On some Modifications of Structure subservient to Respiration in Decapod Crustacea which burrow in Sand; with some remarks on the Utility of Specific Characters in the genus Calappa, and the description of a new species of Albunea.

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With Plates 12—14.

A GOOD deal of scepticism has been expressed in recent years by various writers as to the utility of the more trivial features which distinguish the genera and species of animals from one another. I do not think that such scepticism can excite much surprise if one remembers that the vast majority of " biologists " are almost exclusively engaged in the study of comparative anatomy and embryology. The amount of attention paid to these branches of biology has long been utterly out of proportion to the scant attention devoted to the scientific study of the habits of animals and of the function of the organs and parts composing their bodies. With isolated and noteworthy exceptions, the only naturalists who seriously add to our knowledge of the latter subjects are those who travel in distant countries, and who are thus thrown into close relations with animals in their native haunts. Yet all the time there are thousands of forms living on our own coasts and almost at our very doors of whose detailed habits and life-conditions we know practically nothing. I venture to think that the time has come for consideration whether the

subject of bionomics (in Professor Lankester's sense of the word) should not receive more adequate recognition than it does at present in the biological curriculum of our universities. That such recognition would almost immediately produce effects in a rapid extension of our knowledge is certain; and the subject is invested with so much intrinsic interest, as well as with such important bearings on the problems of evolution, that I believe such recognition would also have the effect of attracting many students to the pursuit of morphology who at present avoid it as a region of mere comparative anatomy.

The present paper contains an account of some modifications of form in certain exotic Crustacea upon which a new light appears to be thrown by my recent researches upon the habits of certain less specialised forms which inhabit British seas (1896, 1897). My thanks are tendered at the outset to Professors Lankester and Poulton for the facilities which they have kindly placed at my disposal during my study of these and numerous other forms of Decapod Crustacea. I am particularly indebted to Professor Lankester for the services of his artist, Mr. Bayzand, from whose beautiful drawings my figures are copied.

1. Calappa granulata, Linn.

The figure (Plate 12, fig. 1) represents a front view of a specimen of this crab as seen when lying flat upon a plane surface.

The genus Calappa is distinguished, among other points, by the extraordinary size and shape of the chelipeds, which in flexion are pressed tightly against the inferior surface of the carapace, and by interlocking with one another form a sort of buckler, the anterior and upper margins of which exactly coincide with the anterior and lateral margins of the crab's carapace. If the "hands" (propodites) of the chelipeds were of the simple form usual among crabs, the anterior part of the buccal apparatus would be visible even when the chelipeds were pressed against the carapace, as is the case, for example, in the species of Atelecyclus or in the species of Matuta

figured in this paper (Plate 12, fig. 1). But in Calappa the buccal apparatus is completely covered by the chelipeds when flexed, owing to the fact that these appendages are here provided with a pair of remarkable cockscomb-like crests on the upper (anterior) margin of the hands (fig. 1, *d*). The margins of these crests are serrated, but otherwise coincide with the outline of the anterior region of the carapace during flexion of the chelipeds.

What is the meaning of this extraordinary opercular apparatus furnished by the chelipeds in this genus, and why do the chelipeds fit so nicely to the carapace during flexion ?

I have found no satisfactory explanation from a study of the literature dealing with the habits of these crabs. Risso (1816, p. 18) states that crabs of this species " inhabit holes in steep rocks 20 to 30 mètres deep. When they are obliged to abandon their usual retreats they withdraw their feet under the carapace, draw their chelipeds together, and let themselves fall like balls to the bottom of the water." He implies, in fact, that the arrangement is an adaptation for defence, similar to the ball-forming habits of the common wood-louse (Oniscus), or of its marine relative Armadillo.

But it is now known that crabs of this genus do not usually live upon rocky, but upon sandy shores, and that they possess markedly fossorial habits (Macgillivray, 1852, p. 102 ; Henderson, 1893 ; Schmidtlein, 1879, pp. 24, 25). I understand that the sand-burrowing habits of this particular species have been frequently observed in the tanks of the Naples aquarium.

The only other suggestion which I have met with as to the function of the chelipeds is contained in Schmidtlein's interesting observations on specimens in the Naples aquarium (l. c., pp. 24, 25). Schmidtlein states that the chelipeds serve " zum Einwühlen und zum Schutze." It would appear from his observations that the crab, if placed in a tank containing a number of hungry fishes, protects from their thievish attacks any morsels of food which it may be engaged in devouring, by hiding them beneath its tightly closing chelipeds. Neither this use, however, nor the act of burrowing, provides any

explanation of the wonderful exactitude with which the chelipeds fit the carapace, nor of certain peculiar relations which they bear to the respiratory channels to be now described.

It is well known that in most, if not in all, of the Oxystome crabs, the exhalant orifice of the respiratory canal is carried to the tip of the snout by a prolongation of the endopodites of the first maxillipeds, either alone as in Calappa (fig. 1, *a, b*), or with the co-operation of the endopodites of the third maxillipeds, as in Matuta (fig. 2, *a, b*).

The inhalant orifice has been shown, on the other hand, by Milne-Edwards to vary considerably in position in the same group of crabs. In most forms it is situated at the base of the chelipeds, between these appendages and the adjacent edge of the branchiostegite ; but in Dorippe,[1] as already shown by Milne-Edwards (1834, i, p. 89), it is situated further forwards, and has the form of a deep emargination of the edge of the pterygostomial portion of the branchiostegite. In Ebalia and the Leucosiidæ in general, the inhalant apertures occupy a position which has hitherto been regarded as unique, being situated beneath the orbits on the outer sides of the exhalant orifice. They lead into a pair of deep afferent gutters excavated in the external wall of the pterygostomial[2] plates. The gutters are converted into closed canals by opercular expansions of the exopodites of the third maxillipeds. In the

[1] Examination of a specimen of this crab has convinced me that in this form also the chelipeds furnish an operculum for the peculiar afferent orifice, but in a way quite different from that described below for Calappa and Matuta.

[2] Not in the prelabial plate, as stated by Milne-Edwards (1839, p. 135) and Dana (1852, p. 62). The language used by the former naturalist is somewhat vague, but Dana at any rate has completely misinterpreted the relations of the afferent gutter to the carapace in this family. I may here draw attention to the fact that in the crab Myctiris platycheles of Australian seas, the edge of the pterygostomial plate also exhibits a deep gutter, which extends from the infra-orbital region to the afferent aperture at the base of the cheliped, and thus closely resembles the afferent canal of the Leucosiidæ. The gutter is clearly subservient to the respiratory function, and interesting results will undoubtedly reward the first careful investigator of the respiratory processes in this aberrant representative of the Catometopa.

remaining Oxystomata the exhalant orifices have been regarded as situated at the base of the chelipeds, i. e. as occupying the normal position.

It is perfectly true that the proximal aperture by which water enters the branchial chamber does occupy this position; but an examination of the crabs Calappa and Matuta has revealed to me that before the water enters the branchial chamber by this aperture, it has in all probability previously traversed certain accessory channels formed by the apposition of the chelipeds to the inferior surface of the carapace.

In the case of Calappa granulata it may be observed that on each side of the median exhalant orifices there exists a well-marked slit-like aperture between the infra-orbital margin of the carapace, and the serrated crests of the apposed chelipeds (fig. 1, e). If one of the chelipeds be now withdrawn from its flexed position, it may be noticed that this slit-like aperture leads downwards and backwards as a well-marked channel to the inhalant aperture at the base of the cheliped. The channel is bounded internally by the ridge-like outer edge of the third maxilliped; its other boundaries are furnished by the approximated surfaces of the inner face of the chelipeds, and the pterygostomial region of the carapace. It is in fact an accessory channel formed by the cheliped; and the inhalant aperture is carried by its means to the tip of the snout in precisely the same way that in the Leucosiidæ the corresponding aperture is carried forward by means of the exopodite of the third maxilliped.

I propose to call this accessory water-channel the "exostegal canal." In its situation on the external side of the pterygostomial portion of the branchiostegite it contrasts with the more primitive branchial canals, which are endostegal in position. It differs from the characteristic afferent canal of the Leucosiidæ in requiring the participation of the chelipeds to complete its external wall, whereas in the Leucosiidæ the third maxillipeds are alone concerned in bringing about the same result.

Attention may now be directed again to fig. 1, which shows

that in Calappa granulata of the Mediterranean, the antero-lateral margins of the carapace are free from denticulations, while the propodial crests of the chelipeds are conspicuously serrated.

On the other hand, it will be remembered that the presence of teeth along the antero-lateral margins of the carapace is a conspicuous feature of a great number of the less specialised types of crab (Cyclometopa), as, for example, in Carcinus and the Portunidæ in general.

Why are these marginal teeth so commonly found among other crabs, while they are absent in Calappa granulata?

I have recently determined (1897) by experiments upon forms such as Atelecyclus and Bathynectes, which possess well-developed marginal teeth, and which adopt sand-burrowing habits, that when these crabs are partially or wholly buried in sand, the chelipeds are approximated to the branchial regions of the carapace, as in Calappa and Matuta, but in such a manner that the marginal teeth of the antero-lateral regions of the carapace exactly overhang the elongated slit-like orifice between chelipeds and carapace. Moreover, during life a current of water can be demonstrated incessantly pouring into this orifice between the marginal teeth of the carapace, whence it traverses the accessory channel between chelipeds and carapace, in order to reach the afferent branchial aperture at the base of the chelipeds.

These types, therefore, possess a pair of functional exostegal canals, which differ from those which I have described in Calappa merely in their greater extent and in their less specialised form. I have, moreover, shown that the marginal teeth which overhang the orifices of these canals act as a "coarse sieve or grating" which prevents the accidental intrusion of foreign bodies, such as grains of sand, into the respiratory canal.

It seems to me to be accordingly probable that the absence of spines and teeth from the antero-lateral margins of the carapace in Calappa granulata is functionally correlated with the restriction of the exostegal orifice in this form to the

infra-orbital region of the carapace, where the teeth on the margin of the propodial crests of the chelipeds have taken over the sieve-function which in more primitive types is discharged by the marginal spines of the carapace.

A similar argument may be employed to explain the absence of marginal teeth on the carapace in Ebalia and the Leucosiidæ in general. In these forms, also, there is a very highly specialised exostegal afferent canal, the aperture of which is restricted to a very narrow area beneath the orbit of the crab. Since the canal is completed in this group by the exopodite of the external maxilliped alone, the respiratory process is independent of chelipeds and carapace margins alike, and there is consequently no necessity for sieve-forming teeth on either of these parts of the body. Whether, however, this independence was maintained throughout the whole ancestral history of the Leucosiidæ is another matter; the considerations advanced in the present paper seem to me to render it probable that the peculiar respiratory adaptations of these forms have also been derived from the more generalised type of adaptation found in the Cyclometopa. In that case the Leucosiidæ have lost the spines on the carapace margins pari passu with the restriction of the area occupied by the exostegal afferent current of water;[1] and the chelipeds have re-acquired their independence simultaneously with the expansion of the third maxillipeds to form an opercular floor to the exostegal gutter. In Calappa, both the chelipeds and the third maxillipeds are concerned in forming the walls of the gutter. It is quite conceivable how the maxillipeds could gradually usurp the whole opercular function to the exclusion of the chelipeds, especially as the specialisation of the Leucosiidæ has clearly been accompanied by a gradual diminution of size, rendering possible

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[1] It is interesting to note that the larger types of Leucosiid appear to have acquired a new set of denticulations at the anterior (infra-orbital) extremity of the narrow afferent gutter. I have observed the presence of such denticulations in species of Ilia, Iphis, and Philyra. Their function is probably the same as that of marginal spines in the Portunids, and of the teeth on the crests of the chelipeds in Calappa.

a continuous relative reduction of the water-supply for the branchiæ, and consequently of the area occupied by the afferent current.

Utility of Specific Characters in the Genus Calappa.

The most recent revision of the genus Calappa, that of Alcock (1896, pp. 140—148), although confined to the nine species found on the Indian coasts, shows that the characters which are employed to discriminate the different species are principally the following:

1. Proportion of length to breadth of carapace.

2. Extent of postero-lateral clypeiform expansions of carapace.

3. Serrations of carapace margins:
    i. Antero-lateral margins.
    ii. Margins of clypeiform expansions.

4. Hairiness of pterygostomial regions.

I make no pretence to be able to explain the possible utility of the varied combinations of these features which the different species of Calappa present, when my only material is the literature upon the genus and some spirit specimens of several species. Nevertheless I venture to point out certain correlations which are not without their significance in this connection.

1. On the whole the more elongated species are restricted to deeper water than the broader species.

2. The clypeiform expansions are largest in the shallow-water species and smallest in those which inhabit deep water; cf. small size of expansions in C. pustulosa (25 fms.), C. Woodmasoni (34 fms.), and C. exanthematosa (100 fms.).

This correlation is confirmed by the fact that the species of the allied genus Mursia, "which is practically Calappa without the wings to the carapace," are found exclusively in the deep sea (e. g. M. bicristimana, 150—400 fms.).

3. The denticulations of the antero-lateral margins I have shown to subserve a sieve-like function in British crabs with an elongated orifice to the exostegal canal. It is probable that

the ancestors of Calappa had a similarly elongated orifice to the exostegal canal, and that the serrations of the antero-lateral margins in the modern species of Calappa are the last relics of the marginal spines which covered the afferent orifices in their ancestors. In C. granulata they have completely disappeared. In support of this contention I may point out that the antero-lateral border of the carapace, which in C. gallus is merely "crenulate" in the adult, is "sharply serrate" in the young (Alcock, 1896, p. 147).

The denticulations of the clypeiform expansions are also known to present a similar process of alteration from youth to maturity (Alcock, l. c. ; Henderson, 1893). No adequate explanation, however, of the function of the clypeiform expansions has been yet put forward. In view of Henderson's remarks concerning the prevalence of protective tints among the arenicolous crabs of the Madras shores (l. c., 1893), the further suggestion may be hazarded that the flattening and expansion of the carapace in the shallow-water species of Calappa may possibly indicate a process of selective assimilation towards the appearance of empty bivalve shells. I am inclined, however, to think that the explanation when found will probably involve something more than mere protective resemblance.

4. Upon the hairiness of the pterygostomial regions I can, I think, throw some positive light. Just as the marginal spines serve as a sieve for fragments of sand and shell, so the pterygostomial hairs serve as a sieve for the finer particles of mud. In Calappa granulata the pterygostomial region forms a triangular area, bounded on all three sides by a dense row of fine hairs—a submarginal series beneath the antero-lateral margin of the carapace, an internal series along the exopodite of the third maxilliped, and a posterior transverse series along the interior edge of the meropodite (arm) of the cheliped. The submarginal series is supplemented by a carpet of fine hairs on the outer side of the branchiostegite, the afferent channel being alone free. In my specimens these hairs are full of mud, indicating that they have efficiently discharged their sieve function during life,

The same remarks apply to my specimens of C. hepatica
from Honolulu and the Sulu Sea. On the other hand, Alcock
states that the pterygostomial region of several species (C.
exanthematosa, gallus, pustulosa, and Woodmasoni)
is characterised by possessing but " few scanty hairs." When
the study of habits is considered worthy of the attention of
men of science, we shall perhaps learn whether or not it is
true, as I venture to believe, that the species with few ptery-
gostomial hairs live in cleaner ground than those having the
outer part of the pterygostomial regions " densely hairy."
That Calappæ do inhabit mud, as well as sand, is certain
from Macgillivray's remark (1852, vol. i, p. 102) that on a
coral reef off the coast of Queensland containing all varieties
of coral, mud and sand, " smooth Calappæ seek refuge . . . .
in the shallow muddy pools . . . . by burrowing beneath the
surface."

2. Matuta picta,[1] Miers.

The figure (Plate 13, fig. 2) which I give of this species
has been carefully drawn by Mr. Bayzand from a specimen
(an adult male) brought back by Mr. G. C. Bourne from Diego
Garcia in 1892. It represents the crab lying in a somewhat
inclined position, the anterior part of the body being elevated
so as to display more effectually the infra-orbital and ptery-
gostomial regions of the carapace.

The genus Matuta is closely related to Calappa, but in
the form of the carapace and chelipeds is less specialised than
the latter type. In the broad swimming plates of the hind-
most pair of thoracic legs, in the obsolescent teeth on the
antero-lateral margins of the carapace, and in the great pair of
epibranchial spines, Matuta betrays obvious signs of deriva-
tion from an early progenitor of the Portunid type, such as

[1] My specimen is identical with M. picta of Miers (1877) and the
synonymous M. lunaris of Leach (1817). It would be referable to the
more comprehensive M. Banksii of Alcock's recent revision (1896), were it
not for the fact that the " posterior granulated ridge " is prolonged as far as
the epibranchial spine, on the posterior border of which it dies away. Alcock's
distinctions under this head are far from satisfactory.

Lupa or Callinectes. All the species of this genus are remarkably specialised for burrowing in sand, as indicated by the great compression of the four hindmost thoracic pairs of legs, and by the spade-like modification of their terminal joints (cf. Rumphius, 1705, and Krauss, 1843).

The chelipeds are curved and moulded to fit the sides of the carapace during flexion, exactly as in the genus Atelecyclus. They are destitute of the cockscomb-like crests which furnish such a characteristic feature of the genus Calappa. The anterior part of the buccal apparatus is consequently exposed even during flexion of the chelipeds. The protection of the mouth parts is, however, ensured by the forward prolongation of the external maxillipeds (fig. 2, b), a feature which is not to be observed in the genus Calappa, but which is a marked characteristic of the allied Leucosiidæ.

If I am right in my interpretations, the exostegal canal in this crab has a most extraordinary course. The orbits, in which the eye-stalks are retractile, have the form of a pair of stony cups. The outer and inferior angle of the orbit is, however, incomplete, and its cavity is continued downwards and outwards over the pterygostomial regions by a deep semicylindrical gutter (fig. 2, e). This gutter is converted into a tube by two dense rows of hairs which arise from the inner and outer edges of the gutter, and by their interdigitation beneath the cavity of the gutter furnish it with a complete hairy floor. So closely are the hairs set to one another, and so intimately do they interlock, that upon a cursory examination the hairy nature of the floor of the orbital gutter is not at first suspected, and Hilgendorf actually figures the gutter (1869, fig. 2) as a completely tubular passage excavated in the substance of the thick calcareous wall of the carapace.

The orbital gutter, as soon as it loses its tubular appearance, turns obliquely outwards and backwards (fig. 2, f) until it is lost in a thick carpet of hairs, which is especially well developed in front of and to the outer side of the afferent aperture at the base of the chelipeds, but which is also continued backwards along the whole inferior edge of the branchiostegite.

The chelipeds are smooth and concave on their inner face, and are capable of being closely apposed to the inferior wall of the carapace, so that they cover the afferent aperture and the whole carpet of hairs in this region, as is well shown in the figure here provided. Their upper margins do not coincide with the edge of the carapace, as they do in Calappa, but during flexion appear to come as far forwards as the posterior aperture of the orbital gutter.

Water clearly seems to enter the orbits, travelling backwards through the orbital gutter into the carpet of hairs (which, when the chelipeds are flexed, must furnish a most efficient sieve for the finer particles of mud and sand), through which it no doubt eventually makes its way to the afferent aperture at the base of the chelipeds.

This aperture is also furnished with a special hair-sieve of its own, since the edge of the branchiostegite which forms its anterior wall is fringed with a special line of stiff hairs, and there is a corresponding series of hairs on the opposing surface of the basal joint of the cheliped. When the cheliped is apposed to the carapace, the two sets of hairs interdigitate and constitute a sieve completely covering the aperture. A similar arrangement exists in Calappa also, but in the latter form the basal portion of the epipodite of the third maxilliped furnishes a much more obvious operculum to the aperture than is the case in Matuta.

The remarkable course of the exostegal canal in Matuta, with the restriction of its principal aperture to the cavity of the orbit, appears explicable to me only on the view which I have set forth in the case of Calappa and the Leucosiidæ, viz. that the common ancestor of all three types possessed a continuous waterway along the whole extent of the antero-lateral margins of the carapace to the base of the chelipeds; that the antero-lateral margins were denticulated; and that a process of restriction of the inhalant orifice began, by which the closure of the whole inhalant gap between chelipeds and carapace became gradually effected, except in the infra-orbital region. This process of restriction was effected as a con-

tinuous process of adaptation to a sand-burrowing existence
The marginal denticulations becoming useless, gradually lost
their sharp and prominent form, until they assumed the blunt,
irregular, variable and obsolescent character which they ex-
hibit in the modern species of Matuta. The great epibran-
chial spine is in itself evidence of the validity of this view, for
it clearly represents the posterior spine of the antero-lateral
series in such genera as Bathynectes, Callinectes, and
Lupa. The same spine is again met with in the allied but
less specialised genus Mursia; and a comparison of M.
armata (De Haan, 1833, pl. xix, fig. 2) with M. cristata
(Milne-Edwards, ' Règne Animal,' pl. xiii, fig. 1) confirms the
views I have put forward. In M. armata the epibranchial
spine is longer, while the antero-lateral teeth are absent; in
M. cristata both are present, but the epibranchial spine is
less elaborately specialised and still forms part of the marginal
series.

The reason for the great elaboration of this epibranchial
spine in Mursia armata and Matuta is less clear, and can
scarcely be found without special study of the living animal.
In its initial stage, however, as presented in Bathynectes
longipes, I have every reason to believe it functions as
a stay or barrier to the cheliped during apposition to the
carapace, thus mechanically maintaining the arm of the cheliped
in the right position for the closure of the exostegal canal
(1897, p. 400). It seems to discharge this function also in
Matuta picta, but I am doubtful whether this function is
the only one which it discharges in cases where it is so highly
developed.[1]

I make no suggestions as to the utility of specific characters
in this genus, owing to the fact that the species of Matuta,

[1] Krauss (1843) remarks on the frequency of similar spines in arenicolous
animals of various groups, e. g. fishes and molluscs, as well as crabs. One
function may be to protect the crab from the danger of forcible dislodgment
from the sand by wave-currents, as ably maintained by my friend Mr. Hunt in
the case of the spiny species of Cardium (' Proc. Linn. Soc.,' xviii, "Zool.,"
p. 269).

and the range of variability in the different species, are as yet very inadequately determined. I would only remark that the beaded ridge which bounds the posterior and postero-lateral borders of the carapace, and which frequently bears a pair of tubercles in its course (see fig. 2), is clearly the homologue of the posterior dentated ridges of Calappa and Hepatus, and is probably degenerate in character. If this is true, the variations presented by this ridge during the stages of its disappearance are little likely to furnish the satisfactory characters for specific discrimination which some systematists have ascribed to them.

3. Albunea symnista, microps, and scutelloides, n. sp.

The problem of a pure water-supply in the case of sand-burrowing crabs has been solved in certain instances, as I have elsewhere shown (1896, 1897) in a manner even more original than that which I have illustrated for Calappa and Matuta. In the forms to which I refer (Corystes cassivelaunus, Portumnus nasutus, and Atelecyclus heterodon of the British coasts) the normal respiratory current of water—the constancy of whose direction has been an accepted maxim among naturalists since Milne-Edwards' classical elucidation of the process nearly sixty years ago,—the normal current is actually reversed in direction, and flows through the branchial chamber from before backwards, instead of from behind forwards. In Corystes cassivelaunus I have shown that it enters the chamber through a long tube formed by the apposition of the second antennæ, whose double rows of hairs interdigitate with one another in a most effective manner (Plate 14, fig. 3).

I now show that the structure of the first antennæ in the genus Albunea is strikingly similar to that of the second antennæ in Corystes, and that the tube formed by their apposition has the same relations to the branchial chamber as in Corystes. The species of Albunea are known to have sand-burrowing habits of life, so that in all probability a reversal of the branchial current takes place in this genus as in Corystes.

Figs. 3 *a* and 3 *b* on Plate 13 illustrate the arrangement of parts in Corystes cassivelaunus, for a detailed description of which I refer to my paper on that animal (1896). The only point that I need emphasise here is that the tube is formed by the outer or second antennæ, the first antennæ being situated in the interior of the tube.

Figs. 4 *a* and 4 *b* illustrate the structure of a Madras specimen of Albunea symnista, Fabr., which belongs to the Hippidea. The systematic position of this group of Crustacea is discussed by Miers (1879). The various naturalists who have previously examined specimens of this genus have all failed to recognise the fact that the hairs on the antennules are arranged along two longitudinal lines, and that they are directed towards the axial line of the body. The figures which have been published are all ludicrously conventional in this respect, and represent the irregularly hairy antennæ of a Palinurus less incorrectly than they do the antennules of an Albunea (see Milne-Edwards, 'Règne Animal,' pl. 42, fig. 3; 'Crustacés,' pl. 21, fig. 9; Miers, 1879, pl. 5; Henderson, 1893, pl. xxxviii). The converging double rows of hairs interdigitate naturally to form a tube, as I have recognised in A. symnista, Fabr. (Pl. 14, fig. 4), Albunea microps, Miers, and another Albunoid form (Pl. 14, fig. 5) which I have not been able to identify with any described species, and which I here name Albunea scutelloides, n. sp.

The antennular tube expands at its base into a prostomial chamber, as does the antennal tube of Corystes. In the latter case the floor of this chamber is formed by the third maxillipeds (fig. 3 *b*); but in Albunea it is formed by the broadly ovate terminal lobes of the endopodites of the first maxillipeds (fig. 4 *b*)—the homologues of the organs which in Calappa form the opercular floor of the exhalant passages (fig. 1 *b*). The prostomial chamber communicates on each side by a wide aperture with the branchial chamber. The channels of communication are bounded externally and ventrally by large lamellate expansions of the basal joints of the first and

second antennæ. The scaphognathite is of unusual size; both in A. symnista and in A. microps its anterior edge touches the basal joint of the antennules, while its posterior extremity is level with the base of the second thoracic leg. It is, in fact, half as long as the body (excluding the antennules) in the attitude represented in fig. 4 a.

In Corystes the roof of the prostomial chamber is largely furnished by the projecting frontal area of that animal (fig. 3 a). In Albunea, however, the frontal area is emarginated (fig. 4 a), and the roof of the prostomial chamber is furnished by the eye-peduncles, whose flattened scale-like form, varying in shape in the different species, is one of the most characteristic features of the genus (figs. 4 a and 5).

In Corystes the three stout basal joints of each antenna are disposed at right angles to one another in the vertical plane, bringing about a characteristic bend in the basal part of the antenna (figs. 3 a and 3 b), a feature which is functionally correlated with the reversal of the branchial current and its course through the antennal tube.

A precisely similar arrangement is recognisable in the species of Albunea, but in connection with the antennules instead of the antennæ (figs. 4 a and 5). In A. symnista (fig. 4 a) the joints are disposed at right angles to one another, as in Corystes cassivelaunus; but in A. scutelloides (fig. 5) the distal joint is pressed much further back than in either of these forms, thereby greatly reducing the angles of inclination. This difference may be readily seen to be correlated with the fact that in the latter form the part played by the frontal region in covering the prostomial chamber is very much less than in Corystes cassivelaunus or A. symnista. In Corystes the roof is provided by the prominent frontal area (fig. 3 a); in A. symnista by the apposed plate-like optic peduncles (fig. 4 a), but in A. scutelloides the optic plates are so small and short that they scarcely project from the orbital emarginations. The increased backward bend of the antennules in the latter species compensates for this deficiency.

In the figure of A. scutelloides (fig. 5) the antennules

are represented after being pulled forwards to some extent, in order to show the cavity of the prostomial chamber beneath and behind them.

Enough has, I think, been said to justify my view that many of the characters which distinguish the species of Albunea, both from one another and from their allies, are correlated with the function of respiration under arenicolous conditions of life. The verification of this inference must rest with those who have the opportunity of examining these animals alive under the proper conditions.

It must in any event, however, remain clear that the great problems which Darwin left us as his heritage, after so greatly illuminating them, are not to be solved by the exclusively morphographical researches which occupy the time and zeal of the great majority of naturalists to-day. Even in the best of hands such researches are capable, as I have shown from the history of the forms discussed in this paper, of obscuring even the simple facts of structure which they profess to elucidate; while the study of the functional relations of parts, side by side with the anatomical elucidation of the parts themselves, provides not only the data for generalisations of intrinsic importance, but assistance of an invaluable character in the field of morphological criticism.

APPENDIX.

DESCRIPTION OF THE NEW SPECIES OF ALBUNEA (A. SCU-TELLOIDES, N. SP.) MENTIONED IN THE FOREGOING PAPER.

By Walter Garstang, M.A.

With Plate 14, fig. 5.

This new species of Albunea closely resembles Albunea microps, Miers, in size, colour (in spirit) and shape. I found a single male individual among a number (placed at my dis-

posal by Professor Lankester) of Albunea microps (both ♂
and ♀) in the Oxford Museum, labelled "Sulu Sea, H.M.S.
Nassau, 1871–2," and the accompanying description is derived
from an examination of this single specimen.[1]

Length of carapace, 9 mm. Sculpture on back closely
resembling that in A. microps, but readily distinguishable by
the following points :—The principal M-shaped transverse
line across the middle of the carapace is relatively more con-
spicuous in A. scutelloides, and the remaining transverse
interrupted step-like ridges are relatively much more nu-
merous (quite twice as numerous). They are consequently
more closely set and give the carapace a still rougher appear-
ance than in A. microps. Under a lens the ridges are seen
to have a minutely tuberculate or beaded character, which is
not seen in specimens of A. microps.

Mid-frontal area emarginated, broadly concave, but the
emargination is wider than in A. microps, and therefore
appears less deep; provided with a median tooth, as in A.
microps, and a pair of small admedian teeth, as in the same
species. Antero-lateral margin (from the admedian tooth to
the antero-external angle of the carapace) divided into two
approximately equal halves by a sublateral prominence; each
half presents a slightly concave curvature. The inner and
outer halves of the antero-lateral margin correspond with the
bases of the antennules and antennæ respectively, and may
therefore be termed the antennular and antennal curves.
Antero-lateral margin without teeth, but with twelve or thir-
teen minute close-set tubercles distributed along the anten-
nular curve and around the border of the sublateral promi-
nence (thus differing from A. microps).

Antennules long ; each provided with two rows of hairs
which interdigitate with those of the other. Antennules pre-
senting a marked double bend at their basal joints.

Antennæ provided with an accessory joint (aciculus), as
long as the joint of the flagellum to which it is approximated,

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[1] The type specimen of this species will be deposited by Professor Lankes-
ter in the British Museum.

i. e. of the same relative length as in A. symnista and A. microps.

Third maxillipeds. The carpal lobe is not produced beyond half the length of the propodite (in this agreeing with A. microps).

Optic peduncles scale-like, elliptical, broader than long, presenting a deep emargination at their antero-internal angles which lodges the cornea. The peduncles occupy the lateral compartments of the median emargination of the frontal area, which may accordingly be termed the orbital emargination.

Telson in the ♂ somewhat like that of A. microps, but more elongated and slender, the broadest part being a little nearer the base of the telson, and the sides more distinctly concave. No transverse rows of hairs on back of telson like those in A. microps and A. Guérinii; but a double ad-median longitudinal series, and a group at each of the basal angles.

This new species approaches in certain features the species Albunea scutellata, described by Milne-Edwards (1834, ii, p. 204, pl. 21, figs. 9—13), which, with two other forms (venusta and myops), has been referred by Stimpson to a new genus, Lepidops (1858, p. 230; Miers, 1879, p. 231). These features are—(1) the absence of frontal denticulations; (2) the broad, scale-like optic plates. In fact, were it not for his remark concerning the truncation of the optic plates, Milne-Edwards' short description would be perfectly applicable to the present species. His figures, however, are not appli-cable. In his figure the carapace breadth is greatest in front; in my specimen it is greatest across the middle (as in A. microps). He figures no accessory joint to the antenna; and if the truncated plates in front of the carapace represent the optic plates, as his account implies, the possible identity of the two forms is altogether precluded. Moreover, there is no projecting lobe at the base of the sickle-shaped dacty-lopodite of the third pair of thoracic legs in my specimen, while such a lobe is clearly indicated in his figure.

Dana's description of A. scutellata (1852, i, p. 406) is

also inapplicable in regard to the form of the frontal margin. My figure (Pl. 14, fig. 5) does not indicate the median orbital emargination as deep as is actually the case.

Stimpson's descriptions (1858, p. 230) of the genera Albunæa (sic) and Lepidopa (sic) render the identity of the two forms still more improbable, owing to the characters of the antennal aciculum and of the carpal lobe of the third maxillipeds which I have described for my specimen. These characters are such as also exist in the species of the restricted genus Albunea, from which Stimpson removes the species scutellata. On these grounds, therefore, I refer my specimen to a new species of Albunea, distinguishable from the other known species by the character of the carapace-sculpture, frontal margin, optic plates, and telson.

On the other hand, Milne-Edwards' figure is clearly bad (note the absence of any distinction between the abdominal tergites and their lateral lamellate expansions); and it is possible that if his (or Desmarest's) specimens could be re-examined, some, if not all, the distinctions upon which I have relied would vanish. If the form of the ocular plates is determined in this genus, as I have rendered probable in the preceding paper, by their opercular relations to the prostomial chamber; and if the emarginations of the frontal area are functionally correlated with the play of the optic peduncles, antennules, and antennæ, as appears to me to be the case after examination of three species of Albunea; then it is perfectly clear that Milne-Edwards' fig. 9 does not correctly represent his specimen in these respects.

BIBLIOGRAPHY.

ALCOCK, A. (1896).—" Materials for a Carcinological Fauna of India " No. 2, "The Brachyura oxystoma," 'Journ. Asiatic Soc. Bengal,' lxv, pt. ii, No. 2, pp. 134—296.

DANA, J. D. (1852).—" Crustacea," 'U.S. Exploring Expedition, 1838—1842,' vol. xiii.

GARSTANG, W. (1896).—"The Habits and Respiratory Mechanism of Corystes cassivelaunus," 'Journ. Mar. Biol. Ass.,' iv, No. 3, pp. 223—232.

GARSTANG, W. (1896).—"On the Function of certain Diagnostic Characters of Decapod Crustacea," 'Report Brit. Ass.,' Liverpool Meeting, pp. 828—830.

GARSTANG, W. (1897).—"The Function of Antero-lateral Denticulations of the Carapace in Sand-burrowing Crabs," 'Journ. Mar. Biol. Ass.,' iv, No. 4, pp. 396—401.

GARSTANG, W. (1897).—"The Systematic Features, Habits, and Respiratory Phenomena of Portumnus nasutus" (Latreille), 'Journ. Mar. Biol. Ass.,' iv, No. 4, pp. 402—407.

HAAN, W. DE (1850).—"Crustacea," Siebold's 'Fauna Japonica.'

HENDERSON (1893).—"A Contribution to Indian Carcinology," 'Trans. Linn. Soc.' (2), v, "Zool.," pp. 325—458.

HILGENDORF (1869).—"Crustaceen," Baron C. C. von der Decken's 'Reisen in Ost-Africa,' iii, pp. 93, 94, Taf. 3, fig. 2.

KRAUSS, F. (1843).—'Die Südafricanische Crustaceen,' Stuttgart, p. 16.

LEACH, W. E. (1817).—"On the Characters of Matuta, with Descriptions of the Species (lunaris, Peronii, Lesuerii, Banksii)," 'Zool. Miscellany,' iii, pp. 12—14, Tab. 127.

MACGILLIVRAY (1852).—'Narrative of the Voyage of H.M.S. "Rattle-snake,"' vol. i, p. 102.

MAN, J. G. DE (1881).—"Remarks on the Species of Matuta," 'Notes from the Leyden Museum,' iii, pp. 109—120.

MIERS, E. J. (1877).—"Notes upon the Oxystomatous Crustacea," 'Trans. Linn. Soc. Zool.,' (2) i, pls. 39, 40.

MIERS, W. J. (1879).—"Revision of the Hippidea," 'Journ. Linn. Soc.,' xiv.

MILNE-EDWARDS, H. (1834).—'Histoire Nat. des Crustacés,' 3 vols.

MILNE-EDWARDS, H. (1839).—"Recherches sur le Mécanisme de la Respiration chez les Crustacés," 'Ann. Sci. Nat.' (2), xi, pp. 129—142.

MILNE-EDWARDS, H. (1849).—'Le Règne Animal, Crustacés.'

RISSO (1816).—'Hist. Nat. des Crustacés des Environs de Nice.'

RUMPHIUS, G. E. (1705).—'D'Amboinische Rariteitkamer,' Amsterdam, pp. 11, 12.

SCHMIDTLEIN, R. (1879).—"Beobachtungen über die Lebensweise einiger Seethiere innerhalb der Aquarien der zoologischen Station," 'Mitth. Zool. Stat. Neapel,' i.

STIMPSON, W. (1858).—"Prodromus descriptionis animalium evertebratorum, &c.," pars vii, pp. 225—252, 'Proc. Acad. Nat. Sci.,' Philadelphia.

EXPLANATION OF PLATES 12—14,

Illustrating Mr. W. Garstang's paper on " Some Modifications of Structure subservient to Respiration in Decapod Crustacea."

PLATE 12.

Fig. 1.—Calappa granulata, Fabr., from the Mediterranean. Front view, showing the closure of the chelipeds beneath the carapace and the respiratory orifices above them. *a.* Exhalant orifice. *b.* Branch of endopodite of first maxilliped, forming opercular floor of exhalant canal. *c.* Antero-lateral margin of carapace. *d.* Dentated crest on propodite of cheliped. *e.* Inhalant orifice of exostegal canal. *f.* Second antenna, forming part of orbital wall.

PLATE 13.

Fig. 2.—Matuta picta, Miers, from Diego Garcia. View from above, the anterior part of the crab's body being elevated to display the buccal region. *a.* Exhalant orifice. *b.* Third maxilliped. *c.* Carpet of hairs on pterygostomial plate. *d.* Propodite of cheliped. *e.* Orbital gutter, having a ventral floor of interlocking hairs. *f.* Postero-lateral extension of orbital gutter on pterygostomial plate.

PLATE 14.

Fig. 3 *a.*—Corystes cassivelaunus from Plymouth. Frontal area, showing tube formed by second antennæ (dorsal view).

Fig. 3 *b.*—Corystes cassivelaunus from Plymouth. Ventral view, showing floor of prostomial chamber.

Fig. 4 *a.*—Albunea symnista, Fabr., ♀, from Madras. Dorsal view, showing tube formed by first antennæ, and the ocular plates which form the roof of the prostomial chamber.

Fig. 4 *b.*—Albunea symnista, ♀, from Madras. Ventral view, showing basal part of antennular tube, lamellate terminal expansions of first maxillipeds, and the pediform second and third maxillipeds.

Fig. 5.—Albunea scutelloides, n. sp., ♂, from Sulu Sea (Oxford Museum). Dorsal view. The antennules are pulled slightly forwards, showing the prostomial chamber beneath. Also showing the double bend of the basal joints of antennules and the broad elliptical optic plates, and eye-spots.

N.B.—The figure does not represent the median emargination as deep as is actually the case. The small admedian teeth, situated on the outer sides of the optic plates, are also inadvertently omitted.
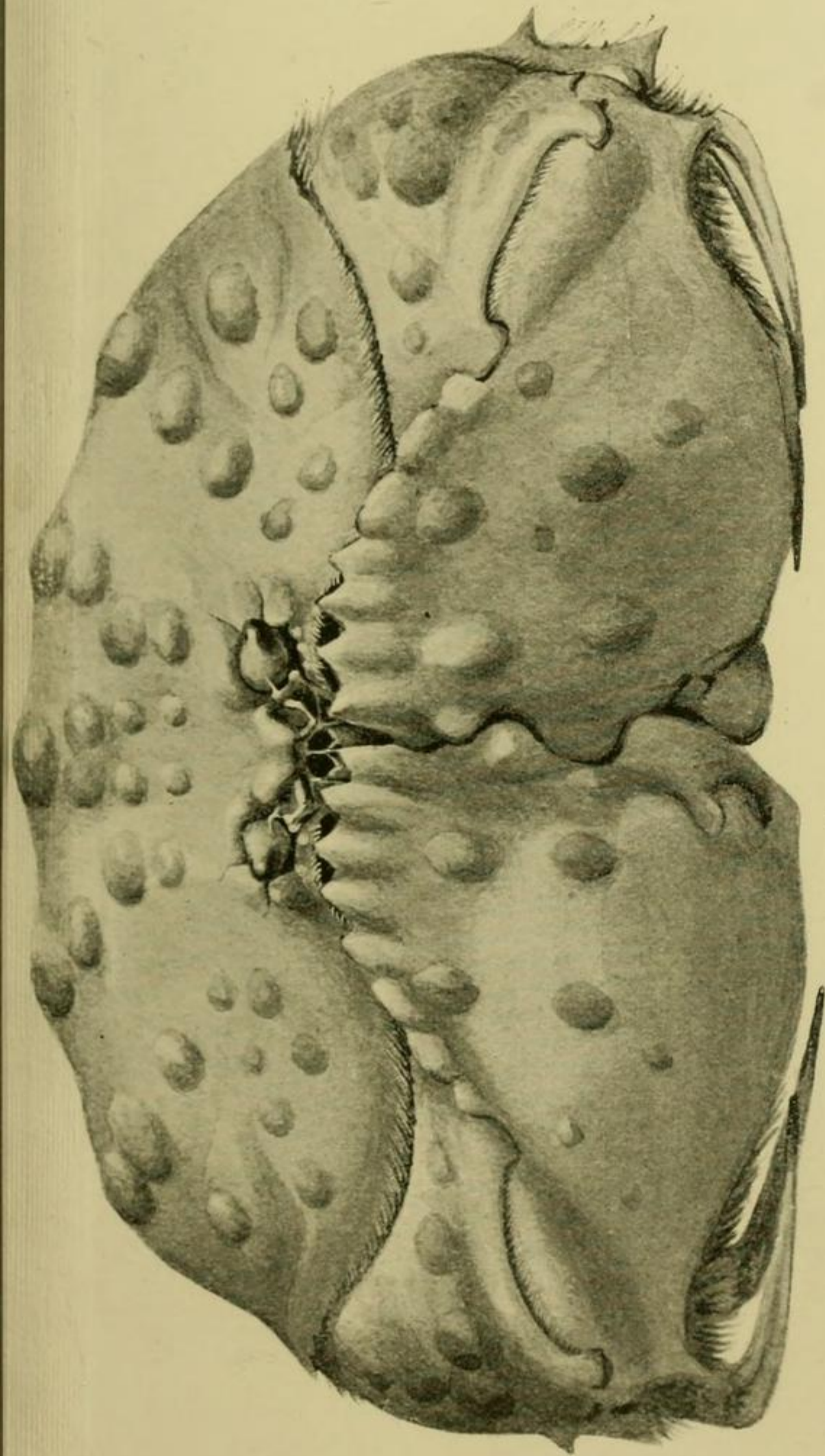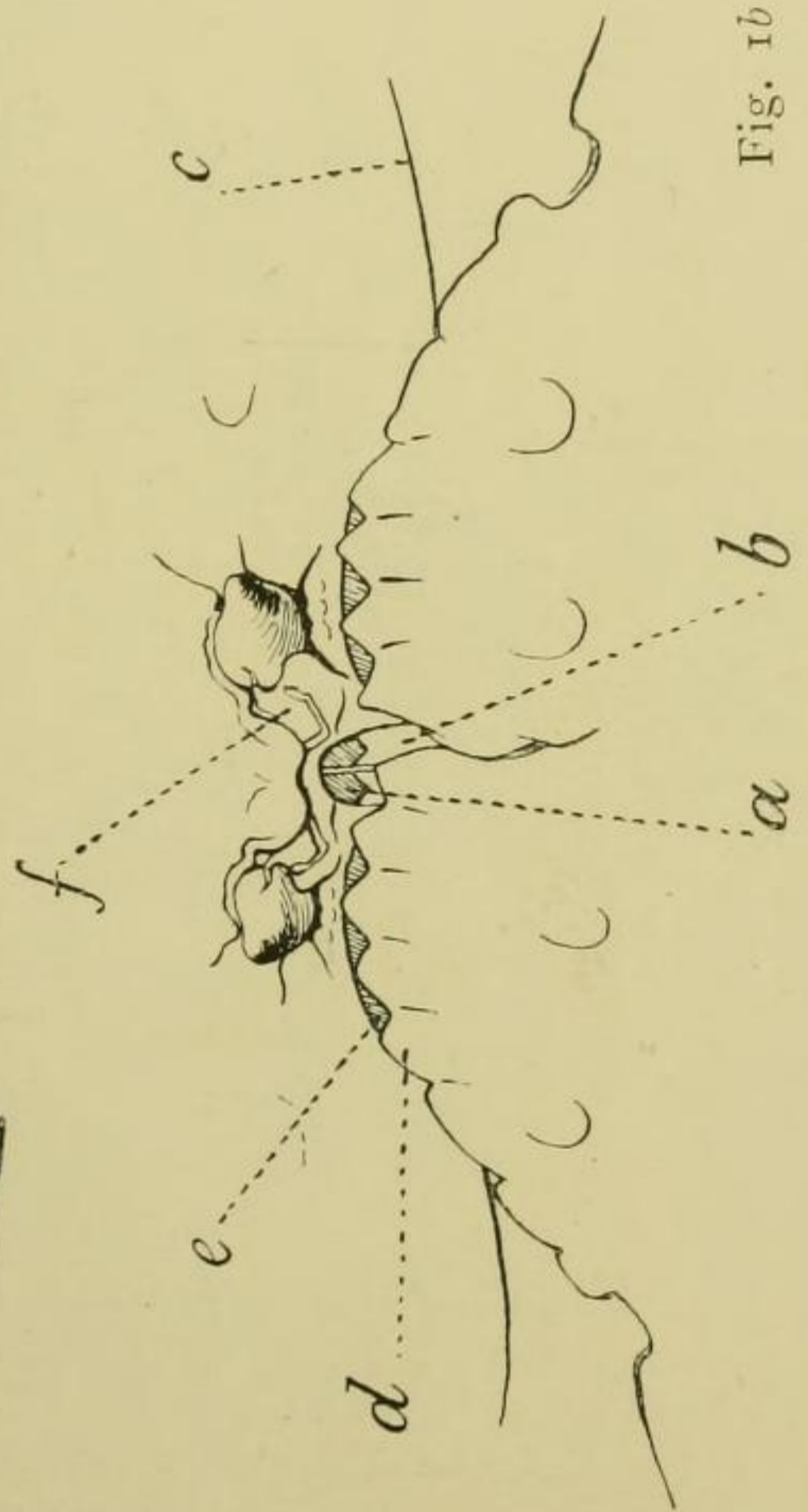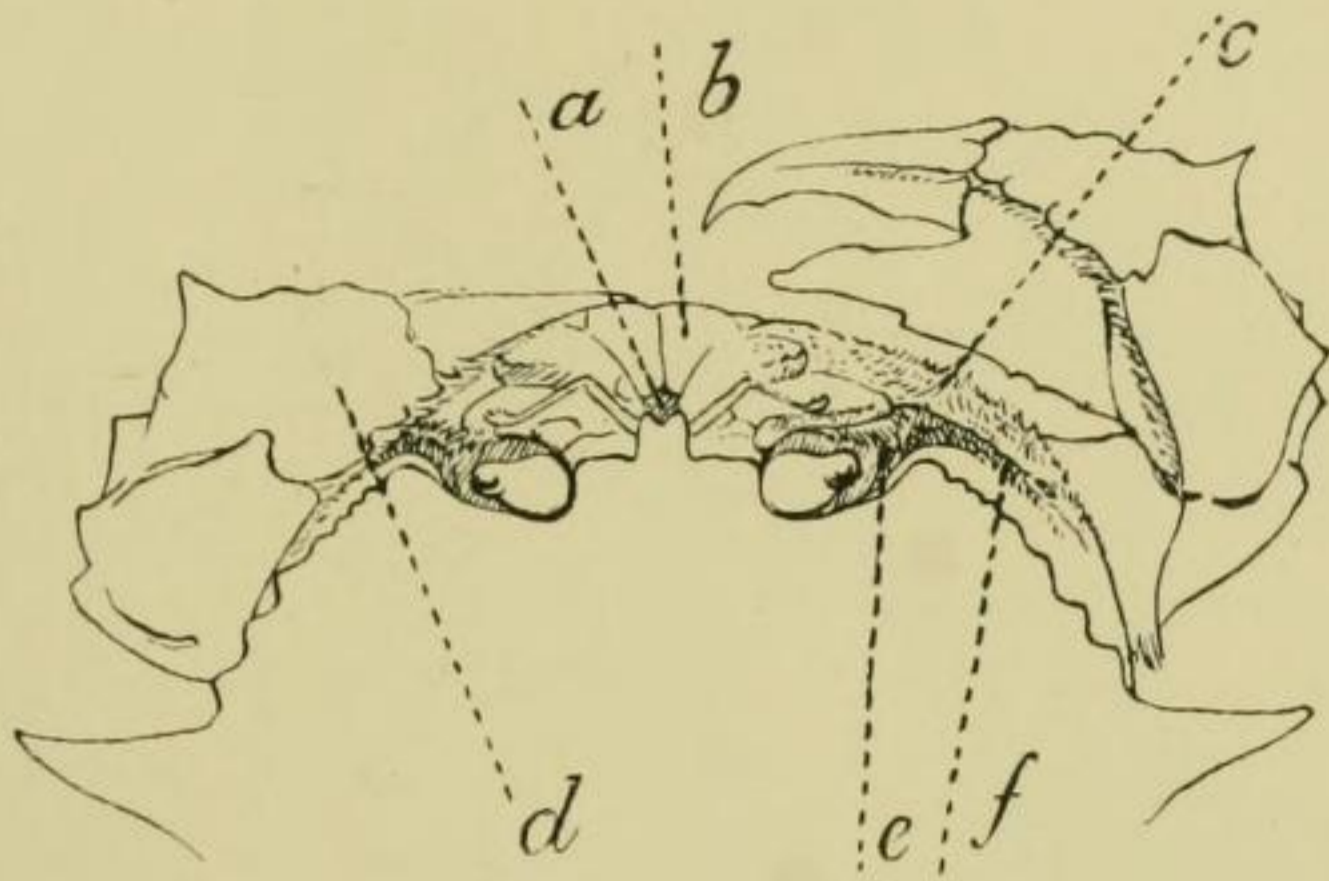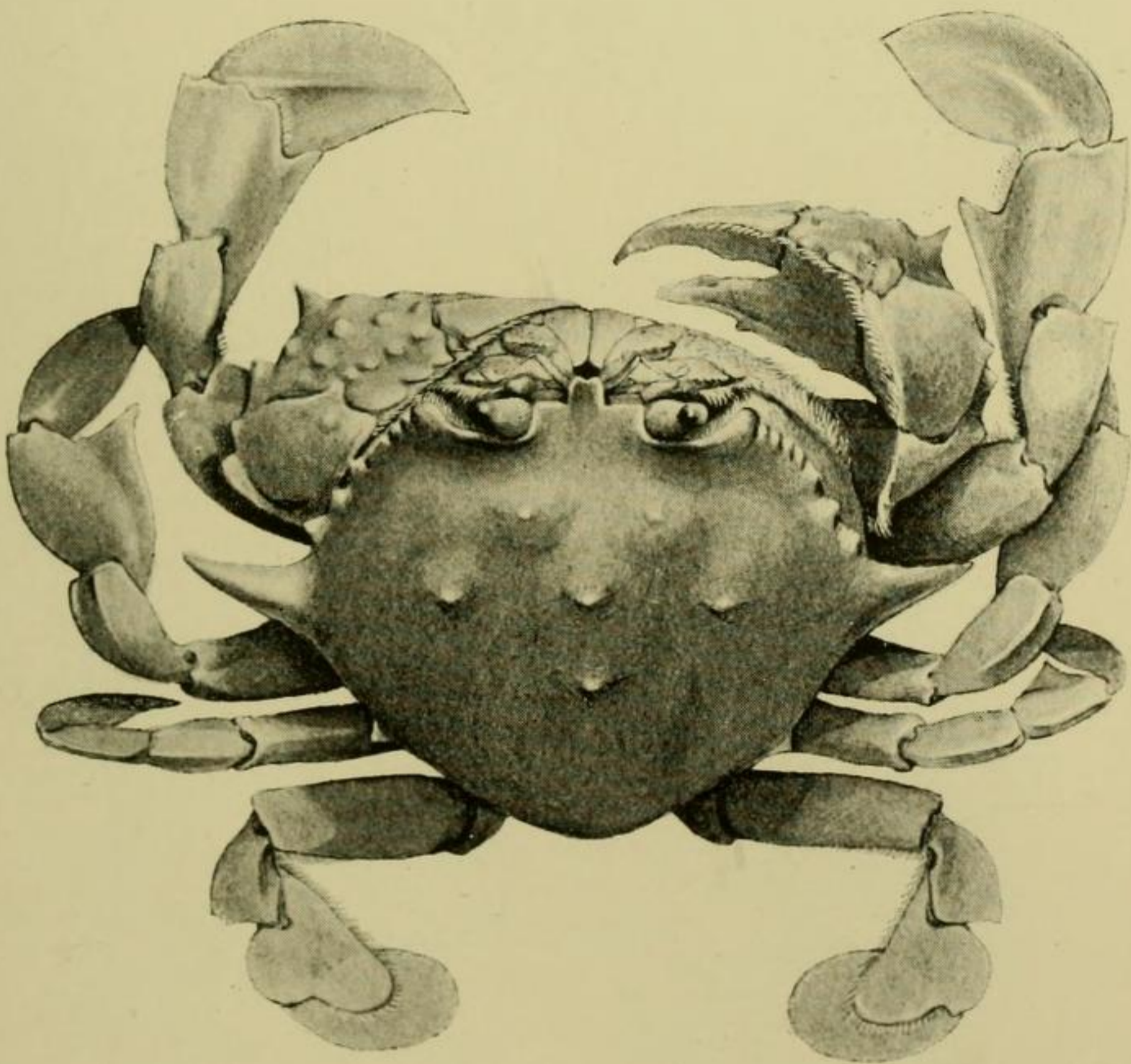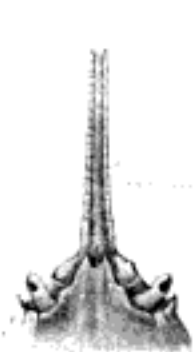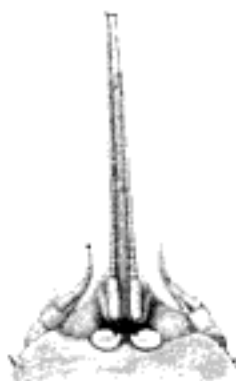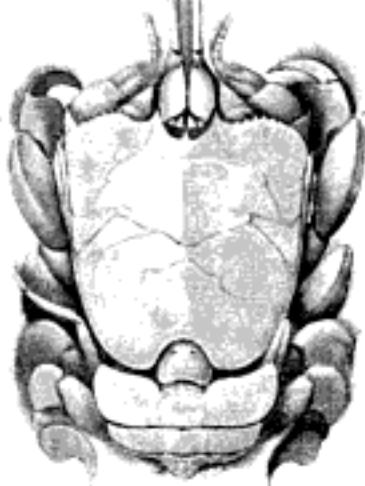
Fig. 1a

Fig. 1b

Fig. *2b*

Fig. *2a*

Fig. 3a

Fig. 5

Fig. 3b

Fig. 4a

Fig. 4b