

On the Classification and the Distribution of the Crayfishes. By T. H. HUXLEY, Sec. R.S., V.P.Z.S.

[Received May 23, 1878.]

- I. Introduction, p. 752.
- II. The Modifications of the Branchiæ in the Crayfishes, p. 756.
 - 1. The branchiæ of *Astacus*, p. 756.
 - 2. The branchiæ of *Cambarus*, p. 763.
 - 3. The branchiæ of *Astacopsis*, p. 764.
 - 4. The branchiæ of *Chærops*, p. 768.
 - 5. The branchiæ of *Engæus*, p. 769.
 - 6. The branchiæ of *Paranephrops*, p. 770.
 - 7. The branchiæ of *Parastacus*, p. 771.
 - 8. The branchiæ of *Astacoides*, p. 773.
- III. The Classification of the Crayfishes, p. 775.
- IV. The Distribution of the Crayfishes considered in relation to their morphological differences, p. 786.

I. INTRODUCTION.

The dismemberment of the genus *Astacus* of the older naturalists, down to the time of Fabricius, was commenced by Leach, who separated the Norway Lobster as the type of a new genus, *Nephrops*¹.

Milne-Edwards advanced a step further by establishing the genus *Homarus* for the Lobsters, and leaving only the freshwater *Astaci*, or the proper Crayfishes, in *Astacus*².

The later proposal of Leach, to use *Astacus* for the Lobsters, and to give a new generic name (*Potamobius*) to the freshwater Crayfishes, would have had the advantage of retaining the primitive signification of ἀστράκος. But *Potamobius* had already been used in another sense; and the change introduced by Milne-Edwards is so generally adopted that it would be confusing to attempt any further alteration.

Guérin³ next proposed to distinguish the *Astacus madagascariensis* of Audouin and Milne-Edwards, as *Astacoides*, from the other Crayfishes; and Erichson, in his valuable Monograph of the group⁴, adopts *Astacoides* for the Madagascar and some of the Australian forms, and establishes the new genera *Cambarus*, *Chærops*, and *Engæus*. In *Cambarus* and *Chærops* the number of the branchiæ is taken into account as an important generic character.

In 1842⁵ Mr. Adam White described some Crayfish from New Zealand, for which he constituted a new genus, *Paranephrops*, under the impression that the New-Zealand form approximated to the genus *Nephrops*. Mr. Wood-Mason⁶ has since "denied the existence of any special relationship between the New-Zealand

¹ Leach, Trans. Linn. Soc. xi. 344.

² 'Histoire Naturelle des Crustacés,' 1837.

³ Revue Zoologique, 1839.

⁴ "Uebersicht d. Gattung Astacus," Archiv für Naturgeschichte, Bd. 6.

⁵ Gray's 'Zoological Miscellany.' See also Dieffenbach's 'New Zealand,' 1843, vol. ii. p. 267.

⁶ Proc. Asiat. Soc. Bengal, 1876, p. 4.

species of freshwater *Astacidae* and the marine genus *Nephrops*;" and "as the species referred to *Paranephrops* differed less from [some of] those of *Astacoides* than these latter did from one another, and as, moreover, the latter name had the priority, he proposed provisionally to refer the New-Zealand species of *Astacidae* to it."

Mr. Wood-Mason is unquestionably right both in denying any special relationship between *Paranephrops* and *Nephrops*, and in asserting that the New-Zealand Crayfish differ less from some of the species of the genus *Astacoides*, as its limits are at present understood, than these do from one another. But I shall have occasion to show that the type of the genus *Astacoides*, the Madagascar Crayfish, differs so widely from the other Crayfishes of the southern hemisphere, that the latter cannot be included in the same genus; while *Paranephrops* is sufficiently different from the Australian and Tasmanian Crayfishes to render its recognition as a distinct generic type desirable¹.

The distribution of the Crayfishes, so far as it is hitherto ascertained, is not a little remarkable. *Astacus fluviatilis* occurs in various parts of England and in Ireland; but I cannot find any record of it in Scotland. Dr. M'Intosh, who has been kind enough to look into this point in aid of my inquiries, assures me that Crayfishes are not indigenous to that part of Britain, that they do not exist in the Tweed and the Teviot, and that an attempt to introduce them into the island of Mull failed; they were placed in various streams, but none were ever seen again. Even in England, Crayfishes appear to be restricted to certain rivers. They abound, for example, in the Thames; but I cannot hear of any in the Cam or the Ouse, though their absence in the latter rivers cannot be ascribed to any want of calcareous matter in the districts through which those rivers flow.

Astacus fluviatilis, however, extends all over the western half of Europe, as far south as the Pyrenees and the northern shores of the Mediterranean; while, eastward, it reaches Sicily, Northern Greece, and the western shores of the Black Sea. In Spain there appears to be no doubt that it occurs about Barcelona; but whether it is found in the rest of the Spanish peninsula is uncertain².

Northwards and eastwards, *Astacus fluviatilis* extends to Sweden and the Baltic provinces of Russia, and through Western Russia, by the basins of the Dniester and the Bug, to the Black Sea.

Over this vast area, marked local varieties appear to be not uncommon; and most authors agree to regard a Crayfish which occurs in Southern Europe, France, Switzerland, and Germany, and which

¹ See on this subject the remarks of Mr. Miers, "Note on the genera *Astacoides* and *Paranephrops*" (Ann. & Mag. Nat. Hist. ser. 4, vol. xviii. 1876).

² See Gerstfeldt, "Ueber die Flusskrebse Europa's" (Mém. présentés à l'Acad. Imp. des Sciences de St. Petersburg, 1859, p. 587). As far back as 1675, Sachs à Lewenbeimb wrote:—"Sic in Hispaniâ licet flumina, negant inveniri ibi *Cancros fluviatiles*, contra in Galliâ frequentissimi, item in Pannoniâ, in Helvetiâ, in Germaniâ; etiam in fluviis Americanis inveniri referunt navigatores. In fluvio Lydiæ Haly cancos invenit Busbequius, Ep. Turc. i. p. 89." But were these Lydian "cancri" crayfishes or fluviatile crabs?

is known in the latter country as the "Steinkrebs," as a distinct species, *Astacus torrentium* or *A. saxatilis*¹.

Eastward of the region inhabited by *Astacus fluviatilis*, from the Arctic to the Black and Caspian Seas, another species, *A. leptodactylus*, ranges, associated with the allied but possibly distinct forms *A. pachypus* and *A. angulosus*, in the southern part of the area; and it is remarkable that these Crayfishes not only frequent the rivers which debouch into the Black Sea and the Caspian, but are said to thrive in the salt waters of those seas.

No Crayfishes are known in the Ob, Jenisei, Lena, or other rivers which flow into the Arctic Ocean²; but the Amur has one or two species (*A. dauricus*). There is a species in Japan (*A. japonicus*); and Dr. Hagen³ enumerates no fewer than six species from British Columbia, Oregon, and California.

East of the Sierra Nevada, all the Crayfishes at present known belong to the genus *Cambarus*, of which Dr. Hagen distinguishes as many as thirty-two species. They extend from the Great Lakes to Mexico, Guatemala, Cuba, and probably other of the West-India Islands. Sloane, in his 'Natural History of Jamaica' (vol. ii. p. 271) describes two species in that island. According to the figure, one of these attains a length of 12 inches.

No Crayfishes are known to occur in the whole continent of Africa, in Syria, the Euphrates valley, Persia, Hindostan, and India beyond the Ganges, nor in China as far as the Corea, nor in the Philippines, nor in any island of the Malay or Papuan archipelagos⁴. The late Prof. Agassiz, though he sought for Crayfishes in the

¹ In 1560, Gesner was acquainted with this distinction:—"Astacus fluviatilis talis apud Helvetios et Germanos est, major silicet et simpliciter dictus *Krebs* vel *Edelkrebs*; eo enim minor est, et colore diversus qui saxatilis cognominatur *Steinkrebs*." ('Nomenclator Aquatiliū,' p. 374). Heller (Die Crustaceen des südlichen Europa, p. 217) refers our English Crayfish to this species; but no specimens I have seen agree with his diagnosis. Whether there is any difference between *A. saxatilis* and the Crayfishes which have been named *A. pallipes* and *A. fontinalis* by Lereboullet and Carbonnier; and whether our English Crayfish is more similar to these than to the form which is commonly known as *A. fluviatilis* on the Continent, is more than I am able to say at present. A critical comparison of large series of specimens from different localities would probably yield results of great interest to the theory of the origin of species.

² Kessler, "Die russischen Flusskrebse" (Bull. de la Soc. Imp. des Nat. de Moscou, 1874).

³ 'Monograph of the North-American Astacidae,' Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College, 1870.

⁴ I have been favoured by Sir Henry Barkly with the opportunity of examining specimens of two kinds of "Cammarons," or so-called Crayfishes, from the rivers of Mauritius. They are large Prawns.

I must confess myself to be in a state of hopeless perplexity respecting the Crayfish or Lobster which is said to occur at the Cape of Good Hope, *Cancer* (*Astacus*) *capensis* of Herbst. At the beginning of his description (Naturgeschichte der Krabben und Krebse, Band ii. p. 49) Herbst says:—"Dieser schöne Krebs hält sich auf den Kap in solchen Flüssen auf, die sich auf den Bergen befinden;" and at the end he states, "die Füße haben insgesamt scheerenförmige Spitzen, da bey dem gemeinen Flusskrebs nur die ersten zwey Paare dergleichen haben." Moreover, the diagnosis runs, "pedibus omnibus cheliferis." It is impossible to suppose that Herbst should have made a mistake on such a point as this; and therefore it must be concluded that his *Cancer ca-*

Amazons, could find none. Two species from Southern Brazil have been described by Dr. von Martens¹ as *Astacus brasiliensis* and *A. pilimanus*; but Von Martens recognizes the affinity of these forms with the *Astacoides* of Erichson.

Several species of *Paranephrops* have been described from New Zealand; and the Fijian Crayfish belongs to the same genus.

Crayfishes occur all over Australia; and the species have been referred to the genera *Astacoides* and *Chærapa*. The only Tasmanian species which have been described constitute the genus *Engæus* of Erichson.

Thus it appears, from what is already published on this subject:—

1. That the Crayfishes of the northern hemisphere are generically distinct from those of the southern hemisphere.

2. That the American Crayfishes, east of the Sierra Nevada, are generically distinct from those west of that range, as well as from the South-American species; and that, while the western North-American Crayfishes belong to the same genus as those of the Old World, the South-American forms are more closely allied with those of Madagascar and Australia.

3. That the New-Zealand species are distinct from the Australian forms; and that the latter are to be placed in the same genus as the Madagascar and South-American species.

4. That there is a negative fact of distribution, not to be accounted for by any apparent difference of climate or other physical conditions—namely, the entire absence of Crayfishes in Equatorial South America, Africa, and the rest of the Old World south of the northern escarpment of the great Asiatic highlands.

The problem thus offered is one of the most remarkable among the many presented by the facts of Geographical Distribution; and it appeared to me that one of the first steps towards attempting its solution was to obtain some more definite conception, than is furnished by extant descriptions, of the actual amount of resemblance and difference between the Crayfishes which are found in the different areas of distribution.

For the most part the Crayfishes are so similar in their general structure, that the characters by which the genera have been distinguished are almost trivial. Erichson, however, has drawn attention

pensis is neither a Crayfish nor a Lobster, and that, unless he was wrongly informed, it is an inhabitant of fresh water.

Milne-Edwards (Hist. Nat. des Crustacés, ii. p. 335) identifies his *Homarus capensis* with the *Cancer capensis* of Herbst; but, as it is stated in the definition of the genus *Homarus* (l. c. p. 333) that the Lobsters “ne se trouvent que dans la mer,” and as *Homarus* has only three pairs of chelate limbs, the identification presents difficulties. Krauss (Südafrikanische Crustaceen, p. 54), under the head of “*Homarus capensis*,” refers to Herbst and Milne-Edwards, and, apparently on the authority of the former, merely says:—“In den Bergflüssen des Kaplandes. Ich habe ihn in Natal nie gesehen.” Elsewhere (p. 20) he gives “*Thelphusa perlata* and *T. depressa* and *Homarus capensis*” as the only South-African freshwater Thoracostraca.

¹ “Südbrasilische Süß- und Brackwasser-Crustaceen,” Archiv für Naturgeschichte, 1869.

to the diminution of the number of the branchiæ in *Cambarus* and *Astacus*, and to an important difference in the structure of those of *Engæus*; and Hagen has pointed out some important peculiarities of these organs in *Cambarus*; while the remarkable fact, that the appendages of the first somite of the abdomen are absent in many of the Crayfishes of the southern hemisphere, has been duly noted by Erichson and several other zoologists.

Having recently had occasion to make a careful reexamination of the structure of *Astacus fluviatilis*, I found two minute filaments attached to the epimera of the penultimate and antepenultimate thoracic somites. The structure and the position of those filaments led me to suspect that they must be rudimentary branchiæ¹; and as the Australian Crayfishes appeared to me to be, on the whole, less specialized forms than the European species, I thought that I should probably find in them fully-formed functional branchiæ occupying the place of these rudiments. Through the kindness of my friend and former pupil, Mr. J. Wood-Mason, a specimen of "*Astacoides*" *franklini* was placed at my disposal; and on examination, I not only found the functional branchiæ I sought, but discovered a number of other interesting differences between the respiratory organs of this Crayfish and those of *Astacus*.

Following up the line of inquiry thus suggested, I have examined examples of all the chief forms of Crayfishes at present known, with the result of establishing some remarkable parallel relations between the morphology and the distribution of these animals.

In order to make these points clear, I must premise a fuller and more precise description of the branchial apparatus of the common Crayfish than has yet been given, in order that it may serve as a standard of comparison for the branchiæ of the other Crayfishes.

II. THE MODIFICATIONS OF THE BRANCHIÆ IN THE CRAYFISHES.

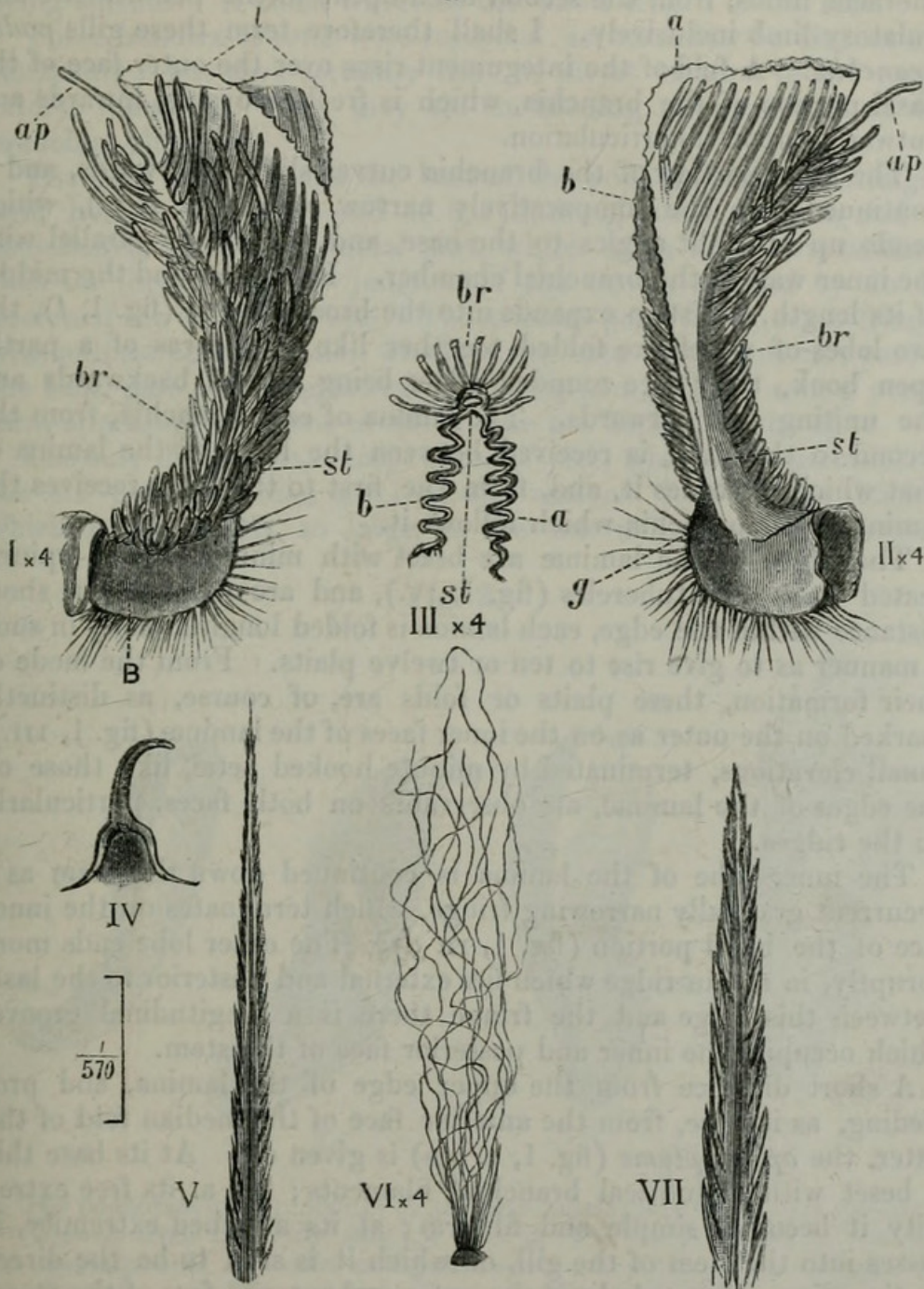
The Branchiæ of Astacus fluviatilis.

When the branchiostegite of a Crayfish is removed, seven branchiæ are seen, running from the base towards the apex of the branchial cavity, parallel with one another, and disposed in curved lines, which are concave forwards and convex backwards. The length of the branchiæ gradually increases from the first to the sixth; the seventh ascends as high as the sixth, but is rather shorter, in consequence of the attachment of its base lying at a higher level.

In each of the six anterior branchiæ, a *basal portion*, a *stem*, an expanded *lamina*, and an *apical plume* may be distinguished. The *basal portion* (fig. 1, I, B) is broad, with a convex posterior and inferior free edge, beset with long setæ; and it is articulated by its

¹ I have met with no allusion to these structures, unless the following passage in Brandt's and Ratzeburg's description of the Crayfish (Med.-Zoologie, ii. p. 61) refers to them:—"Ueber jeder der obersten Kiemen der beiden mittlern Fusspaare steht etwa 1''' entfernt ein kleiner fadenförmiger, unten breiterer, bärtelähnlicher Theil." I do not quite see the applicability of "unten breiterer," unless "unten" applies to the attached ends of the filaments; but in other respects the description fits the rudimentary branchiæ very well.

Fig. 1.

*Astacus fluviatilis.*

- I. The outer face of the podobranchia of the antepenultimate thoracic limb of the left side ($\times 4$): B, the basal portion; st, the stem; l, the lamina; br, the branchial filaments; ap, the apical plume. II. The inner face of the same podobranchia ($\times 4$): the letters as before, except g, the decurrent fringe, continued from the inner lobe of the lamina. III. A transverse section of the podobranchia, taken a little above the level of b in II. ($\times 4$): a, the inner lobe of the lamina; b, its outer lobe; st, the stem; br, the branchial filaments. IV. One of the hooks of the lamina; and V The extremity of one of the setæ of the base of the podobranchia: the vertical line indicates the scale to which these figures are drawn, and represents $\frac{1}{570}$ of an inch. VI. The coxopoditic setæ of the same limb ($\times 4$). VII. The free end of one of these setæ, magnified to the same degree as IV. and V.

truncated anterior end with the coxopodite of one or other of the thoracic limbs, from the second maxillipede to the penultimate ambulatory limb inclusively. I shall therefore term these gills *podobranchiæ*. A fold of the integument rises over the outer face of the basal portion of the branchia, which is freely movable, inwards and outwards, upon its articulation.

The basal portion of the branchia curves slightly upwards, and is continued into the comparatively narrow *stem* (fig. 1, *st*), which bends up at right angles to the base, and lies nearly parallel with the inner wall of the branchial chamber. Rather beyond the middle of its length, the stem expands into the broad *lamina* (fig. 1, *l*), the two lobes of which are folded together like the leaves of a partly open book, their free rounded edges being turned backwards and the uniting fold forwards. The lamina of each branchia, from the second to the sixth, is received between the lobes of the lamina of that which precedes it, and, from the first to the fifth, receives the lamina of the branchia which follows it.

The edges of the laminæ are beset with minute hooked spines, seated upon low tubercles (fig. 1, *iv.*), and are flat; but, a short distance within the edge, each lamina is folded longitudinally in such a manner as to give rise to ten or twelve plaits. From the mode of their formation, these plaits or folds are, of course, as distinctly marked on the outer as on the inner faces of the laminæ (fig. 1, *iii.*). Small elevations, terminated by minute hooked setæ, like those on the edges of the laminæ, are observable on both faces, particularly on the ridges.

The inner lobe of the lamina is continued down the stem as a decurrent gradually narrowing fringe, which terminates on the inner face of the basal portion (fig. 1, *ii. g*). The outer lobe ends more abruptly, in a thin ridge which lies external and posterior to the last. Between this ridge and the fringe there is a longitudinal groove, which occupies the inner and posterior face of the stem.

A short distance from the upper edge of the lamina, and proceeding, as it were, from the anterior face of the median fold of the latter, the *apical plume* (fig. 1, *i. a p*) is given off. At its base this is beset with cylindrical branchial filaments; but at its free extremity it becomes simple and filiform; at its attached extremity, it passes into the stem of the gill, of which it is seen to be the direct continuation. The whole of the outer and anterior face of the stem, as far as the basal fold, is beset with branchial filaments, of which those in the region of the lamina are the longest, while towards the base they are shorter and more closely set.

Close to the attachment of the podobranchia, the upper surface of the coxopodite presents a rounded elevation, from which a great number of long, flexible and tortuous setæ proceed (fig. 1, *vi.*). When undisturbed, they ascend vertically between the gills on the sides of the branchial chamber. The apex of each of these *coxopoditic setæ* is acute; and at a short distance from its extremity it is beset with numerous short foliaceous scales, which gives it the aspect of a minute catkin (fig. 1, *vii.*). Further down these scales become

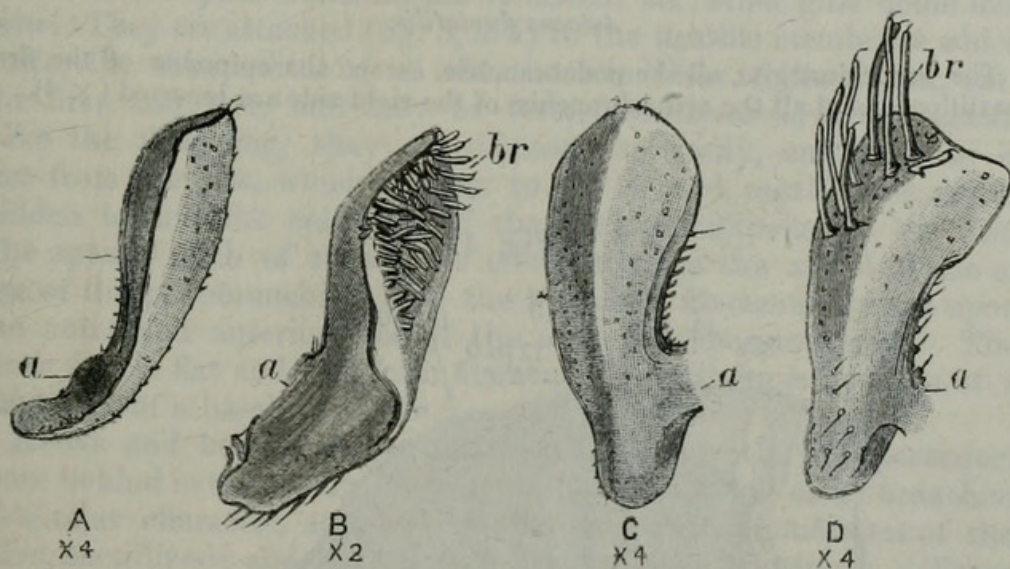
more widely separated, and at length disappear, the base of the seta being smooth. A canal traverses the whole length of the seta.

These bundles of setæ were regarded as branchiæ by Brandt and Ratzeburg; but they certainly have no direct relation to the respiratory function. They may aid in keeping parasites out of the branchial chamber.

The setæ which fringe the base of the podobranchia are straight, stiff, hollow, and composed of a cylindrical basal portion, and an acuminate acicular terminal part, which often appears articulated with the foregoing; the junction of the two is marked by an inflexion of the wall of the seta. The acicular part (fig. 1, v.) is fringed with minute pointed scales, which, in the setæ of the anterior part of the base, pass into long lateral processes, and give the seta a penniform appearance. None of these setæ are hooked at the apex.

The only differences, except those of size, which are observable in the six podobranchiæ, are, that the external lobe of the lamina, which is not nearly so large as the internal, in the hindermost

Fig. 2.

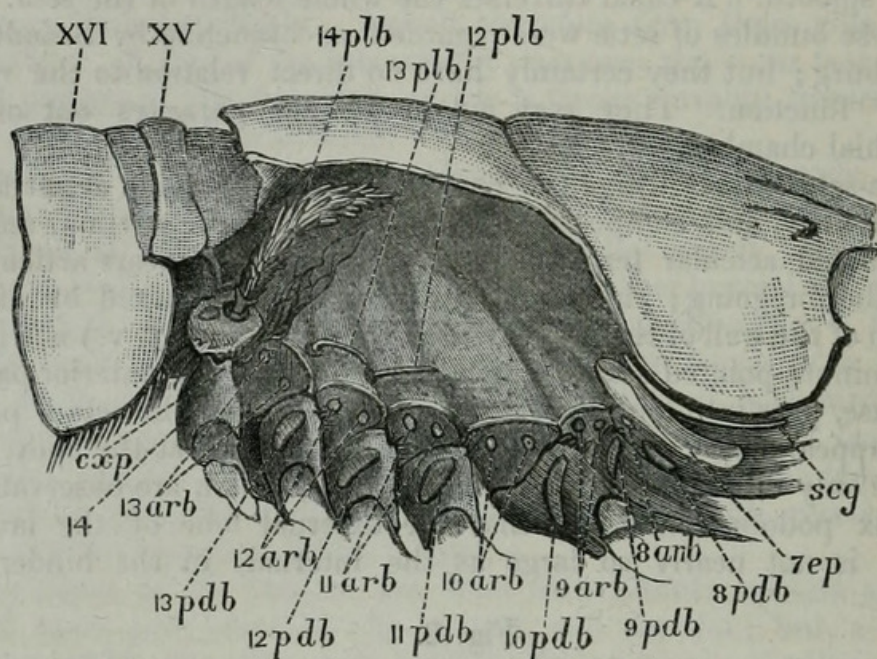


- A. The podobranchia (epipodite) of the first maxillipede of *Astacus fluviatilis*, viewed from the outer side ($\times 4$). B. The podobranchia of the first maxillipede of *Astacoides madagascariensis*, outer side ($\times 2$): *br*, branchial filaments. C. The podobranchia (epipodite) of the first maxillipede of *Astacus fluviatilis*, viewed from behind ($\times 4$). D. The podobranchia of the first maxillipede of *Parastacus brasiliensis*, from behind ($\times 4$); *br*, branchial filaments. In each figure *a* marks the pedicle by which the more or less modified podobranchia is attached to the coxopodite.

branchia increases in relative size, until, in the most anterior branchia it becomes larger than the internal lobe. The penniform setæ are more numerous on the bases of the anterior podobranchiæ.

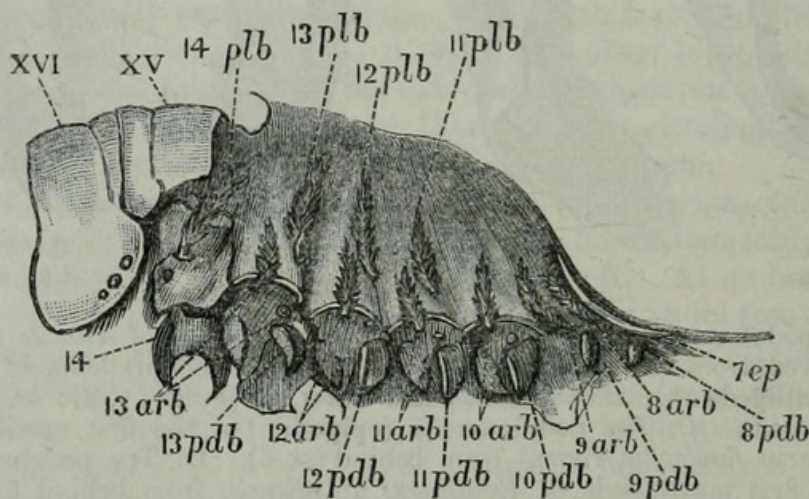
The first maxillipede is said, and, in a physiological sense, rightly, to possess no branchia; but it is provided with an appendage (fig. 2, A, C) which is undoubtedly the homologue of the podobranchia of the other thoracic limbs. This is a soft membranous

Fig. 3.

*Astacus fluviatilis.*

The branchiostegite, all the podobranchiæ, except the epipodite of the first maxillipede, and all the arthrobranchiæ of the right side are removed ($\times 4$).

Fig. 4.

*Astacopsis franklinii.*

The branchiostegite, all the podobranchiæ, except that of the first maxillipede, and all the anterior arthrobranchiæ, except the first, of the right side are removed ($\times 2$).

scg, scaphognathite (not shown in fig. 4); 7ep, the podobranchia of the first maxillipede; 8pdb to 13pdb, the other podobranchiæ; 8arb to 13arb, the arthrobranchiæ or their attachments to the arthrodial membranes of the second and following thoracic appendages; 11plb to 14plb, the pleurobranchiæ; 14, the coxopodite of the hindermost ambulatory limb; exp, the coxopoditic setæ of that limb in *Astacus*.

plate, which broadens at its upper extremity, and sends a short process downwards beyond its articulation with the coxopodite of the maxillipede. The plate is slightly folded upon itself longitudinally, but in such a manner that it is concave forwards instead of backwards. It bears no branchial papillæ, and has no longitudinal plaits; but, on its posterior face and along its inner edge, it presents hooked tubercles, like those of the laminæ of the podobranchiæ. It is obvious that this structure, which lies immediately behind and parallel with the scaphognathite of the second maxilla (but, as I have ascertained, does not share its function of scooping the water out of the branchial cavity¹), is a modified podobranchia, reduced, as it were, to the part which, in the other podobranchiæ, is represented by the base, stem, and lamina.

Thus every thoracic limb, except the last, is provided with the representative of a podobranchia—though, in the case of the first maxillipede, this structure, if it plays any part in the respiratory process, does so simply in virtue of its thin and soft texture, and not by means of any special branchial filaments. The podobranchia of the first thoracic appendage is, in fact, reduced to a mere *epipodite*.

When the podobranchiæ are removed, six other gills come into view. They are attached (fig. 3, *arb*) to the flexible membrane which unites the coxopodites of all the thoracic limbs to the thorax, save the first and last, and may be termed *anterior arthrobranchiæ*. Like the foregoing, they are disposed vertically, and increase in size from the first, which belongs to the second maxillipede and is hidden behind the epipodite of the first maxillipede, to the last. The apex of each of these gills is exactly like the apical plume of one of the podobranchiæ; and the branchial filaments are set upon the outer and anterior face of the stem in the same way. The inner face is flat and free from filaments; and there is no trace of a lamina or of a basal dilatation.

Above and behind these, more directly above in the posterior, more behind in the anterior limbs (fig. 3, *arb*), are five other branchiæ of similar character, attached to the arthrodial membranes of the third maxillipede and the anterior four ambulatory limbs. These may be termed the *posterior arthrobranchiæ*.

After the removal of all these functional branchiæ, there will be found, immediately above the bases of the penultimate and antepenultimate thoracic limbs (fig. 3, 12 *plb*, 13 *plb*), two minute filamentous processes, the longer of which was not more than one sixth of an inch in length in any specimen I have examined, while both are so delicate as to be invisible except under a simple lens. The posterior of these is the larger: it has the structure of an ordinary branchial filament, with a somewhat swollen base, which is attached to the margins of a foramen in the lower part of the epimeron of the penultimate thoracic somite, just below a transverse depression which separates this from the upper part of the epimeron. The position

¹ If the branchiostegite of a living Crayfish is carefully removed, the rapid rhythmical motion of the scaphognathite is readily seen; but the modified podobranchia of the first maxillipede remains quiescent.

of this filament is sometimes vertical, but more frequently horizontal. The anterior filament is sometimes a mere papilla; it is attached to the margins of a small foramen which occupies a similar position in the antepenultimate epimeron—namely, close to the anterior edge and just below the transverse depression. These are two rudimentary gills, of the same order as that next to be described.

The seventh, and most posterior branchia of those which become visible when the brachistegite is removed (fig. 3, ¹⁴ *plb*), has yet to be considered. It resembles one of the arthrobranchiæ in all essential characters, but it is not attached to the arthrodial membrane; on the contrary, the base of its stem is fixed to the margins of a circular aperture situated close to the edge of a peculiar shield-shaped plate, the posterior and outer surface of which is covered with strong setæ. Immediately behind and below the attachment of the gill there is an oval space, occupied by a soft and flexible portion of the cuticle, like a tympanic membrane. By its lower margin this plate furnishes an articular surface to the outer condyle of the coxopodite of the last thoracic limb, while its anterior and upper angle, bending sharply upwards, passes into a curved prolongation, which extends upwards and backwards in the soft integument of the flank, and articulates with a slender process of somewhat similar form sent forward from the first abdominal somite. Internally this shield-shaped branchiferous plate is continuous with the sternum of the last thoracic somite. It is obvious that this plate, with its anterior process, represents the epimeron of the last thoracic somite, which is thus adherent to the penultimate somite only by the slender anterior and superior process and the soft integument. Hence, the last thoracic somite moves easily upon its predecessor, though, in strictness, the usual statement that the last thoracic somite in *Astacus* is "free" is not altogether exact.

It follows from this determination of the nature of the shield-shaped plate, that the gill which it bears is attached to the epimeron, or side-wall, of the last thoracic somite; and it may be termed a *pleurobranchia*. The similarly attached filaments (¹² *plb* and ¹³ *plb*) represent reduced or rudimentary pleurobranchiæ.

We may suppose that the total number of branchiæ which a thoracic somite can possess is eight, four on each side, namely:—one podobranchia, connected with the coxopodite of the appendage; two arthrobranchiæ, fixed to the articular membrane; and one pleurobranchia, attached to the epimeron. And if four places for branchiæ are assigned to each somite, the extent to which the hypothetically complete scheme or formula is actually filled up will be readily seen, and the branchial arrangements of different Crayfishes will be easily compared.

*The Branchial formula of Astacus fluviatilis*¹.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0 (ep)	0	0	0	= 0 (ep)
VIII.....	1	1	0	0	= 2
IX.....	1	1	1	0	= 3
X.....	1	1	1	0	= 3
XI.....	1	1	1	0	= 3
XII.....	1	1	1	<i>r</i>	= 3 + <i>r</i>
XIII.....	1	1	1	<i>r</i>	= 3 + <i>r</i>
XIV.....	0	0	0	1	= 1
	6 + ep + 6	+	5	+	1 + 2 <i>r</i> = 18 + ep + 2 <i>r</i>

“ep” here signifies a podobranchia which has lost its branchial filaments and become completely metamorphosed into an epipodite, while *r* indicates that a rudiment of a branchia exists.

It will be observed that, in this species of Crayfish, no somite possesses its hypothetically full complement of branchiæ except XII. and XIII.; and even in them the pleurobranchiæ are rudimentary. The representatives of eleven possible branchiæ are altogether wanting.

2. *The Branchiæ of Cambarus.*

The principal distinction between this genus and *Astacus*, as it was established by Erichson, lies in the absence of the single pleurobranchia of the latter, and the consequent reduction of the number of the branchiæ to seventeen on each side.

In his elaborate monograph of the genus, Dr. Hagen observes, “But there is also another difference, not before noticed². In *Astacus* each pair of gills, except the single one on the fifth set of legs, has a broad deeply-folded membrane, closely fixed behind the most external gill-lobe. In *Cambarus*, this membrane is always wanting in the gills of the fourth pair of legs, but exists, as in *Astacus*, in all the others.

“In the true *Astacus*, all the gills with a folded membrane behind have a basal external bundle of shorter but broader and irregularly placed gill-tubes; these are never to be found in *Cambarus*.”

In a species of *Cambarus* from Guatemala, of which a number of specimens have been presented to the British Museum by Mr. Salvin³, I find Dr. Hagen’s first remark fully borne out. The last

¹ In this, as in all other cases, it is to be understood that the branchial formula gives the branchiæ of only one side of the body, and that the total number of branchiæ is therefore double that given in the formula.

² Dr. Hagen appears to have overlooked De Haan’s definition of the distinctive characters of the American Crayfishes known to him:—

“Branchiæ 17; nulla supra pedes quintos; externæ supra quartos tantum e tubulis liberis, externæ supra sequentes infra e tubulis, supra e laminis tuberculatis compositæ” (Fauna Japonica, Crustacea, p. 164).

³ Mr. Salvin informs me that they were obtained in a river near Coban, in Vera Paz, at an elevation of about 4300 feet above the sea.

podobranchia is devoid of even a trace of a lamina; in the five which precede it, on the other hand, the lamina is very large, and folded into two longitudinally plaited lobes, as in *Astacus*. The edges and the surfaces of the laminae present tubercles, which are more prominent than in *Astacus*, and bear similar hooked spines.

The inner decurrent prolongation of the lamina is wider than in *Astacus*, particularly in the anterior podobranchiae. It is also beset with hooked setae mounted on low tubercles.

The setae of the upper part of the base are relatively shorter. As in *Astacus*, their apices are straight and not hooked.

The coxopodites bear bundles of twisted setae, which are similar to those of *Astacus*, but are more obtusely pointed.

The arthrobranchiae are similar in number and in form to those of *Astacus*. Those of the posterior series are proportionately larger.

I cannot discover a trace of the hindermost pleurobranchia, nor of the rudiments of the anterior ones, in this species; but it is not improbable that they may be discovered in larger forms.

The modified podobranchia (epipodite) of the first maxillipede is soft, and folded longitudinally in such a manner as to present a broad and shallow anterior groove. It bears no branchial papillae, nor any setae; but there are a few short hooks here and there.

The Branchial formula of Cambarus.

Somites and their appendages.	Podo- branchiae.	Arthrobranchiae.		Pleuro- branchiae.	
		Anterior.	Posterior.		
VII.....	0 (ep)	0	0	0	= 0 (ep)
VIII.....	1	1	0	0	= 2
IX.....	1	1	1	0	= 3
X.....	1	1	1	0	= 3
XI.....	1	1	1	0	= 3
XII.....	1	1	1	0	= 3
XIII.....	1	1	1	0	= 3
XIV.....	0	0	0	0	= 0
	6 + ep	6	+ 5	+	0 = 17 + ep.

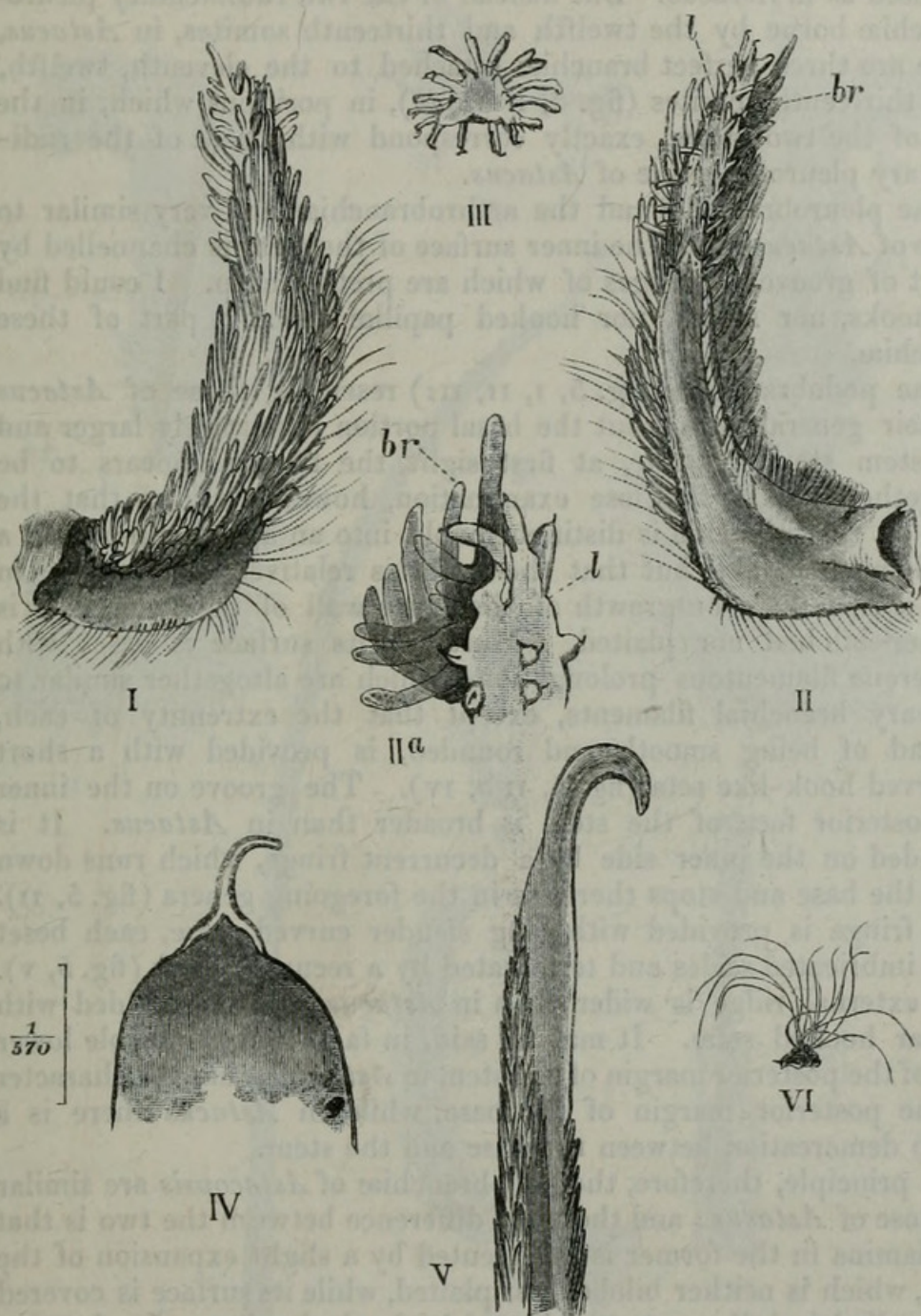
In comparison with *Astacus*, there is obviously a reduction of the branchial system, arising from the complete disappearance of all the pleurobranchiae in *Cambarus*.

3. *The Branchiae of Astacopsis*¹ *franklinii*.

When the branchiostegite is removed, seven branchiae are seen, having the general appearance and disposition of those of *Astacus*; and, as in *Astacus*, the six anterior are podobranchiae, attached to the coxopodite of the second maxillipede and the five following appendages, while the seventh is a pleurobranchia, fixed to the epimeron of

¹ Since, as will be shown below, those Australian Crayfishes which neither belong to *Cheraps* nor to *Engæus* are distinct from *Astacoides*, as represented by the Madagascar species, I propose to apply the generic name of *Astacopsis* to them.

Fig. 5.

*Astacopsis franklinii.*

- I. The outer face of the podobranchia of the antepenultimate thoracic limb of the left side ($\times 3\frac{1}{2}$). II. The inner face of the same podobranchia: *br*, branchial filaments; *l*, rudimentary lamina. II *a*. The apex of the same, more highly magnified. III. A transverse section of the podobranchia at about the junction of its middle and upper thirds. IV. The extremity of one of the hooked filaments; and V, that of one of the hooked setae. In these two figures the vertical line represents $\frac{1}{370}$ of an inch magnified to the same extent. VI. The coxopoditic setae ($\times 3\frac{1}{2}$).

the last thoracic somite. There is also an anterior series of six arthrobranchiæ, and a posterior series of five (p. 760, fig. 4, *arb*), disposed as in *Astacus*. But instead of the two rudimentary pleurobranchiæ borne by the twelfth and thirteenth somites, in *Astacus*, there are three perfect branchiæ attached to the eleventh, twelfth, and thirteenth somites (fig. 4, 11-13 *plb*), in positions which, in the case of the two latter, exactly correspond with those of the rudimentary pleurobranchiæ of *Astacus*.

The pleurobranchiæ and the arthrobranchiæ are very similar to those of *Astacus*; but the inner surface of the stem is channelled by a sort of groove, the edges of which are pretty sharp. I could find no hooks, nor spines, nor hooked papillæ on any part of these branchiæ.

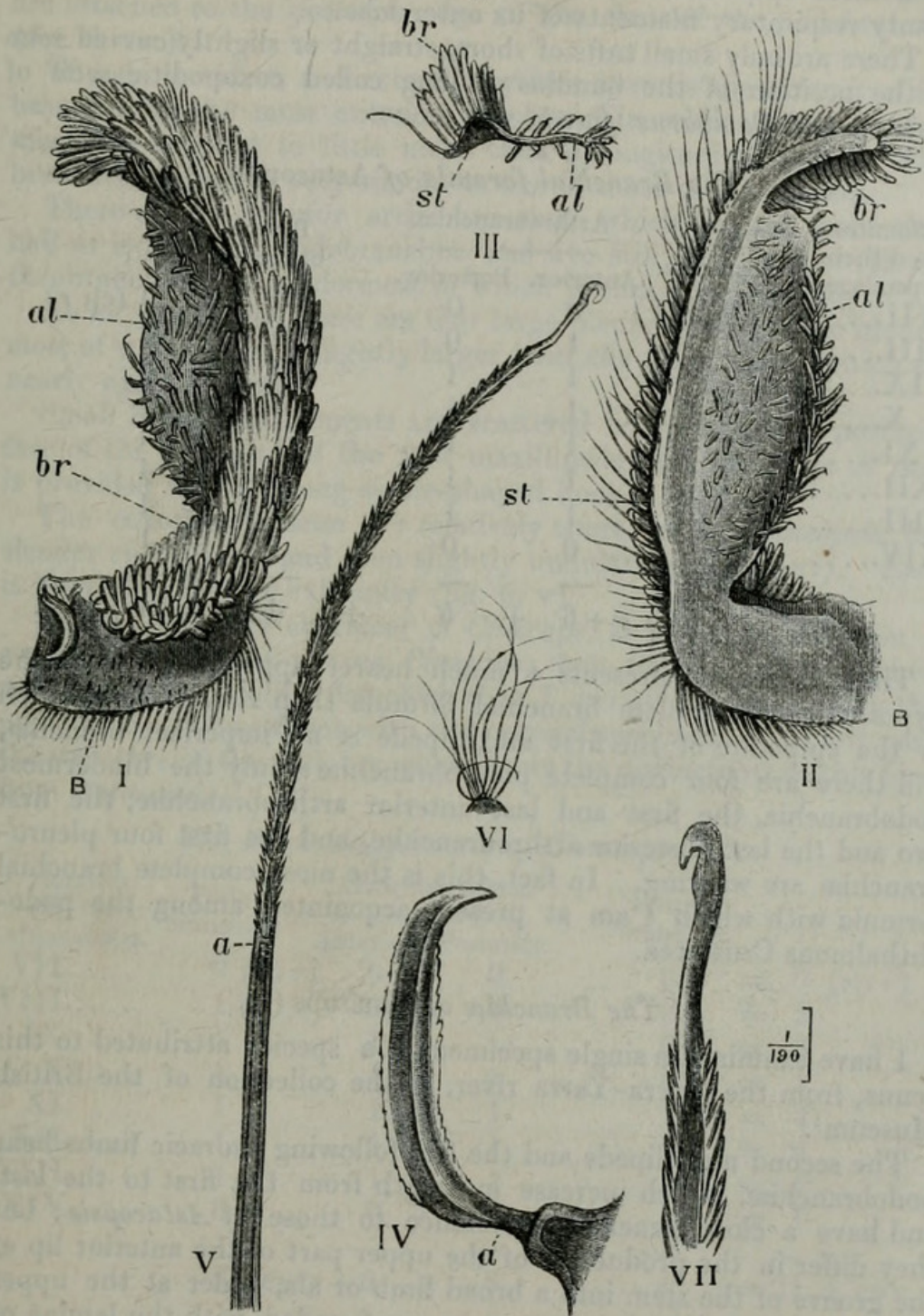
The podobranchiæ (fig. 5, I, II, III) resemble those of *Astacus* in their general form; but the basal portion is relatively larger and the stem stouter, while, at first sight, the lamina appears to be altogether wanting. Close examination, however, shows that the apex of the branchia is distinguishable into an apical plume and a lamellar appendage, but that the latter is relatively very small; in fact, it is a mere outgrowth of the inner wall of the stem, and is neither bilobed nor plaited. Moreover its surface is beset with numerous filamentous prolongations, which are altogether similar to ordinary branchial filaments, except that the extremity of each, instead of being smooth and rounded, is provided with a short recurved hook-like seta (fig. 5, II *a*, IV). The groove on the inner or posterior face of the stem is broader than in *Astacus*. It is bounded on the inner side by a decurrent fringe, which runs down onto the base and stops there, as in the foregoing genera (fig. 5, II). This fringe is provided with long slender curved setæ, each beset with imbricated scales and terminated by a recurved hook (fig. 5, V). The external ridge is wider than in *Astacus*, and is provided with similar hooked setæ. It may be said, in fact, that the whole lower half of the posterior margin of the stem in *Astacopsis* has the character of the posterior margin of the base, while in *Astacus* there is a sharp demarcation between the base and the stem.

In principle, therefore, the podobranchiæ of *Astacopsis* are similar to those of *Astacus*; and the main difference between the two is that the lamina in the former is represented by a slight expansion of the stem, which is neither bilobed nor plaited, while its surface is covered with cylindrical filaments terminated by hooked spines. In *Astacus*, as in *Cambarus*, on the other hand, the lamina is large, bilobed, plaited, and the place of the filaments is taken by mere papillæ terminated by similar hooks. Moreover, in *Astacus* and *Cambarus* the setæ of the base are not hooked.

The appendage of the first maxillipede is similar to that of *Astacus* in form; but on the outer surface of the outer lobe there are sixteen or eighteen short branchial papillæ, some of which, but apparently not all, are terminated by hooks; in fact, except in size, they quite resemble the filaments of the other branchiæ.

In this Crayfish, therefore, the first podobranchia is not reduced

Fig. 6.

*Cheraps* (?).

- I. The outer face of the podobranchia of the antepenultimate thoracic limb of the left side ($\times 3$). II. The inner face of the same podobranchia: B, basal portion; st, stem; al, ala; br, branchial filaments. III. A transverse section of the middle of the podobranchia ($\times 3$). IV. A sickle-shaped hook of a branchial filament $\frac{1}{190}$ of an inch in length. V. One of the coxopoditic setae more highly magnified: a, the circumferential inflexion of the wall of the seta. The central canal does not stop at this point, but is continued to the end of the seta. VI. A bundle of coxopoditic setae ($\times 3$). VII. The extremity of one of the long setae of the posterior edge of the stem. The vertical line represents $\frac{1}{190}$ of an inch magnified to the same extent.

to a mere epipodite, but retains true branchial characters in the scanty respiratory filaments of its outer lobe.

There are only small tufts of short, straight or slightly curved setæ in the position of the bundles of long coiled coxopoditic setæ of *Astacus* and *Cambarus* (fig. 5, vi).

The Branchial formula of Astacopsis.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0 (ep <i>r</i>)	0	0	0	= 0 (ep <i>r</i>)
VIII.....	1	1	0	0	= 2
IX.....	1	1	1	0	= 3
X.....	1	1	1	0	= 3
XI.....	1	1	1	1	= 4
XII.....	1	1	1	1	= 4
XIII.....	1	1	1	1	= 4
XIV.....	0	0	0	1	= 1
	—	—	—	—	—
	6 + ep <i>r</i>	6	5	4	= 21 + ep <i>r</i> .

Thus *Astacopsis* presents a much nearer approximation to the hypothetically complete branchial formula than *Astacus*, inasmuch as the epipodite of the first maxillipede is an imperfect branchia, and there are four complete pleurobranchiæ: only the hindermost podobranchia, the first and last anterior arthrobranchiæ, the first two and the last posterior arthrobranchiæ, and the first four pleurobranchiæ are wanting. In fact, this is the most complete branchial formula with which I am at present acquainted, among the podophthalmous Crustacea.

4. *The Branchiæ of Chærapis* (?).

I have examined a single specimen of a species attributed to this genus, from the Yarra-Yarra river, in the collection of the British Museum¹.

The second maxillipede and the five following thoracic limbs bear podobranchiæ, which increase in length from the first to the last, and have a close general resemblance to those of *Astacopsis*; but they differ in the production of the upper part of the anterior lip of the groove of the stem into a broad limb or ala, wider at the upper end than below, which must not be confounded with the lamina of *Astacus*, as it corresponds only with part of the inner lobe and the decurrent fringe in that genus (fig. 6, i, ii, iii *al*). Both faces, as well as the free posterior margin of this fringe, are beset with cylindrical branchial filaments, the apex of each of which is terminated by a strong sickle-shaped hook (fig. 6, iv). The majority of the branchial filaments of the stem are also terminated either by smaller hooks or by short straight spines. Long setæ, hooked at

¹ My best thanks are due to Dr. Günther, F.R.S., for the readiness with which he has aided my investigations by giving me free access to the Crustacean collection under his charge.

the ends, and otherwise similar in structure to those of *Astacopsis*, are attached to the posterior edge of the stem of the podobranchia (fig. 6, VII).

The ala is widest, and extends furthest towards the summit of the branchia, in the most anterior podobranchia, while in the hindermost it is reduced to little more than a longitudinal ridge. This branchia, in fact, is very similar to one of those of *Astacopsis*.

There are six anterior arthrobranchiæ, which are not more than half as long as the podobranchiæ, and five still smaller posterior arthrobranchiæ, the hindermost of which is almost rudimentary.

As in *Astacopsis*, there are four large pleurobranchiæ, the hindermost of which is only slightly larger than the other three, which are nearly equal in size.

Small branchial filaments are scattered over the whole posterior face of the epipodite of the first maxillipede; and the apex of each is provided with a strong sickle-shaped hook.

The coxopoditic setæ are relatively short, as in *Astacopsis*, but slender and curved, and even slightly undulating (fig. 6, VI). Each is hooked at its free extremity (fig. 6, V).

If the distinctive character of *Chærapis*, as given by Erichson, is correct, this is not a true *Chærapis*; but the branchiæ of these animals are so readily detached, that I can give no opinion on this point without comparison with the original specimens. In any case, the structure of the podobranchiæ shows the distinctness of this form from *Astacopsis*.

The Branchial formula of Chærapis (?).

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0 (ep r)	0	0	0	= 0 (ep r)
VIII.....	1	1	0	0	= 2
IX.....	1	1	1	0	= 3
X.....	1	1	1	0	= 3
XI. ...	1	1	1	1	= 4
XII....	1	1	1	1	= 4
XIII....	1	1	1	1	= 4
XIV.....	0	0	0	1	= 1
	6 + ep r	6	5	4	= 21 + ep r.

5. *The Branchiæ of Engæus.*

The number, the general disposition, and the structure of the branchiæ are the same as in *Astacopsis* and *Chærapis*.

The podobranchiæ have no vestige of a lamina. The first podobranchia has a small ala, much as in *Chærapis*; but only a few of the branchial filaments have terminal hooks.

The arthrobranchiæ are very small, those of the posterior series being the smaller; and the three anterior pleurobranchiæ are much smaller than the hindermost.

In all the branchiæ, and especially in the arthrobranchiæ and pleurobranchiæ, the terminal filament is exceptionally long and thick.

There are only a few very small hooked papillary elevations on the epipodite of the first maxillipede; in fact the podobranchia is reduced to nearly the same condition as in *Astacus*. The hooks of the setæ are very slender.

The branchial formula is the same as in *Astacopsis* and *Chærap*s, viz.:—

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.		
		Anterior.	Posterior.			
VII.....	0 (ep <i>r</i>)	0	0	0	=	0 (ep <i>r</i>)
VIII.....	1	1	0	0	=	2
IX.....	1	1	1	0	=	3
X.....	1	1	1	0	=	3
XI.....	1	1	1	1	=	4
XII.....	1	1	1	1	=	4
XIII.....	1	1	1	1	=	4
XIV.....	0	0	0	1	=	1
		6 + ep <i>r</i> + 6	+	5	+	4 = 21 + ep <i>r</i> .

6. The Branchiæ of Paranephrops.

In *Paranephrops planifrons* I find the branchiæ to have the same general character and disposition as in *Astacopsis* and *Engæus*.

The podobranchiæ are devoid of any trace of a lamina. The branchial filaments on the posterior faces of these branchiæ are, for the most part, provided with terminal hooks, while the rest have smooth and rounded apices.

The anterior arthrobranchiæ have not half the size of the podobranchiæ, while the posterior arthrobranchiæ are very minute, and the hindermost is rudimentary, being a mere simple filament, like one of the rudimentary pleurobranchiæ of *Astacus*. The pleurobranchiæ are larger, but the three anterior ones are small. None of these branchiæ have hooked papillæ.

The external and posterior face of the epipodite of the first maxillipede is beset with short hooked branchial filaments.

The coxopoditic setæ are few, slender, short, and hooked at the extremity.

The Branchial formula of Paranephrops.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.		
		Anterior.	Posterior.			
VII.....	0 (ep <i>r</i>)	0	0	0	=	0 (ep <i>r</i>)
VIII.....	1	1	0	0	=	2
IX.....	1	1	1	0	=	3
X.....	1	1	1	0	=	3
XI.....	1	1	1	1	=	4
XII.....	1	1	1	1	=	4
XIII.....	1	1	<i>r</i>	1	=	3 + <i>r</i>
XIV.....	0	0	0	1	=	1
		6 + ep <i>r</i> + 6	+	4 + <i>r</i>	+	4 = 20 + ep <i>r</i> + <i>r</i> .

The branchiæ of two specimens of a *Paranephrops*, from the Fiji Islands, like the foregoing in the British Museum, are in such bad condition, the specimens having apparently got dry before they were placed in spirits, that I cannot make out all the details of their structure; but, so far as it can be ascertained, they agree with those of the preceding species.

7. *The Branchiæ of Parastacus.*

By the kindness of Prof. Peters, I have been able to examine two well preserved males of the *Astacus brasiliensis* and *A. pilimanus* of Von Martens; and the results are very interesting.

The branchiæ of the two species are so much alike that they may be described together. In many points they resemble those of *Chærapa*; but the structure is by no means identical; and as these Crayfishes are peculiar in other respects, I think it will be most convenient to consider them as members of a distinct genus, *Parastacus*.

There are six ordinary podobranchiæ, of which, as usual, the first is the smallest, the next two are longer, and the last three are longest of all and nearly equal. In the podobranchia of the second maxillipede, the inner lip of the groove of the stem of the branchia is produced into a broad ala, as in *Chærapa*; but the ala becomes broader towards the apex, and is there abruptly truncated. The truncated edge is fringed by a single series of branchial papillæ. The posterior lip of the groove is beset with long hooked setæ. In the four following podobranchiæ the ala is a little narrower, especially at its apex, but it has essentially the same characters. In the last the ala is present in the basal half of the stem, but narrows to a mere ridge in the apical half.

The modified podobranchia of the first maxillipede bears from ten to sixteen longer or shorter branchial filaments on the outer half of the posterior surface of its apical end (fig. 2, D, p. 759).

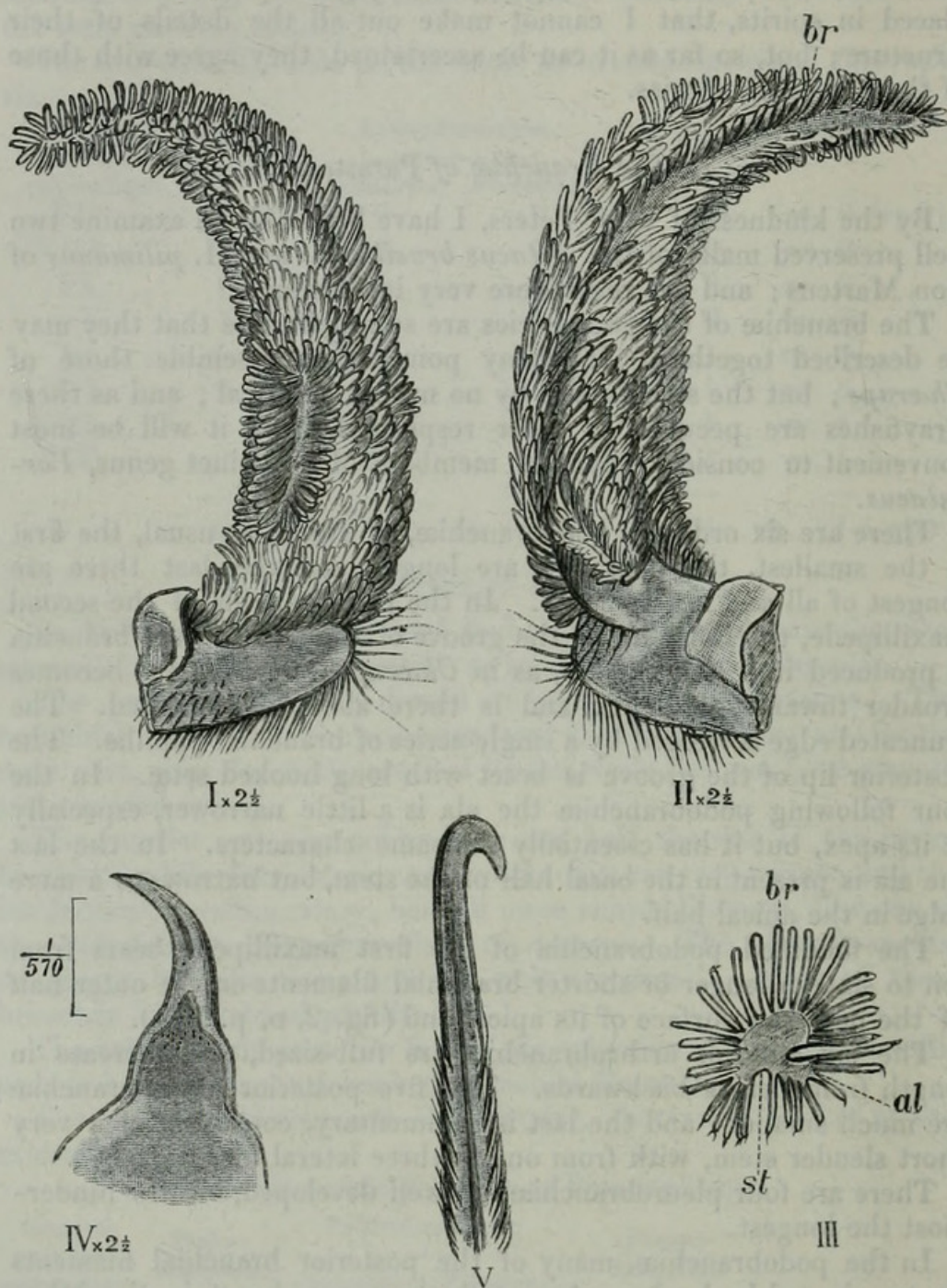
The six anterior arthrobranchiæ are full-sized, and increase in length from before backwards. The five posterior arthrobranchiæ are much smaller; and the last is rudimentary, consisting of a very short slender stem, with from one to three lateral filaments.

There are four pleurobranchiæ, all well developed, but the hindmost the longest.

In the podobranchiæ, many of the posterior branchial filaments are terminated by hooks. As usual, these are absent in the other branchiæ.

The coxopoditic tubercles give origin to bundles of long and tortuous setæ, with hooked apices. These are neither so long, nor so numerous, as in *Astacus* and *Cambarus*, but are more like them than are those of any other *Parastacidae*.

Fig. 7.

*Astacoides madagascariensis.*

- I. The outer face of the podobranchia of the antepenultimate thoracic limb of the left side ($\times 2\frac{1}{2}$). II. The inner face of the same: *br*, branchial filaments. III. A transverse section of the middle of the podobranchia: *st*, the grooved inner face of the stem. IV. The terminal hook of a branchial filament; and V. The apex of a coxopoditic seta. The straight line represents $\frac{1}{570}$ of an inch magnified to the same extent as these.

The Branchial formula of Parastacus.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.		
		Anterior.	Posterior.			
VII.....	0 (ep r)	0	0	0	=	0 (ep r)
VIII.....	1	1	0	0	=	2
IX.....	1	1	1	0	=	3
X.....	1	1	1	0	=	3
XI.....	1	1	1	1	=	4
XII.....	1	1	1	1	=	4
XIII.....	1	1	r	1	=	3+r
XIV.....	0	0	0	1	=	1
	6 + ep r	6	+	4 + r	+	4 = 20 + ep r + r.

8. *The Branchiæ of Astacoides.*

I am indebted to the courtesy of Prof. Alphonse Milne-Edwards for the opportunity of examining the branchiæ of a male specimen of the Crayfish of Madagascar, *Astacoides madagascariensis*. On account of the rarity of this species, it is desirable to describe its branchial apparatus in some detail. The length of the specimen was 5·7 inches.

The branchiostegite of the left side being carefully removed, the six large podobranchiæ were seen. The first, 0·9 inch long (measured from its attachment to its apex), was directed upwards and backwards in the cervical depression. The second, 1 inch long, took a similar direction, but was concave forwards. The third, slightly shorter, lay parallel with the second. The fourth (fig. 7, 1, 11) was much longer; bent round the third, its summit touched the apex of the second; the total length of the branchia when straightened out was about 1·3 inch. The fifth branchia was still longer, curving round the posterior edge of the last, so that its apex touched the front boundary of the branchial cavity. The sixth branchia started from a higher level than any of the others, in consequence of the great size of the coxopodite of the penultimate thoracic limb; its length was 1·05 inch; and it was nearly straight, its apex fitting into the summit of the branchial cavity. The base of each podobranchia is elongated upwards, as in *Astacopsis*; and there is a soft fold of integument over its attachment. There is no trace of any lamina.

On the removal of the podobranchiæ the arthrobranchiæ came into view. But, in contradistinction to all other known Crayfishes, there are only five of them fully developed, and even these are remarkably small in comparison with the podobranchiæ. The first is the shortest (0·5 in.); and they increase in length to the hindermost, which is 0·35 in. long. Each is concave forwards and convex backwards; and the apex of the hindermost comes within 0·15 inch of the nearest part of the anterior superior boundary of the branchial cavity. In all these branchiæ the branchial filaments are very numerous, stiff, relatively short and close-set; so that they

approach the characters of the branchiæ of the Lobster. The groove on the inner face of the stem seems, at first, to be reduced to nothing in the upper part of the podobranchiæ. However, a transverse section (fig. 7, III) shows that it exists and is bounded by two lips, the anterior of which is produced into a narrow ala. But the numerous hooked branchial filaments, which arise from the posterior face of the stem, fill the groove and appear to obliterate it.

The hindermost of the arthrobranchiæ is attached close to the articulation of the coxopodite with the epimeron, and is therefore in the same position as one of the anterior series of arthrobranchiæ in other Crayfishes. There is not the slightest trace of the attachment of another branchia on the arthrodial membrane behind this. But on the epimeron, just above the margin of the articular cavity, and 0.1 inch behind the root of the anterior branchia, a minute filament, 0.05 in. long, which I take to be a rudiment of the posterior branchia, enclosed by the downward extension of the epimeron, projects.

The attachment of the next arthrobranchia is like that of its predecessor, but not quite so far forward. At a distance of 0.5 in. behind and above its root, an exceedingly minute papilla, not more than a fifth of the length of the foregoing, is enclosed in the articular edge of the epimeron. This is doubtless the rudiment of the posterior arthrobranchia. The three remaining arthrobranchiæ are fixed into the arthrodial membranes of the other ambulatory and prehensile limbs, in a position corresponding with that occupied by the fourth. In the case of the hindermost of these, or that of the eleventh pair of appendages, there is, above and behind the root of the gill, and 0.08 inch distant from it, a filamentous rudimentary branchia, rather less than 0.1 inch long, attached within the articular margin of the epimeron. Three or four minute unequal processes are given off from the posterior edge of this filament. There is another very small papillary rudiment immediately above and behind the root of the next arthrobranchia; but none could be discovered above that of the most anterior arthrobranchia.

In addition to the five conspicuous and functional outer arthrobranchiæ, there was another very small one, only 0.18 inch long, and almost rudimentary, attached to the second maxillipede.

The pleurobranchia of the last thoracic somite was only 0.3 inch long, and was hardly visible at first, from being overlapped by the hindermost podobranchia. I could not discover the slightest trace of any other pleurobranchiæ.

The upper part of the modified podobranchia of the first maxillipede is sharply folded upon itself longitudinally; and its outer lobe is beset with numerous short branchial filaments, most of which have terminal hooks. Similar hooked filaments are to be found about the base and the posterior region of the other podobranchiæ; but a large proportion of the filaments of these branchiæ, and all of those of the arthrobranchiæ, appear to be hookless.

The tubercles of the coxopodites give rise to small tufts of short and straight setæ, which are hooked at the end, like those of *Asta-*

copsis (fig. 7, v). The hinder and upper setæ of the bases of the podobranchiæ are similarly hooked; but, as in the other species, the anterior setæ are straight, or only slightly curved at the extremities.

The Branchial formula of Astacoides madagascariensis.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.		
		Anterior.	Posterior.			
VII.....	0 (ep <i>r</i>)	0	0	0	=	(ep <i>r</i>)
VIII.....	1	<i>r</i>	0	0	=	1 + <i>r</i>
IX.....	1	1	0	0	=	2
X.....	1	1	<i>r</i>	0	=	2 + <i>r</i>
XI.....	1	1	<i>r</i>	0	=	2 + <i>r</i>
XII.....	1	1	<i>r</i>	0	=	2 + <i>r</i>
XIII.....	1	1	<i>r</i>	0	=	2 + <i>r</i>
XIV.....	0	0	0	1	=	1
		—	—	—	—	—
		6 + ep <i>r</i> + 5	+ <i>r</i> + 4 <i>r</i>	+ 1	=	12 + ep <i>r</i> + 5 <i>r</i>

In *Astacoides*, therefore, the branchiæ have suffered more reduction than in any other known Crayfish; and this reduction is, as it were, a continuation of the process already commenced in *Engæus* and *Paranephrops*, in which the anterior pleurobranchiæ and the posterior arthrobranchiæ are small, or even rudimentary.

III. THE CLASSIFICATION OF THE CRAYFISHES.

Whatever may be the variation in the structure of the branchiæ of the different species of Crayfish, it will be observed that they all agree in possessing podobranchiæ, or branchiæ attached to the coxopodites, of the six middle thoracic appendages, and that these are either not at all, or incompletely, differentiated into a branchial and an epipoditic division. Moreover *Astacopsis*, *Chærapis*, *Engæus*, *Paranephrops*, *Parastacus* and *Astacoides*, in which the apices of the podobranchiæ are not separated into a branchial plume and a well developed lamina, present a less-differentiated type of branchial structure than that which obtains in *Astacus* and *Cambarus*.

Thus the structure of the branchiæ in the Crayfishes separates them into two groups, of which I propose to term the latter the POTAMOBIDÆ, and the former the PARASTACIDÆ.

In the PARASTACIDÆ the podobranchiæ are devoid of more than a rudiment of a lamina, though the stem may be alate. The podobranchia of the first maxillipede has the form of an epipodite; but, in almost all cases, it bears a certain number of well-developed branchial filaments.

The first abdominal somite possesses no appendage in either sex; and the appendages of the four following somites are large.

The telson is never completely divided by a transverse suture.

More or fewer of the branchial filaments of the podobranchiæ are terminated by short hooked spines; and the coxopoditic setæ, as well

as those which beset the stems of the podobranchiæ, have hooked apices.

In the POTAMOBIIIDÆ the podobranchiæ of the second, third, fourth, fifth, and sixth thoracic appendages are always provided with a large plaited lamina. The podobranchia of the first maxillipede is converted into an epipodite, entirely devoid of branchial filaments.

The first abdominal somite invariably bears appendages in the male, and usually in both sexes. In the male these appendages are styli-form, and those of the second somite are always peculiarly modified.

The appendages of the four following somites are relatively small.

The telson is usually completely divided by a transverse suture.

None of the branchial filaments are terminated by hooks; nor are any of the coxopoditic setæ or the longer setæ of the podobranchiæ hooked, though hooked tubercles occur on the stem and on the lamina of the latter.

The coxopoditic setæ are always long and tortuous.

It is worthy of notice that the Parastacidæ agree with the Palinuridæ and Scyllaridæ in the abortion of the appendages of the first abdominal somite, and in possessing hooked setæ, while in the Potamobiidæ, as in the Lobsters, the setæ are not hooked, and, as in almost all the Podophthalmia, except the Palinuridæ and Scyllaridæ¹, the appendages of the first abdominal somite are present, and are specially modified in the males.

Of the six genera of the Parastacidæ, *Astucoides* is widely separated from all the rest by the reduction of the number of its functional branchiæ to twelve, while all the other genera at present known have, at fewest, twenty, and usually twenty-one, branchiæ.

Astacopsis, *Chærap*s, *Engæus*, and *Parastacus* have, in common, a long epistoma, the surface of which is flattened, the basal joint of the antennæ fixed by the overlapping edge of the cephalostegite, the posterior thoracic sterna narrow, the coxopodites of the hinder thoracic limbs large and approximated in the middle line. The rostrum and the antennary squame are short. *Engæus* is distinguished among these, not only by the narrowness of the first abdominal somite, but by the form of the anterior part of the head, with its short and deflexed rostrum, and very small antennary squame.

In *Chærap*s the podobranchiæ are alate, in *Astacopsis* they are not. *Parastacus* somewhat resembles *Chærap*s in its alate podobranchiæ, but differs from all the rest by possessing long and tortuous coxopoditic setæ.

I have nothing to add to the distinctive characters of the two genera of the Potamobiidæ, *Astacus* and *Cambarus*, already given by Erichson, Hagen, and others.

All the branchiæ of the Crayfishes consist of a stem beset with numerous cylindrical filaments. In fact, they are typical examples of what are termed by Milne-Edwards "branchies en brosse," and may be called "trichobranchiæ," in contradistinction to the lamellar

¹ In *Gebia*, *Callinaxis*, and *Porcellana*, the first abdominal appendages are rudimentary or abortive in the male sex.

gills or "phyllobranchiæ," which are met with in a large number of other Crustacea. The whole of the Macrurous Podophthalmia, excepting the genera *Gebia* and *Callianassa*, the Prawns, the Shrimps, and the Mysidæ, have trichobranchiæ.

In the Mysidæ the branchiæ are rudimentary or absent, and in the Euphausidæ and Penæidæ they are peculiarly modified. In the Prawns and Shrimps, in *Gebia* and *Callianassa*, in all the Anomura and Brachyura, the gills are phyllobranchiæ.

Thus the Podophthalmia or Thoracostraca (to use the convenient name proposed by Prof. Claus) are divisible in respect of the structure of their respiratory organs into three groups, which may be termed Abranchiata, Trichobranchiata, and Phyllobranchiata.

Among the trichobranchiate Podophthalmia, the Euphausidæ possess no other than podobranchiæ¹. These are mere respiratory plumes presenting no differentiation even into base and stem. All the rest of the Trichobranchiata have arthrobranchiæ, either with or without functional podobranchiæ and pleurobranchiæ. Among those which possess all three kinds of branchiæ, the Parastacidæ and the Palinuridæ are highly exceptional among the Thoracostraca in the absence of the appendages of the first abdominal somite in both sexes. They further, as a rule, possess 21 branchiæ (*pdb.* 6, *arb.* 11, *p/b.* 4), though the number is, in some cases, reduced by the suppression of more or fewer of the arthrobranchiæ and pleurobranchiæ.

In most, if not all the other Trichobranchiata, the first abdominal appendages of the males are present and specially modified. Among these, the Potamobiidæ are characterized by the imperfect division of their podobranchiæ into a proper branchial and an epipoditic portion.

In *Homarus* and *Nephrops*, *Axius* and *Thalassina*, the podobranchiæ are completely differentiated, from their bases onward, into a proper branchial and an epipoditic portion. In this condition the podobranchia is usually described as an epipodite, to the base of which a branchia is attached.

In *Homarus* the branchial filaments are numerous and multiserial, and the branchial formula is:—

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII. . . .	0 (ep)	0	0	0	= 0 (ep)
VIII. . . .	1	0	0	0	= 1
IX. . . .	1	1	1	0	= 3
X. . . .	1	1	1	0	= 3
XI. . . .	1	1	1	1	= 4
XII. . . .	1	1	1	1	= 4
XIII. . . .	1	1	1	1	= 4
XIV. . . .	0	0	0	1	= 1
	6 + ep	+ 5	+ 5	+ 4	= 20 + ep.

¹ Possibly some of the branchial plumes in *Sergestes* may be attached to the arthrodiol membranes. A critical examination of the species of *Sergestes* in reference to this point would probably yield interesting results.

In *Nephrops* the branchiæ have the same structure, but the branchial plume of the podobranchia of the second maxillipede is absent or rudimentary; hence the number of the branchiæ is reduced to 19.

In *Axius* the podobranchia of the penultimate thoracic limb is reduced to an epipodite by the disappearance of the branchial plume, and the hindermost pleurobranchia is also wanting. The arthrobranchia of the second maxillipede is represented by a mere rudiment.

The Branchial formula of Axius stirhynchus.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0 (ep)	0	0	0	= 0 (ep)
VIII.....	1	<i>r</i>	0	0	= 1 + <i>r</i>
IX.....	1	1	1	0	= 3
X.....	1	1	1	0	= 3
XI.....	1	1	1	1	= 4
XII.....	1	1	1	1	= 4
XIII.....	0 (ep)	1	1	1	= 3 + ep
XIV.....	0	0	0	0	= 0
	5 + 2 ep	+ 5 + <i>r</i>	+ 5	+ 3	= 18 + 2 ep + <i>r</i> .

The branchial filaments in this genus, again, are arranged only in two series on the stem, though, as they remain filiform, the approximation to the phyllobranchiate type is but slight.

In *Homarus*, *Nephrops*, and *Axius* the epipoditic divisions of the podobranchiæ are very large; but in *Thalassina*, *Stenopus*, and *Penæus* they are much reduced in size, and the branchial element disappears in more than the hindermost.

In *Thalassina scorpioides* the last thoracic somite is provided with no branchiæ of any kind, nor have its limbs any epipodite, and there are no pleurobranchiæ. The podobranchiæ of the twelfth and thirteenth somites are reduced to stout curved setose epipodites. In the eleventh there is a similar epipodite, but a branchial plume springs from its base. The tenth had a small epipodite, without a branchia in the specimen examined; but I am inclined to think that the branchia may have become detached; for the similar epipodite of the external maxillipede bore a mutilated, or rudimentary, small branchia. The small epipodites of the second maxillipedes figured by Milne-Edwards were broken off; but the places to which they were attached were discernible. The first maxillipede had no epipodite, in which respect *Thalassina* approaches *Callianassa*.

There are twelve arthrobranchiæ attached in pairs, from the second maxillipede to the penultimate thoracic limb inclusively. All these branchiæ are remarkable from the fact that, for a greater or less distance from the base of the gill, the stem is provided with broad imbricated foliaceous expansions, which are traversed by ramified

vessels, and take the place of the branchial filaments, which are sometimes very few, and confined altogether to the basal region of the branchia. These branchial plates differ from those of the true phyllobranchiæ in their small number and in their disposition, inasmuch as they are directed obliquely to the stem and not at right angles to it. Nevertheless it is interesting to find, in both *Axius* and *Thalassina*, a certain approach to the phyllobranchiate type, which is completely reached in *Gebia* and *Callianassa*.

The Branchial formula of Thalassina.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0	0	0	0	= 0
VIII.....	0 (ep)	1	1	0	= 2 + ep
IX.....	1	1	1	0	= 3
X.....	1	1	1	0	= 3
XI.....	1	1	1	0	= 3
XII.....	0 (ep)	1	1	0	= 2 + ep
XIII.....	0 (ep)	1	1	0	= 2 + ep
XIV.....	0	0	0	0	= 0
3 + 3 ep + 6 + 6 + 0 = 15 + 3 ep.					

In *Stenopus hispidus* the branchiæ resemble those of *Astacopsis* in structure, the filaments being loose, slender, and multiserial. But the disappearance of the branchial plumes from the podobranchiæ has gone still further than in *Thalassina*; and all these organs are reduced to delicate, almost vesicular epipodites entirely devoid of any proper branchial filaments, except in the case of the second maxillipede, in which a few such filaments are attached to the base of the epipodite. Moreover the number of the pleurobranchiæ is increased to seven.

The Branchial formula of Stenopus.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0 (ep)	?	0	0	= (ep)
VIII.....	0 (ep <i>r</i>)	1	1	1	= 3 + ep <i>r</i>
IX.....	0 (ep)	1	1	1	= 3 + ep
X.....	0 (ep)	1	1	1	= 3 + ep
XI.....	0 (ep)	1	1	1	= 3 + ep
XII.....	0 (ep)	1	1	1	= 3 + ep
XIII.....	0 (ep)	1	1	1	= 3 + ep
XIV.....	0	0	0	1	= 1
0 + 7 ep + <i>r</i> + 6 + 6 + 7 = 19 + 7 ep + <i>r</i>					

I am inclined to suspect the existence of a rudimentary anterior arthrobranchia in VII.; but I could not make sure of it.

By the structure of its branchiæ *Stenopus* is sharply separated from *Penæus*, with which it has hitherto been associated, although it approaches *Penæus* in the almost complete abortion of the branchial element of the podobranchiæ. In the Penæidæ, in fact, each branchia consists of a stem which is pointed at both ends and gives off two series of opposite lateral branches. This stem is attached by a pedicle near its lower end. Near each end of the stem the lateral branches are very short, and stand straight out; but they rapidly become longer; and as they do so they curve outwards towards one another, and eventually meet in the middle line. The middle of the branchia consequently assumes the form of a hollow cylinder.

The outer face of each lateral branch gives off a close-set series of secondary branches, which diminish in size towards the free end of the lateral branch, and at the free end are simple undivided filaments. But towards the attached end of the branch the secondary branches are themselves dichotomously subdivided in the direction of their length; so that the most complicated of these secondary branches presents a short stem whence two branches proceed, each of these again gives off two, and these may terminate in yet other two. Hence each secondary branch is like a flat triangular plate slit by fissures of varying depths, and attached by its apex to a lateral branch. All these secondary branches are directed upwards and outwards.

A detached lateral branch closely resembles one of the branchiæ of *Thysanopoda*; while, so far as I can judge from the figures given by Krøyer¹ and Sars², the branchiæ of *Sergestes* and *Lophogaster* still more closely approach those of *Penæus*.

A similar structure was described by Duvernoy in *Aristæus*, and was supposed by him to be characteristic of that genus; but Dana has already justly expressed a doubt whether, in this respect, *Aristæus* differs from the other Penæidæ.

In *Penæus*, the last and the penultimate thoracic limbs present no trace of podobranchiæ; and in all the rest the podobranchia is reduced to a small epipodite, which, in the middle of the series, is bifurcated at its free end. The latter lies between the arthrobranchiæ of its own somite and the next following. There are seven pleurobranchiæ, of which the hindmost is the largest, while the most anterior is very small.

¹ Forsøg til en monographisk Fremstilling af Kraebdyrslagten *Sergestes*: 1855.

² Beskrivelse over *Lophogaster typicus*: 1862.

The Branchial formula of Penæus brasiliensis.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.		
		Anterior.	Posterior.			
VII.....	0 (ep)	1 (small)	0	0	=	1 + ep
VIII.....	0 (ep)	1	1	1	=	3 + ep
IX.....	0 (ep)	1	1	1	=	3 + ep
X.....	0 (ep)	1	1	1	=	3 + ep
XI.....	0 (ep)	1	1	1	=	3 + ep
XII.....	0 (ep)	1	1	1	=	3 + ep
XIII.....	0	1	1	1	=	3
XIV.....	0	0	0	1	=	1
	0 + 6 ep	+ 7	+ 6	+ 7	=	20 + 6 ep.

The arthrobranchia of VII. is very small; in fact, it is a mere tuft of dichotomously divided branchial filaments.

The results of this examination of the principal forms of those Trichobranchiata which possess more than one kind of branchiæ may be thrown into a tabular form, as follows:—

- I. No appendages to the first abdominal somite in either sex. *Astyla*.
 1. Podobranchiæ undivided..... PARASTACIDÆ.
 2. Podobranchiæ divided into branchial and epipoditic portions PALINURIDÆ.
- II. Appendages of the first abdominal somite almost always present, and specially modified in the males. *Stylophora*.
 1. Podobranchiæ partially divided..... POTAMOBIIDÆ.
 2. Podobranchiæ completely divided or reduced to epipodites.
 - a. Pleurobranchiæ not more than four.
 - a. Posterior pleurobranchia present, and the most posterior of the podobranchiæ complete HOMARIDÆ.
Homarus, Nephrops.
 - β. Posterior pleurobranchia wanting, and more or fewer of the posterior podobranchiæ reduced to epipodites.
 - a. Branchiæ with only filamentous processes..... *Axius.*
 - b. Branchiæ with foliaceous as well as filamentous processes *Thalassina.*
 - b. Pleurobranchiæ more than four.
 - a. Branchiæ filamentous *Stenopus.*
 - β. Branchiæ ramose..... *Penæus.*

All the Trichobranchiata are Macrura, in the sense of having the abdomen and its appendages well developed; but, in *Ibacus* and *Thenus*, the abdomen becomes shortened and the cephalothorax wide, while the antennary and the ocular regions are modified in a manner very similar to that which gives rise to the peculiar "face" or "metope" of the typical Brachyura. A very little further modification would convert *Thenus*, for example, into a trichobranchiate Crab. Such forms as these, which simulate the Brachyura, and yet differ profoundly from them, may be termed "pseudo-carcinoids."

If the branchial filaments of *Axius* were shortened and widened, the structure of the branchiæ would approach that which obtains in *Gebia* and *Callianassa*, which are truly phyllobranchiate. But in other respects there is a wide interval between these genera, on the one hand, and *Axius* and *Thalassina*, which are ordinarily associated with them among the Thalassinidæ, on the other hand; for the podobranchiæ have entirely disappeared on the six hinder thoracic limbs, and even on the first or second maxillipede they are represented only by rudimentary epipodites.

There are no pleurobranchiæ; and the total number of gills is reduced to five pairs of arthrobranchiæ on each side.

The Branchial formula of Gebia and Callianassa.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.					
		Anterior.	Posterior.						
VII.....	0	0	0	0	=	0			
VIII.....	0	0	0	0	=	0			
IX.....	0	1	1	0	=	2			
X.....	0	1	1	0	=	2			
XI.....	0	1	1	0	=	2			
XII.....	0	1	1	0	=	2			
XIII.....	0	1	1	0	=	2			
XIV.....	0	0	0	0	=	0			
	—	—	—	—		—			
	0	+	5	+	5	+	0	=	10

In the almost complete abortion of the podobranchiæ, and in the presence of ten arthrobranchiæ attached in pairs to the middle thoracic somites, *Gebia* and *Callianassa* agree with *Porcellana*, *Galathea*, *Lithodes*, *Pagurus*, and *Remipes*. But in *Galathea* and *Porcellana* the four hindermost pleurobranchiæ are present, making fourteen gills on each side; in *Lithodes* and *Pagurus* the penultimate pleurobranchia exists, making eleven; in *Remipes* there is no pleurobranchia, and only nine arthrobranchiæ, viz. one on the ninth and two for each of the four following somites, are present.

In this group, which nearly corresponds with the Anomala of De Haan, and which I propose to term the "Anomomorpha," there is every degree of modification—from such typically Macrurous forms as *Gebia* and *Galathea* to such pseudo-carcinoids as *Lithodes* and *Porcellana*. It is interesting to remark, however, that, while in *Thenus* and *Ibacus* the process of modification has chiefly affected the head, in the Anomomorpha the characteristic changes are more marked in the abdomen. In none of the latter are the basal joints of the antennæ fixed, nor are distinct orbits formed.

It is easy to understand the possibility of the derivation of the Anomomorpha from some form allied to *Axius* and *Thalassina* (but with four pleurobranchiæ) by the further reduction, and final almost complete disappearance, of the podobranchiæ, while the biserial filaments of the other gills flattened out and became lamellar.

The Prawns and Shrimps ("Salicoques" of Milne-Edwards, *Carides*

of De Haan), if we exclude the Penæidæ, constitute a natural assemblage, to which I will apply the name of "Caridomorpha." They are all eminently Macrurous; and the characteristic feature of their branchial system is the predominance of the pleurobranchiæ, and the concomitant diminution in the number and the importance of the arthrobranchiæ and of the podobranchiæ. In fact, so far as I am aware, there are never any traces of the latter except upon the maxillipedes.

In both *Palæmon* and *Crangon* I find five pleurobranchiæ attached to the posterior thoracic somites, from the tenth to the fourteenth inclusively. In *Palæmon*, two arthrobranchiæ, one of which is very small, are attached to the arthrodial membrane of the external maxillipede, which has a very short and rudimentary epipodite. The second maxillipede bears a podobranchia divided into a small branchia and an oval epipoditic plate. In the first maxillipede the place of the podobranchia is occupied by a rounded bilobed lamella.

In *Crangon* none of the maxillipedes bear gills. The epipodite of the first maxillipede is relatively much larger and triangular; that of the second is tongue-shaped and almost vesicular; that of the third is a mere rounded process.

I can find only one arthrobranchia on the ninth somite.

The Branchial formula of Palæmon.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0 (ep)	0	0	0 =	0 (ep)
VIII.....	1	0	0	0 =	1
IX.....	0 (ep)	1	1	0 =	2 + ep
X.....	0	0	0	1 =	1
XI.....	0	0	0	1 =	1
XII.....	0	0	0	1 =	1
XIII.....	0	0	0	1 =	1
XIV.....	0	0	0	1 =	1
	1 + 2 ep	+ 1	+ 1	+ 5	= 8 + 2 ep.

From the number of their pleurobranchiæ the Caridomorpha cannot be regarded as a reduced modification of any of the Trichobranchiata, except the Penæidæ and *Stenopus*. But it is easy to derive them from a *Stenopus*-like primitive form by the reduction of the podobranchiæ and the arthrobranchiæ, and the conversion of the five posterior pleurobranchiæ into gills of the lamellar type.

In the Brachyura of Milne-Edwards the disposition of the branchial apparatus is well known to be definite and characteristic. In *Cancer pagurus*, for example, there are nine branchiæ; seven of these are pyramidal in form, and take a general direction from the base towards the apex of the branchial chamber, to the inner walls of which they are applied. The two posterior of these gills are pleurobranchiæ, being attached respectively to the epimera of the eleventh and the twelfth somites. The fifth and fourth, the third and second,

are fixed in pairs by a common pedicle to the arthrodistal membrane of the appendages of the tenth and ninth somites—that is, the great forceps and the third maxilliped. The most anterior gill, slenderer than the others, is attached to the arthrodistal membrane of the second maxilliped. There are therefore five arthrobranchiæ.

The podobranchia of the first maxilliped is represented only by the large curved epipodite, which sweeps over the surface of the arthrobranchiæ and the pleurobranchiæ. The podobranchia of the second maxilliped is divided into a branchial plume, which lies horizontally under the bases of the four anterior arthrobranchiæ, and an epipodite, which ascends between the arthrobranchia of its somite and those of the next, and lies internal to the latter, close to the inner wall of the branchial cavity.

In the third maxilliped the epipodite is very long, and forms the valve to the afferent aperture of the branchial cavity. Attached to its base is a short truncated branchia, which fits in between the bases of the second and the third arthrobranchiæ.

The Branchial formula of Cancer pagurus.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.		
		Anterior.	Posterior.			
VII.....	0 (ep)	0	0	0	=	0 (ep)
VIII.....	1	1	0	0	=	2
IX.....	1	1	1	0	=	3
X.....	0	1	1	0	=	2
XI.....	0	0	0	1	=	1
XII.....	0	0	0	1	=	1
XIII.....	0	0	0	0	=	0
XIV.....	0	0	0	0	=	0
	2 + ep	+ 3	+ 2	+ 2	=	9 + ep.

A considerable reduction of the branchial apparatus occurs in some Brachyura, especially the *Catometopa*. Thus, in *Gelasimus* the hinder pleurobranchia and the most anterior arthrobranchia have disappeared, and the two podobranchiæ are so small as to be almost rudimentary.

In the Raninidæ and in *Latreillia*, the Brachyurous metope is incompletely formed; but the branchial system is essentially that of the true Crabs. The same may be said of *Dromia*, although the branchial apparatus of this crustacean presents some very interesting approximations to the less-modified type from which it cannot be reasonably doubted that the Brachyura have proceeded.

The epipodites of the three maxillipedes are very similar in form and disposition to those of the ordinary Crabs; and that of the second bears a small horizontal branchial plume. That of the third sometimes bears a small branchia. The coxopodite of the fourth thoracic limb has a small epipodite; but I find no trace of such an appendage on the rest of the thoracic limbs. Moreover there are five pairs of arthrobranchiæ attached to consecutive somites from the ninth to

the thirteenth—and four pleurobranchiæ, one for each of the four posterior thoracic somites.

The Branchial formula of Dromia.

Somites and their appendages.	Podo- branchiæ.	Arthrobranchiæ.		Pleuro- branchiæ.	
		Anterior.	Posterior.		
VII.....	0 (ep)	0	0	0	= 0 (ep)
VIII.....	1	0	0	0	= 1
IX.....	1	1	1	0	= 3
X.....	0	1	1	0	= 2
XI.....	0	1	1	1	= 3
XII.....	0	1	1	1	= 3
XIII.....	0	1	1	1	= 3
XIV.....	0	0	0	1	= 1
		—	—	—	—
		2 + ep.	+ 5	+ 5	+ 4 = 16 + ep.

On comparing this branchial formula with that of *Homarus*, the relation between the two is obvious. In fact, if the three posterior podobranchiæ of the Lobster are suppressed, and the next is reduced to an epipodite, the branchial formula becomes the same as that of *Dromia*, and the remaining differences between the respiratory organs of the two result from the modification in form and structure of the branchial elements which remain. Thus it is a permissible, if not a probable, suggestion that, just as the Anomomorpha may have been derived from the modification of some form allied to *Axius*, and the Caridomorpha from some form allied to *Stenopus* and *Penæus*, so the Carcinomorpha (= the Brachyura and the Raninidæ, with *Homola* and *Dromia*) may have proceeded from some Homarine stock.

However this may be, the actual morphological relations of the Thoracostraca appear to me to be represented with tolerable accuracy by the following scheme :—

CRUSTACEA.

THORACOSTRACA OR PODOPHTHALMIA.

III. PHYLLOBRANCHIATA.

CARIDOMORPHA.

ANOMOMORPHA.

CARCINOMORPHA.

II. TRICHOBRANCHIATA.

Penæidæ. *Stenopidæ.*

Thalassinidæ. *Axiidæ.*

Homaridæ. *Potamobiidæ.*

Palinuridæ.

Parastacidæ.

Euphausidæ.

I. ABRANCHIATA.

Mysidæ.

STYLOPHORA.

ASTYLA.

IV. THE DISTRIBUTION OF THE CRAYFISHES CONSIDERED IN RELATION TO THEIR MORPHOLOGICAL DIFFERENCES.

From what has been said above, it will be obvious that there is a remarkable correspondence between the morphological and the geographical divisions of the Crayfishes. Thus, all the Crayfishes of the northern hemisphere are Potamobiidæ, and all those of the southern hemisphere are Parastacidæ. In the northern hemisphere, again, the *Astaci* are Eurasiatic and West-American, while the *Cambari* are characteristic of the North-American region east of the Sierra Nevada—in other words, of the river-basins which flow into the Gulf of Mexico and the West Atlantic.

The *Astacine* region nearly answers to the Palæarctic province of Mr. Sclater, minus the southern shores of the Mediterranean, and plus Western North America; while the *Cambarine* region takes in most of the Palæarctic region, with the Neotropical region as far as Guatemala and the West Indies.

In the southern hemisphere, *Astacopsis*, *Chærapa*, and *Engæus* are confined to the Australian region, *Paranephrops* to New Zealand and the Fijis; while the South-American *Parastacus* is distinct from either of these, though closely allied with the Australian forms; and the peculiarity of the Madagascar fauna is vindicated by *Astacoides*.

Thus, if we were to establish provinces of distribution on the Crayfishes alone, they would bear only a partial resemblance to those based on the association of terrestrial animals. On the other hand, if we compare the distribution of the Crayfishes with that of the freshwater fishes, there are, as might be expected, some curious points of resemblance. The distribution of the Salmonidæ, for example, corresponds pretty closely with that of the Potamobiidæ, though the range of the Salmonidæ extends less far to the south in North America, and a little further, namely, as far as Algeria in the Old World. Again, the Salmonidæ to the east of the Rocky Mountains are, for the most part, distinct from those to the west, while the genus *Onchorhynchus* is, like *Astacus*, common to both the Asiatic and the American shores of the North Pacific.

With the singular exception of *Retropinna*, there is no true Salmonoid in the southern hemisphere; but, as Dr. Günther has pointed out, the Haplochitonidæ and the Galaxiadæ, which stand in somewhat the same relation to the Salmonidæ as the Parastacidæ do to the Potamobiidæ, represent the Salmonidæ in the fresh waters of New Zealand, Australia, and South America.

It is worthy of remark that the Salmonidæ, the Haplochitonidæ, and the Galaxiadæ are singular among Teleostean fishes for the embryonic character of their female reproductive organs, which have no oviducts—just as, among the Podophthalmous Crustacea, the Crayfishes are distinguished by the undifferentiated character of their podobranchiæ.

With the exception of one or two species in Algeria and Asia Minor, the Salmonoids and their allies are wanting in the whole of

Africa and Asia south of the great Asiatic highlands, just as the Crayfishes are. It will be very interesting to learn, from the thorough investigation of the fauna of Madagascar, which is now being carried out, whether the Salmonoids or their allies are in any way represented there.

The broad similarity in distribution between the Salmoniform fishes and the Crayfishes is doubtless due to the likeness of the conditions under which the two groups have reached their present development. I do not think that there can be any reasonable ground for questioning the assumption, that both the freshwater fishes and the freshwater Crustacea are modifications of a marine prototype, which has more or less completely adapted itself to freshwater conditions. In the case of the Crayfishes, at any rate, there is abundant analogical evidence in support of this hypothesis. It is well known that, in many parts of the world, the Prawns ascend rivers, and become fluvatile. The *Palæmon lacustris* (*Anchistia migratoria*, Heller) of the Lago di Garda is identical with a Prawn now living in the Mediterranean. Again, the *Mysis relicta* of the lakes of Norway, Sweden, Western Russia, and North America (Michigan and Superior) is only a variety of the *Mysis oculata* of the Arctic seas¹. Nor do I think it can be seriously questioned that the fluvatile and the land Crabs are modified descendants of marine Brachyura.

Let it be supposed that, at some former period of the earth's history, a Crustacean, similar to *Paranephrops* or *Astacopsis* in its general characters, but with the first pair of abdominal appendages fully formed, which we may call provisionally *Protastacus*, inhabited the ocean, and that it had as wide a distribution as *Palæmon* or *Penæus* have at the present day. Let us suppose, further, that the northern form of the genus tended towards the assumption of the Potamobiine, and the southern towards that of the Parastacine type. Under these circumstances, it is easy to understand how such rivers as were, or became, accessible in both hemispheres, and were not already too strongly tenanted by formidable competitors, might be peopled respectively by Potamobiine or Parastacine forms, which, acquiring their special characters in each great river-basin, would bring about the distribution we now witness. As time went on, the *Protastacus* stock might become extinct, or might be represented only by rare deep-water forms, as the Homaridæ are represented in the Indian Ocean only by *Nephropsis*.

Some such hypothesis as this appears to me to be fully justified by the present state of knowledge; and though it cannot as yet be said to be directly supported by palæontological facts, these facts agree with the hypothesis very well as far as they go. For the Mesozoic marine

¹ G. O. Sars, 'Histoire Naturelle des Crustacés d'eau douce de Norvège.' In the British Museum there is a species of that especially marine genus *Penæus*, which is affirmed by the Messrs. Schlagintweit to have been obtained from an affluent of the Sutlej, at the foot of the Himalayas. *Penæus brasiliensis* ascends the North-American rivers for long distances (Smith, in Prof. Baird's Report, 1872-72).

strata abound in Crustacea, such as *Glyphæa* and *Hoploparia*, which are evidently closely allied to the Crayfishes.

The great difficulty is, not to account for the Crayfishes where we find them, but to understand their absence over so large a part of the Old World and of intertropical America. Whether this is to be explained by extensive alterations in geographical conditions since the extinction of the *Protastacus* stock, or by the competition of Prawns and freshwater Crabs, or by some other circumstance at present unknown, is a very interesting subject for further inquiry.

Postscript, Oct. 24, 1878.

Since this paper was read, my friend Mr. Moseley, F.R.S., has written for and obtained specimens of the "Crayfish" said to exist in the fresh waters of the Cape-Verd Islands. They belong to the genera *Atya* and *Palæmon*. Moreover, by the intervention of Sir Joseph Hooker, I have procured a considerable number of freshwater Crustacea from Jamaica. But these also all belong to *Atya* and *Palæmon*. I suspect that all Sloane's "Crayfishes" are simply Prawns. The largest example of one of the species sent to me measures sixteen inches in length when the great chelate limbs are fully extended.—T. H. H.

November 5, 1878.

Arthur Grote, Esq., V.P., in the Chair.

The Secretary read the following reports on the additions to the Society's Menagerie during the months of June, July, August, September, and October 1878:—

The total number of registered additions to the Society's Menagerie during the month of June was 159, of which 35 were by birth, 75 by presentation, 29 by purchase, 14 were received on deposit, and 6 by exchange. The total number of departures during the same period, by death and removals, was 73.

The most noticeable additions during the month of June was as follows:—

A Japanese Wolf (*Canis hodophylax*, of the 'Fauna Japonica,' Mamm. t. 9, p. 38), presented by H. Heywood Jones, Esq., F.Z.S., June 26th, being the first example of this little-known animal we have ever received alive.

Judging from the present specimen the Japanese Wolf, although nearly allied to *Canis lupus*, would seem to be a distinct species, to be recognized by its smaller size and shorter legs.

The Japanese Dog sent to us by Mr. Pryer (see P. Z. S. 1878, p. 115) is quite a different animal, and is, I have no doubt, only a variety of the domestic dog or a hybrid.



Huxley, Thomas Henry. 1879. "On the classification and the distribution of the crayfishes." *Proceedings of the Zoological Society of London* 1878, 752–788.

View This Item Online: <https://www.biodiversitylibrary.org/item/90451>

Permalink: <https://www.biodiversitylibrary.org/partpdf/67240>

Holding Institution

Natural History Museum Library, London

Sponsored by

Natural History Museum Library, London

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.