

MARINE CRUSTACEANS.

I. ON VARIETIES. II. PORTUNIDAE.

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(With Text-figures 35—38.)

INTRODUCTION.

THE collection of Crustaceans from the Island of Minikoi¹ and the Maldive Group has been divided, for purposes of description and comment, into two halves of widely different biological interest. Of these the first, containing the land forms, has been reported upon in Part I. of this publication. The second, containing the marine forms, is too bulky to be described in a single article, and has accordingly been divided into a series of sections which will be dealt with by instalments, of which these pages form the first. Most of the sections will be undertaken by the writer of this introduction, but the collection of prawns of the family Alpheidae is in the hands of Professor Couzière, of Paris.

In reporting on such a collection as this, various questions of a general nature arise, such as that of the crustacean fauna of the several zones of depth, which are best left over for consideration till the whole of the material has been examined. Meanwhile, however, there is one such question which seems to demand attention at an earlier stage. In former papers² I have often had occasion to describe and classify groups of individuals to which

¹ By one of the fatalities that wait upon all expeditions, a great part of the Crustaceans from Minikoi were destroyed on the way to England. Fortunately the accident is mitigated by the fact that it is often possible to recognise in the Maldive collection forms seen at Minikoi. It will be necessary to allude to this in the course of the following sections, but the warning must now be given that the absence of mention of Minikoi as a locality for any species is not to be taken to mean that it is not to be found there.

[A large spirit-tank was apparently tapped on the way home and the greater part of the fluid withdrawn. It contained in numbered packages Mr Borradaile's and my collections of

Crustacea from Minikoi, which were almost completely rotted. The loss is greatly to be regretted, as the habitat, mode of life, etc., in short the natural history of the specimens in each bag was carefully noted and there is now no means of ascertaining to what species Mr Borradaile's notes apply. ED.]

² "On some Crustaceans from the South Pacific," Pts. i. ii. iv. and v., *P. Z. S.* 1898, pp. 32 and 457; and 1900, pp. 568 and 795; and "On the Stomatopoda and Macrura brought by Dr Willey from the South Seas," Willey's *Zool. Results*, Pt. iv., Cambridge, 1900.

I gave the recognised name of "variety," without attempting to define what that name meant. In many of the sections of this series similar groups of individuals occur, and it seems well to indicate at the outset what value is put upon them, both for the immediate purpose of the better description of the collection in hand, and in the hope of helping other workers in the same field. From these considerations there arise certain others regarding the ultimate nature and fate of varieties, and I shall endeavour to show in what direction my own speculation on this subject has led me. I am well aware that an experience, not of four years, but of forty would barely qualify an investigator to speak with sufficient authority for his words to carry conviction on such intricate and disputed points. But it seems well to indicate in general terms what are the problems involved from the point of view of the systematist.

The first article in the series will therefore be devoted to some remarks on the subject of varieties in the Decapoda. The second and following ones will contain the systematic lists, and the whole will be brought to an end by a discussion of such general questions as may be suggested by the material. Wherever possible the only references will be to Major Alcock's excellent lists of the Indian crabs, which contain full bibliographies and accurate descriptions of the species. These papers appeared in the *Journal of the Royal Asiatic Society of Bengal*: Part 1 (Oxyrhyncha) in Vol. LXIV. ii. p. 157 (1895): Part 2 (Oxystomata) in Vol. LXV. ii. p. 296 (1896): Part 3 (Xanthidae) in Vol. LXVII. ii. p. 67 (1898): Part 4 (Portunidae, etc.) in Vol. LXVIII. ii. p. 1 (1899): Part 5 (Dromiidae) in Vol. LXVIII. ii. p. 123 (1899): Part 6 (Catometopa) in Vol. LXIX. ii. p. 279 (1900). A reference to this work is to be understood by the mention of Major Alcock's name and the numbers of the part and page of the article referred to. In other cases references will be limited, as far as may be, to indicating a single paper in which a reliable synonymy may be found.

The classification adopted is that of Ortmann in Bronn's "Thierreich," with certain modifications of my own, proposed in a paper in the *Proceedings of the Zoological Society* for 1900 (pp. 568—596).

The several sections will not deal with groups of equal taxonomic value, nor will these necessarily be considered in systematic order. Section II, included in the present instalment, is devoted to the Swimming Crabs (Portunidae).

In conclusion I may be allowed to repeat the acknowledgements I have already made to the Managers of the Balfour Memorial Fund and the Drapers' Company of London for their aid. Nor can I sufficiently express my obligation to Mr Stanley Gardiner for the assistance his great knowledge of tropical marine biology has been to me, confirming, as it has, my own less experienced observations, and for much kind advice on other points.

I. VARIETIES¹ IN THE DECAPOD CRUSTACEANS.1. *The Nature of Varieties.*

In sorting out a collection of Crabs or Prawns, it is probably the habit of many systematists to separate groups of specimens which seem to belong to single species, and afterwards to examine each of these groups with more care. Now in many cases such a group will prove to be homogeneous, that is, to consist of individuals, differing from one another, it is true, in a greater or less degree, but not separable by their differences into sub-groups. Such a group will be regarded as a *species*. But in other cases careful examination of the specimens will reveal amongst them well-marked differences by which they can be separated into two or more sub-groups. Further, these sub-groups may either be entirely independent of one another, in which case we are dealing with two species confounded at first sorting, or they may be connected by specimens² intermediate between them with regard to the features by which they are separated, and not otherwise sharply marked off from them. Such sub-groups are called *varieties*. It must, however, be borne in mind that the intermediate specimens between varieties are much less numerous than those which exhibit the peculiarities of the varieties in a typical development. Otherwise it is only possible to say that the species exhibits considerable range of variation, but that definite varieties are not established. In my own experience, however, wide variability without the formation of definite varieties is rare among Decapods.

The difference, then, between species and varieties as recognised in systematic Carcinology is, or should be, that *species are unconnected by intermediate forms, while varieties are united into species by the existence of specimens intermediate between them in structure*. This is of course a purely empirical distinction, but it has the merit of being easily understood, workable, not likely to be very differently applied by different workers, and, which is decisive, the only one practicable in the present state of our knowledge. With the advantages of empiricism, however, the method of distinction outlined above combines one of its disadvantages, being somewhat too rigid for universal application. It has therefore to be modified in practice by the judgment of the worker in certain cases; that is to say, in those in which the trend of variation in each of two or more groups of individuals makes it probable that a more extensive series of specimens would show complete continuity, though there be, for the time, a gap between them. In such cases it is legitimate to unite the forms in question as varieties of a single species; though at the time of doing this the uncertainty should be distinctly stated. In point of fact surmises of this sort have repeatedly been justified by later knowledge³.

¹ In this paper the word *variety* is used to denote an assemblage of individuals (as defined below). A *variation* is a peculiarity of a single individual (though it is often repeated in other individuals, in which case the word may be used collectively). *Variation*—without the indefinite article—is the fact of the existence of variations, and *variability* is the name given to the phenomenon of the occurrence of variation in a species or higher group, or between the like parts of an individual. The adjective *varietal* indicates connection with a variety.

² Either in the collection or described by former writers on the species.

³ It is, indeed, a mere commonplace that many so-called species are mere varieties, to which rank some are degraded every year. In the end it will probably be found that every true species has definite habits and habitat, which have brought about its specific distinctness. It is not, of course, on this account any the less important that varieties should be named and registered.

Two or three more characteristics of varieties remain to be alluded to. In the first place it must be noted that varieties, like species, may be sundered by more than one difference, and that these differences, while they are, no doubt, smaller than those between most kindred species, can be easily paralleled by the latter in many cases, both in kind and in magnitude. Again, though the range of variation within a single variety is generally somewhat greater than that found in most homogeneous species, the latter will sometimes almost, if not quite, equal varieties in that respect. The differences between varieties are often less marked in the young than in old specimens, but this is the case with all the peculiar features of individual organisms. Lastly, there is, in many cases, no ascertained connection between varieties and locality, either geographical or bathymetrical, and they are not known to have any peculiar habits.

As an example of a varietal¹ species we may take *Thalamita admeta* (Hbst.), of whose varieties a key is given below in the second section of this report (p. 202). Here there are six varieties, resembling one another closely (that is, having the same range of variation) in most characters, but capable of separation by means of others, such as the depth of the frontal cleft, the fulness and granulation of the hand (propodite of the first leg), the size of the fourth side-tooth of the cephalothoracic shield; and so forth. These characters, be it noticed, are just such as are used in other cases to separate species of swimming crabs. Again, any two of the varieties may differ in one point only, or in more than one; and the varietal differences are less marked in the young than in old specimens.

With the exception of two new varieties, which appear for the first time in the Maldive collection, but will probably be found ere long in some other part of the range of the *T. admeta*, the geographical distribution of these varieties is practically identical. There would be little doubt of finding all of them in a sufficiently large collection from any part of the Indopacific region. Their bathymetrical distribution, on the other hand, would, if we confined ourselves to the data on p. 203, appear to show clear evidence of limitations of range. For the var. *admeta* was only taken by the Expedition as a littoral form, var. *granosimana* and var. *savignyi* at a depth of not less than 20 fathoms. But var. *savignyi* has been constantly taken elsewhere on the shore, and var. *intermedia* extends down to 30 fathoms, and is also taken on the shore², while of the varieties *granosimana* and *admeta* we have certainly not sufficient captures to allow of dogmatic statement.

Again, there is no evidence of any difference in either the habits or the habitat of the varieties. In the Island of Minikoi I was able to recognise, besides the type variety of *T. admeta*, another, differing in the slenderness of the chela, which I suspect to have belonged to *savignyi* (or possibly to *intermedia*, see the footnote to p. 191). Between the type and this variety there appeared to be no difference of habit or habitat. Of course, such differences would probably be hard to find, but the negative evidence on this point is supported by the results of dredgings in the Maldives. These dredgings supply data for recognising the connection, if any exist, between three factors of the environment at least and the organisms dredged. The factors are—the nature of the bottom, the presence or absence of weed, and the presence or absence of currents bringing water from without the

¹ By the term "varietal species" I propose to distinguish a species in which definite varieties have been recognised from a "homogeneous species" in which no such varieties have yet been found.

² In this paper the word *shore* will be used to denote that part of the littoral belt which lies between tidemarks, including both the reef and the sand-flats of the lagoon.

reef, as indicated by the nearness or remoteness of passages. In four dredgings var. *granosimana* was taken on a bottom of muddy sand, on another with coarse sand and small rubble, on coarse sand with rubble, and on a hard (rocky) bottom. In two of these dredgings weed was present, in two it was not. The number of captures was not enough to make it possible to come to any conclusion as to the effect of the neighbourhood of passages on the distribution of this variety, but in a similar case—that of the varieties of *T. exetastica*—it is quite clear that this factor is without influence. Var. *savignyi* was only taken twice, but *admata* and *intermedia*, which were found four and six times respectively, showed no greater tendency to restriction to special environments than did *granosimana*.

2. *The Relation between Varieties and Species.*

Among the Decapod Crustaceans, then, species are paralleled by other assemblages of individuals, known as varieties, which differ from them neither in the nature of their characteristic features nor in the magnitude of these, but only in being connected into groups of two or more by the existence of intermediate individuals. It is hardly possible to resist the conclusion that, in many cases at least, species have arisen from such definite varieties as these by the extinction of the intermediate individuals. And it will be interesting to consider of what nature and origin varieties may be, and what processes may turn them into species.

The orthodox explanation of the origin of varieties such as those we are now dealing with would, no doubt, be that they are produced by natural selection of the variations (generally smaller in degree than those which characterise varieties) which are found within the limits of homogeneous species and varieties. Now there can, of course, be no reasonable doubt that natural selection is at work among the Decapoda, and it is probable that in some cases (as, for instance, in that which Professor Weldon has investigated in *Carcinides maenas*) it brings about transformations of species by accumulating small variations. This is especially likely to be taking place where a variety is locally restricted¹. But in the case of varieties not so restricted, as we are now using the term, it is very difficult to accept the same view, and that for three reasons.

1. *There is no evidence of isolation* such as is presupposed in the evolution of two or more varieties simultaneously from a single species. And it should be observed that this is the problem now before us, not the replacement of an outworn type of the species under stress of uniformly changing environment over its whole range.

Isolation in the organic world may be of four kinds:

i. "Geographical."

ii. "Habitative"—a name which I propose to give to the separation of allied organisms which, living in the same locality, are nevertheless separated by their habits of life—as one prawn will hide among the branches of corals and another in a sponge, one crab burrow just below high-water mark and another just above, and so on. With this kind of isolation

¹ To these cases the name of "subspecies" might well be confined, leaving that of "variety" for non-local forms such as those now under consideration. The ultimate result of such a process is probably to be seen in genera like *Sesarma*,

Potamon, and perhaps *Pilumnus*, where large numbers of species, differing in small points from one another, are of local distribution.

may be included that brought about by limitation of an organism to certain zones of depth, or bathymetrical isolation.

iii. "Physiological," due to a greater or less degree of infertility accompanying structural differences between allied organisms.

iv. "Sexual," due to a preference by the members of a species or variety for mating with their own kind.

Local variation is, of course, far from unknown in the Decapoda, but of the class of varieties we are now dealing with one of the most marked characteristics is their independence of geographical limitations. In fact it may generally be safely foretold of a Decapod crustacean that, if one variety be taken in a given locality, any others that may be known will probably also be found there, if only the collection be large enough. In the great majority of cases, if not in all¹, the varieties of the Decapoda are not known to affect *special habits or habitats*. Of course it is also true that very little is known about the habits of the group at all; but this does not justify us in assuming that non-local varieties are adapted to special habits. In a few cases of varietal species which I have examined "in the field," I have been unable to find any evidence of such a phenomenon. We have seen that, in the case of *Thalamita admeta*, there is no sign either of varietal habits or of varietal habitats as far as our present knowledge goes. An even better example is *T. exetastica* Alc., whose three varieties have been taken on every kind of bottom and in varying positions with regard to the passages of the reef. To take another instance, from a different group of Decapods, the porcelain crab *Petrolisthes lamarcki* has four varieties which show no divergence either in habits or in habitat. Regarding bathymetrical isolation there is again no evidence of varietal separation. We have seen that the case of *T. admeta* is somewhat doubtful. That of *T. exetastica* is beyond question in this respect, all the varieties having been taken within a few fathoms of one another in the Maldives. Yet *T. exetastica* is a species with a well-marked specific bathymetrical range, the thirteen recorded captures (including that made by the "Investigator") being all below 26 (or possibly below 30) fathoms.

As to *physiological* and *sexual isolation* in the Decapoda there is no evidence.

2. *There is no evidence of adaptation of varieties to special varietal habits or habitats.* This, which is really an entirely different question from that of isolation, resolves itself into a restatement of the evidence just given. For, so long as hardly anything is known of the adaptation of species by their structure to their specific habitats or habits, it is idle to argue that there is no evidence of the utility of varietal characters. But we do know, or at least are beginning to know, that every species has its specific habitat and habits, to which we conclude, from the few cases that we understand, that its specific characters are adapted. It is therefore quite pertinent to argue that, unless varieties can be shown to have definite habitats and habits, their varietal characters cannot be assumed to be adapted to such circumstances. And it is of just this phenomenon—the existence of varietal habitats and habits—that there is at present no evidence.

3. *There is no clear evidence of intermediate stages in the formation of varietal from homogeneous species.* There are plenty of species in which it is impossible to pick out two

¹ Contièrre [*Les Alpheidae*, Paris, 1899] seems to have found at Jibuti examples of habitative isolation among one or two Alpheid varieties, but at present there is always a doubt as to the interpretation put on the term variety.

well-characterised non-local varieties, and again there is a certain proportion in which two or more such varieties are seen. But in all these latter, so far as I have met with them, the varieties are sundered by well-marked gaps. That is to say, in sorting fifty specimens of two varieties, there would not, in my experience, be more than two or three whose position would be doubtful. This is, of course, merely negative evidence, but it would not be right to assume that positive evidence in the opposite direction exists till it be forthcoming¹.

In view of the facts just stated, it is, I think, clear that there are considerable difficulties in the way of explaining the origin of varieties in the Decapoda by means of natural selection. Time and research may remove these difficulties, but it is equally likely that they will not. It will be well, therefore, to consider shortly the alternatives. A Lamarckian view of the question, as compared with the Darwinian, is equally difficult to reconcile with the want of any correlation of varietal characters with the environment, which is implied by the absence of geographical and habitative isolation. There is left, if both these fail us, but one alternative possible. Like smaller variations, those which characterise varieties would appear to be produced by intrinsic forces alone, of whose equilibrium they are perhaps the outcome². But questions so momentous are not to be decided by an examination of one group only, nor by any but those who have made variation a study. In their hands may be left the question "*Are varieties the outcome of inward or of outward forces; does the solution of the problem of their origin lie with Physiology or with Natural History?*"

Turning now to an examination of the ways in which varieties might become species, and assuming that natural selection is the transforming agent, we may consider in what manner it would act. There are two conditions under which natural selection can come into play upon a varietal species. Either the environment may alter, or the species may spread into a new area where the environment is different from that under which it has hitherto been living.

¹ Throughout this article statistics have been avoided, as any attempt to draw exact conclusions in a particular case from less than, say, a thousand specimens would be hazardous. But, to take the first example to hand, out of 36 specimens of the type variety of *Thalamita admeta* collected in the Maldives, two only show characters which caused hesitation as to whether they should be placed with the remaining 34 or with examples of var. *savignyi*. These two were of middle size. One small specimen showed some resemblance to var. *edwardsi*, but its position could not be said to be doubtful.

² This alternative, if, as seems probable, it coincide with Bateson's theory of Discontinuous Variation, will receive from that fact an advocacy which will make it worth careful consideration. The chief point in which it amplifies Mr Bateson's theory would seem to be that it is now suggested that discontinuous variations may coincide, and so produce entities still more like species than assemblages of individuals separated on one character only, and that there is no evidence of this coincidence being brought about by natural selection, but on the other hand a possibility of its being due to intrinsic causes (correlation). The same cause, for instance, which produces ridges in one part of the body

may, under the different conditions of growth prevailing in another region, make tubercles or granulations, and the swelling of a surface may lessen automatically the relative area of granulation or the height of the granules. Of course very many varieties are separated by one character only, or at all events only one such has yet been detected in them. The origin of such a form is a simpler problem than that of one characterised by two or more special features, and is that which has been chiefly discussed above.

No doubt cases exist of discontinuous variations which do not coincide. But in that case one would probably be more conspicuous than the others, and its use for systematic purposes would cause the others to be overlooked. An examination of a key to the varieties of a species will sometimes reveal such characters of secondary prominence by the fact that it is possible to rearrange the key in two or more ways. In these cases it is easy to see that the key by no means necessarily represents genetic affinities, but merely classifies possible combinations of characters. But I am not here concerned to uphold Mr Bateson's theory, and shall enter no farther into a discussion of this point, which concerns variation, not varieties.

(a) Let us suppose the environment to alter. Its effect upon a varietal species might take one of several forms: (i) It might affect all varieties equally, either favourably, unfavourably, or not at all. (ii) It might extinguish all but one. In either of these events the species as a whole would change its characters, but there would be no transformation of a group of varieties into a group of species. (iii) In a species with three or more varieties, in which the extreme varieties are connected (structurally, not necessarily genetically) by intermediate varieties, it might extinguish the intermediate variety or varieties, leaving the extreme ones as separate species. (iv) In a species with two or more varieties, it might affect all or some of the varieties favourably in their most marked form and prove prejudicial to the intermediate individuals between the varieties. By this means it might polish the varieties, so to say, into species.

(b) Supposing, on the other hand, the species to migrate into a new environment, either geographical or habitative, the possibilities which we have just discussed again present themselves with the addition of a new factor to determine which of them is to come into play. For clearly either one or more than one of the varieties might migrate, and it is probable that the effect of changed conditions on a single variety would be different from that which they would have on a group of varieties. In the one case we should have the new factor of isolation, in the other this would still be wanting.

But here we are brought face to face with a difficulty due to our lack of knowledge of the reproductive physiology of the Decapoda. The above paragraphs dealing with the effect of a changed environment all presuppose that the varieties breed more or less true, that is, that at least the great majority of the offspring of members of one variety belong to that variety. If, on the other hand, any variety give rise plentifully to all, it is clear that the task of natural selection will be much harder, for it will have to reduce this tendency in the surviving varieties as well as to extinguish the unfitted ones. On this point, however, it is useless to say more in the present state of our knowledge.

[*Note.* Jan. 16, 1902. Since the foregoing was written, Mr Bateson's paper on "Heredity, Differentiation, and other Conceptions of Biology" (*Proc. Roy. Soc.* LXII.) has appeared. It seems that I have reached conclusions somewhat similar to those outlined in the later pages of that paper. What I have called "varietal characters" are probably the same as those which are there called "specific variations," while the "normal variations" are with me "variations within a homogeneous species or variety." If Mr Bateson's conceptions, and the terms by which he designates them, be accepted, a very great advance in Systematic Zoology will be possible. But some confusion is likely to result if either of the terms "varietal" and "specific" be applied to phenomena which are at the base of *both* varietal and specific entity. Would not the word "specifactive" meet the case better?]

II. PORTUNIDAE (SWIMMING CRABS).

1. *General.*

The family Portunidae are distinguished from the rest of the round-fronted (cyclometope) crabs by the adaptation of some of their legs for swimming, to which end these limbs are transformed into flattened paddles. The result is often to confer upon the crabs a power of darting at high speed through the water, which would hardly be credited by those who have not watched them. Corresponding to this mobility they have a thin flattened form of body, enabling them to pass sideways through the water, and a lightness gained at the expense of the protective cuticle. These peculiarities give the swimming crabs a strikingly different bodily form from the heavily-built, slow-moving Xanthids, which is moreover accompanied by an equally marked difference of habitat. The Xanthids are usually to be found on the reef or shore exposed to the full force of the breakers. In this position the lightly-built swimming crabs would be dashed to pieces against the rocks. Their proper haunt is a space of quiet waters, such as the lagoon of a coral atoll, and as these places are, in the tropics, generally bottomed with white or greyish coral sand, on which the crabs lie, and in which they often hide their bodies, they frequently mimic it by their pale greyish colour¹, often in a manner as striking as that in which flat-fish resemble the shingly bottom they live on.

At the same time the swimming crabs are by no means entirely confined to a bottom of coral sand even in the tropics. In deep water, where rocks are not associated with danger, they are found on every kind of bottom in about equal numbers, and here, if they hide, it must be under stones. They even occur, though not so very often, on the reef. But the individuals, found in this position, may possibly have strayed from the lagoon with the outgoing tide. Probably, when more is known about the lives of the species, it will be found that certain of them maintain their existence on the reef by sheltering under stones or in blocks of coral, where if anywhere they are always found, and that others—certainly the bulk of individuals—prefer the lagoon. In their habits these crabs are active and intelligent, escaping capture with cleverness. The lagoon forms usually keep close to the sand and do not rise more than a few feet into the water, but others swim as boldly and strongly as fish.

The bodies of most Portunidae are adorned or protected with sharp thorns or teeth, and it is on such characters as the number and size of these and the shape of the lobed front that the species are generally distinguished, though in most cases enough is not known of their habits to make it possible to say whether, and if so how, these be of use to the animals.

The family is highly variable and varietal and is probably undergoing rapid evolution in many directions.

¹ This colouring would also resemble, though not so closely, that of coral blocks or rubble.

2. *Systematic List.*Subfamily **Carupinae.**Genus *Lupocyclus* Ad. and Wh., 1848.

- 1.
- Lupocyclus strigosus*
- Alc. 1900. Alcock, IV. p. 24.

Dredged in Kolumadulu on a bottom of dead and broken shells in 35 fathoms of water. All previous specimens have been dredged in the neighbourhood of India in 15—58 fathoms.

Subfamily **Thalamitinae.**Genus *Lissocarcinus* Ad. and Wh., 1848.

- 2.
- Lissocarcinus laevis*
- Miers, 1886. Alcock, IV. p. 21.

Dredged in South Nilandu on a bottom of hard sand in 36 fathoms of water.

- 3.
- Lissocarcinus polybioides*
- Ad. and Wh., 1848. Alcock, IV. p. 19.

Dredged in Mulaku on a bottom of mud with weed, in 28 fathoms of water.

- 4.
- Lissocarcinus orbicularis*
- Dana, 1852. Alcock, IV. p. 20.

This crab lives symbiotically¹ with the teat-fish (*Holothuria nigra*). It hides under or among the tentacles, coming out from shelter at times, perhaps to feed, and crawling all over the body of its host on which it crouches if disturbed. Its dark purple colouring with white spots is protective, resembling the sticky black skin of the teat-fish with grains of coral sand adherent. Paler brown forms live on other Holothurians to whose colour their own is adapted. The other two species taken by the Expedition are roughly speaking sand-coloured, and there is no record of their living symbiotically with other organisms. The females of *L. orbicularis* show a very perfect condition of an arrangement found in various other swimming crabs. That is to say, there is a well-developed brood-pouch formed by a deep sternal hollow surrounded with a fringe of hair and floored by the abdomen, whose sides are also edged with hair. One specimen had many fully hatched zoeas in this pouch, and it would be interesting to know how long these young remain there, and how much of their development is passed there.

The species was taken on the shore and also dredged. It was found in Minikoi, Hulule, Male Atoll, Furnardu velu², Miladumadulu, South Nilandu, and Mulaku.

Genus *Charybdis* de Haan, 1835.

- 5.
- Charybdis (Gonioneptunus) truncata*
- (Fabr.). Alcock, IV. p. 67.

The size and shape of the teeth on the antero-lateral edge are not constant. This is probably the reason why the descriptions of different writers do not quite agree. Alcock

¹ The words "symbiosis" and "commensalism" appear to be often used as synonymous, but the latter should obviously be restricted to cases where the food of two

associated organisms is of the same nature.

² [For definition of this term see p. 155. Ed.]

says that the propodite of the last leg has its hinder edge smooth. It is not serrate, but it bears 4 or 5 minute curved spines, indicated in de Haan's figure of the female.

The species was dredged in depths of more than 28 fathoms, on bottoms of sand and mud, in Haddumati, Kolumadulu, and Mulaku.

Genus *Thalamita* Latr., 1829.

6. *Thalamita prymna* (Hbst.), 1803.

Var. *picta* Stimps., 1859. Alcock, IV. p. 79.

Found sheltering in a coral mass on the outer reef at Minikoi.

Var. *danae* Stimps., 1859. Alcock, IV. p. 77.

Taken on the reef at Minikoi.

It would be interesting to know the difference between the habits of this species and those of the equally common and somewhat similarly built, though quite distinct, *T. admeta*. I am under the impression, though the loss of my Minikoi specimens leaves me somewhat in doubt on this point, that *T. prymna* is a reef crab of a darker, more greenish hue than *T. admeta*, generally found in the neighbourhood of living corals, and perhaps of rather more sluggish habits than the latter. *T. admeta* on the other hand, though also found on the reef, is, I fancy, a lagoon crab of a paler colour, sometimes almost white, fond of lying on the sand, and of extremely active habits.

7. *Thalamita sima* H. M. Edw., 1834. Alcock, IV. p. 81.

There is considerable variation in the depth of the frontal cleft of this species, and same also in the granulation of the under side of the hand. A few specimens came near *T. poissoni*. The absence of spines from the hinder edge of the meropodite is, however, always to be relied on as a distinction between the two. The var. *granosimana* of *T. admeta* tends to approach this species, as will be stated later.

Specimens were dredged in Haddumati, Nilandu, Kolumadulu, Suvadiva, Fadifolu, Felidu, and Mahlos on every kind of bottom below 19 fathoms. Elsewhere it appears generally to have been taken as a shore form. Possibly its small size may have caused it to escape collection on the shore in the Maldives. On its absence from Minikoi no stress can be laid, for the reasons stated in a footnote to p. 191. In dredging, the liability of a swimming crab to capture depends, not on its conspicuousness, but on its powers of swimming, which are usually greater in larger crabs. The small average size of dredged specimens of many swimming crabs is probably due to this.

8. *Thalamita poissoni* Aud. and Sav., 1825. Alcock, IV. p. 81.

The hands of the female (and to a less extent the small hand of the male) have well-marked ridges on the outside and are not full but narrow, like those of *T. admeta*, var. *savignyi*. One male specimen from Suvadiva has the spines on the fore edge of the meropodite of the *cheliped* blunt, as they are said to be in *T. chaptali*. The shape of the frontal lobes and of the frontal notch varies considerably, and some specimens can hardly be told from *T. admeta*, var. *savignyi*, when young, or from var. *edwardsi* of the same species when full grown. In other cases there are traces of scaly markings on the under side of the chelipeds

which recall *T. admeta*, var. *granosimana* on the one hand, and *T. sima* on the other. From the latter species, however, as well as from *T. chaptali*, *T. poissoni* is sharply distinguished, as yet, by the presence, on the hinder edge of the propodite of the last leg, of several spinules, of which there is no trace in *T. sima* or *T. chaptali*. From *T. admeta* it is sundered by its much smaller size.

At present, therefore, it is necessary to keep separate the four forms of *Thalamita* known as *T. admeta*, *T. sima*, *T. poissoni* and *T. chaptali*; but it is far from impossible that they may eventually prove to be all varieties of one species, perhaps in process of separation as independent species.

Dredged in Suvadiva, South Nilandu, Mulaku, Addu, Haddumati, Miladumadulu, Fadifolu, Kolumadulu, and Minikoi, on all kinds of bottoms, in from 7—43 fathoms. Elsewhere has generally been taken on the shore, but the same remarks apply here as in the case of *T. sima*.

9. *Thalamita admeta* (Hbst.), 1803.

T. admeta and *T. quadrilobata*, Alcock, iv. pp. 82—85.

Among the numerous specimens of this very variable species collected by the Expedition, were examples of two varieties hitherto unrecorded. One of these has characters in common with both *T. quadrilobata* Miers and the type of *T. admeta*, having the front of the latter but resembling the former in all other respects. I propose the name of *intermedia* for this form, and have also taken the step contemplated by Alcock, of including *quadrilobata* with *admeta*. The other variety, which I propose to call *granosimana*, resembles var. *savignyi*, but has the under side of the cheliped granular as in *T. sima*, which it also resembles in a rather less flattened body and more arched front than those of *T. admeta*.

The following key includes all the varieties of this species at present recorded:

I. Crest on the basal joint of the second antenna toothed or granular, not spinose.

1. Space between the two lower ridges of the hand (propodite of cheliped) smooth or only very sparsely granular. Fingers shorter than the palm, dactylopodite hooked. At least the big chela of the male deep and full in shape. Median cleft of the front always deep. Fourth side-tooth of carapace usually quite vestigial.

i. Outer surface of hand more or less granular; ridges strongly developed.

Var. A, *admeta* (Herbst.), 1803.

ii. Outer surface of hand smooth; ridges slight.

Var. B, *edwardsi* Borradaile, 1900.

2. Space between the two lower ridges on the hand strongly granular. Fingers as long as palm, straight. Chelae slender in shape. Median cleft of the front often shallow. Fourth side-tooth of carapace small, but not vestigial.

i. Under side of hands smooth.

Var. C, *savignyi* A. Milne-Edwards, 1861.

ii. Under side of hands granular.

Var. D, *granosimana* n.

II. Crest on basal joint of second antenna with three large spines.

1. Front two-lobed.

Var. E, *intermedia* n.

2. Front four-lobed.

Var. F, *quadrilobata* Miers, 1884.

Admeta was taken on the shore in Minikoi, Goidu, Fadifolu, and S. Mahlos; *intermedia* on the shore in Goidu and Fadifolu, in 5 fathoms at North Male and in 30 fathoms at Haddumati; *granosimana* in 20—43 fathoms on bottoms of varying description in Mahlos, Kolumadulu, South Nilandu and Suvadiva; and *savignyi* in 23—28 fathoms at North Male and Mahlos. The latter variety was probably also seen at Minikoi.

Admeta, *savignyi* and *intermedia* are, to the best of my knowledge, found both on the reef and in the lagoon¹. With them go probably *edwardsi* and *quadrilobata*. *Savignyi* and *intermedia* certainly, and probably also the other three, extend from the shore down to 30 or 40 fathoms at least. *Granosimana*, which shows features which tend to ally it with *T. sima*, has, like the latter species, been found only in deep water in the Maldives. If this be a real and not an apparent limitation (see above p. 201), the same cause is probably at work in both cases, and *granosimana* very likely exists elsewhere on the shore with *T. sima* and *T. poissoni*. In that case it is probably an incipient species in a somewhat earlier stage than *T. sima* and *T. poissoni*. On the other hand it may be a genuine local subspecies.

10. *Thalamita exetastica* Alc. 1900. Alcock, iv. p. 86.

The collection contains a number of specimens which are at least closely allied to this species and may all be for the present classed as varieties of it. Some of them approach very closely to Alcock's definition, but there is one point in which all fall somewhat short. This is in the squamiform markings on the chelipeds, which never completely cover the limb but are always replaced to a greater or less extent by more rounded granulations on the upper side, and are often wanting over a part of the lower side.

Three varieties are present:

1. Var. A. Typical, that is, agrees with Alcock's definition in all points (except the granulation of the chelipeds as above).

2. Var. B, *spinifera*. Differs from the type in having a varying number of spines on the hinder edge of the propodite of the last leg. In this point it approaches *T. investigatoris*, Alcock, 1900.

3. Var. C, *macrodonta*. Has no spines on hinder edge of last propodite, but differs from type in that:

(i) The last side-tooth is nearly as large as the third and projects somewhat more than the rest. Fourth tooth rudimentary.

(ii) The median frontal lobes are distinctly narrower than the submedian. About 1 : 2 in the Kolumadulu specimen, and 2 : 3 in the Suvadiva specimen.

In both these respects the variety approaches *T. investigatoris*.

¹ See footnote to p. 191.

Var. A was dredged in 30 and in 37 fathoms in Suvadiva, on a rough stony bottom and on the hard smooth bottom of a passage.

Var. B was dredged in Suvadiva, Kolumadulu, South Nilandu, Haddumati, Mulaku, and Felidu in 30—45 fathoms on every kind of bottom.

Var. C was dredged in Suvadiva and Kolumadulu in 34 and 35 fathoms on bottoms of rubble and broken shells respectively.

It seems not unlikely that the dredgings of the "Investigator" and of Mr Gardiner's Expedition have revealed a new and highly varietal species of *Thalamita* in deep waters near India, of which *T. exetastica*, var. *spinifera*, var. *macrodonta*, *T. investigatoris* and *T. imparimanus* are but varieties. The habitat of this species is probably in moderately deep water only. Allied to it, but separated from it by the form of the chelipeds and their equality in the male, is the species next described of which the only known specimen has been taken on the littoral.

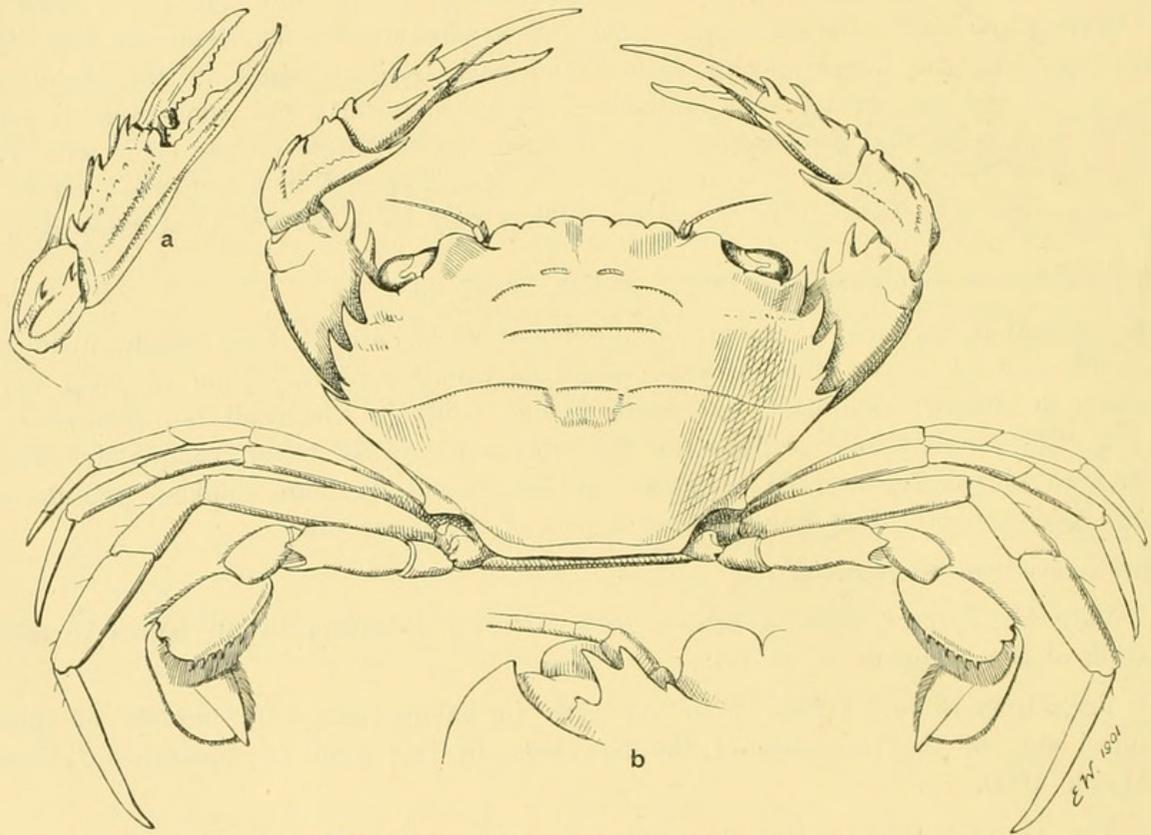


FIG. 35. *Thalamita tenuipes*; a. outside of chela, b. base of antenna.

11. *Thalamita tenuipes* n. sp.

Closely allied to *T. imparimana* Alc. 1900 (IV. p. 87), but separated from it by the following characters:

(i) Basal joint of antenna has a short crest consisting of two large teeth fused at their bases.

(ii) Chelipeds of male equal, smooth, with a few scattered warts and scanty hairs. Outside the wrist are two ridges, and three spines, at the inner angle one spine. Outside

the hand two distinct ridges, with another less distinct above them; on the upper side two pairs of spines. Fingers as long as palm, slender, hooked at tip, grooved within and without.

(iii) Line between 6th and 7th abdominal terga very slightly concave.

(iv) Habitat the shore (?).

Length 10 mm.; breadth 13 mm.

Colour in spirit, ochreous yellow.

One male from Goidu, Goifurfehendu Atoll.

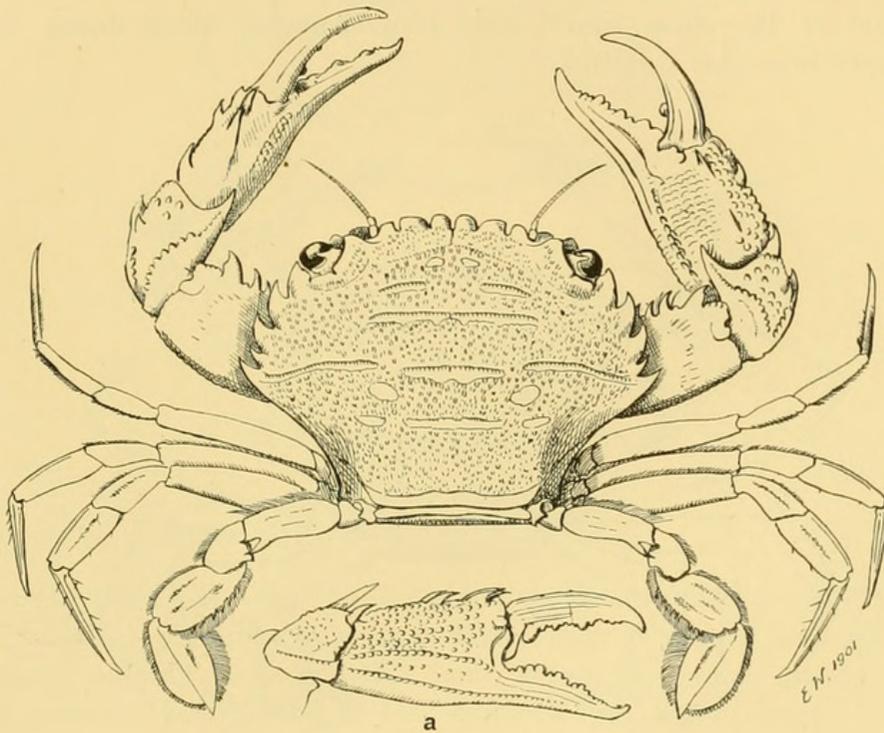


FIG. 36. *Thalamita gardineri*; a. outside of chela.

12. *Thalamita gardineri* n. sp.

The *exetastica* group of *Thalamita* approach *Charybdis* in some respects. The present species is allied by its features both to *Charybdis* and to the *exetastica* group. From the latter it is sundered by the following characters:

(i) The transverse ridges of the carapace are disposed as in *T. exetastica* but are rather more prominent than in the type variety.

(ii) The antero-lateral edge slopes outwards, making a greater angle with the middle line of the body than in *T. exetastica*.

(iii) The median frontal lobes are distinctly narrower than the submedian (2:3), and on a lower plane than, though not overlapped by, the latter.

(iv) The last side-tooth projects much more than the rest, and is as long as the 2nd or 3rd, though not so broad. The 4th side-tooth is small, but not rudimentary. There is no small tooth at the base of the first side-tooth.

(v) The chelipeds of the adult male are almost absolutely equal. Transverse squamiform markings are almost wanting. The upper side of the hand is covered with rounded granules, but on the inside squamiform markings remain.

(vi) There are about 10 spines on the hinder edge of the last propodite.

Length of longest specimen (♂), 13 mm. Breadth of same specimen, 17 mm.

Colour in spirit, sandy mottled with reddish.

Taken in Minikoi, sheltering under stones on the reef. This species is transitional to *Charybdis* (*Goniosoma*), but is separated from that genus by having only five side-teeth. The outward trend of the antero-lateral edge is a character which makes its position in the genus *Thalamita* somewhat doubtful.

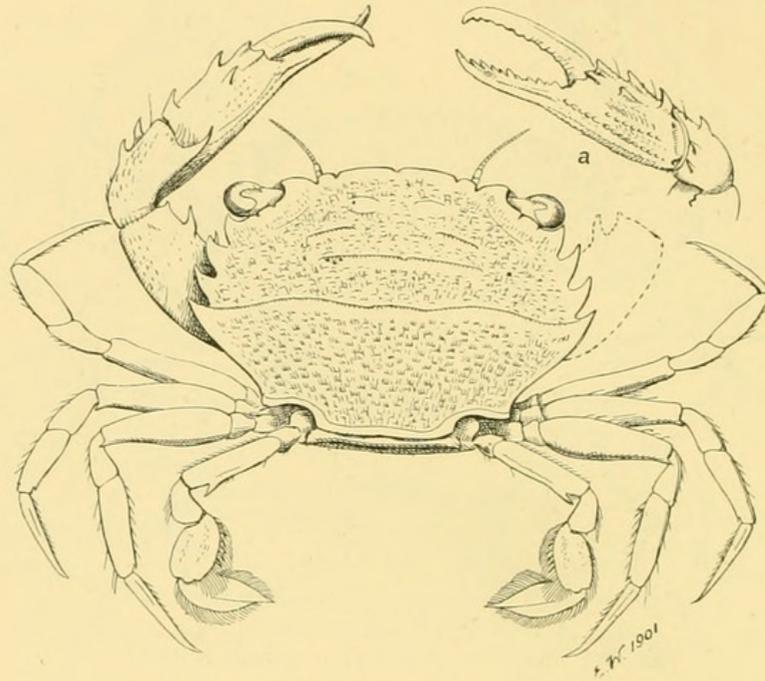


FIG. 37. *Thalamita cooperi*; a. outside of chela.

13. *Thalamita cooperi* n. sp.

Closely allied to *T. invicta* Thallw. 1890¹, of which it is possibly only a variety. It differs from Thallwitz' species however in the following points:

- (i) The fourth side-tooth is wanting, and not merely vestigial as in *invicta*.
- (ii) The outer side of the hand bears the usual five spines, instead of only three.

The front is lobed (excluding the orbital lobes), the middle lobes being the widest and somewhat recalling the frontal lobes of *T. admeta*. There are four side spines including the orbital angle, the fourth of those usually present being lost. The antennal ridge is granular. On the outside of the hand are the usual five spines and three granulated ridges. The fingers are shorter than the hand. The last propodite bears about half-a-dozen spinules.

¹ Thallwitz, *Abh. Zool. Mus. Dresden*, 1890—1891, No. 3, p. 46.

Taken at Goidu, Hulule and Minikoi, on the shore in each case. At the latter island it was sheltering in a coral block on the outer reef.

I have called this species after my friend Mr C. Forster Cooper, who was a member of the Expedition.

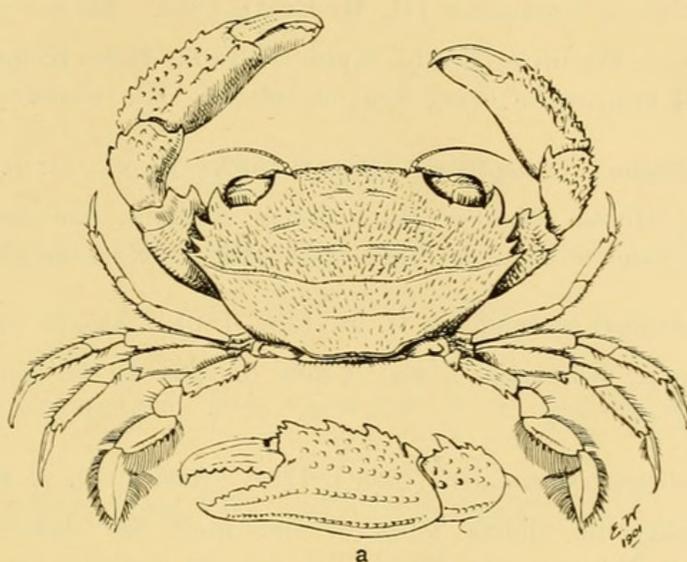


FIG. 38. *Thalamita pilumnoides*; a. outside of chela.

14. *Thalamita pilumnoides* n. sp.

Diagnosis: "A *Thalamita* with the body and limbs very hairy; the ridges of the back much as in *T. admeta*; the front bent downwards, slightly arched, and bilobed, the angles of each lobe being slightly produced; the inner supraorbital lobes nearly straight, sloping backwards and inwards, less than half the width of the frontal lobes; side-teeth four in number (including the orbital tooth), the third being the smallest; the hinder edge of the carapace concave, forming a gentle curve with the side edge; the sixth abdominal segment of the male broader than long; the basal joint of the antenna about equal to the orbit in width, its crest with four blunt teeth; the chelipeds stout, unequal (in ♂ at least), with three granular ridges on the outside of the hand, the areas between the ridges smooth, the under side smooth, the upper side covered with sharp tubercles, a row of three teeth along the inner edge of the upper side and one tooth at the articulation with the wrist, the fingers shorter than the palm, the wrist with one spine at the inner angle and three smaller ones on the outside, while the upper side bears some granules as on the hand, the arm with a series of teeth on its fore edge, diminishing from without inwards, and part of the upper surface granular; a spine on the hinder edge of the last meropodite and two or three spinules on the hinder edge of the last propodite."

Length, 4 mm.; breadth, 6.5 mm.

Colour in spirit, pale yellow with minute green spots in places, especially on the front.

One male from a small shoal in the middle of the lagoon at Minikoi.

G.

Subfamily **Portuninae.**Genus *Neptunus* de Haan, 1833.

15. *Neptunus (Achelous) granulatus* (H. M. Edw.), 1834. Alcock, iv. p. 45.

Taken in Haddumati, Suvadiva, Felidu, South Nilandu, Male, Kolumadulu, Miladumadulu and Mahlos from 0—43 fathoms on every kind of bottom. Not recorded from a tidal reef.

16. *Neptunus (Hellenus) longispinosus* (Dana), 1852. Alcock, iv. p. 40.

Taken in Minikoi, Hulule, Mahlos, Male, South Nilandu, Kolumadulu, Haddumati and Miladumadulu in 2—4 fathoms on every kind of bottom. Not recorded from a tidal reef.

17. *Neptunus (Hellenus) tuberculosus* H. M. Edw. 1861. Alcock, iv. p. 42.

Taken in Haddumati, Kolumadulu, and Felidu in 22—40 fathoms on bottoms of sand with weed or rubble.

18. *Neptunus (Hellenus) hastatoides* (Fabr.), 1798. Alcock, iv. p. 38.

In all the specimens the middle lobes of the front are distinctly shorter than the others. Taken in South Nilandu and Mulaku in 19—30 fathoms on hard and on muddy bottoms respectively.

19. *Neptunus (Hellenus) tenuipes* (de Haan), 1835. Alcock, iv. p. 42.

The last side-spine in nearly all the specimens is considerably more than three times the length of any of the others, which is the proportion given by Alcock, but it varies in length a good deal.

Taken in Mulaku, Haddumati, Felidu, South Nilandu, and Suvadiva in 28—40 fathoms on sandy or muddy bottoms.



Borradaile, L. A. 1902. "Marine crustaceans. I. On varieties. II. Portunidae." *The fauna and geography of the Maldive and Laccadive archipelagoes : being the account of the work carried on and of the collections made by an expedition during the years 1899 and 1900* 1, 191–208.

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