

ON ACANTHEPHYRA PURPUREA
AND ITS ALLIES (CRUSTACEA
DECAPODA: HOPLOPHORIDAE)

BY STANLEY KEMP

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*On Acanthephyra purpurea and its Allies (Crustacea
Decapoda: Hoplophoridae).* By STANLEY KEMP, Sc.D.,
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ONE of the most striking features of collections made with large plankton nets in the open ocean is the great number of prawns of a vivid scarlet or blood-red colour which are obtained. They include both Penæidea, represented by such genera as *Sergestes* and *Gennadas*, and Caridea with Hoplophoridae as the dominant family. The Hoplophoridae appear to be exclusively pelagic in habitat; though scarce in high latitudes they occur in all the oceans of the world, and in temperate and tropical waters they are frequently abundant.

There are many species of Hoplophoridae which are extremely scarce and are known only from few specimens, often obtained at widely distant localities; but, with a few exceptions to be noted below, the abundant species in every part of the world belong either to *Acanthephyra purpurea* A. Milne-Edwards or to a form which bears a very close resemblance to it. In any large collection of oceanic Caridea more than 80 per cent. of the material will belong to the *A. purpurea* group.

In 1906, when attempting the identification of certain Hoplophoridae from the west coast of Ireland, I went somewhat fully into the characters by which the various forms related to *A. purpurea* were supposed to be distinguished. In so doing I examined the 'Challenger' specimens, pointed out numerous discrepancies in Spence Bate's account, and gave a partial revision of the genus. So far as *A. purpurea* and its allies were concerned, I convinced myself that only a single highly variable species could be maintained. This opinion has not remained unchallenged in the years that have intervened: it has

been effectively contested by Stephensen (1923) and is not accepted by Balss (1925).

The ships of the Discovery Committee, on the numerous voyages which they have made to the Antarctic during the past fourteen years, have taken every opportunity to explore the pelagic fauna of the South Atlantic, and large plankton nets have also been used in all sectors of the Antarctic and on the East African coast. The extensive Decapod collections made in this way have been placed at my disposal by the Committee, and I have also had the opportunity of examining the still more abundant Hoplophorid material obtained by the late Dr. Johannes Schmidt during his celebrated voyage round the world in the 'Dana.' I am greatly indebted to Dr. Å. Vedel Tåning and the authorities of the Carlsberg Foundation for the privilege of reporting on this unrivalled collection. A full account of the Hoplophoridæ from these sources will, it is hoped, be published before long; but in the meantime, for the assistance of others engaged in similar work, it appears desirable not only to recant my former views, but to put on record the conclusions which have been reached regarding *A. purpurea* and its allies after examining the largest collection hitherto made.

There is perhaps something to be said in extenuation of the opinion I formerly held. In *A. purpurea* and its relatives the rostrum, its length and the characters of its dentition, is of minor taxonomic importance, and apart from details concerned with the presence or absence of a tooth on certain abdominal somites, the only obvious differential character is the number of dorso-lateral spines on the telson—a feature which at first sight would not appear to be of special significance. In the group the number of pairs of these spines varies from 3 to 19*, and since, with sufficient specimens, practically every intermediate number may be found, it was perhaps pardonable to believe that the character had no real validity. It is now apparent, however, that the number of telson spines is very definitely correlated with geographical distribution, and the study of several thousand specimens from all parts of the world leads me to the

* In reckoning the number of spines, those which form the terminal cluster at the tip of the telson are omitted.

conclusion that eight distinct forms should be recognized in the *A. purpurea* group.

The facts which have emerged may be briefly stated thus :—

In the North Atlantic, as Stephensen (1923) has already shown, two forms only are represented; one of these has 4 pairs of spines on the telson, while the other, which reaches a larger size, has from 7 to 11. The 4-spined form is *A. purpurea* A. Milne-Edwards, and in adults the dorsal carina of the fourth abdominal somite terminates bluntly and does not end in a tooth. The northern limits of this species are not easily ascertained owing to confusion with the allied form, but probably do not extend much beyond 53° N.; its southern limit on the eastern side of the Atlantic is in about 17° N.

The form with 7 to 11 telson spines has a tooth at the end of the carina on the fourth abdominal somite. It is known to occur as far north as Davis Strait, S.W. Greenland and Iceland. There are indications that it lives generally at lower levels than *A. purpurea*, and it is probably able to reach higher latitudes by taking advantage of the warm intermediate layer of water. It is the only member of the *purpurea* group which penetrates into the Mediterranean, and here, as Stephensen has noted, there is a difference in the growth of the rostrum, which in adults is proportionately longer than in Atlantic specimens. The southern limit of this form on the eastern side of the Atlantic is in about 13° N. This species has frequently been referred to as *A. multispina*, but its correct name appears to be *A. hæckeli* (von Martens). Von Martens (1868) described it from the Mediterranean as *Ephyra hæckeli*, and I have examined the types in the Berlin Museum.

Passing down the Atlantic from north to south a sudden change occurs in the species of the *purpurea* group at the limits noted above. In place of a 4-spined form one with 6 (less commonly 5) telson spines now appears and, in place of the 7- to 11-spined, one with 13 to 19. The form with 6 spines has not been described hitherto, and I propose for it the name *A. sexspinosa*. Apart from the telson, adults of this species differ from all other members of the group in the absence of teeth at the posterior ends of the carinae of both fourth and fifth

abdominal somites. *A. sexspinosa* reaches its southern limit in the neighbourhood of 18° S.

The form with 13 to 19 spines is Spence Bate's *A. acanthitelsonis*, described from the 'Challenger' collections. It appears to live in rather deeper water than *A. sexspinosa* and its southern limit is about 28° S. The collections examined indicate that these two species, *A. sexspinosa* and *A. acanthitelsonis*, occur only in the Central and South Atlantic, and occupy this area to the complete exclusion of all other members of the group.

Continuing southwards there is once again an abrupt change in the species. At 35° S. *A. sexspinosa* has given place to a form with 4 telson spines, and at 24° S. *A. acanthitelsonis* begins to be replaced by one with 7 to 11 spines: we have, strangely enough, returned to species closely similar to those in the North Atlantic. The 4-spined form can, however, be distinguished from its northern counterpart, for the dorsal carina of the 4th abdominal somite invariably ends in a tooth. The only name available for this form, *A. batei* Stebbing, is preoccupied in the genus, and I propose therefore to call it *A. quadrispinosa*. The form with 7 to 11 telson spines does not appear to differ from *A. hæckeli* in any feature of importance, and in the proportionate length of the adult rostrum it is intermediate between Mediterranean and North Atlantic specimens. In the absence of distinctive characters the same name, *A. hæckeli*, should be used for both northern and southern forms, the species thus having a widely discontinuous distribution. In the Atlantic sector of the southern ocean *A. quadrispinosa* extends nearly to 40° S., while *A. hæckeli*, living at greater depths and, as in the north, taking advantage of the warm intermediate layer of water, is able to reach 55° S.

Balss (1925, pp. 254-5) has recorded specimens from twenty-four stations in the Atlantic under the names *A. purpurea* and *A. acanthitelsonis*, and from the particulars he gives of the numbers of telson spines it is clear that his material is in good agreement with the statements made above: unfortunately, he does not give details of the teeth on the abdominal somites. He had 4-spined and 8-9-spined forms both in the north and south, with *A. acanthitelsonis* and a form with 5 or 6 spines in the intervening latitudes. The only discrepancy

is an 8-spined specimen from 4° S., which may perhaps be an abnormal *A. sexspinosa*.

Turning now to other parts of the world, the first point to be noted is that *A. haeckeli* and *A. acanthitelsonis*, with 7 or more telson spines, have no representative in the equatorial or northern waters of the Indian and Pacific Oceans. In southern latitudes *A. haeckeli* evidently has a circumpolar distribution. It was taken by the 'Dana' only at her southernmost stations in the New Zealand area, and it has been found by the 'Discovery II' to the west and south-west of Kerguelen and in the Bellingshausen Sea, south-west of Cape Horn. In the Indo-Pacific it does not extend so far north as in the Atlantic, not reaching north of 32° S. Its southern limit, so far as is known, is 57° S.

A. quadrispinosa has a wide Indo-Pacific distribution, which, in sharp contrast with that in the Atlantic, extends far north of the Equator. Its latitudinal limits are from 25° N. to 42° S., and it ranges from the East African coast to mid-Pacific in 163° W. The species has been recorded from the Indo-Pacific under the name of *A. purpurea* by various authors: by de Man (1920), (Balss 1925), Calman (1939), and others.

In the warmer parts of its Indo-Pacific range *A. quadrispinosa* is associated with two other members of the *purpurea* group. One of these, also with 4 spines on the telson, is an abundant form long recognized as distinct under the name of *A. sanguinea* Wood-Mason. This species is easily separated by the structure of the branchiostegal spine of the carapace, which exists merely as a small projection of the frontal margin and is not flared outwards and flanked by a short carina as it is in *A. quadrispinosa*. *A. sanguinea* extends from the Gulf of Aden (Calman) to the East Indian Archipelago in 138° E. Its southern limit is in 12° S. and in the east it reaches 18° N.

The other species associated with *A. quadrispinosa* is a large heavily-built form not hitherto recognized. In its proportions it differs widely from other members of the group; the carapace and abdomen are conspicuously deeper in proportion to their length, and the abdomen is relatively shorter than in any of the others, the length excluding the telson being less than twice as long as the

carapace. It has, constantly, only 3 pairs of spines on the telson. I propose for this species the name *A. smithi*, in recognition of the American carcinologist Sidney I. Smith, who was far in advance of any of his contemporaries in the accuracy of his work on deep-water Crustacea. *A. smithi* has a range extending from the East African coast to mid-Pacific (131° W.) and in the east it occurs from 20° N. to 24° S.

Only one other form remains to be mentioned. It occurs on the west coast of Central and South America and was recorded by Faxon as *Acanthephyra agassizi*? (a name which is synonymous with *A. purpurea*). This form appears to be closely related to *A. sanguinea*, for it has the same reduced branchiostegal spine and in the peculiar pitting of the carapace resembles this species and differs from all other members of the group. The rostrum, however, is very much shorter and, like *A. smithi*, it has only three pairs of spines on the telson. To this species, or variety, I give the name *trispinosa*. I have seen fewer specimens of it than of any of the others, and the rather meagre records indicate that it is found off the West Coast of America from 7° N. (Faxon) to 4° S. Specimens obtained by the 'Dana' show that it extends westwards into the Pacific as far as 116° W.

A point that will be noticed in this review is that certain oceanic regions, such as the North Pacific and that lying off the western coast of South America, are apparently not inhabited by any members of this otherwise universally distributed group of species. The deep-water pelagic fauna of the Pacific coasts of S. America no doubt needs further exploration, but so far as the North-west coast of America is concerned it seems that the deficiency is a real one. No representatives of the *A. purpurea* group were taken by the Harriman Alaska Expedition, and Mr. Fenner A. Chace of the Harvard Museum, to whom I am indebted for much information on the Hoplophoridae, tells me that he knows of no records from this area.

A question which naturally arises is the amount of variation in the number of telson spines and the extent to which the character is reliable. In the telson, though to a lesser degree than in the rostrum, abnormalities sometimes occur, and these appear generally to be due

to injury. A moult succeeding the injury may result in a telson more or less normal in form, but either by its reduced length or from other evidence abnormalities can usually be detected. As to normal variation, it is comparatively common to find some irregularity in the disposition of the spines on the two sides of the telson; but with the lower numbers, 3 and 4, any deviation from the specific number occurs, on one side only, in a very small percentage of specimens, while it is exceedingly rare (though not unknown) for a 3-spined species to possess 4 pairs of spines or *vice versa*. In *A. sexspinosa* 5 spines are not uncommon on one side only, and throughout the area of its distribution 5 pairs are occasionally found. In *A. hæckeli* and *A. acanthitelsonis* there is naturally a range of numbers rather than a fixed number. The observed limits are 7 to 11 in the former* and 13 to 19 in the latter. Stephensen records a specimen of *A. multispina* (= *A. hæckeli*) with 13 pairs—presumably an abnormality. Specimens with 12 spines are extremely scarce: I have not seen any myself.

The species of *Acanthephyra* discussed in this paper may be distinguished from other representatives of the genus †:—

Carapace without a dorsal carina in posterior half; laterally not carinate or with a short branchiostegal carina not nearly reaching to hepatic groove. Rostrum well formed, reaching almost to or beyond end of antennal scale, with teeth along whole length of upper margin and with three or more teeth below. Cornea wider than eyestalk. Abdomen dorsally carinate on second to sixth somites; carinæ of at least third and sixth somites ending in teeth. Telson dorsally sulcate at proximal end, with three or more pairs of dorso-lateral spines, excluding those at apex.

The eight forms in the group may be diagnosed thus:—

Acanthephyra acanthitelsonis Spence Bate, 1888.

Branchiostegal spine of carapace strong, flared outwards and supported by a sharp carina extending back-

* Stephensen notes that six spines are sometimes found in Mediterranean specimens.

† In Chace's recent key to *Acanthephyra* (1936) the species fall under section 11.

wards on to carapace for fully three times length of spine. Surface of carapace very finely and evenly pitted. Dorsal carinæ of third to sixth abdominal somites ending posteriorly in a tooth; that of third somite longer than any other. Telson with 13 to 19 pairs of dorso-lateral spines*. Form slender; dorsal length of sixth somite, without spine, twice or rather more than twice its depth at posterior end. Rostrum in adults usually not reaching to end of antennal scale and shorter than carapace †. Length ‡ up to 134 mm.

Central and South Atlantic, from about 14° N. to 28° S.

Acanthephyra hæckeli (von Martens), 1868.

Resembling *A. acanthitelsonis* in most characters, but with 7 to 11 pairs of dorso-lateral spines on telson. Rostrum in adults sometimes extending beyond antennal scale and longer than carapace. Length up to 147 mm.

Distribution discontinuous. N. Atlantic from Davis Strait and Iceland to about 13° N. Mediterranean. S. Atlantic from 24° S. southwards. Circumpolar in southern latitudes, extending north to 32° S. Length up to 134 mm.

Synonyms: *A. sica* Spence Bate, *A. rectirostris* Riggio, *A. parva multidentis* Coutière, *A. multispina* Coutière (Sund).

Acanthephyra sexspinosa, sp. n.

Branchiostegal spine of carapace strong, directed somewhat outwards; not buttressed by a definite carina but forming the termination of a short, smoothly rounded swelling. Surface of carapace finely and uniformly pitted. Dorsal carinæ of both fourth and fifth abdominal somites, in adults, not ending posteriorly in a tooth; dorsal tooth of third somite long, much exceeding that on sixth somite. Form slender, dorsal length of sixth somite, without spine, about twice its posterior depth. Rostrum in adults extending beyond antennal scale, but usually shorter than carapace. Length up to 96 mm.

Central and South Atlantic from 17° N. to 18° S.

* Excluding those which form the terminal cluster at the apex of the telson.

† Measured from the back of the orbit to the mid-dorsal point of the posterior margin.

‡ From tip of rostrum to tip of telson.

Acanthephyra purpurea A. Milne-Edwards, 1881.

Branchiostegal spine of carapace strong, flared outwards and supported by a conspicuous carina extending backwards on to carapace for fully twice length of spine. Surface of carapace coarsely and uniformly pitted. Dorsal carina of fourth abdominal somite, in adults, not ending posteriorly in a tooth; tooth of third somite much longer than that of fifth or sixth somites. Telson with 4 pairs of dorso-lateral spines. Form slender, dorsal length of sixth somite, without spine, more than twice its depth at posterior end. Rostrum in adults extending much beyond antennal scale and longer than carapace. Length up to 105 mm.

North Atlantic to the north of 20° N.

Synonyms: *Miersia Agassizi* Smith, *Acanthephyra parva paucidens* Coutière.

Acanthephyra quadrispinosa, sp. n.

Resembling *A. purpurea* in all the characters noted above except for the constant presence of a tooth at the distal end of the dorsal carina of the fourth abdominal somite; this tooth is a little smaller than that on the fifth somite. The pitting on the carapace is uniform but is finer than in *A. purpurea*. Length up to 111 mm.

South Atlantic from 32° S. to 40° S. Indo-Pacific from the E. African coast to 163° W., and from 25° N. to 42° S.

Synonym: *A. batei* Stebbing (*nec* Faxon).

Acanthephyra sanguinea Wood-Mason, 1892.

Branchiostegal spine extremely small, in large specimens sometimes obsolete, forming merely a small projection on frontal border of the carapace and not supported by a carina or swelling. Surface of carapace finely pitted; pits aggregated so as to form narrow, slightly curved bands, disposed vertically and with smooth interspaces between*. Dorsal carinae of third, fourth, fifth, and sixth somites ending in a tooth; that

* The pits, in all species of the *purpurea* group, form the points of attachment of small lanceolate scales which overlap each other, with the tips directed forwards. In preserved specimens of most species these scales are usually rubbed off, but in *A. sanguinea* they are more persistent and patches of scales, forming a thick tomentum, are frequently seen.

of third somite the largest and of fourth the smallest. Telson with four pairs of dorso-lateral spines. Form moderately slender; dorsal length of sixth somite, without spine, usually twice or nearly twice its posterior depth, one and two-thirds times in very large specimens. Rostrum long, in adults extending beyond antennal scale and exceeding length of carapace. Length up to 126 mm.

Indo-Pacific from the Gulf of Aden and East African coast to 138° E., and from 18° N. to 12° S.

Synonym: *A. kempii* Balss, which is based on a specimen with a malformed rostrum.

Acanthephyra trispinosa, sp. n.

Closely related to *A. sanguinea*, with which it agrees in the disposition of the pits on the surface of the carapace. Branchiostegal spine very small, on frontal margin, with only the barest indication of a swelling at its base. Dorsal carinae of third to sixth abdominal somites ending in a tooth; that of third somite much the largest, that of fourth scarcely smaller than that on fifth. Telson with three pairs of dorso-lateral spines. Form moderately slender, dorsal length of sixth somite, excluding spine, about twice its posterior depth. Rostrum in adults extending to or slightly beyond end of antennal scale, but always shorter than carapace. Length up to 86 mm.

West coast of Central America from 7° N. to 4° S., extending westwards to 116° W.

Acanthephyra smithi, sp. n.

Branchiostegal spine of carapace not strong, scarcely directed outwards; not buttressed by a definite carina but forming the termination of a short smoothly rounded swelling. Surface of carapace very finely and uniformly pitted. Dorsal carina of second to sixth abdominal somites exceptionally high; carinae of third to sixth somites ending in large teeth, that of third little if at all larger than the others. Telson with three pairs of dorso-lateral spines. Form unusually stout; abdomen short, its length, excluding telson, less than (in large specimens much less than) twice length of carapace*; dorsal length

* In all the other species of the group the abdomen is more than twice as long as the carapace.

of sixth abdominal somite not more than one and a half times its posterior depth. Rostrum, in adults, not extending beyond end of antennal scale and always shorter than carapace. Length up to 127 mm.

Indo-Pacific from the East African coast to mid-Pacific in 131° W. At the western end of its range it extends to 14° S. and at the eastern end from 20° N. to 24° S.

In this paper I have called all the forms species, though it must be admitted that the characters which differentiate them are for the most part of minor importance when compared with those which serve to separate other members of the genus. Some may prefer to regard *A. quadrispinosa* as a subspecies of *A. purpurea*, and *A. trispinosa* as a subspecies of *A. sanguinea*. But though the distinctions between these pairs of forms are confined to a single character, except for an occasional freak specimen they are absolute, and the component forms in each pair are geographically isolated from each other. *A. acanthitelsonis*, with perhaps more reason, might be considered a subspecies of *A. hæckeli*, and the distribution of the former abuts on that of the latter in the North Atlantic and overlaps it by some 4° in the South Atlantic, but here again the character, so far as is known, is absolute, and there is no intergradation between the two forms at their points of contact.

I have found it particularly difficult to reach any feeling of certainty about *A. hæckeli*, here regarded as a single form with a discontinuous distribution in the North Atlantic and Mediterranean and in southern latitudes. Caridea are animals with such a large number of parts that it is not easy to convince oneself of the identity of specimens from different regions. I have failed to find any valid differential characters between the two groups, but it is quite possible that such characters exist and will ultimately be discovered.

The distributional facts brought to light in this group of species appear to me to be noteworthy. Marine animals show a fixity of specific characters not usually seen in land faunas, and this is generally attributed to the uniformity of their environment and the lack of

barriers to a wide dispersal. And of all marine environments the open ocean is commonly regarded as presenting the most uniform conditions. In consequence, it was by no means unexpected to find, as we do both in the Hoplophoridae and in many other groups of pelagic oceanic animals, that a single species might be found at a number of widely distant localities without exhibiting the slightest deviation from a set pattern of structural characters. It is thus not a little astonishing to find that these abundant pelagic Caridea have become differentiated in the various oceans.

Improved hydrographic knowledge will perhaps reveal environmental differences in the oceans which will throw light on the distribution of *A. purpurea* and its allies, and eventually, by this means, it may be possible to explain how such species as *A. sexspinosa* and *A. acanthitelsonis* are able to occupy a well-defined area in the Atlantic without being dispersed by ocean currents into regions inhabited by other forms.

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