown enlarged. The limbs of the second, third, and fourth abdominal segments are exposed by the removal of the eggs which they carried; a few of the eggs remain attached to the long hairs of the appendages. The tergal vestiges upon which these limbs stand are shown. The tergum of the first abdominal segment may be seen in front of the foremost egg-bearing limb. The fifth segment has no hard tergite. That of the sixth segment, composed of four large and two small pieces, is seen behind, between the uropods. *c*, Cervical groove; *r*, rostrum; 1–4, side-lobes of the cephalothorax.

in *Eupagurus*. In the male, only the slightest traces of segmentation are recognisable. The sixth tergite in both sexes is represented by two stout plates, one behind the other, each divided by a deep median groove into two, with a pair of small nodules at the sides against the junction of the main plates. In *Eupagurus* each pair of plates is represented by a single structure. The tergite of the telson is softer than that of the

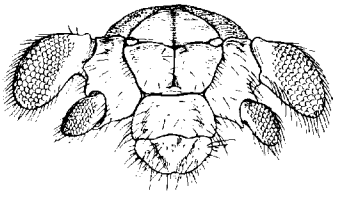


FIG. 6. — *Porcellanopagurus*: dorsal view of the end of the abdomen of the specimen shown in Fig. 1, × 5.

sixth segment, and consists of two successive plates. The two lateral pieces of the hinder edge are less independent than in *Eupagurus*, and there is a median notch, not a point, as in Chilton's and Lenz's figures. The sub-anal valve* is present, though soft. The telson is carried folded under the sixth segment. The dorsal side of the abdomen, which in life is covered by the flat shell of a mollusc, as will be explained later, is smooth and only sparsely hairy, but the sides and ventral surface, which are exposed, are rough-skinned and much more hairy. I can detect no trace of sterna.

The eyes, antennules, and antennae (Figs. 1 and 2) closely resemble those of *Eupagurus*. The scales on the bases of the eyestalks are present, but hidden by the

FIG. 7.—*Porcellanopagurus*: mouth-limbs of the left side of the specimen shown in Fig. 1.—*a*, Mandible, ventral view; a^1, the same, dorsal view; *b*, maxillule, ventral view; b^1, the same, lateral view; *c*, maxilla; *d*, first maxilliped; *e*, second maxilliped; *f*, third maxilliped.

rostrum. The antennary exopodite, by an extraordinary error, is figured by Filhol (*loc. cit.* fig. 2) on the ventral side of the limb, and Lenz omits it altogether in his figure of *P. platei*. In *P. edwardsi* and *P. tridentatus* it is, as a matter of fact, situated in the

* See Gardiner's "Fauna of the Maldives," Art. "Land Crustaceans," vol. I, pp. 73, 81.

ordinary position, and well developed, as a blunt-ended and sparsely hairy, movable spine. The fixed basal spine of the antenna is also present, and is shorter than the exopodite, directed almost straight forwards, and provided with several teeth. The mouth-limbs (Fig. 7) also show no remarkable features. The molar process of the mandible is fairly wide, and the cutting edge has one low tooth near the middle and another at the hinder angle. As in *Eupagurus*, the outer edge of the endopodite of the maxillule is turned forwards. The small process on this edge, which perhaps represents the true end of the limb, is directed forwards, not backwards as in *Eupagurus bernhardus*. In *E. prideauxi* it is wanting. The first pair of legs, incorrectly figured by Filhol as equal, has been shown by subsequent writers to be unequal, the right the larger. The hand of this limb (Fig. 8) is much broader and heavier than in *Eupagurus*. The fingers are white-tipped, not spoon-shaped, and open nearly vertically. The legs of the second and third pairs are those of an ordinary hermit-crab, but rather stouter than usual, and symmetrical. The little ridges to which allusion has been made cover them on both sides, and, standing out in profile along the anterior edge, make it seem toothed. In fact, only one ridge, situated at the end of the carpopodite, is drawn out into a tooth. Under the propodite of each leg is a double row of movable spines, under the dactylopodite a single row. The fourth pair are subchelate as in an ordinary hermit-crab, and have the usual scaly patch on the palm. The fifth pair are like those of *Eupagurus* (Fig. 9), with a clumsy chela, whose fingers are spoon-shaped, lined with hair, and finely toothed around the edge. Whitelegge is incorrect in stating this limb to be simple in *P. tridentatus*, but the mistake is an easy one to make, for when the fingers are closed the dactylopodite, hidden among the long hairs at the end of the leg, looks merely like a low mound upon the tip of the propodite. This leg also has the scaly patch by which it is characterized in hermit-crabs, only somewhat reduced.

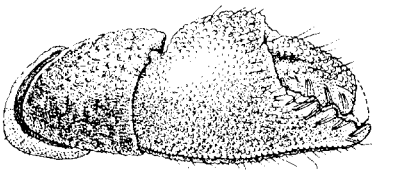
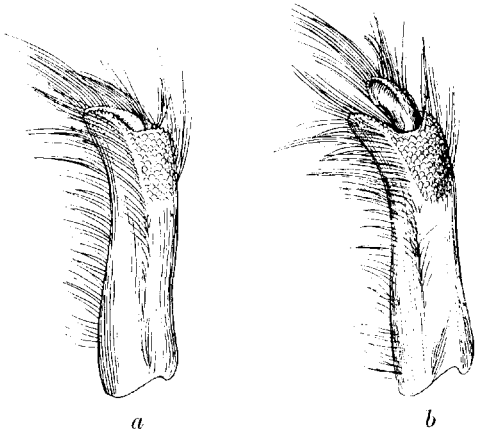


FIG. 8.—*Porcellanopagurus*: outer view of the great cheliped of the specimen shown in Fig. 1, × 3.



a *b*

FIG. 9.—*Eupagurus bernhardus*: end of the last leg—*a*, from the inner side, with the chela closed; *b*, slightly different view, with the chela open, × 7½.

The gill-formula is the same as that of *Eupagurus*, consisting of eleven gills on each side—five pairs of arthrobranchiae and a pleurobranchia. The gills are phyllobranchiae.

The abdomen of the female bears, besides the uropods, three limbs, placed on the second, third, and fourth segments (Fig. 5). I make this statement on the evidence of

the "Terra Nova" specimen, which is a female. Filhol, describing what may have been either a male, or a female deprived of her egg-bearing limbs, mentions a pair of small appendages on the forepart of the abdomen, presumably on the first abdominal segment, though they do not appear in his figure. Lenz even figures such limbs in *P. platei*, of which his specimens were females. I am unable to find any traces of appendages in this position in the "Terra Nova" specimen, nor are they mentioned or figured by any other author. Probably they do not exist.* In *Eupagurus* this segment is without limbs in either sex: in various other Eupagurinae it bears them, sometimes in the female, sometimes in the male. The limbs of the second, third, and fourth segments of the female *Porcellanopagurus* (Fig. 10*a*) resemble those of the same sex of *Eupagurus* (Fig. 10*b*) in being biramous, and in the shape of both branches, but not in the size of the exopodite, which is so minute that the limb appears at first sight to be uniramous. Outside (that is, above) the exopodite, the end of the protopodite has a strong, blunt angle, upon which is a bunch of long hairs, whose function is to supplement those of the endopodite in bearing the eggs. The position of these limbs is interesting. They are all dorsal, and the first is almost median: the other two lie successively more to the left, so that the three form a slanting row. Here is a reminiscence of the relation which the same appendages bear to one another in an ordinary hermit-crab, where, although they lie directly one behind the other if the abdomen be untwisted, yet in its normal spiral position they form a row slanting to the left. In correspondence with this is the fact that in *Porcellanopagurus* the exopodite, which stands in front of as well as above the endopodite in the limb of the second segment, is more dorsally placed in that of the third, and directly above the other branch in that of the fourth segment, and thus has in each case the position which it would have if the abdomen were spirally twisted. It would appear, therefore, that the secondary straightening of the abdomen of *Porcellanopagurus* has been brought about by a process of telescoping rather than by untwisting, so far as the greater part of its length is concerned: the telson and sixth segment have to a considerable extent been rotated backwards into their original position. That the limbs are more dorsal in position than usual, is no doubt in connection with the manner in which the abdomen is protected, and serves to bring the eggs under shelter of the shallow shell which the animal carries over its back. I have been unable to find in this genus any trace of the little appendage which is borne on the fifth abdominal segment in *Eupagurus*.

The only male *Porcellanopagurus* which I have been able to examine is that of *P. tridentatus*. In it the abdomen bears no limbs on any segment but the sixth. This is a sharp distinction from some species of *Eupagurus*, but not from others.

* It is not clear that Filhol is not alluding to the limb of the second abdominal segment, or even to the last thoracic appendage. Lenz's figure is probably very inaccurate. I have already stated that it omits the antennal exopodite. It also shows a pair of appendages in the first abdominal segment, but none on the second, third or fourth. If these be not serious errors, *P. platei* differs very remarkably from the other species of the genus to which it has been assigned.

E. bernhardus (Fig. 10*c*) has appendages of moderate size on the third, fourth, and fifth segments of the male. *E. prideauxi* (Fig. 10*d*), however, shows only simple, microscopic vestiges of these limbs. It is interesting to note that in the male *E. bernhardus* the appendages in question are biramous with one branch reduced, but that this is the endopodite, whereas in the female of *Porcellanopagurus* it is the exopodite that has undergone reduction. Chilton describes the male of *P. edwardsi*, and as he makes no reference to any abdominal limbs save the uropods, it is probable that the latter alone are present. Balss, however, figuring what he states to be the male of *P. japonicus*, shows three unequally biramous limbs on the same segments as in the female. It is

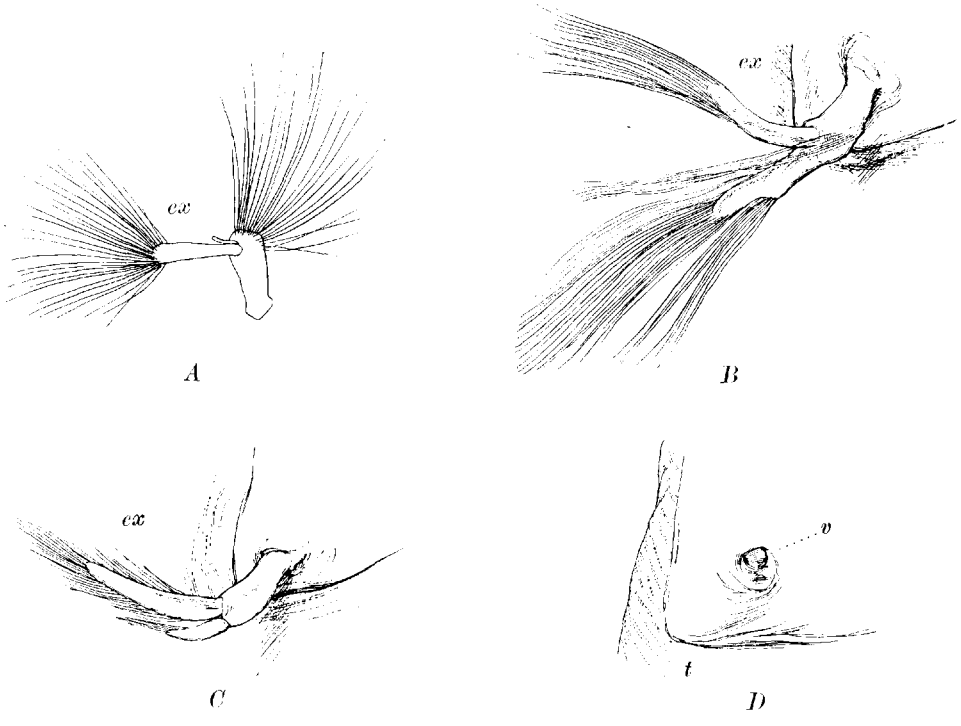


FIG. 10.—Dorsal views of the limb of the third abdominal segment in Eupagurinae—*A*, *Porcellanopagurus*, sp., ♀, × 6; *B*, *Eupagurus bernhardus*, ♀, × 5; *C*, the same, ♂, × 5; *D*, *Eupagurus prideauxi*, ♂, × 8. *ex*, Exopodite; *v*, vestige of pleopod; *t*, postero-external angle of tergum.

possible that he may be mistaken in the sex of his specimen, but in that case it is to be observed that, as they are represented in his figure, the reduced rami appear to be the endopodites as in male *E. bernhardus*. If the male of *P. japonicus* be rightly figured by Balss, then there is in *Porcellanopagurus* a difference between species in regard to the development of the abdominal limbs of the male, as there is in *Eupagurus*. The question needs reinvestigation.

The uropods (Fig. 6) of the two sexes are alike, and resemble those of the ordinary hermit-crabs, except in that they are almost completely symmetrical in shape and not very asymmetrical in position, though they are still obviously placed at an angle with

the horizontal plane. It is noticeable that they retain the scaly patches on both rami which are used, by the hermit-crabs which inhabit hollow objects, to give foothold on the inside of their homes.

With regard to the habits of *Porcellanopagurus*, some information may be gained from the statements of the naturalists who collected the specimens at present known to science. *P. edwardsi* was originally taken in shallow water (down to 5 m.) at Campbell Island and Stewart Island, living among sea-weeds, and was expressly stated by Filhol not to live in a shell. Chilton records it dredged at the Snares in 60 fathoms. The "Terra Nova" specimen, which I have rather doubtfully referred to the same species, was trawled in 70 fathoms off the North of New Zealand, on a bottom of sand and rock. *P. platei* was obtained on the shore at Juan Fernandez, and Plate, who collected it, stated that it *deckt die Eier mit einer Muschelschale zu.* Lenz, for no very obvious reason, distrusted Plate's statement, and held that the animal's abdomen *kann nach vorn auf den Rücken geklappt werden*, and in that position was mistaken by Plate for the shell of a bivalve mollusc! This very improbable supposition may be dismissed, in view of the subsequent evidence by which Plate's statement is confirmed for other species. *P. tridentatus* has been obtained in 54–59 fathoms off Wata Mooli in New South Wales, and between tidemarks in the Kermadec Islands. Oliver, by whom it was collected in the latter locality, found it under stones, and states that it was not common, and that it never uses a spiral shell, but manages to keep on its back a single valve of a bivalve mollusc's shell, or a vacant *Siphonaria* or limpet shell. *P. japonicus* is as yet only reported from the Uraga Channel in Japan, where a single specimen was taken. No information is available as to the depth or nature of the habitat in which it was found, but it is stated to have carried over its back a *Cardium* shell, held in position by the telson of the crab fixed in the umbo.

It appears that *Porcellanopagurus* has a wide distribution in the extra-tropical parts of the Pacific, that each of the several as yet widely separated localities in which it has been taken possesses its own representative of the genus, that it ranges from near high-water mark to a depth of at least 70 fathoms, and that the same species may extend throughout this vertical range. As will be explained later, while the distinctions and affinities of the species are as yet obscure, it seems that the New Zealand, Chilian, and Japanese forms resemble one another more closely than any of them resembles the Australian–Kermadec species. In most respects there is no indication that the habits of the genus differ substantially from those of the ordinary hermit-crabs, but the mode in which the abdomen is protected is unique among Paguridea. Some kind of shallow, non-spiral shell found by the animal is held over the back, covering, to judge by the extent of the egg-mass, the abdomen and the soft part of the cephalothorax. How the shell is kept in position is not clear. That the telson and uropods should be wedged into the umbo suggests itself at once, and this was the case in Balss' specimen, but if, as Oliver states, a limpet shell is sometimes used, the abdominal organs alone will not suffice to retain the protecting structure. It may well be that the hinder two

pairs of legs take part in holding the shell in position. Speculation as to how this may be done, and whether their scaly pads are used for the purpose, does not at present seem likely to be profitable. The eggs, which are of rather small size (·5 mm.) in my specimen, must pass into the deep furrow on the ventral side to which I have already alluded. Thence they must by some means, perhaps by the last pair of legs, be transferred to the back and attached to the hairs of the abdominal limbs. The mass which they then form is moulded to the shape of the covering shell.

The species of *Porcellanopagurus* have as yet been very inadequately described for systematic purposes, with the exception of *P. tridentatus*, of which Whitelegge's account is full and good. This member of the genus differs from the rest more, as it seems at present, than they do from one another. It is smaller, measuring 10 mm. in length, whereas the others probably all reach a length of 15 mm. or more. Its scaly sculpture is finer and its hairs shorter, the lobes of its carapace-edge are less marked, and probably its great chela has a more swollen hand. *P. platei* and *P. japonicus*, to judge by the figures of them which have been published, lack the third cusp of the second carapace-lobe and have the point of the third lobe more forwardly directed than in *P. edwardsi*. *P. japonicus* has a small, sharp spine at the tip of each of the lobes, which is wanting in Lenz's figure of *P. platei*, and the two species differ also in the greater smoothness of the legs of the latter. I have already alluded to the question of the abdominal limbs. The "Terra Nova" specimen agrees pretty well with the descriptions of *P. edwardsi*, but its great chela shows considerable unlikeness to that of the male of Filhol's species as described and figured by Chilton. The scales on the wrist are coarser and less regular, the upper edge of the palm has a well-marked, though irregular, crest of sharp granules or teeth, and along the lower edge there runs a strong, regular line of fine granules. This is evidently also present in *P. japonicus*. Possibly, however, these differences are sexual, and in any case the examination of a series of specimens would be necessary before a new species could be established for the form taken by the "Terra Nova."

Porcellanopagurus is a quite independent case of the phenomenon which may be called "carcinization," and which consists essentially in a reduction of the abdomen of a macrurous crustacean, together with a depression and broadening of its cephalothorax, so that the animal assumes the general habit of body of a crab. To this end, by devious routes, evolution has proceeded throughout the Anomura. In the lower members of most divisions of that tribe the abdomen is a strong and important organ, and the cephalothorax little, if at all, depressed. Their higher members are "crabs." Among the Paguridea, the widening of the region between the bases of the third maxillipeds of the Eupagurinae may perhaps be regarded as a first step in this direction, the broad-backed *Eupagurus splendescens* (Fig. 11) represents a further advance, and besides *Porcellanopagurus* two other members of the sub-family—*Tylaspis*

and *Ostraconotus* *—may fairly be said to have become carcinized. It would be natural to expect that these three genera would be closely related, but, in fact, that is not the case. As regards the mode of reduction of the abdomen, *Tylaspis* and *Ostraconotus* do show some resemblance, though the process has been carried much further in the latter genus than in the former. In both of them the abdomen is straight and slender, and carries its unpaired limbs in the usual position on the ventral side. But when the appendages of the male are regarded it becomes evident that *Tylaspis* belongs to the group of genera which have paired limbs on the forepart of the abdomen (in point of fact it has two pairs), whereas *Ostraconotus* resembles *Eupagurus* in having no paired pleopods at all. The condition of *Porcellanopagurus* in this respect is, as we have seen, at present still a little doubtful, but in any case, with its unique arrangement in the female of three limbs dorsally placed in a slanting row, it is obviously the result of an entirely different process from that which produced either of the others, so that, even if there were any grounds on which it could be supposed to be related to one of them, its carcinization must have occurred independently. The cephalothorax tells the same tale. In *Tylaspis* the soft hinder region found in an ordinary hermit-crab has become inflated and then hardened.† In *Ostraconotus* the whole cephalothorax has taken something of the shape of that of a Galatheid, the hinder region being hardened as in *Tylaspis*. In *Porcellanopagurus*, while the hinder region remains soft, the forepart is quite unlike that of either of the others, as will be gathered from the description I have given of it. In the shape of the legs there is again the widest difference between the three. The sole point of resemblance between them lies in the fact that the last leg of each has the same minute, clumsy, spoon-fingered chela, and this they share with other Eupagurinae. The fourth leg is subchelate in *Porcellanopagurus*; simple, with a wide propodite for the protection of

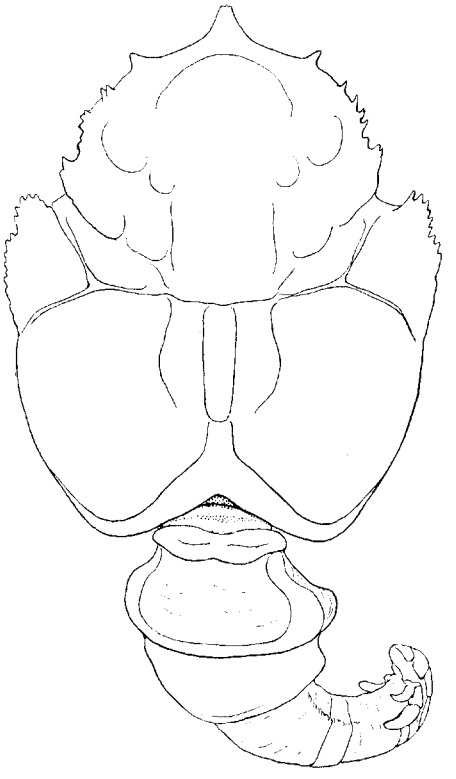


FIG. 11.—*Eupagurus splendescens*: outline dorsal view, × 2½.

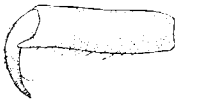


FIG. 12.—End of fourth leg of *Tylaspis*, × 7½.

* For descriptions and figures of these crustaceans, see Henderson, "Challenger" Anomura, p. 81, pl. VIII, fig. 5, 1888 (*Tylaspis*), and Milne-Edwards and Bouvier, Mem. Mus. Harvard, XIV, iii, p. 167, pl. XII, 1893 (*Ostraconotus*).

† This is also the case in *Eupagurus splendescens*.

the eggs, in *Ostraconotus*; simple,* slender, and unusually small in *Tylaspis*. The walking legs (pairs 3 and 2) in *Ostraconotus* have very remarkable flattened dactylopodites that almost suggest a swimming function; in *Tylaspis* they are very long and slender; in *Porcellanopagurus* little modified from those of an ordinary hermit-crab. The chelipeds are of quite different types in all three, as inspection of the figures will show. In short, there is not the least resemblance between the three cases, and when all the facts are known, there is little doubt that it will appear that the crab-like habit of body has arisen in different circumstances, and is made viable by different modes of life, in all of them. I have indicated the explanation of the case of *Porcellanopagurus*. In the other two genera there is great likelihood that the soft abdomen is somehow protected in life. Perhaps, as they are both deep-water animals, it is merely buried in the ooze of the sea floor. Certainly in *Ostraconotus* it is not carried under the cephalothorax, and its unarmoured dorsal side makes it unlikely that this is the case in *Tylaspis*.

Superficially, the abdomen of *Porcellanopagurus* resembles that of *Birgus* more than that of any other pagurid, but the position of its egg-bearing limbs is different, and in any case *Birgus* belongs undoubtedly to the Pagurine stock, while *Porcellanopagurus* and the other genera we have been discussing are as certainly Eupagurine, so that there can be no question of relationship in this case.

The Lithodidae,† with their flat, hard-backed abdomen, deprived of uropods and pressed against the sterna of a very crab-like cephalothorax, present a more advanced case of the carcinization of Paguridea than those we have hitherto mentioned, but there appears no likelihood that any of them are connected with those less highly modified forms. They are, in truth, probably diphyletic, the Lomisinae being derived from primitive, trichobranchiate Pagurinae, and the Lithodinae from Eupagurinae, which differed from *Eupagurus* in keeping a pair of limbs on the first abdominal segment of the female, although they had lost that feature in the male. They must therefore have left the Pagurid stock at a point not very far removed from that at which *Porcellanopagurus* took origin, but there is no possibility of reconciling the two cases in the crucial matter of the course of evolution of the abdomen.

Still less, of course, can the Hippidea, the Porcellanidae, or the true crabs, all primarily symmetrical groups, be supposed to have arisen either from a hermit-crab — or, for that matter, from one another. The descent of the true crabs, indeed, must be traced from a decapod which, though its structural features would bring it under the Anomura, as that group must be defined,‡ was more primitive than any existing member of the tribe.

* At the end of the propodite of the fourth leg of *Tylaspis* (Fig. 12) there is a slender process, but this is not in the plane in which the dactylopodite works, so that there is no chela.

† The evolution of this group is discussed by Bouvier, Ann. Sci. Nat. (7), XVIII, p. 157 (1895).

‡ See Ann. Mag. Nat. Hist. (7), XIX, p. 473 (1907).

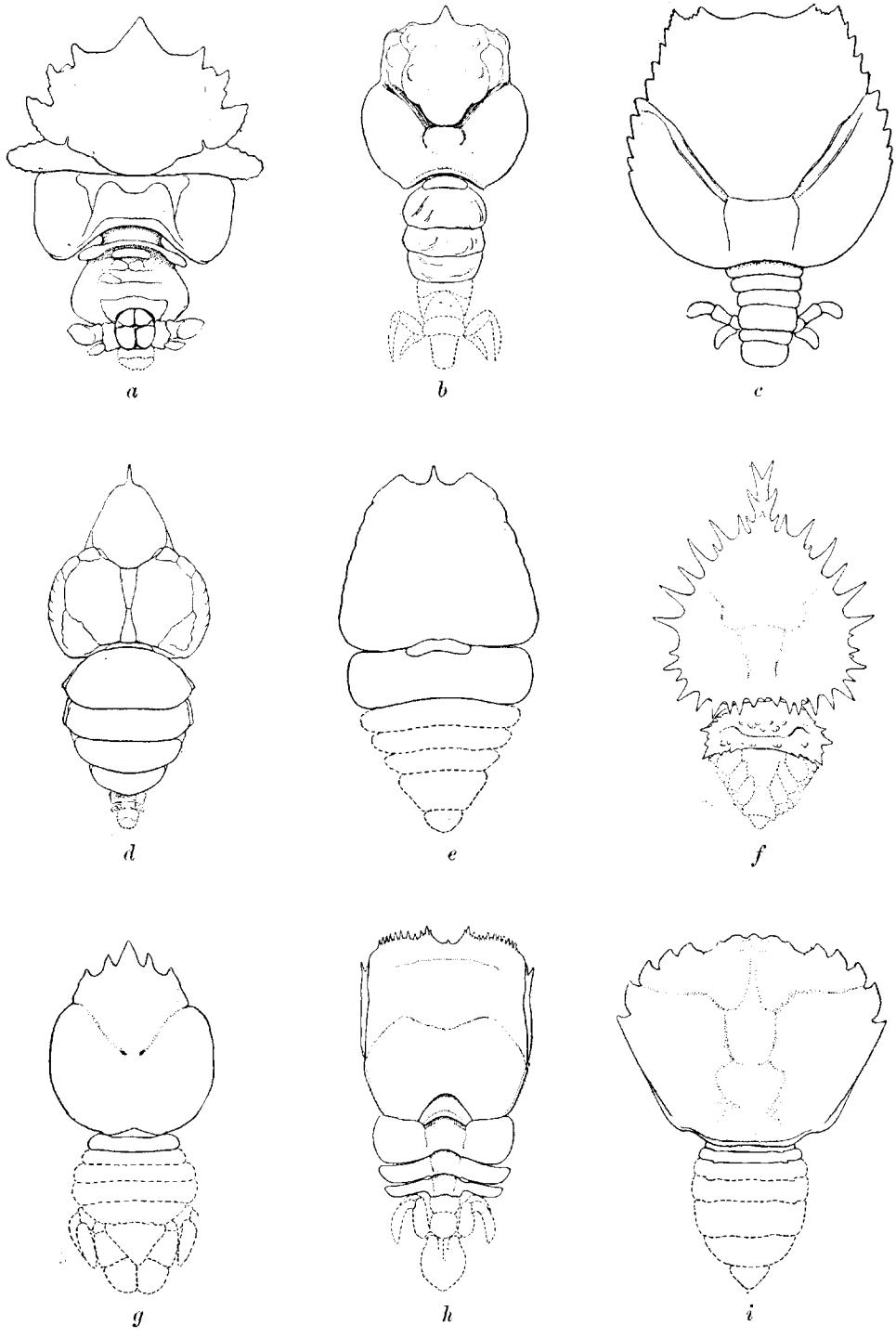


FIG. 13.—Outline dorsal views of the bodies of a series of "crabs"—*a*, *Porcellanopagurus*; *b*, *Tylaspis*; *c*, *Ostraconotus* (after Milne-Edwards); *d*, *Birgus*; *e*, *Lomis*; *f*, *Lithodes*; *g*, *Porcellana*; *h*, *Albunea*; *i*, *Carcinus*. Not drawn to scale. In each case the part indicated by a dotted line is normally carried under the rest of the body.

Discussion of the affinities of *Porcellanopagurus* has brought into view all the various crab-like Crustacea. It is not possible to make such a survey without being struck, on the one hand, by the persistence with which their habit recurs quite independently, and, on the other, by the fact that examples of it are found solely upon one branch of the decapod tree. I have elsewhere* shown reason for regarding the Anomura and the Brachyura as ultimately forming a single stock of the Reptantia. Outside that stock crabs do not occur. Now this fact cannot be attributed to special conditions of life. The Anomura are subject to no common conditions which they do not share with other Reptantia, and, if conditions of life have induced the origin of crabs among Anomura, we are faced with the question why they have not done so among other groups of Reptantia or among such reptant Caridea as many Alpheidae and Pontoniinae. The habit of body of these Macrura does not, upon the face of things, present any greater difficulty to the evolution of something like a crab than that of the hermit-crab which gave rise to *Lithodes*. The conclusion seems inevitable that there is in the constitution of the Anomura a disposition or tendency—only the vaguest terms can be used here—to achieve that special conformation of body which constitutes a crab, and such is not the case with other Decapoda. Whether this tendency be primarily one of morphology or of habits is another question; but seeing that a similar form of body has been reached independently in circumstances which must have needed very different changes in the habits of the animals, it would appear likely that a morphogenetic tendency is the primary factor, but that it can only be realized in the event of the development of suitable habits.

It may be doubted whether the conditions of life play any part other than a purely permissive one in the realization of the tendency to carcinization. The circumstances in which the life of reptant Decapoda is passed cannot be supposed to have in this respect the kind of stringency which dictates, for instance, the special features which are common to the pelagic or to the endoparasitic fauna. An incalculable number of modes of life is open to them, to be taken advantage of according to the special physique of each. The tendency to carcinization, emerging independently from time to time, has led in each case to different habits, but the obligation to the change must have lain always within, not without the organism. The history of the abandonment by hermit-crabs of their habit of living in a shell when they became Lithodidae must have been very different from that of the case in which certain Galatheidea, perhaps when the broadening of the thorax was permitted by the habit of placing their bodies upside down with the flexed abdomen pressed against a stone, became Porcellanidae. The true crabs, again, must have arisen in a different manner, perhaps when a lobster took to backing into shallow crevices with the abdomen doubled under the thorax—a habit which would naturally lead on the one hand

* The subject of the genealogy of the Reptantia is discussed in the article in Gardiner's "Fauna of the Maldives," already quoted above.

to that of the Dromiacea and Dorippidae of carrying their shelter with them by means of the hinder legs, and on the other to that of the free-wandering crabs. But none of these organisms lives in a habitat locally removed from that of other Reptantia. Crabs and lobsters, *Porcellanopagurus* and ordinary hermit-crabs may be taken in the same locality. It is with their habits rather than with their habitats that their structure is correlated. Nor is it possible, in view of the fact that they possess free larvae, and those of the same type, and therefore persistent from their common ancestor, to construct any hypothesis which shall account for their unlikeness by supposing that at some former time they were isolated in unlike conditions of life. They owe their differences to themselves alone.

There are few better instances than those afforded by carcinization of the fact that the organism is, after all, the dominant factor in evolution. What is bred in the bone will come out in the flesh, and Nature is no more able than Man to make silk purses out of sows' ears.

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