PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the Feeding Mechanism of the Branchiopoda: Appendix on the Mouth Parts of the Branchiopoda

H. Graham Cannon and F. M. C. Leak

Phil. Trans. R. Soc. Lond. B 1932 **222**, 340-352
doi: 10.1098/rstb.1932.0018

APPENDIX.

On the Mouth Parts of the Branchiopoda.

By H. GRAHAM CANNON, *Sc.D., and Miss* F. M. C. LEAK, *Ph.D.*

Introduction.

Very little is known concerning the mouth parts of the Branchiopoda, with the exception of the mandibles, which, being comparatively large, have been accurately described in numerous forms. There are references and isolated figures occurring from time to time in the literature of the subject. Thus, as early as 1840, JOLY (p. 254) mentions the maxilla in *Artemia salina*, and later BUCHHOLZ (1866, Plate 3, fig. 5), SPANGENBERG (1875, Plate 1, fig. 5) and CLAUS (1886, Plate 5, fig. 1) published figures of the maxillary region of various Anostraca. In SPANGENBERG's figure the maxilla is undoubtedly distorted, and in the figure illustrating CLAUS's paper the maxillule is unfortunately labelled the maxilla. SARS (1896, Plate 7, figs. 1 and 8) later figured the comparatively large maxilla of *Branchinecta*, but here again it was undoubtedly out of place in the specimen figured. More recently BORRADAILE (1926, p. 210) mentions the difficulty of finding the maxillule of *Chirocephalus*, and refers to CANNON's brief description of the limb which was based on a series of transverse sections. Finally, WAGLER (1927, p. 316) in his account of the Branchiopoda gives a general account of the maxillules and maxilla. He maintains, among other things, that the maxilla of the Anostraca still shows a trace of its biramous constitution and that the maxilla of the Cladocera consists of a small setose prominence. The first statement, we maintain, is incorrect and is unsupported by any published evidence, and the second is impossible as the Cladoceran maxilla varies from a well-defined but minute limb to complete absence. Unfortunately, WAGLER quotes no authority for these statements.

There is thus no published comparative account of the Branchiopodan mouth parts, and the present note is an attempt to supply this deficiency. We have not dealt with the mandibles as these have been described elsewhere, but have included a short account of the upper and lower lips.

The neglect of this problem is undoubtedly due to the difficulty of minute dissection of the parts—especially of the maxillæ. The maxillules are comparatively easy to remove as they usually remain attached to the paragnaths, but the maxillæ are exceedingly difficult to isolate. We have not worked, however, to any great extent on isolated limbs, but have studied the maxillæ in position on the body. The difficulty, then, is to see them, as, besides being so minute, they are extremely transparent and are always wedged in between the maxillules and the first trunk limb. We have used the method of microtome dissection described by CANNON (1927, p. 355) and of plain dissection with fine needles, the specimens always being dissected in pure glycerine.

We have to thank Dr. R. GURNEY for identifying most of the species used.

Note.—Part of the work recorded in this appendix was submitted by Miss F. M. C. LEAK (Mrs. E. HOLMAN), B.Sc. (London) for the degree of Ph.D. (Sheffield).

The Upper and Lower Lip.

Although it has been generally supposed that the lower lip is absent in all Branchiopoda except the Notostraca (Calman, 1909, p. 36, and Wagler, 1927, p. 316), it is evident on examining various genera from the sagittal plane that it is present in the typical position, immediately behind the mandibles and guarding the posterior edge of the mouth. With the exception of the aberrant Gymnomera it exhibits a constant form similar to that described by Zimmer (1927, p. 281) as characteristic of the Crustacea Malacostraca. It is bifid and consists of two triangular hairy lobes—the paragnaths—situated one on each side of a median food groove. The paragnaths, to a varying degree in different genera, overlie the bases of the maxillules on the ventral side, while the setæ from the latter project forward against their inner faces into the median food groove, fig. 26.

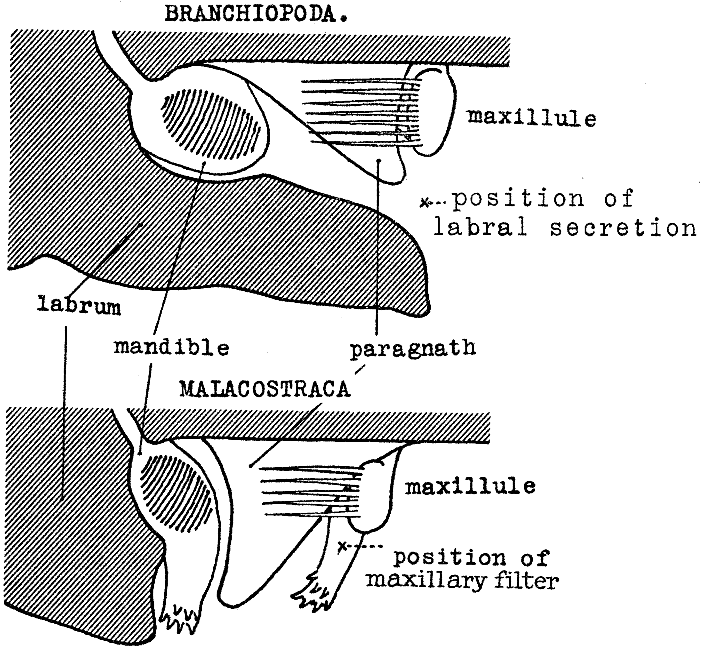

Fig. 26.—Diagram showing relative position of upper (labrum) and lower (paragnaths) lips and associated mouth parts in Malacostraca and Branchiopoda.

An interesting comparison may be made between the lower lips of the Branchiopoda and the Malacostraca. The shape of the paragnaths in the two groups is similar, but their position relative to the mandibles and the labrum is different. In both groups the paragnaths are triangular in side view, but while in the Malacostraca the ventral tip—the apex of the triangle—is level with the anterior point of origin of the paragnath from the body wall, in the Branchiopoda this has shifted backwards and is level with the posterior point of origin.

Parallel with this is the difference in extent and position of the labrum in the two groups. In the typical Branchiopod the upper lip extends backward beyond the maxillary region. In extreme cases, such as *Limnetis,* it reaches more than half-way down the mid-ventral groove. In the typical Malacostracan, on the other hand, it stops short at the mandible, or at most the maxillary level, fig. 26.

These differences may be correlated with the feeding mechanisms of the two groups. The primitive Malacostracan, according to CANNON (1927, p. 367) exhibited a filtratory mechanism by which an anteriorly directed food current along the mid-ventral groove was filtered by the maxilla. The latter acted both as suction and filter pump, and so forced the food stream through the filtratory setæ on its basal endite. The food so obtained was scraped off by the maxillule and first trunk limb and pushed forwards on to the mandibles. In the Branchiopoda, as described in the main part of this paper, a similar anteriorly directed food current is produced along the mid-ventral line (CANNON, 1928, p. 808; LUNDBLAD, 1920, p. 36), but no such maxillary filtratory mechanism exists. In both groups the food current, on reaching the maxillary region, passes outwards into the swimming stream. In the Branchiopoda, therefore, there must exist some means by which the particles carried on the food stream are retained in the mouth region. According to CANNON (*supra*, p. 279; 1922, p. 229; 1928, *a* p. 813) this is brought about by the development of labral glands which pour out a viscid secretion into the food groove, and so entangle the food particles and enable the maxillules to push the entangled mass on to the mandibles. A labrum of the extent and position of that of a typical Malacostracan would not serve this purpose, since any secretions would pass out anterior to the maxillary region. Hence the Branchiopod labrum has extended backwards so that its secretion is passed into the food stream just posterior to the maxillules, and this backward development has carried with it the lower lips.

The Maxillule.

Throughout the whole of the Branchiopoda, with the exception of the Notostraca, the maxillule exhibits a remarkably uniform structure, consisting of a single lobe curving round the posterior end of the paragnath and terminating in a single endite armed with orally directed spines on the anterior edge.

In the Anostraca the setæ are all long and straight and armed with lateral interlocking setules. The only variations in this group are the presence or absence of a single short spine on the ventral tip of the limb, fig. 27, and the difference in number of the long setæ, ranging from twenty-two in *Branchinecta* and *Eubranchipus* to twenty-eight in *Polyartemiella.*

In the Conchostraca and Cladocera, while the basal structure of the limb is the same, the setæ are curved and not straight as in the Anostraca, figs. 28 and 29. This may be correlated with the head flexure in these two groups. In the Conchostracan *Estheria,* in addition to the setæ being curved, the plane of the plate from which they arise also curves towards the median plane, the two maxillules thus arching over the median food groove, fig. 28. The same arrangement is found in *Lepidocaris,* fig. 32.

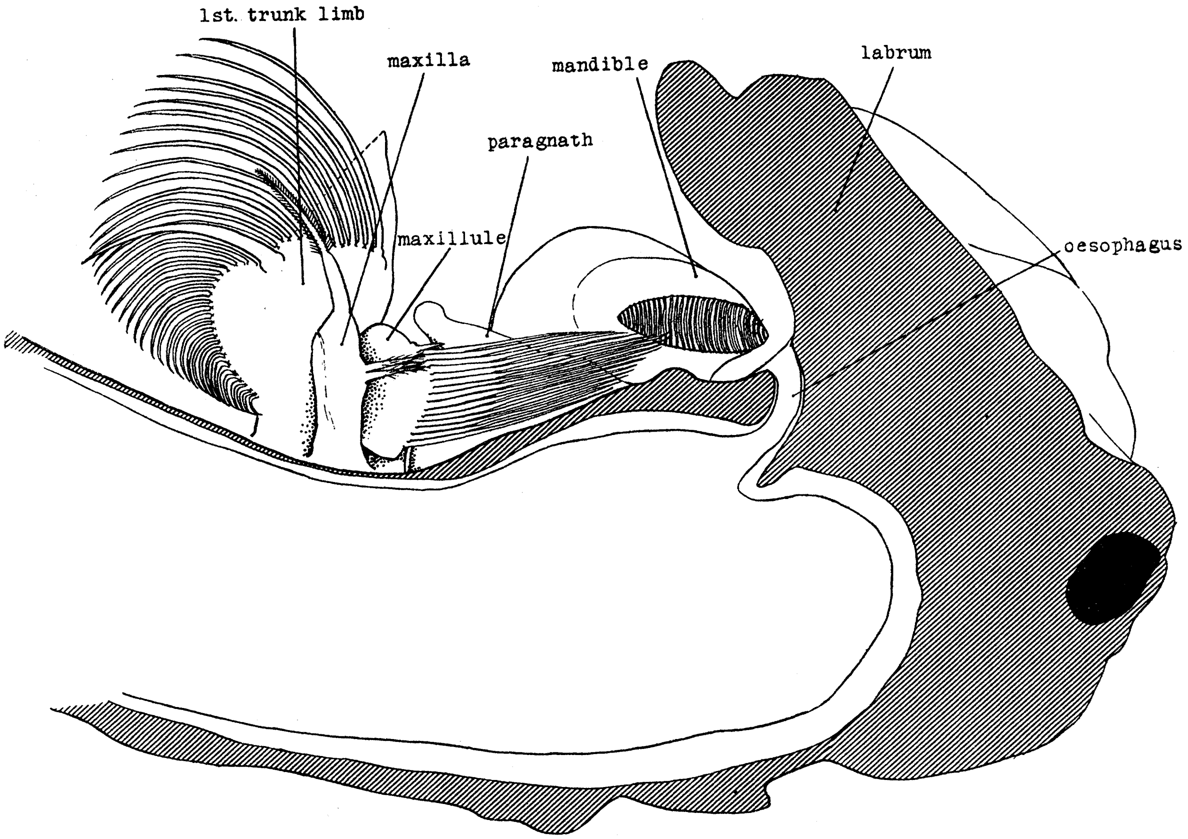

FIG. 27.—*Artemia salina* × 88. Sagittal view of anterior end of right side.

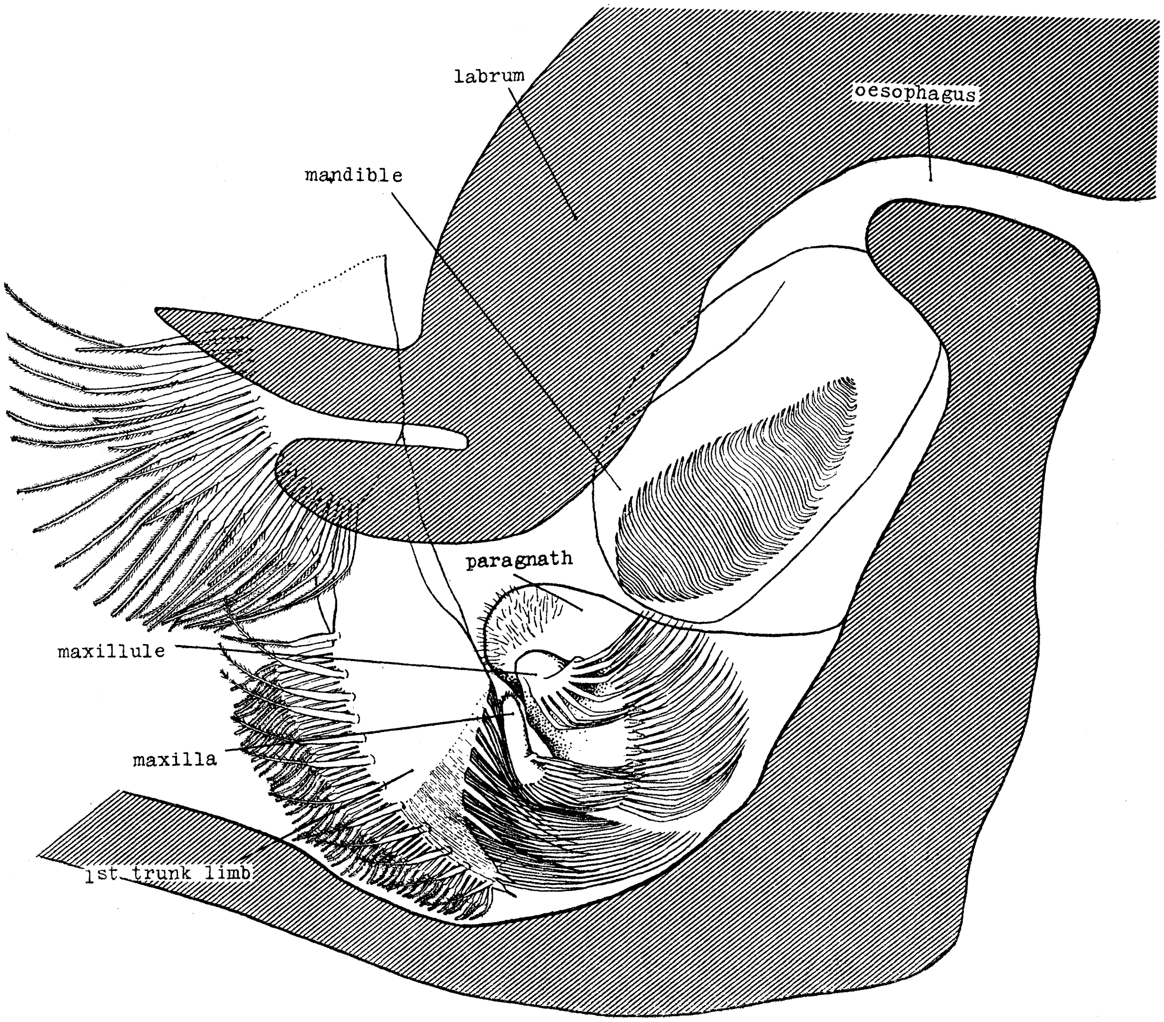

FIG. 28.—*Estheria siberica* × 140. Sagittal view of anterior end of right side.

Among the Cladocera the maxillulary setæ are less numerous than in the other groups, and this is most marked in the Anomopoda. It suggests that the limb is becoming progressively less important as a result of the head flexure which, by bringing the first trunk limb gnathobase nearer to the mandibles, has resulted in this structure partly taking over the functions of the maxillules. Thus Cannon has shown that the gnathobases of all Branchiopoda, except the Notostraca, are primitively filtratory in function, but that in the Cladocera Ctenopoda the first trunk limb of the gnathobase has become modified, fig. 29, to act in a true gnathobasic manner, pushing food forwards on to the maxillules and maxillæ, while in the Daphniidæ this has happened on the second trunk limb, the first having probably lost its gnathobase.

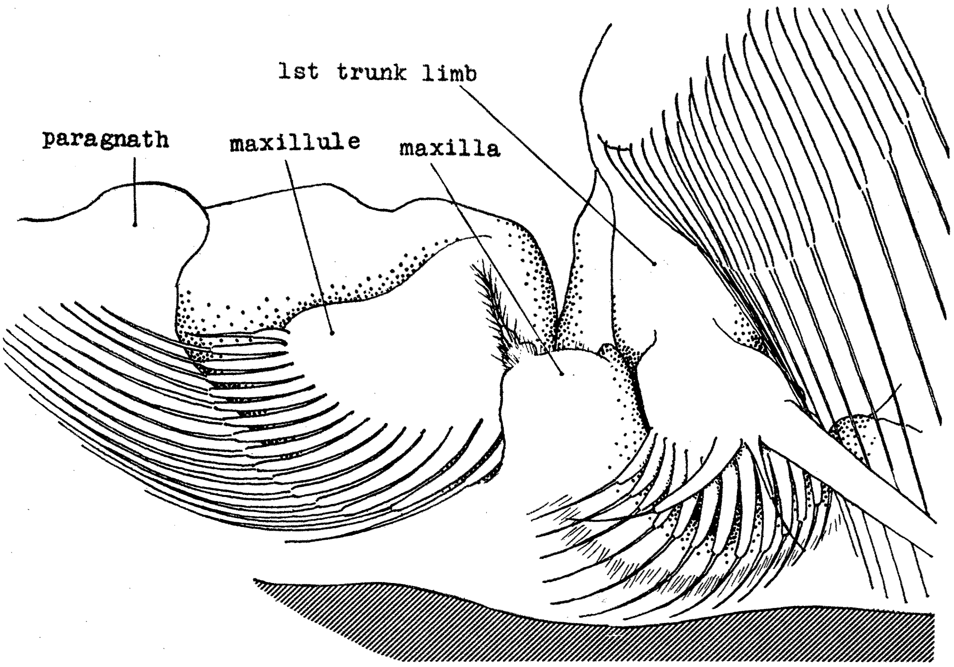

Fig. 29.—*Sida crystallina* × 375. Sagittal view of anterior end of left side. (Note, the paragnath has been displaced slightly forwards.)

The maxillule of the Notostraca, fig. 24, differs considerably from those of the other Branchiopoda. The recent statement that it is biramous (Wagler, 1927, p. 316) is incorrect, the supposed inner branch being the paragnath, as originally stated by Claus (1886, p. 14), and corroborated by Sars (1896, p. 73). It consists of a single endite armed with setæ, but both setæ and limb are much stouter than in the other groups. The setæ, however, do not all point towards the mouth. The dorsal setæ pass forwards close against the paragnaths and are armed with setules, but the more ventral setæ are stout spines or teeth which project towards the middle plane. The limb can thus be divided into two potential endites, a proximal, bearing orally directed setæ, and a distal, biting against its fellow on the other side, and can be compared with the typical Malacostracan maxillule (Cannon, 1927, text-fig. 4*d*). Cannon (1928, p. 820) has recently suggested that the Malacostraca and Branchiopoda evolved from a common stock after the first and second post-mandibular limbs had become modified as maxillules and maxillæ and that the development of the "phyllopodial" type of feeding led to a progressive disappearance of these limbs in the Branchiopodan stem, while they persisted in the Malacostraca. It is possible, then, that the maxillule of the Notostraca represents the most primitive Branchiopodan maxillule directly comparable with that of an unspecialised Malacostracan. In the Conchostraca and Cladocera the distal setæ have disappeared, while in the Anostraca the single stout spine at the tip of the maxillule may be the remains of the primitive distal group.

The Maxilla.

The maxilla, when present, is throughout the whole of the Branchiopoda, relatively of small size, and in consequence easily overlooked. It exhibits two well-defined types—on the one hand that found in the Notostraca and Conchostraca, and on the other, that exhibited by the Anostraca, Cladocera and Lipostraca.

The maxilla of the Notostraca is too well known from CLAUS's description to need a fuller detailed account. It consists of two distinct parts—an inner setose lobe or endite, and an outer tubercle on which opens the duct of the maxillary gland. WAGLER (1927, p. 316) states that the moving up of this tubercle towards the endite portion of the limb gives a false impression of a biramous constitution. There is no evidence, however, that the duct is moving towards the middle line, but rather the reverse, as in the Anostraca it opens on the limb itself. Its position so far removed from the middle line and pointing outwards is probably correlated with the fact that in the Notostraca there is little, if any, forward current along the mid-ventral line, certainly in the region behind the mouth. Hence there will be no continuous stream of water to sweep away the excretion as it leaves the duct, and so the opening of the duct is placed at a distance from the mouth. Similarly, in *Limnetis* which, like the Notostraca, is a mud-eater, the opening of the maxillary duct is on a tubercle situated immediately outside the maxillules, the remainder of the maxilla having disappeared. This agrees with SARS's description (1896, p. 123).

Thus, neglecting the excretory tubercle, the maxilla of these two orders may be said to consist of a single small setose endite. In the Notostraca this curves round the median face of the basal part of the maxillule, that is, the part on which the setæ point forward. In the typical Conchostracan, *Estheria*, it occupies a similar position, so that its setæ point forwards under the arch formed by the maxillulary setæ. The edge of the endite is slightly curved in a manner similar to the maxillules, so that the two maxillæ together form a smaller arch of setæ, fig. 28.

In the remaining orders of the Branchiopoda the maxilla, when present, consists of a sub-cylindrical lobe variously armed with plumose setæ. It is wedged in between the first trunk limb and the maxillule on the median side, these two limbs being contiguous more laterally.

In all the Anostraca which we have studied, the maxilla is of about the same height as the maxillules. It is armed anteriorly with a few setæ, but these are quite unlike the maxillary setæ of *Apus* and *Estheria*, which are rigid, constant in direction, and similar to the maxillulary setæ. They are, on the contrary, extremely delicate and flexible, and point irregularly forwards. The most marked difference, however, is that they are plumose, that is, armed all round with setules. In *Polyartemia*, *Polyartemiella* and *Chirocephalus*, these are the only setæ present, and vary in number from two in *Chirocephalus*, fig. 30, *b*, to six in *Polyartemiella*. In *Eubranchipus*, fig. 30, *a*, *Artemia* and *Dendrocephalus*, an additional seta is present attached to the inner posterior margin and projecting backwards into the food grove. This seta is of a different type from those on the anterior surface, being considerably stronger and more rigid, though it is probably capable of a certain amount of movement at the tip.

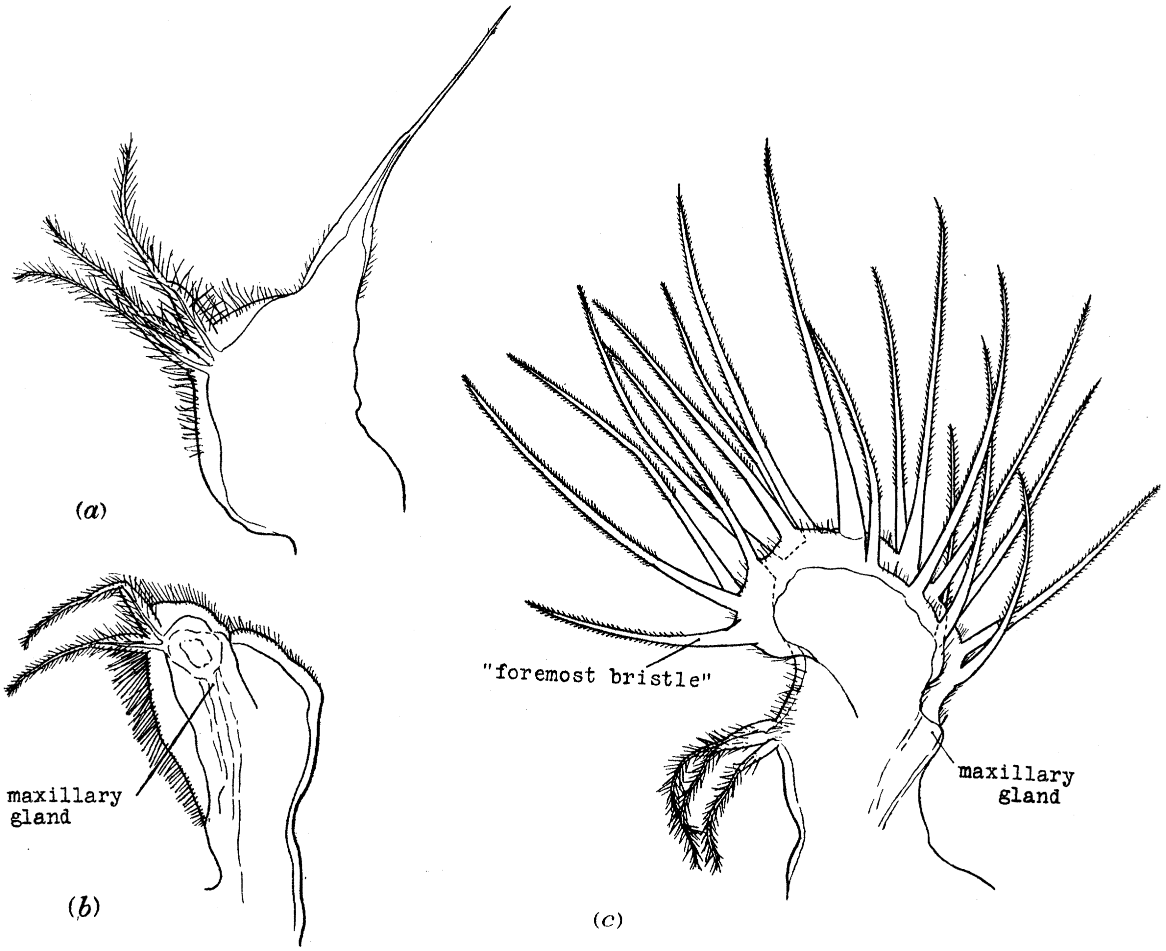

FIG. 30.—Isolated left maxillæ of (*a*) *Eubranchipus vernalis* × 114; (*b*) *Chirocephalus diaphanus* × 114; (*c*) *Branchinecta paludosa* × 84.

The maxilla of *Branchinecta*, figs. 30, *c* and 31, at first sight appears entirely different from those of the other Anostraca, though from three to five flexible spines are present on the anterior margin in the usual position. It is considerably larger in comparison, and the distal portion is flattened out into a plate bearing a fringe of long setæ. This flat plate is bent in a median direction and the setæ mostly project across the food groove so that an arch is formed by the two maxillæ, but one seta—that placed most anteriorly and described by SARS (1896, p. 47) as the " foremost bristle "—is always directed laterally outwards into the space between the first trunk limb and the base of the maxillule, fig. 31.

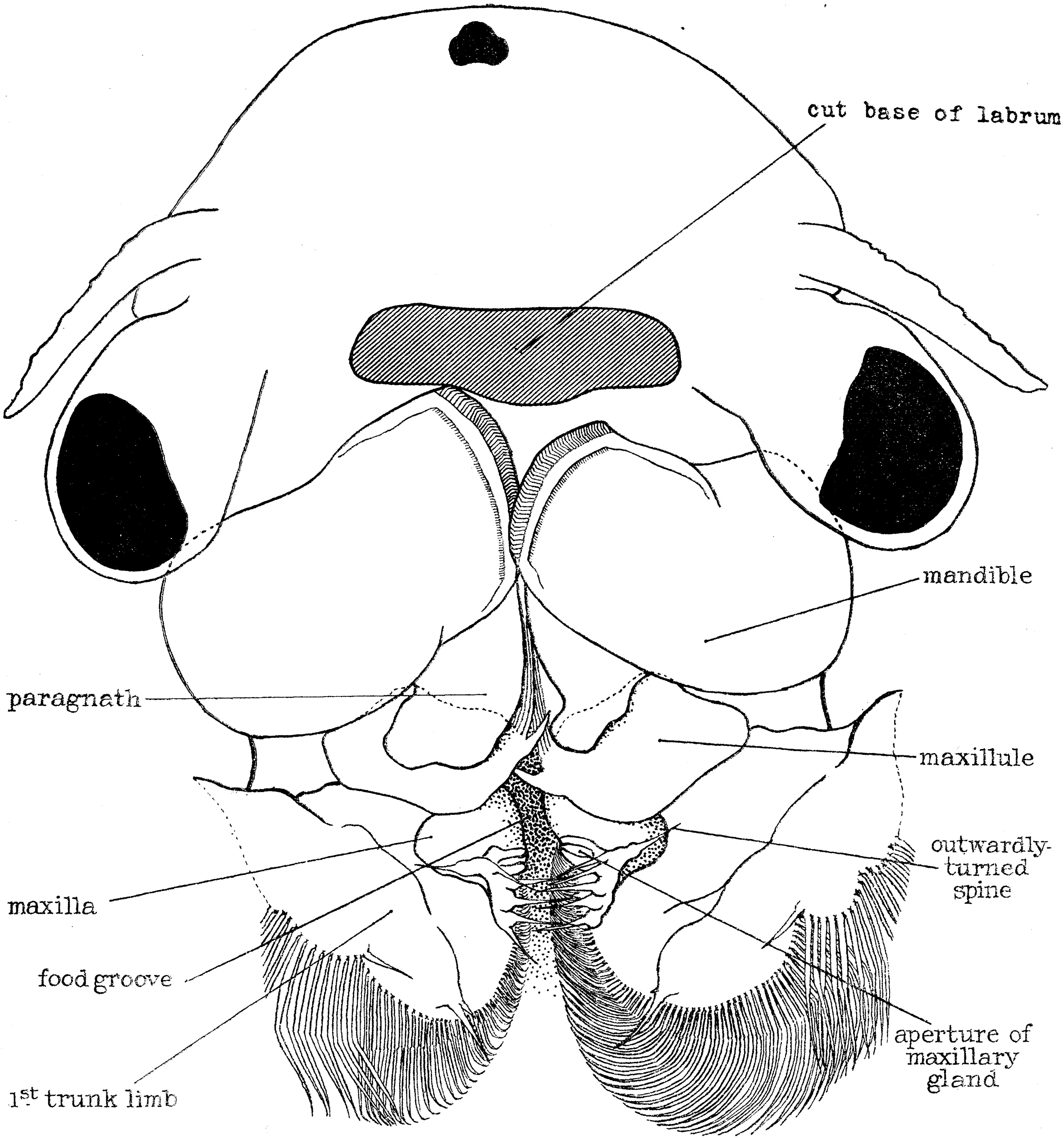

FIG. 31.—*Branchinecta gaini* × 60. Ventral view of anterior end, the labrum having been removed.

SARS (1896, Plate 7, figs. 1 and 8) for *Branchinecta paludosa* figures the limb turning outwards, but this is obviously not the natural position in the living animal as there is insufficient space between mandibles and first trunk limb. The position figured by Sars is only possible when all the limbs have been outwardly compressed. In all the specimens of *Branchinecta gaini* and *Branchinecta paludosa* examined by means of frontal slices we found that the maxillary plate was bent medially and the setæ were directed across the food groove.

The outwardly turned spines lie one in each channel through which the ventral food stream passes to the exterior. Immediately posterior and slightly dorsal to this seta on each maxilla is the very conspicuous opening of the maxillary gland, the secretions of which, therefore, are removed in the ventral stream immediately on leaving the gland.

In the Lipostraca, Scourfield (1926) figured a tubercle immediately behind the maxillule of *Lepidocaris*, which he suggested might represent the opening of the maxillary gland. Figures of two specimens, figs. 5 and 7, pp. 281 and 282, show that, in addition to this tubercle, there was a lobe situated more medially which bore two or three flexible plumose setæ closely similar to those of modern Anostraca. The maxilla of *Lepidocaris* is thus the same as that of *Chirocephalus*, but the opening of its excretory duct has shifted to a more lateral position.

In the Cladocera no true maxilla has hitherto been described. However, a well-formed maxilla occurs in *Sida*, and the series *Sida—Holopedium—Moina—Daphnia* shows a gradual disappearance of the limb.

The maxilla of *Sida*, fig. 29, consists of a small lobe similar to that of *Chirocephalus* but only about half as high as the maxillule. It is similarly wedged in between the maxillule and the gnathobase of the first trunk limb and is extremely difficult to find. It bears only one short flexible plumose seta. In *Holopedium*, fig. 16, the plumose seta has disappeared, but the body of the maxilla forms a distinct lobe covered with setules. The distal part is slightly bent forwards, but it is doubtful whether it is capable of being moved. In *Moina* all that remains of the maxilla is a slight hillock covered with setules in the typical position between the maxillule and first trunk limb, while in *Daphnia* all trace of the maxilla has disappeared.

General.

In the foregoing account we have demonstrated that while the Branchiopodan maxillule is remarkably constant throughout the group, the maxilla exhibits two district types—that of the Notostraca and Conchostraca, in which it resembles the maxillule, and that of Lipostraca, Anostraca and Cladocera, where it is totally different and is always characterised by the presence of a small number of soft, flexible, plumose setæ, The most unexpected fact emerging from this division is the grouping of the Cladocera with the Anostraca rather than with the Conchostraca. It is generally accepted that the Cladocera evolved from an ancestor similar to the modern Conchostraca (Sars, 1896, p. 37), and it would be expected at first sight that the two groups would exhibit the same type of maxilla. However, we were fortunate in obtaining some larval Conchostraca from Dr. G. S. Carter which he had collected in South America, probably *Eulimnadia chacoensis*, and a study of these unexpectedly explained the anomalous grouping.

We found that the maxilla in the larval Conchostraca closely resembled that of *Sida*, and was quite unlike that of an adult *Estheria*. Its inner portion consisted of a minute lobe bearing near its tip a soft plumose seta which pointed roughly forwards and which was exactly of the type we have described in the Anostraca and Cladocera.

If the Cladocera evolved from the Conchostraca, this has been brought about by the abbreviation of the body, by the reduction of trunk segments. Now all the Conchostraca typically hatch as nauplius, and as development proceeds new limb-bearing segments appear at the hind end; that is, an *Estheria* passes through a larval stage in which the number of trunk limbs is the same as that of, *e.g.*, *Sida*. In fact, a larval *Estheria* with six trunk limbs looks like a Cladoceran, as at this stage it has biramous swimming antennæ, the head is not yet enclosed in the shell, and the adductor muscle has not yet come into play to produce the laterally compressed adult form. The Cladocera may thus be regarded in a sense as pædogenetic Conchostraca. They are sexually mature larval Conchostraca exhibiting larval characters in the type of swimming antennæ, the carapace, the number of trunk segments, and now, we may add, in the maxilla.

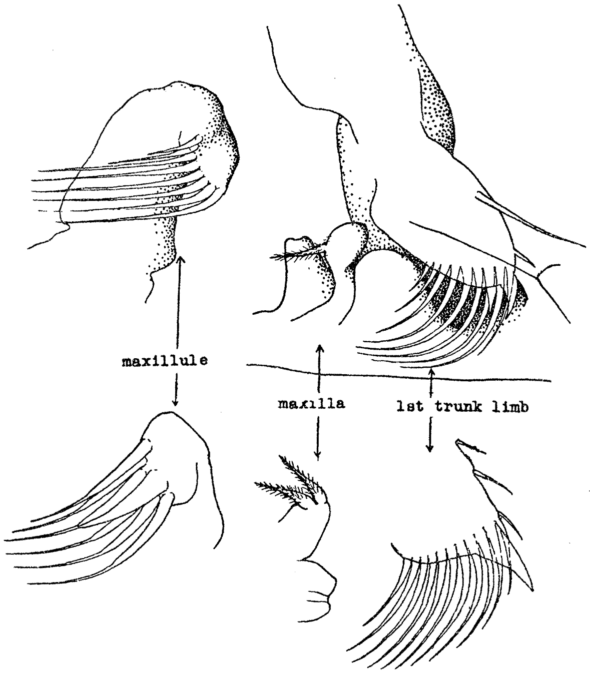

Fig. 32.—Comparison between maxillules, maxillæ and 1st trunk limbs of larval Conchostraca (above × 175) and adult *Lepidocaris* (below × 350).

More interesting than the comparison of the larval Conchostraca with the adult Cladocera is that with the adult *Lepidocaris*, for here we find that maxillules, maxillæ and gnathobases are essentially the same, fig. 32.

The adult gnathobase of *Estheria* is an extremely complicated structure, figs. 22 and 28, and yet from fig. 32 it can be seen that the larval gnathobase closely resembles that of an adult *Lepidocaris*, fig. 8.

The only difference between the maxillules is the presence of a stout claw at the base of the setæ on the maxillule of *Lepidocaris*, which is absent on that of the larval Conchostracan figured. This claw, however, is covered all over with minute subsidiary claws—this has been omitted in the figure for the sake of clearness—and is of the type that occurs all along the bases of the maxillulary setæ of an adult *Estheria*, fig. 28. Undoubtedly, therefore, the maxillule of a larva later than that figured would show one or more of these claws.

The maxilla of *Lepidocaris* figured is a ventral view. It shows that the inner cylindrical lobe bears two plumose setæ and only differs from that of the larval Conchostraca in that in this form there is only one. The number of such setæ, however, is probably of little significance ; it is the type of setæ which is important, for, as we have previously shown, the number varies from two to six in closely allied Anostraca. We can be certain that these are the only setæ on the maxilla. There are no forwardly directed setæ of the type that occurs on the maxillule or on the maxillæ of adult *Estheria*—long, straight, or slightly curved setæ armed only laterally with setules. The two preparations which we possess showing the maxilla are extremely good and show the bases of all the limbs absolutely clearly for a considerable distance behind the mouth.

On the outer side of the maxilla of the larval *Estheria* is a well-defined papilla on which opens the duct of the maxillary gland. An identical structure is to be found on the maxilla of *Lepidocaris*, as first shown by SCOURFIELD (1926, p. 164).

The maxilla of the larval Conchostracan is thus not only totally different from that of the adult, but is closely similar to that of an adult *Lepidocaris*. This can only represent a definite case of recapitulation. Without going so far as to say that the maxilla of *Branchipus*, of *Sida*, or of *Lepidocaris* is functionless, the fact of its minute size and that we can see it disappearing in the Cladocera suggests, at least, that it is a dwindling structure, and probably of little importance as a limb. Hence, that the comparatively large and armed maxilla of an adult Conchostracan goes through this simple but characteristic stage would appear purposeless unless it indicates that the ancestor of the Conchostraca possessed such a degenerate maxilla. Now there is ample evidence that the ancestral Crustacean possessed a maxilla of the typical biramous type. The maxilla of typical Malacostraca and of certain Ostracods is of this common type from which all Crustacean limbs can be derived. Hence, when the Branchiopods were definitely established, the maxilla must already have dwindled to the simple type such as occurs to-day in the Anostraca and Cladocera. In the Conchostraca, therefore, and presumably in the Notostraca, since the maxillæ of these two groups are essentially the same, the maxilla has re-developed. It is a new structure *sui generis*, and as such cannot be compared directly with any other limb.

Summary.

1. A bifid lower lip is present in the typical position in all Branchiopoda consisting of two triangular paragnaths, one on either side of a median food groove. The upper lip extends obliquely backwards beyond the tips of the paragnaths, thus differing from the Malacostracan labrum, which stops short at the level of the anterior margin of the paragnaths. The backward extension of the labrum serves to exude the secretion of the labral glands on to the food filtered off by the trunk limbs and then carried forward to the mouth.

2. The maxillules are remarkably constant throughout the group. Each maxillule consists of a single lobe curving round the hind end of the paragnath and terminating in a single endite. This is armed with spines which project forwards towards the mouth close against the median face of the paragnath. These spines are laterally beset with setules. The maxillule of the Notostraca differs from that of other groups in that the setæ on the distal part of the endite are very stout and point medially instead of forwards. Thus, while the proximal parts can push food forwards on the mandibles, the distal parts can bite together as jaws, and the Notostracan maxillule thus resembles functionally that of a typical Malacostracan.

3. The maxillæ can be divided into two distinct types. The Notostraca and Conchostraca possess maxillæ which are small but otherwise resemble the typical Branchiopodan maxillule. The Lipostraca, Anostraca and Cladocera exhibit maxillæ which consist of a minute lobe carrying a small number of soft, flexible, plumose setæ near the tip.

4. The maxilla of a larval Conchostracan is closely similar to that of an adult *Lepidocaris*. This indicates that the maxilla of the ancestral Branchiopod must have been of the simple type found in *Sida* or *Chirocephalus*, and that the maxilla of an adult *Estheria* or *Apus* is a newly developed structure.

REFERENCES.

Behning, A. (1912). ‘Int. Rev. Hydrobiol.,’ Leipzig. Biol. Suppl., ser. IV, p. 1.

Borradaile, L. A. (1926). ‘Ann. Mag. Nat. Hist.,’ vol. **17**, p. 193.

Borradaile, L. A., Eastham, L. E. S., Potts, F. A., and Saunders, J. T. (1932). “The Invertebrata,” Cambridge.

Buchholz, R. (1866). ‘Sch. phys-ökon. Ges. Königsberg,’ Jahrg. **5**, p. 100.

Calman, W. T. (1909). “A Treatise on Zoology,” pt. VIII, fasc. iii, Crustacea, London.

Cannon, H. G. (1922). ‘Quart. J. Micr. Sci.,’ vol. **66**, p. 213.

Cannon, H. G. (1927). ‘Trans. Roy. Soc. Edin.,’ vol. **55**, p. 355.

Cannon, H. G. (1928, *a*). ‘Trans. Roy. Soc. Edin.,’ vol. **55**, p. 808.

Cannon, H. G. (1928, *b*). ‘Brit. J. Exp. Biol.,’ vol. **6**, p. 131.

CANNON, H. G., and MANTON, S. M. (1927). 'Trans. Roy. Soc. Edin.,' vol. **55**, p. 219.

CANNON, H. G., and MANTON, S. M. (1929). 'Trans. Roy. Soc. Edin.,' vol. **56**, p. 175.

CLAUS, C. (1886). 'Arb. zool. Inst. Univ. Wien,' vol. **6**, p. 267.

EKMAN, S. (1902). 'Bih. svensk. Handl.,' vol. **28**, p. 1.

ERIKSSON, S. (1928). 'Zool. Bidr. Uppsala.,' vol. **12**, p. 93.

JOLY (1840). 'Ann. Sci. nat. (Zool.),' vol. **13**, p. 251.

LANKESTER, E. RAY (1881). 'Quart. J. Micr. Sci.,' vol. **21**, p. 343.

LUNDBLAD, O. (1920). 'Ark. Zool.,' vol. **13**, p. 1.

NAUMANN, E. (1921). 'Acta. Univ., lund,' vol. **17**, No. 4, p. 1.

SARS, G. O. (1896). "Fauna Norwegiæ," Christiania.

SCOURFIELD, D. J. (1926). 'Phil. Trans.,' B, vol. **214**, p. 153.

SPANGENBERG, F. (1875). 'Z. wiss. Zool.,' vol. **25** suppl. p. 1.

STORCH, O. (1924). 'Ergbn. Zool.,' Jena, vol. **6**, p. 125.

STORCH, O. (1925, *a*). 'Int. Rev. Hydrobiol.,' vol. **12**, p. 369; vol. **13**, p. 68.

STORCH, O. (1925, *b*). 'Z. wiss. Zool.,' vol. **125**, p. 299.

STORCH, O. (1925, *c*). "Biologie der Tiere Deutschlands.," Berlin, Part 15, p. 23.

STORCH, O. (1926). 'Zool. Anz.,' vol. **67**, p. 145.

STORCH, O. (1929). 'Biol. Generalis Wien.,' vol. **5**, p. 1.

WAGLER, E. (1927). "Handbuch der Zoologie," Berlin, vol. **3**, p. 305.

ZIMMER, C. (1927). "Handbuch der Zoologie," Berlin, vol. **3**, p. 553.