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D. J. Scourfield

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V. *On a New Type of Crustacean from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire)*—Lepidocaris rhyniensis, *gen. et sp. nov.*

By D. J. Scourfield, *I.S.O., F.Z.S., F.R.M.S.*

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[Plates 21–23.]

Contents.

1. Introduction.

The Chert Bed of Middle, or possibly Lower, Old Red Sandstone age discovered by Dr. W. Mackie (1914) at Rhynie, in Aberdeenshire, has become famous among palæobotanists on account of the beautifully preserved remains of the earliest known land plants, described by the late Dr. Kidston and Prof. Lang (1917–1921).

In addition to the plants, however, the Rhynie Chert also contains animal remains, for the most part very small and in a very fragmentary condition, although the fragments themselves are in many cases exceedingly well preserved. The vast majority of these animal remains are evidently Crustacean in character, and it was at first thought (see British Association Report, 1919, p. 110) that they belonged to several, or at least to two, different species. Subsequent work has, however, convinced me that all the

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Crustacean remains so far seen in the Rhynie Chert belong to the one species described in this paper.

Next to the Crustacean remains in order of abundance, but very far behind in actual number, are the traces of small Arachnids. These, so far as at present discovered, have been described by Mr. S. Hirst (1923), and comprise a true Mite, a small spider-like creature, and several forms belonging to the extinct Order Anthracomarti. A few fragments of other animals have also been seen, but they are too vague and uncertain to allow of description at present. Strangely enough, although the Chert evidently represents a fossilised swamp or the shallow margin of a lake, no certain traces of any of the characteristic microscopic organisms of such situations, such as Desmids, Diatoms, Peridinians, Rhizopods, &c., have been seen, although constantly looked for. When it is remembered that in addition to the cellular structure of the larger plants, delicate hyphal threads and spores are also found most perfectly preserved in the Chert, this absence of all representatives of our modern "pond-life" organisms is very strange. The explanation is possibly to be found in the theory, which in fact has been already advanced to account for the origin of the Chert, that the water in which the Chert Bed was formed came from a hot spring or geyser, and was highly charged with silica. In this case the paucity of aquatic life would be comparable with what is known to occur in concentrated saline waters, and the presence of only a single species of Crustacean would be easily explained on the assumption that it was the only form which could adapt itself to the very special conditions of the environment.

Technique.—Owing to the fragmentary condition of the remains of the Crustacean and the entire uncertainty as to where they would most likely be found in the Chert, it was soon realised that some simpler method than that of preparing ordinary rock sections would be necessary if excessive labour and expense were to be avoided. The expedient of examining small, thin flakes or chips of the Chert immersed in oil was therefore tried, and found to work admirably. The chips are simply struck off with a hammer, the flattest and thinnest being as a rule selected for examination. When covered with oil (usually cedar oil or oil of cloves—preferably the latter, as it is less troublesome to use), the roughness of the surface is obliterated as effectually as if the chips had been ground and polished. Examination under the microscope can be made with or without a cover-glass, and as a rule no difficulty is found in using objectives up to $\frac{1}{6}$ inch (4 mm.). Even immersion-lenses up to $\frac{1}{12}$ inch (2 mm.) can be used in many cases if required, and in fact a certain number of details of the Crustacean to be described were only noticed in this way. The chips can also, of course, be mounted in balsam if desired, the balsam naturally having the same effect as the oil in obliterating all traces of surface roughness. Incidentally, it may be mentioned that both in the work of searching for traces of the Crustacean and in the elucidation of its structure, the use of a strong light is very helpful, especially, of course, in the case of chips of any considerable thickness. For this reason a good artificial illuminant is generally preferable to daylight. In many instances a 100 c.p. "Pointolite" lamp has been employed with advantage.

Although the bulk of the work has been done by means of chips of the Chert immersed in oil, a fair number of sections prepared in the usual way have also been examined. Such preparations, however, have no particular advantage over the rough chips for the end in view in this case. Frequently they have two disadvantages, for they are often ground too thin, thus hindering the elucidation of the connection of the various parts, and also it is not usually possible to examine the sections from the back of the slide with any objective higher than $\frac{1}{3}$ inch or $\frac{1}{4}$ inch (8 mm. or 6 mm.) owing to the thickness of the glass slip. No record of the total number of chips and sections examined has been kept, but it must have been very considerable, probably about two thousand. Although, relatively speaking, the animal remains in the Chert may be referred to as fairly numerous, not more than a quarter of the chips and sections examined have yielded traces of animals of any kind, and of these not more than about one in five has proved of any value in the work of elucidating the structure and determining the relationships of the different parts of the Crustacean described in this paper.

Most of the material used in this research has been supplied by the authorities of the British Museum, to whom I wish to express my sincere thanks. This material resulted from the special digging operations undertaken by the Committee of the British Association appointed to excavate critical sections of the Rhynie Chert, who were assisted by a grant from the Royal Society. (See British Association Reports, 1919 and 1920.)

My grateful thanks are also due to many friends who have assisted me in various ways, and especially to the Rev. W. Cran, of Skene, Aberdeenshire, from whom, through the good offices of Miss G. Lister, I first received specimens of the Rhynie Chert. Mr. Cran has most generously placed at my disposal all his Crustacean remains, the result of what must undoubtedly have been a very large amount of careful search. To my wife I am indebted for undertaking a large share in the laborious work of preliminary search for traces of the Crustacean; to Mr. C. H. Caffyn for making sections; to Dr. W. Mackie for the gift of sections; to Mr. S. Hirst for many chips containing parts of the Crustacean; to Mr. J. H. Pledge for taking the photo-micrographs; and in a very special degree to Dr. W. T. Calman, who has taken the greatest interest in the progress of the work, and whose advice and suggestions have been invaluable.

2. Detailed Description of *Lepidocaris rhyniensis*, gen. et sp. nov.

A.—*Female.*

General appearance.—There can be no doubt that in general appearance the Rhynie Chert Crustacean (male as well as female) must have looked exceedingly like a very diminutive *Branchipus*, *Chirocephalus*, or other typical Anostracan. The elongated tapering form, the many body segments, the caudal furca, and the entire absence of a dorsal shield or shell, make the comparison inevitable. But there were some striking points of difference from any known form of the order referred to. The chief of these,

to anticipate a little, were the absence of stalked eyes and the presence of large biramous second antennæ.

On Plate 21 a few photographs of specimens of *L. rhyniensis* have been reproduced in order to give some idea of their actual appearance under the microscope. It must be pointed out, however, that, owing to the large amount of débris of various kinds embedded in the Chert, the photography of the Crustacean remains is a very difficult proposition, and that much more can usually be made out from an examination of the specimens under the microscope than appears from the photographs.

On Plate 22 an endeavour has been made to give restorations of the probable general appearance of the female and of the anterior part of the male, while on Plate 23 restorations of the principal appendages have been attempted. Most of the evidence upon which these restorations are based will be found in the text-figures, although naturally it has not been possible to include a drawing of every specimen that has been seen and taken into account in the course of this work.

Size.—As already mentioned, the Crustacean remains in the Chert are mostly fragments, and only four specimens have been found which allow of the actual length of the animal being determined with any certainty. Three of these are of apparently more or less fully grown individuals preserved in an extended position. The most convincing, perhaps, is the peculiar section showing simply the edges of all the somites on one side (fig. 1). This specimen measures a trifle more than $\frac{1}{10}$ inch (2·5 mm.), and this was very probably about the original length of the animal, as the evident drawing out of the middle somites is compensated for by the telescoping of some of the anterior and posterior ones. Judging by the length of the one remaining ramus of the caudal furca, the animal was probably not quite fully grown. Another extended specimen, which shows indications of all somites from head to tail, though exceedingly badly preserved, measures $\frac{1}{9}$ inch (2·7 mm.) without the caudal rami, which are missing. With these the specimen must have measured about $\frac{1}{8}$ inch (3 mm.). The third extended specimen (fig. 2) measures about $\frac{1}{9}$ inch (2·7 mm.), but the anterior somites are somewhat telescoped, and the head is not quite complete, so that the original length may well have been about $\frac{1}{8}$ inch (3 mm.). This specimen, by the way, appears to have been a male, judging by the sole remaining portion of an appendage attached to it. I believe, therefore, that $\frac{1}{8}$ inch (say, 3 mm.), may be safely accepted as the normal length of a full-grown individual (male or female), inclusive of the caudal rami.

Confirmation of this is obtained indirectly from the fourth specimen alluded to above. This is the most perfect specimen yet found (figs. 3 and 4, also Plate 21, photos 1, 2 and 3), but it is bent upon itself almost exactly in the middle. The two halves together measure about $\frac{2}{37}$ inch (1·4 mm.), without allowing for the bend in the body. Experiment shows that about one-sixth of the observed length must be added in such a case as this to obtain the real length, and this would give a length of about $\frac{1}{16}$ inch (1·6 mm.). The specimen, however, is obviously a young one, as shown by the rudimentary condition of the caudal rami and other characters, and if the sizes of its separate organs (*e.g.*,

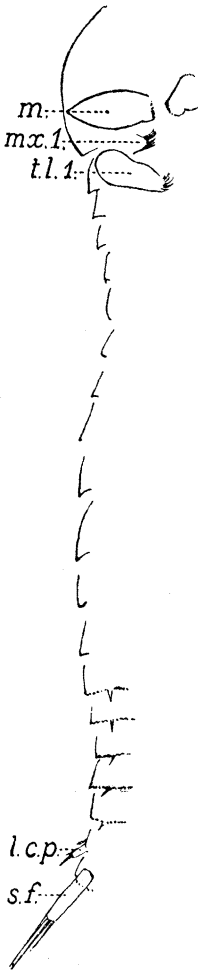

FIG. 1.—Specimen (adult, or very nearly so) showing full series of somites, 19 in number, indicated, however, solely by their edges in section and on one side only. Parts of the mandibles, maxillula and first trunk limbs visible. × 50. (In. 25688.)*

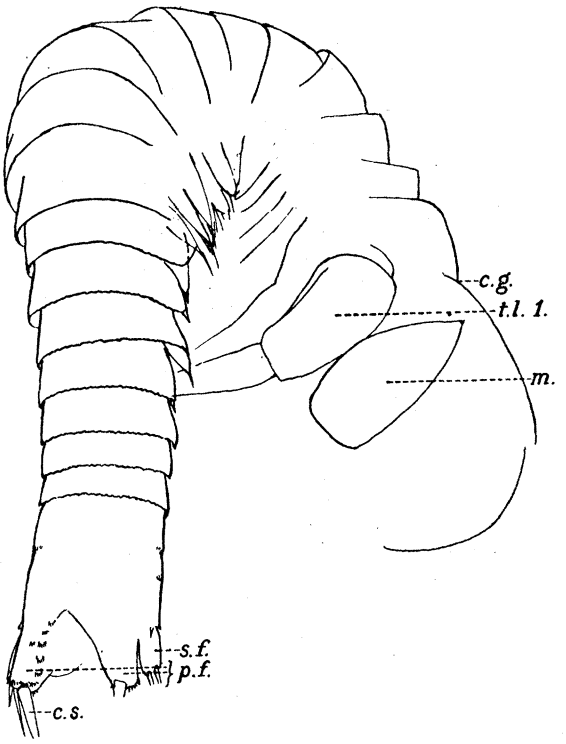

FIG. 3.—Specimen (probably about half-grown) showing complete series of somites, apparently 19 in this case also. This represents the most perfect specimen that has yet been found. Seen from side of chip approached most nearly by posterior half of body. The anterior half only imperfectly visible in this view, but well seen from the other side of the chip (see Fig. 4). Secondary furca only just beginning to appear. × 130. (In. 24493.)

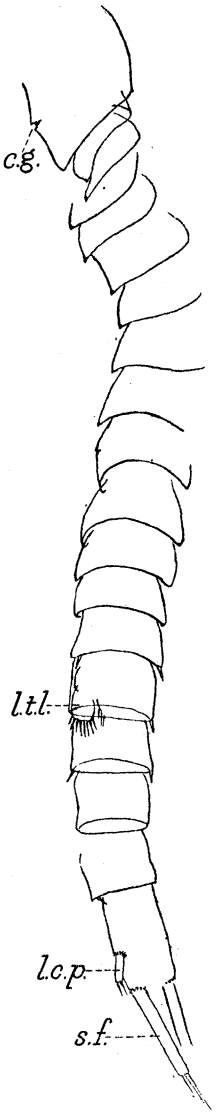

FIG. 2.—Specimen (adult) showing full series of somites, 19 in number, the anterior being very imperfect, the posterior more or less complete. Only part of one appendage remaining, viz., the last trunk limb, this, however, showing that the specimen was a male. × 50. (In. 25689.)

* The pieces of Rhynie Chert containing the specimens from which the figures were drawn have been deposited in the British Museum (Natural History), and the numbers in brackets are the Museum Register numbers. For explanation of the lettering, see p. 186.

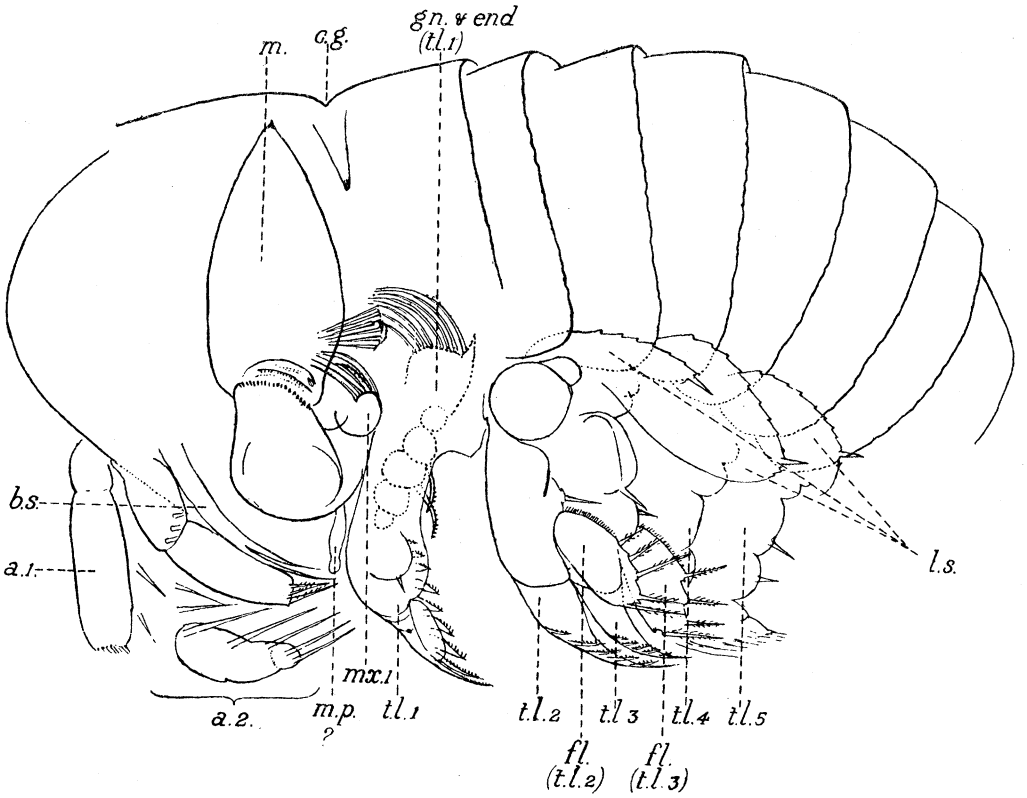

FIG. 4.—Anterior part of specimen shown in fig. 3. Almost perfect, but part of left side of head, with part of left mandible and second antenna, &c., cut away by section. By deeper focussing the right antennæ of the first and second pairs, and other details not shown, can be made out, though necessarily only in rather vague outline. × 200. (In. 24493.)

mandibles, last joint of first antennæ, &c.) be compared with the largest of these structures which have been found either isolated or in parts of other individuals, a ratio of about 7 : 12 is obtained, which, applied to the length, would give for the maximum size about $\frac{1}{9}$ inch (2·7 mm.). To this must be added the length of the caudal rami, which in this young specimen do not project beyond the end of the body, making about $\frac{1}{8}$ inch (3 mm.), as mentioned above, as the probable length of a fully-grown individual.

Body Segments (Somites).—The first, third and fourth specimens referred to above (figs. 1 to 4, see also Plate 21, photos 1–3) show pretty definitely that there were nineteen somites in all. The first somite was by far the largest, being much longer and probably slightly broader than any of the others. It was apparently bluntly rounded in front, whether seen from above or from the side, and covered not only the head proper, but also the first pair of trunk limbs. At about one-third of its length from the posterior margin and just above the mandibles, there was a well-marked transverse groove (the "cervical" or "mandibular groove"), as in recent Anostraca. No traces of any eye-stalks projecting from the head have ever been seen, but of course it does not follow that the animal was blind. The probability is that at least a simple median eye was present under the anterior part and possibly also compound eyes as in *Apus*. The

underside of the first somite was produced backwards into a large, more or less rectangular labrum, covering the mouth, mandibles and maxillulæ. The sides and posterior edge of the labrum were covered with minute fimbriated scales. (See figs. 28, 32 and 51. The labrum can also be made out in the specimens from which text-fig. 4 and photo 5, Plate 21, were taken, although not shown in the figures.)

The succeeding seventeen somites, *i.e.*, all those between the cephalic and caudal segments, appear to have been sub-equal in length, but decreasing somewhat in width posteriorly. Only the last three of these seventeen were simple rings, the fourteen anterior somites showing lateral pleura, and, in addition, the twelve anterior segments possessed large lateral scales, about which a few remarks will be made later. In the case of the two somites without scales but with pleura, the latter were pointed and ended in a spine. The three somites consisting of simple rings carried a single spine on each side posteriorly, the spines being in line with the spinous terminations of the pleura of the preceding somites, and also with the lateral outgrowths on the last segment. (See figs. 3, 4, 6 and 7, also 21 and 22.)

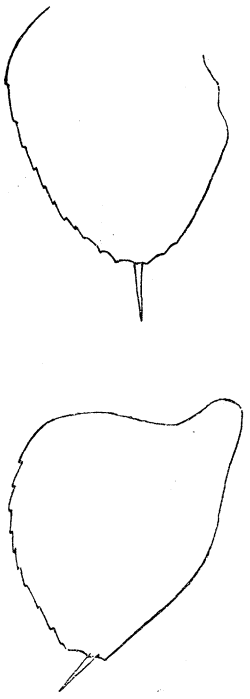

Fig. 5.—Two specimens of lateral scales. One of these (the only one ever seen) seems to show the entire scale, including the point of attachment. × 210. (In. 25719 and In. 25690.)

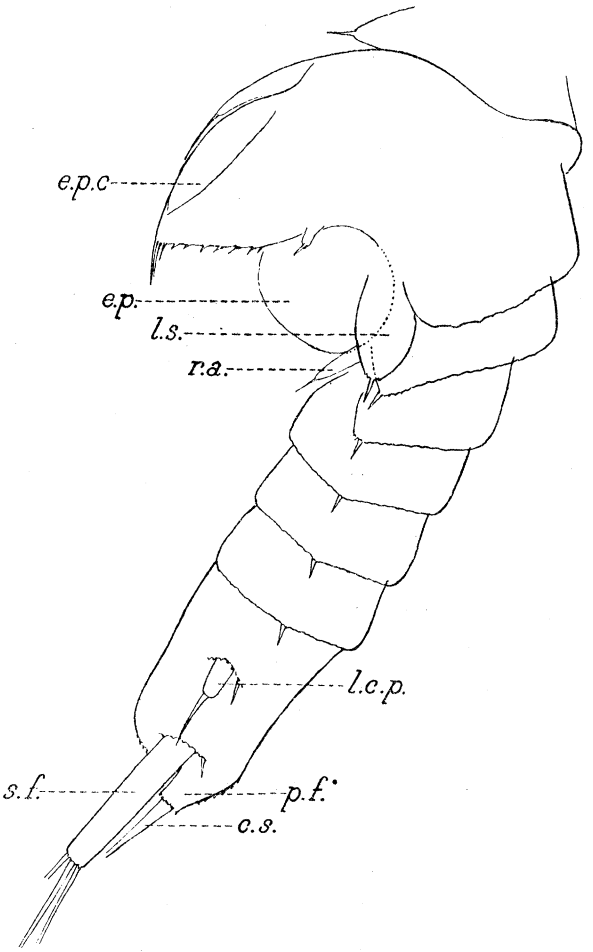

Fig. 6.—Side view of posterior part of body of female (probably not quite full grown), showing egg-pouch and cover, last lateral scale, rudimentary appendage, &c. × 130. (In. 25691.)

The last or caudal somite (see figs. 6, 7 and 8) was about equal in length to the two preceding somites, and was consequently the second in length of the whole series. It

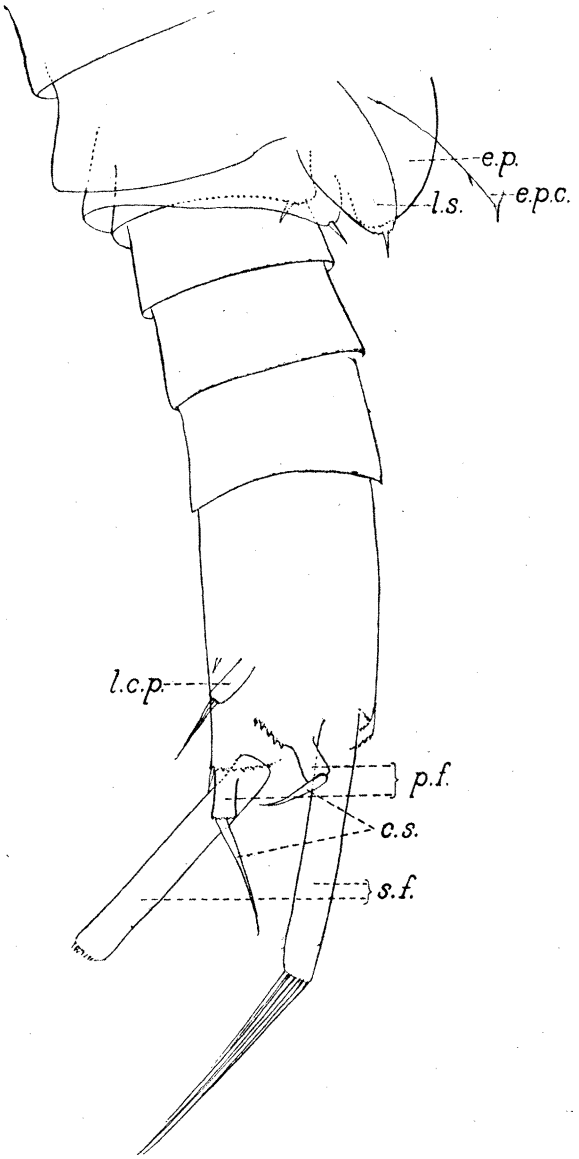

FIG. 7.—Side view (slightly twisted) of posterior part of body of full-grown female, showing almost the same details as fig. 6. × 130. (In. 25692.)

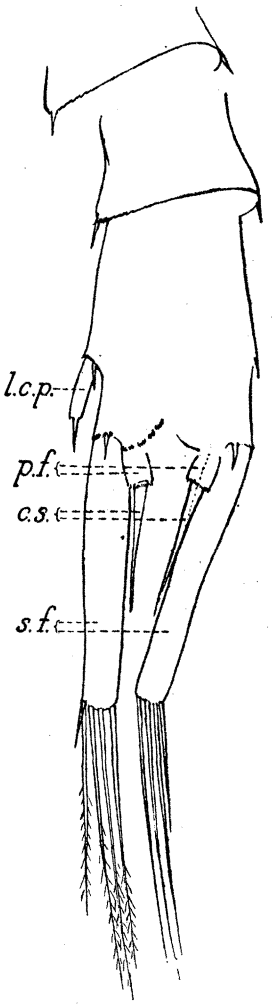

FIG. 8.—Dorsal view of tail of adult, showing primary and secondary furca, &c. × 130. (In. 25693.)

was provided with a pair of small lateral processes, directed more or less outwards, somewhat posterior to the middle; a pair of long processes directed backwards also arising laterally, but almost terminally, forming a well-marked furca, and two smaller terminal knob-like projections on the dorsal surface forming a less conspicuous furca. The small lateral processes were jointed (? movably) to the segment, and each carried

two terminal setæ (sometimes only one) and was accompanied by a stout spine at the base dorsally. The long processes were also jointed (? movably) to the segment, and each terminated in four long plumose setæ, three probably of approximately equal length, and the fourth shorter. A short, slender spine arising from the outer distal angle was also probably present; at least, it occurs in the specimen shown in fig. 8. Each of these processes was also accompanied by a strong spine at the base dorsally. The smaller terminal knob-like projections were not jointed to the segment but were directly continuous with it. Each bore a single peculiar seta, very stout at the base and tapering in the form of an elongated cone. It will be shown later, when the question of development is dealt with, that these projecting knobs, with their characteristic conical setæ, represent the primary furca of the terminal segment of the body, whereas the larger terminal processes were a later outgrowth and constitute what may be called the secondary furca.

The lateral scales referred to above as being connected with the twelve anterior trunk segments must have been a very prominent feature of the animal, and deserve special mention. As will be seen from fig. 5 (see also figs. 4 and 21) they were more or less ovoid in shape with a well-developed spine at the free end. The dorsal edge (also posterior owing to the scales being placed somewhat obliquely) was strongly chitinised and notched along most of its length. The ventral edge (also anterior) was apparently not so strongly chitinised; it was usually smooth, except for an occasional notch or two near the tip. The scales came out from under the pleura, but it has been impossible definitely to determine their point of attachment. By analogy with modern Anostracans it might have been expected that they would be proximal exites, but no example has been found showing clearly that they were actually attached to the appendages. On the other hand, the last pair of the series, which was rather smaller than the others, gives the impression that they may have originated by the pinching-off, so to speak, of a part of the pleura (see also figs. 38 and 50). The possession of the spine at the tip is also peculiar, as, so far as I know, none of the proximal exites found in recent Anostraca show such a feature.

Appendages.—The appendages of the adult female were as follows:—Two pairs of antennæ, mandibles, maxillulæ (? also vestigial maxillæ), three pairs of trunk limbs adapted for scraping or rasping, eight pairs (probably) of copepodoid trunk limbs adapted for swimming, one pair of trunk limbs modified into a flap covering the egg-pouch, and one pair of rudimentary appendages behind the egg-pouch. It is a matter for speculation whether the two pairs of lateral caudal processes already alluded to might not also be regarded as in some sense appendages.

First Antennæ (*Antennules*). (Fig. 9.)—These were uniramous and distinctly three-jointed. The first or basal joint was the shortest and the third joint the longest. All three were of approximately the same diameter, so that these antennæ looked somewhat thick and clumsy. The first and second joints were without outgrowths of any kind, but the last joint had a very small projection on one side just beyond the middle, and its

truncated end almost certainly gave rise to delicate setæ of some kind. Nearly all the specimens of this joint show a dotted appearance on the truncated distal end, with vague filaments arising therefrom (see also fig. 30). In two cases (fig. 10) I have been

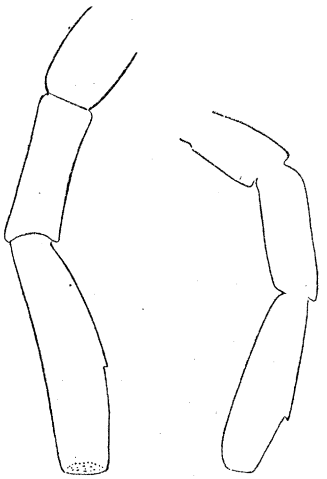

Fig. 9.—Two specimens of first antennæ, showing the three-jointed character of these organs, and in one case the "dots" on the truncated tip of the last joint. × 210. (In. 25720 and In. 25694.)

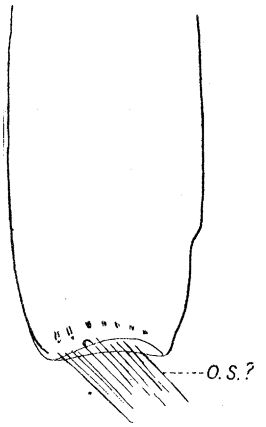

Fig. 10.—Tip of terminal joint of first antenna, showing traces of sensory setæ (? olfactory setæ), and the appearance of the "dots" under a high power. × 700. (In. 24493.)

able to make out under a high power ($\frac{1}{12}$-inch N.A. 1·4) that the dots consist of two parallel lines, thus reproducing the appearance commonly seen at the base of the so-called olfactory setæ on the first antennæ of the Cladocera. I have very little doubt that these dots and vague filaments do really represent the remains of structures very similar to, if not identical with, the sensory organs alluded to.

Second Antennæ. (Figs. 11 & 12, also Plate 23, fig. 1.)—These were a very characteristic feature, for they were large and biramous with long plumose setæ, retaining in fact almost exactly the general form found in the larval stages of all Branchiopods. The basal portion, apparently consisting of three short joints, gave rise to an outer branch of five joints and a shorter inner branch of two joints.

The first joint of the outer ramus was rather short, the second slightly longer, and they were armed apparently with two and three strong spines respectively. The three succeeding joints were rather more slender, about equal in length but decreasing somewhat in diameter. Each gave rise to a series of long plumose setæ, the numbers being probably as follows: first joint, four; second joint, three; last joint, five, two being from the tip. The extreme end of the last joint was always sharply reduced in diameter.

The basal joint of the inner ramus was rather shorter than the second joint and was armed with three spines on the distal margin and five or six spines on the inner face. The second joint bore four rather long, slender spines at its tip and a shorter one slightly below the others.

FIG. 11.—Second antenna of female (incomplete), showing very clearly the last three joints of the outer branch, with their long plumose setæ, terminal joint of inner branch, &c. × 240. (In. 25695.)

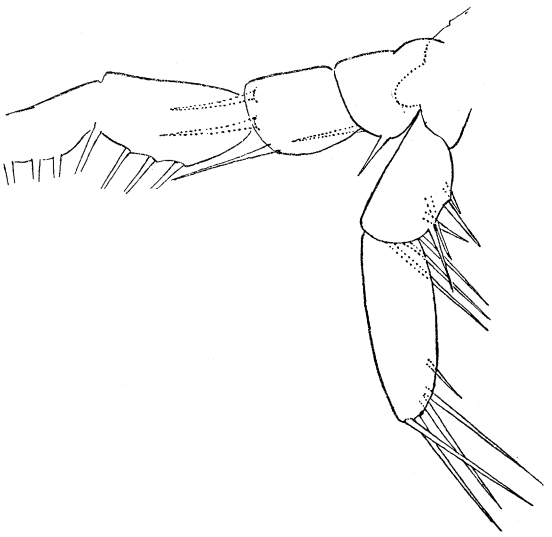

FIG. 12.—Second antenna of female (incomplete), showing two-jointed inner branch, &c. × 210. (In. 25696.)

Mandibles. (Fig. 13 *a*, *b*, *c*, also Plate 23, figs. 3, 4 and 5.)—These organs are the most abundant of all the fragments of Crustacean remains found in the Chert. This is probably due to the fact that they were more strongly chitinised than any other part of the body. They were powerful organs of the typical Branchiopod form without the slightest trace of a palp in the adult. The triturating surfaces, oval in shape, were formed by rows of minute denticles and some larger teeth. The two mandibles were not quite symmetrical in this respect, however; for whereas the triturating surface of the left mandible was bordered on its upper edge by a row of teeth, diminishing in size from behind forwards, the right mandible only possessed a single large tooth posteriorly, *i.e.*, approximately in the same position as the first (largest) tooth of the series on the left mandible.

Maxillulæ. (Fig. 14.—See also figs. 4, 29, 30, 31 and 32.)—These were quite small, as in most modern Branchiopods, and (as far as can be made out) consisted of a single nearly semi-circular plate fringed on the free curved edge with a series of eight or nine long plumose spines. From near the centre of the plate there arose a single long spine, slightly thicker than the others, and covered with short prickles. All the spines pointed forwards. It will be seen at once that these organs were very similar to the corresponding appendages in most of the modern Branchiopods. As will appear later, they were also very similar to the distal ends of the gnathobases of the anterior pairs

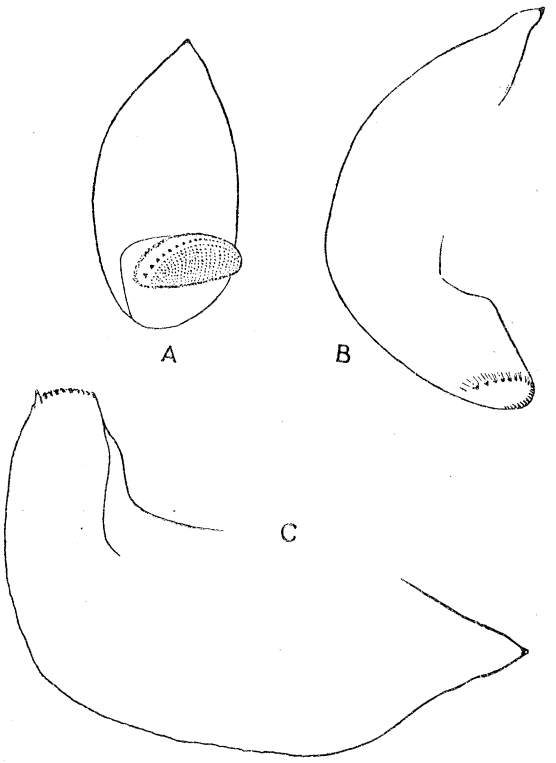

FIG. 13.—Three specimens of mandibles.—A. Left mandible from inner side, showing the triturating area and row of small teeth. × 210. B. Left mandible from behind. × 210. (In. 25721.) C. Right mandible showing the single tooth. × 210. (In. 25722.)

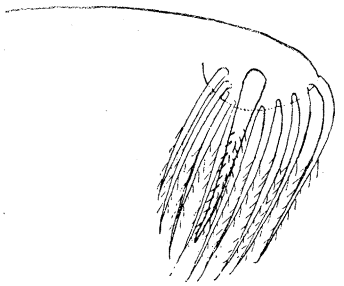

FIG. 14.—First maxilla (maxillula). × 400. (In. 25697.)

of trunk limbs, and it has often been found difficult, when examining a particular specimen, to decide whether part of a gnathobase or a maxillula was in question. The principal difference to be noted is the greater length in the maxillula of the spine with the prickles on its surface as compared with the stout spine on the gnathobase to which it apparently corresponds.

Maxillæ?—Practically the only evidence of the existence of a pair of appendages between the maxillulæ and the first pair of trunk limbs is that shown in fig. 32. It is not clear what the structures indicated really were, but if they do represent maxillæ, then these organs must have been exceedingly rudimentary. The specimen in which these supposed maxillæ occur was not quite adult (it was a male), as is shown by the sizes of the other structures, and it seems probable that in the adults at least there were no recognisable maxillæ, as otherwise better evidence would have been obtained of their existence.

The Trunk Limbs.—The appendages so far described have been almost typically Branchiopodan in character. We now come to appendages which, although closely related to the foliaceous type of foot characteristic of the Branchiopoda, differ from all

the forms hitherto known in that group. They were moreover divided rather sharply into two distinct series or tagmata. The first series consisted apparently of the three anterior pairs of trunk limbs and were much nearer the typical foliaceous foot than the others. They ended, however, in peculiar hand-like structures, the "fingers" of which were provided with strong combs on one side, and they no doubt functioned as scraping or rasping organs. The second series seem at first sight to have little, if any, relationship to the foliaceous type of foot, as they are paddle-like organs of the Copepod type, but it will be shown later that they are in reality most closely related to the foliaceous foot.

First Pair of Trunk Limbs. (Figs. 4, 15, 16, 29, and 31, also Plate 21, photo 5, and Plate 23, fig. 7.)—As already mentioned, this pair of appendages was attached to the

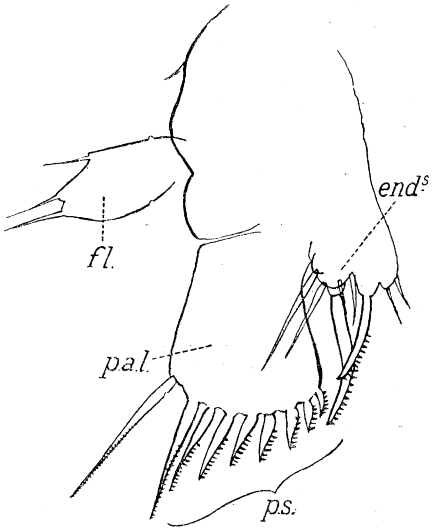

FIG. 15.—First trunk limb, showing flabellum, palmate terminal rasping organ, &c. The endites are not properly displayed owing to foreshortening, but the pectinate setæ arising from two of them are well shown. × 210. (In. 25698.)

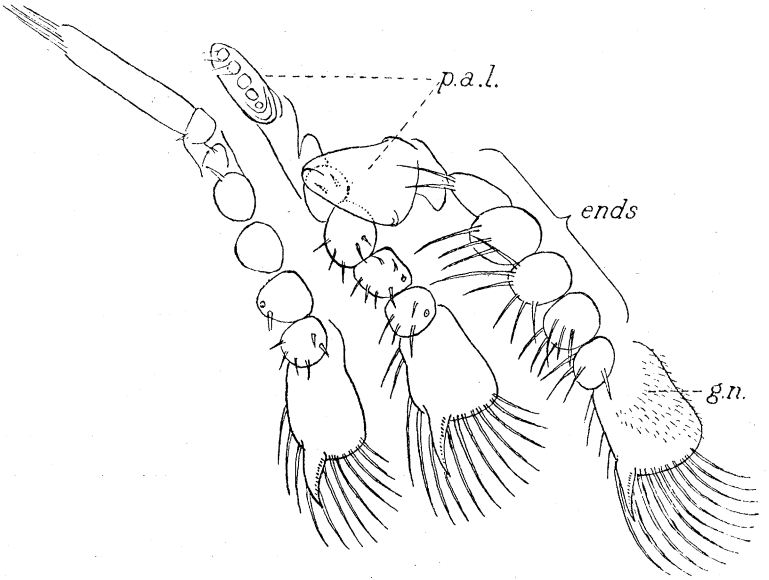

FIG. 16.—Section through first three pairs of trunk limbs, showing gnathobases, endites in section, &c. × 240. (In. 25699.)

cephalic segment. Each limb consisted of a broad, somewhat triangular, plate (the corm or axis), bearing on the inner edge six processes (lobes, not articulated to the corm), on the outer edge one process (articulated to the corm), and terminating in a large palmate extension fringed distally with strong pectinate spines. The foliaceous ground-plan is unmistakable. The inner processes are the endites, the proximal being an exceedingly well-developed gnathobase, the outer process is almost certainly the exite known usually as the flabellum, and the palmate terminal piece is either a seventh endite or more probably the apical lobe. No evidence has been obtained of the existence on this limb, or indeed on any of the others, of an exite corresponding to the branchial

lobe known as the "bract" or sometimes as the "epipodite." Such an organ may have been present, though not preserved on account of its peculiarly soft and very slightly chitinised nature; but on the whole this seems unlikely.

The most striking feature of this limb is evidently the large terminal palmate lobe or plate with its strongly chitinised comb-like spines. This hand-like organ was distinctly articulated at the base, although the joint does not appear to have extended completely across the limb. It was turned obliquely inwards, so as to approach the middle line and probably acted in concert with the corresponding lobe of the other limb of the pair. Its convex distal margin carried a number, eight to eleven, of strong spines gradually diminishing in length from the outer to the inner margin. All the spines were provided with teeth on the inner side only. The outermost (longest) was also the most slender and its lateral teeth were very small. The teeth of the other spines were much more robust, giving these spines a comb-like appearance. In passing, it may be mentioned that possibly an incipient form of this lobe may be seen in such species as *Branchinecta paludosa* (see Sars, 1896, Tab. VII), *Branchipodopsis kalaharensis*, *B. wolfi*, &c. (see Daday, 1910, figs. 49*g*, 52*h*, &c.).

The other striking feature of this limb is the gnathobase—a large, sub-quadrangular lobe armed with a powerful pectinated tooth and a series of long plumose setæ. Much of its surface was covered with minute hairs.

The five endites between the gnathobase and the palmate terminal lobe were small rounded knobs armed with setæ, the fifth with only one seta apparently. In addition, the second and third of these endites were each provided with a characteristic long, curved, stout spine, bearing teeth on one side only, similar to the comb-like spines of the terminal lobe.

The exite (flabellum) of this limb was a small sub-ovoid plate armed with four spines, three sub-terminal and one on the outer edge. Its point of insertion was about the middle of the outer edge of the limb and just above it there was a stout spine.

Indications have been seen in some cases of what was probably an incipient articulation dividing the basal portion carrying the gnathobase from the rest of the limb.

Second Pair of Trunk Limbs. (Figs. 4, 16, 17, also Plate 23, fig. 8.)—These were very similar to the first pair, but somewhat more slender in all respects. The terminal palmate plate or lobe was more elongated and was armed with only six pectinate spines of a less robust character, the outermost again being the most slender. The gnathobase was almost exactly similar, but was perhaps devoid of the general hairiness of the surface. The five intermediate endites were also practically the same except that the second and third did not possess the characteristic curved pectinate spines. The exite or flabellum was much larger and more quadrangular than in the first trunk limbs and was usually armed with six spines instead of four.

Third Pair of Trunk Limbs.—So far as it has been possible to determine, these very closely resembled the second pair in all details, but were apparently slightly more slender. The exite was perhaps a trifle larger.

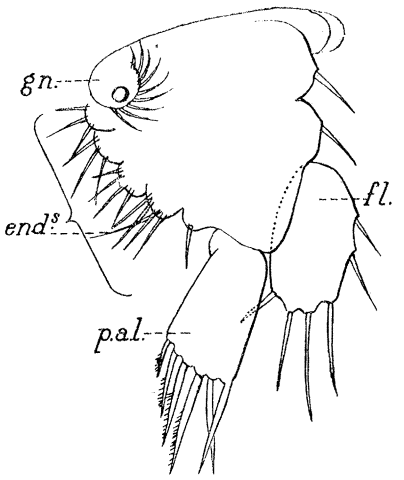

FIG. 17.—Second (or third) trunk limb. The gnathobase is shown in a foreshortened position. × 240. (In. 25694.)

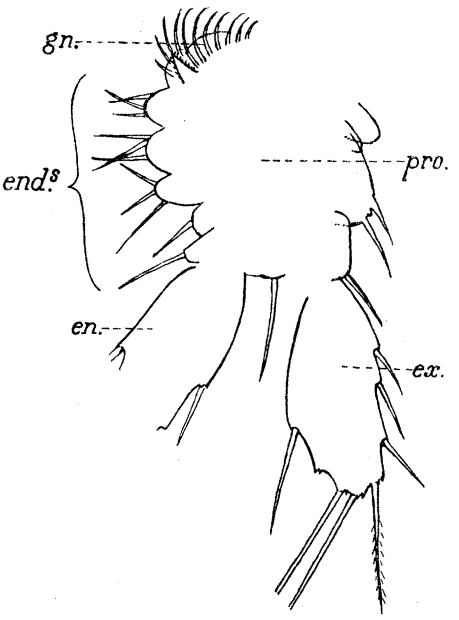

FIG. 18.—Fifth trunk limb, showing distinct division into protopodite, endopodite and exopodite (copepodoid type), but with endites and gnathobase still present on the inner edge of the protopodite. (The fourth trunk limb in this specimen appears to be similar, but it is twisted and difficult to figure.) × 240. (In. 25700.)

Fourth to Eleventh Pairs of Trunk Limbs. (Figs. 18, 19 & 20, also Plate 21, photo 6, and Plate 23, figs. 9 & 10.)—Commencing probably with the fourth pair, the trunk limbs took on quite a different aspect from those already described. Each foot consisted of a very large, almost rectangular, basal portion, to which were attached distally two flat, elongated, sub-rectangular plates, presenting a most striking resemblance to the two rami of a typical Copepod swimming foot (*e.g.*, *Cyclops*), the rami, however, being only one-jointed as in the young forms of recent Copepods. The large basal portion (protopodite) on its outer edge was indented so as to form two (or three ?) lobes, each of which bore a seta, or perhaps two. On its inner edge it was cut into five or six lobes, each of the distal ones with one long seta and the proximal with a few spines. In at least the two or three anterior pairs of these limbs (see fig. 18, also Plate 23, fig. 9) the proximal lobe on the inner side was a true gnathobase similar to that occurring on the first three pairs of trunk limbs. In the middle of the distal edge of the protopodite, between the two rami, was a single, rather long, seta. No clear evidence has been obtained that the protopodite was divided into segments, but the apparent grouping of the inner lobes in pairs corresponding to the outer lobes seems to suggest that there may have been two transverse lines of extra pliability dividing the protopodite into three incipient segments.

The two rami were almost exactly similar in shape and size, the outer being perhaps slightly the larger. They were rather more than twice as long as broad, somewhat

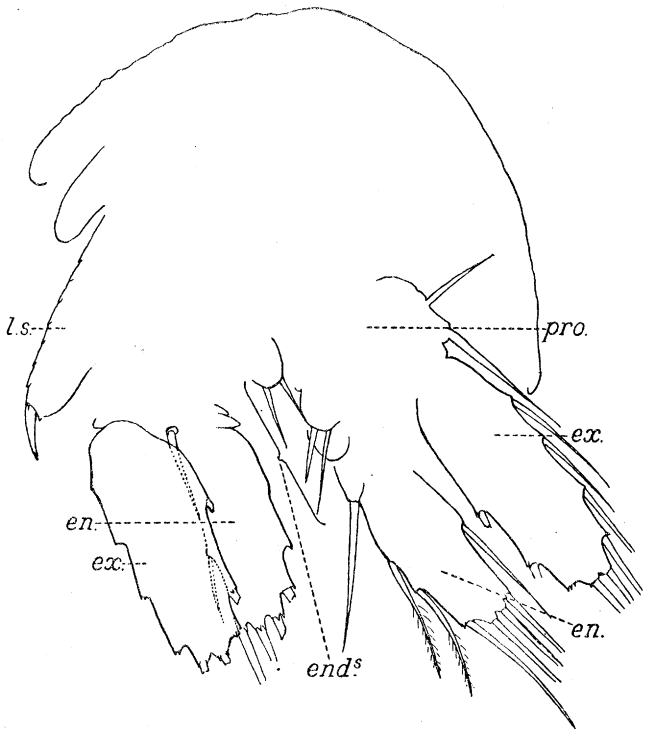

FIG. 19.—A pair of copepodoid trunk limbs (incomplete), more or less in position under section of somite. (Several overlapping pairs are actually present in this specimen.) × 210. (In. 25726.)

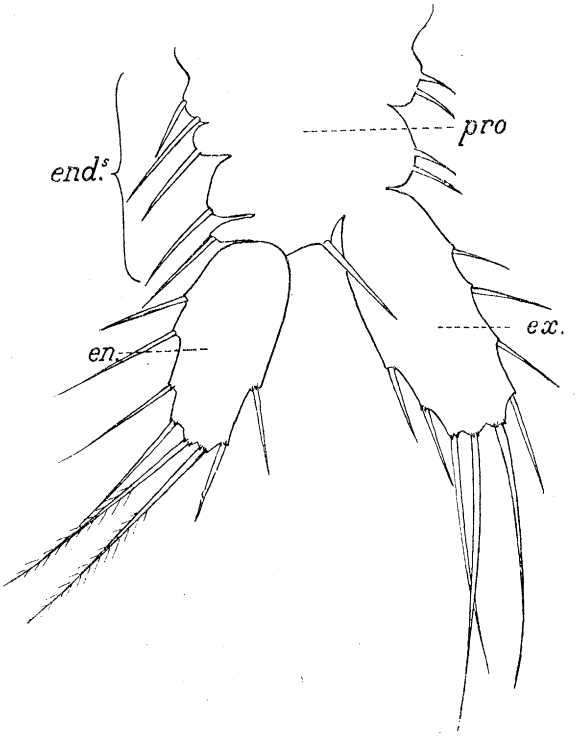

FIG. 20.—A nearly complete specimen of a copepodoid trunk limb. × 210. (In. 25698.)

rounded proximally, and furnished distally with four long setæ, the two median being longer than the others and inserted on two little projections. The edges of the rami were also provided with setæ, usually as follows: three on the outer and two (or one) on the inner edge of the outer ramus, and one (or two) on the outer and two (or one or three) on the inner edge of the inner ramus. At the points of insertion of the four terminal setæ—and of the more distal, at any rate, of the lateral setæ—there were two or three very minute thorns. Probably all the setæ on these feet were plumose, the delicate lateral barbs being quite distinctly preserved in numerous cases.

From the foregoing it will be seen that the group of limbs described were essentially the same as biramous Copepod swimming feet, the chief differences being the excessively large size of the protopodite, the unjointed rami, and the presence of gnathobases on some of the anterior members of the series. Notwithstanding this resemblance to Copepod feet, it is evident that these appendages are closely related to a limb of the foliaceous type. If the first three pairs of trunk limbs, which are unmistakably Phyllopod in plan, be compared with one another, it will be seen that there is an increase in size and armature of the "flabellum" from the first to the third, and a corresponding decrease in the terminal palmate lobe, so that the two tend to approximate to one another in size and structure (see figs. 4, 15, 17 and 29). There seems little doubt, therefore, that the two rami of the fourth to the eleventh pairs of trunk limbs represent these two processes

still more closely approximated in size and structure. At the same time, by a modification of the distal part of the corm (protopodite), the points of attachment of the two processes (rami) are brought very nearly into the same horizontal line. The lobes on the inner edge of the protopodite are evidently homologous with the endites of the first three pairs of limbs.

Egg-pouch Cover. (Figs. 6, 21 & 22.)—Fqllowing the biramous swimming feet there was a large flap covering the egg-pouch. Viewed ventrally, it appeared rather longer than

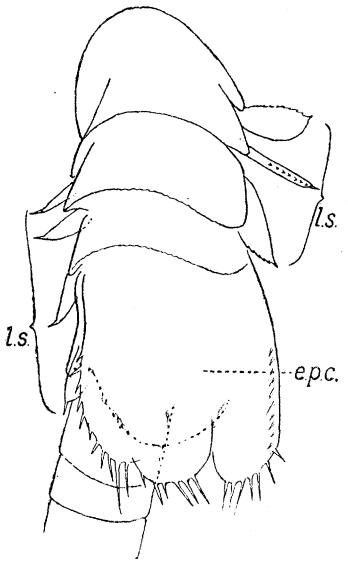

FIG. 21.—Ventral view of middle part of female, showing egg-pouch cover, lateral scales, &c. × 75. (In. 25701.)

FIG. 23.—Rudimentary appendage behind egg-pouch. × 360. (In. 25702.)

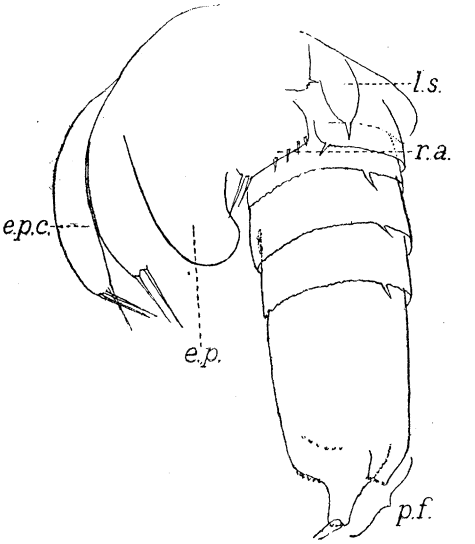

FIG. 22.—Posterior part of female, showing egg-pouch and cover, rudimentary appendage, &c. × 130. (In. 23031.)

broad, and showed a distinct division into two lateral halves. The outer edge of each half was nearly straight, but curved round distally to meet a rounder inner lobe, there being an evident notch where the two joined. The outer edge was armed with about eleven spines, and the inner lobe with about six. Viewed laterally, the flap appears to have been well arched so as to form a saucer-shaped cover for the egg-pouch below. From the evident division into two lateral halves, and the further partial division of these again into two parts, together with the presence of the fringing setæ, it seems clear that the egg-pouch cover was a modified pair (probably the twelfth) of trunk limbs.

Egg-pouch. (Figs. 6 & 22.)—This appears to have arisen from the thirteenth body segment, or possibly from the thirteenth and fourteenth together, and to have been usually more or less spherical, though sometimes elongated posteriorly, with a tendency for the free end to turn towards the body of the animal. Unfortunately, in no case have any remains of eggs been seen within the egg-pouch.

Rudimentary Pair of Appendages behind the Egg-pouch. (Fig. 23.)—In several instances it has been noticed that posterior to the egg-pouch, though covered, of course, by its free portion, there existed a pair of rudimentary appendages. Their exact shape has not

been quite satisfactorily determined, but they were characterised by having a nearly straight outer edge which carried four spines proximally and two spines at the distal extremity. The inner part appears vague in all cases, so that the appendage may not have been much more than a projecting ridge armed with spines as indicated. It is not quite certain whether these rudimentary appendages arose from the fourteenth or the fifteenth somite, although probably from the former.

Caudal Processes considered as Rudimentary Appendages.—As already mentioned, it is rather tempting to speculate as to whether the small lateral and large terminal processes on the caudal segment may not possibly be regarded as appendages. They were certainly jointed to the segment, but whether movably (*i.e.*, actuated by muscles) or not cannot of course be determined. It will be seen, however (see fig. 6), that each process is accompanied by a spine placed dorsally at its base, that these spines are in line with the lateral spines on the three segments immediately in front of the caudal segment, and that these spines again are in line with the pointed rudimentary pleura of the fourteenth and fifteenth somites, the whole line becoming more ventral as it is traced forwards. The position of the caudal processes is not inconsistent, therefore, with the idea that they are modified appendages, and that they represent the posterior remnants of a once continuous series, a pair to each segment, which were originally situated more laterally than was afterwards the case with the ordinary appendages.

B.—*Male.*

Except for one important feature—the great claspers—the general appearance and nearly all the appendages of the male appear to have been the same as in the female. The size also appears to have been about the same. The differences were as follows :—

Second Antennæ. (Figs. 24 & 26, also Plate 23, fig. 2.)—The basal portion and the

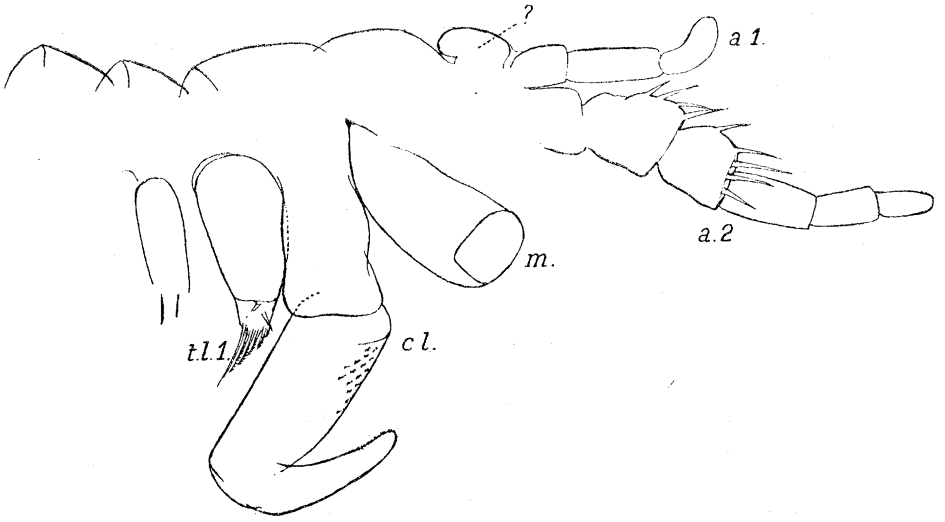

Fig. 24.—Anterior part of male, showing first and second antennæ, mandible, clasper and first trunk limb of right side. × 130. (In. 25696.)

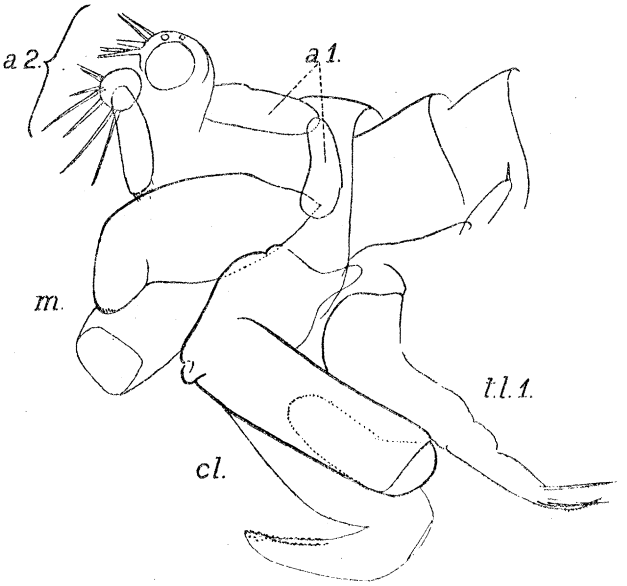

FIG. 25.—Same specimen as in fig. 24 from the left side (the mandible and clasper of the right side indicated below the left). × 130. (In. 25696.)

outer branch were seemingly identical with the same parts in the female, except that the first and second joints of the outer branch carried more spines—namely, four and five respectively as against two and three. The inner branch, however, was distinctly different from that of the female. It was somewhat longer and consisted of three instead of two joints. The basal joint was more heavily armed with spines, there being about thirteen altogether, the most distal being exceptionally large. The second joint—the longest of the three—was without any spines. The terminal joint (fig. 27), about as long as the

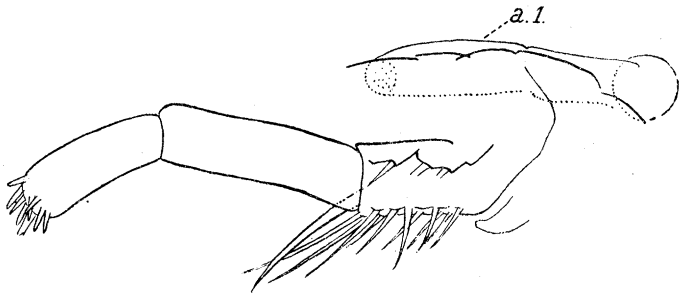

FIG. 26.—Inner branch of second antenna of male, showing its three-jointed structure, papillæ at end of third joint, &c. × 210. (In. 25703.)

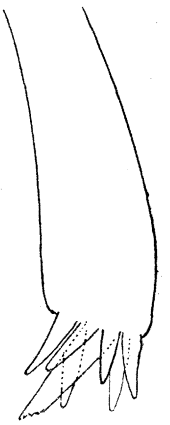

FIG. 27.—Last (third) joint of inner branch of second antenna of male, showing papillæ at tip. × 500. (In. 25694.)

basal joint, was peculiar, in that it was somewhat curved and slightly expanded towards its extremity, which, instead of bearing long setæ, as in the female, was provided with nine

to twelve short conical papillæ. In one or two cases a rather larger papilla, with an irregular point, has been seen amongst the others. Probably these characteristic papillæ were modified setæ specialised for some sensory function.

Claspers. (Figs. 24, 25, 28, 29, 30 & 31, also Plate 23, fig. 6.)—These powerful organs,

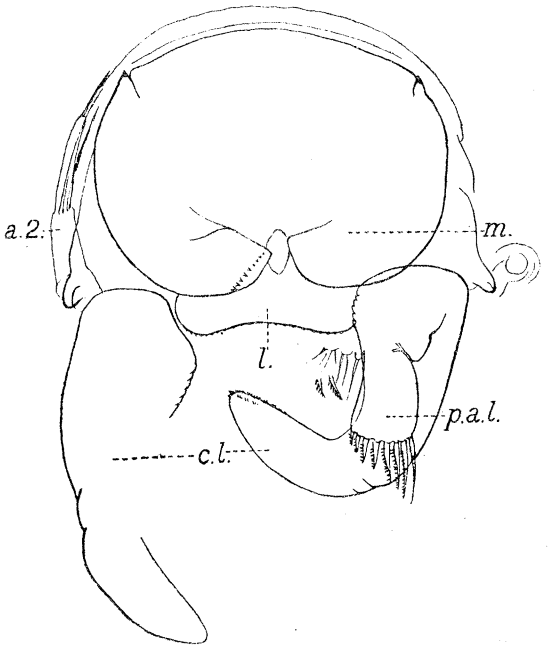

Fig. 28.—Transverse section through head of male just behind claspers, looking forward, showing labrum, mandibles, claspers, part of right first trunk limb, &c. × 130. (In. 25704.)

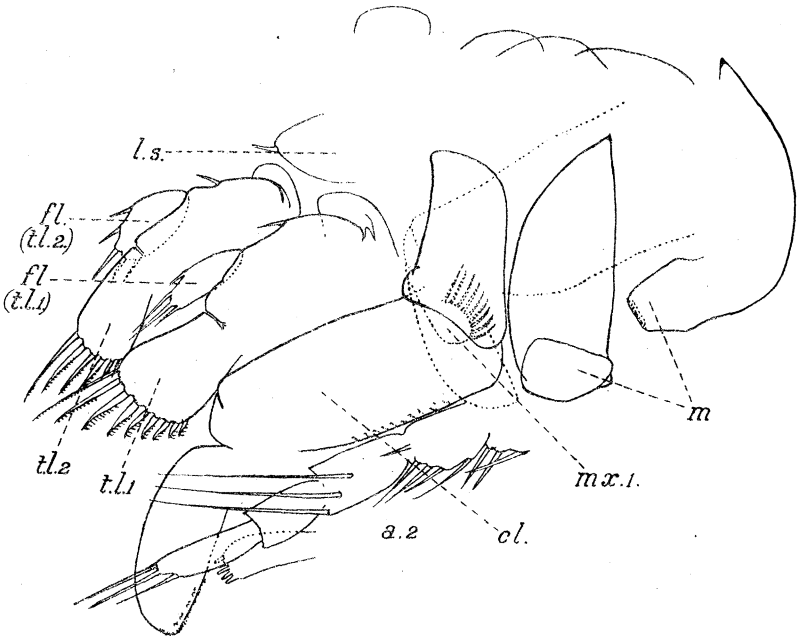

Fig. 29.—Portion of anterior part of male, showing outer branch and part of inner branch of right second antenna, mandibles, claspers, maxillula, first and second trunk limbs. × 150. (In. 25705.)

the most striking of the peculiarities of the male, had a remarkably close general resemblance to the claspers occurring in the males of certain modern Anostraca. Instead, however, of being modified second antennæ, they originated immediately behind the mandibles and in front of the first pair of trunk limbs. Each consisted of a strong basal

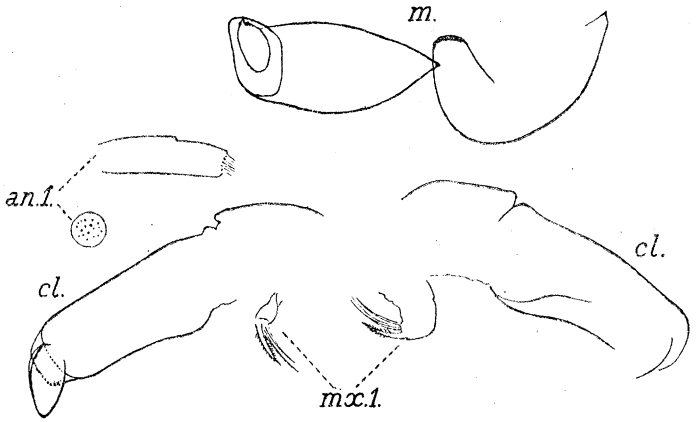

Fig. 30.—Parts of a male (portions of first antennæ, mandibles, claspers and maxillulæ), chiefly to show apparent connection between the claspers and the maxillulæ. The little circle with dots represents an end view of the tip of a first antenna. × 130. (In. 25706.)

portion, to which was attached the clasper proper, consisting of three joints. The first joint was by far the largest. Seen from the front, or from behind, it was slightly convex on the outer and concave on the inner margin, tapering rather rapidly from a very broad base to a much smaller distal end. There was a recess on the inner edge, starting from a point near the base and spreading out distally, which was roughened with rows of little teeth or fimbriated scales. Seen from the side (see fig. 25), the first joint appeared as an elongated rectangle of a thickness considerably less than the width of the base seen from the front. The second joint was very small. The third joint was about two-thirds the length of the first joint. It was about the same size at the base as the distal end of the first joint, and, as seen from the front, tapered from base to tip, the outer edge being at first nearly straight and then rapidly curving up, while the inner edge was somewhat concave. As seen when viewed from the side, the width of the joint was maintained from base to tip, or even in some cases slightly expanded, so that the free end was somewhat spoon-shaped. The edges of the depressed area, and to some extent this area itself, were covered with little teeth or fimbriated scales. This joint was apparently capable of being folded upon the first joint, and fitting into the recess on its inner face, thus securing a very firm grip.

The position of the claspers between the mandibles and the first pair of trunk limbs suggests at once that they represent a development from either the first or second pair of maxillæ. As, however, practically the only specimen seen showing even a problematical trace of a second pair of maxillæ (fig. 32) also shows the claspers apparently connected

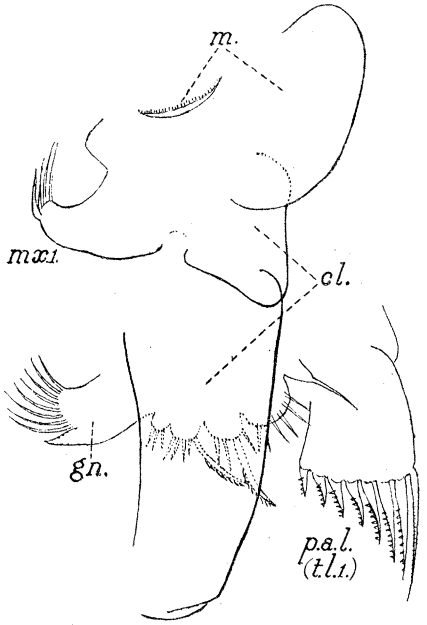

Fig. 31.—Basal part of clasper of male with maxillula, to show apparent connection between the two. Inner part of first trunk limb below. × 210. (In. 25707.)

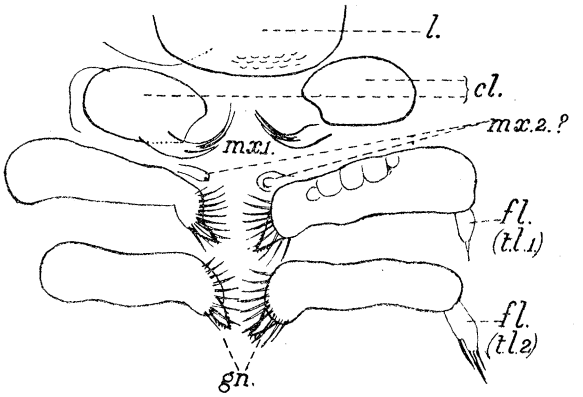

Fig. 32.—Section through bases of claspers and two first pairs of trunk limbs of male, showing apparent connection between claspers and maxillulæ, possible rudimentary second maxillæ, &c. × 150. (In. 23034.)

with the first pair of maxillæ, it seems reasonable to conclude that they arose from the first pair. The direct evidence of connection is not absolutely conclusive, but many examples have been seen where the connection seems so intimate (see figs. 30, 31 & 32) that there can be little doubt that the claspers did actually arise as outgrowths from the maxillulæ.

The last two Pairs of Trunk Limbs. (Figs. 33 & 34.)—The trunk limbs of the male seem to have been the same as in the female, with the exception apparently of the last two

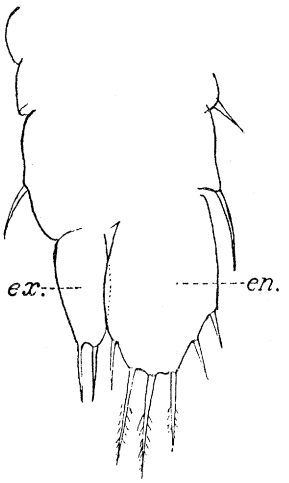

Fig. 33.—Penultimate appendage of male. × 240. (In. 23034.)

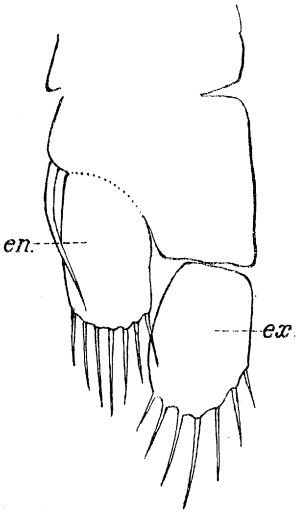

Fig. 34.—Last appendage of male. × 240. (In. 25708.)

pairs. These, although still of the biramous type, were distinctly different from the immediately preceding appendages. Instead of the rami being elongated and armed with setæ on the edges as well as distally, they were broad plates with the setæ practically on the distal margin. In the penultimate pair the two branches arose from about the same level, but the outer branch was much smaller than the inner, and it was only armed with two (or three) setæ, whereas the inner branch was provided with about seven setæ. In the last pair the two branches were sub-equal, but they did not arise from the same level owing to the protopodite being somewhat extended on the outer side. Both branches bore about seven setæ on their distal margins. The whole of the protopodite has not been observed in either the penultimate or the last pair of limbs, but the distal part of it, forming perhaps a true joint, was different in the two cases. The outer edge of the former was slightly convex, with a spine arising from near the middle, while in the last limb the outer edge was almost perfectly straight, without a spine, and longer owing to the extension already referred to. In both cases there was a rather long seta from the inner distal angle, but none from the middle of the distal margin between the two rami. Owing to the imperfection of the specimens it is impossible to say exactly to which appendages of the female these last two pairs of limbs of the male correspond.

It may be mentioned here that, judging by the number of specimens of claspers and other characteristic appendages seen, the males of *L. rhyniensis* must have been almost as numerous as the females.

C.—*Developmental Stages.*

Eggs ?—Numerous examples of empty cases (see fig. 35) have been seen which may have been the egg-cases of this Crustacean. Usually they appear to be more or less

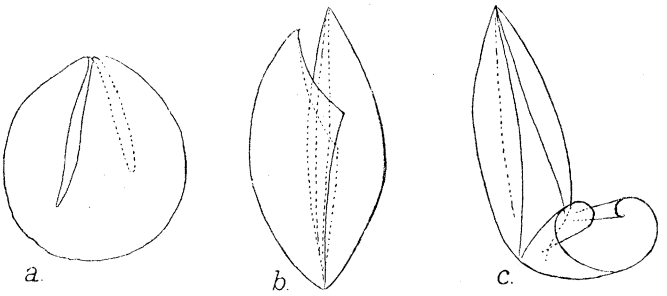

Fig. 35.—Egg cases ? × 210. (*a*) Just commencing to split into two parts. (In. 25692.) (*b*) Split extending almost to base, with edges of the two halves curling in. (In. 25692.) (*c*) Ditto, one-half in section showing curling in of the free edges very plainly. (In. 25709.) (*a*) and (*b*) are lying between the rami of the furca of the specimen shown in fig. 7.

rolled up and remind one very strongly of the rolled-up cases thrown off from the eggs of a *Daphnia* when hatching in the brood-chamber. In no instance have any contents been noticed, nor have such cases been seen either in the egg-pouch or attached in any other way to the remains of the animals. These cases may just possibly have been spore cases, of which several different kinds occur in the Chert, but I am inclined to look upon them as at least of animal origin and quite probably as the egg-shells of the Crustacean now being described.

Youngest Forms Found.—Owing to the excellent preservation of small, delicate structures in the Chert, it has been possible to distinguish some very young specimens in various stages of growth and to follow, to some extent, their gradual development into the adult form. No actual nauplius or metanauplius has so far been found, and such may of course never have existed in a free-swimming condition, but the youngest form discovered (fig. 36) was apparently not very far removed from the metanauplius state. It measures only about 1-80th inch (0·3 mm.), or, say, one-tenth of the length of an adult, and shows but four somites, the cephalic and caudal being by far the largest. The distal margins of the cephalic and intermediate somites are strongly notched, while the end of the caudal somite is provided with fimbriated scales. The labrum is very well developed and also the second antennæ, but the most remarkable feature, perhaps, is the pronounced Branchiopod character which the mandibles have already assumed. No trace of palps on the mandibles can be made out in this specimen, although they were certainly present at this stage as is evident from the specimen shown in fig. 46. The commencement of lateral scales seems to be indicated, or they may be the developing limbs. The cauda

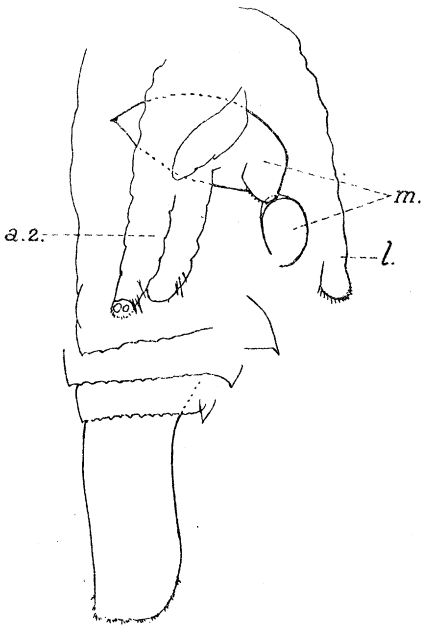

Fig. 36.—Youngest specimen so far found, with only four somites, but showing well-developed mandibles of characteristic Branchiopod type. × 240. (In. 25710.)

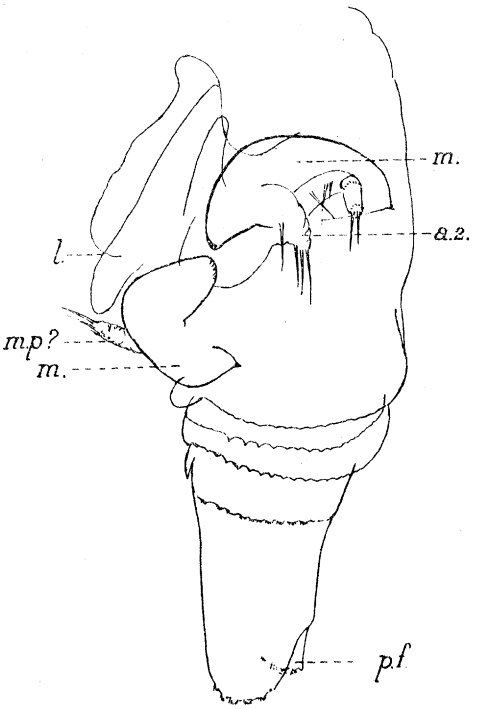

Fig. 37.—Young with five somites. × 240. (In. 25711.)

segment is no doubt forked at its extremity, although this cannot be seen in the view obtainable, and it was almost certainly provided with the two characteristic conical setæ as will become evident presently.

A later stage, actually the next in all probability, is represented in fig. 37. It closely resembles the foregoing, but has five somites, and is about 1-70th inch (0·36 mm.) in length. The bifurcation of the caudal segment is clearly shown. A very vague structure by the side of the left mandible may be the remains of a palp.

The next stage in the development which has been found is shown in fig. 38. It has apparently nine somites and is about 1-40th inch (0·6 mm.) long. The large bifid seta ("masticatory process") arising from the base of each of the second antennæ, which is such a marked feature in the larval forms of the most recent Branchiopoda, is well shown. This no doubt existed in the earlier stages, being clearly seen in the specimen shown in fig. 46. No palp can be made out on the mandible, although it no doubt existed; but behind the mandibles at least three pairs of appendages are easily recognisable—namely, the maxillulæ and the first and second pairs of trunk limbs, the first pair already assuming the shape so characteristic of the adult. The anterior lateral scales are clearly shown, and their origin, by a process of "pinching-off" from the angles of the pleura, seems to be distinctly indicated. The forked character of the caudal segment is also well shown.

A stage possibly the same as the above, although it has ten clearly marked somites, is shown in fig. 39. The general outline, especially of the head, is much better preserved than in the other examples of the young forms, and shows the two characteristic conical setæ still attached to the end of the caudal segment. There can be no reasonable doubt

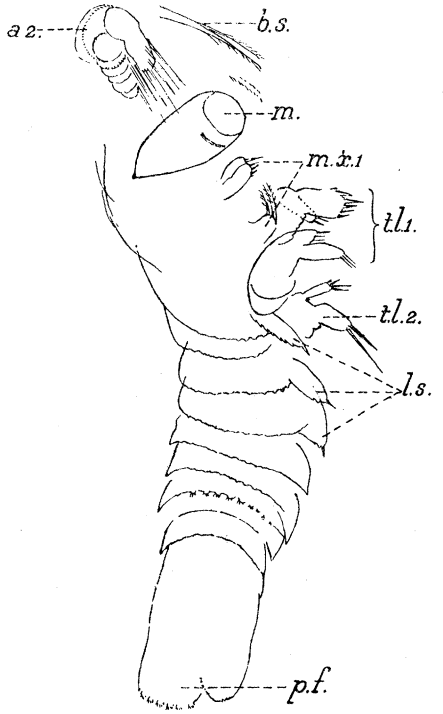

FIG. 38.—Young with nine somites. × 150. (In. 25723.)

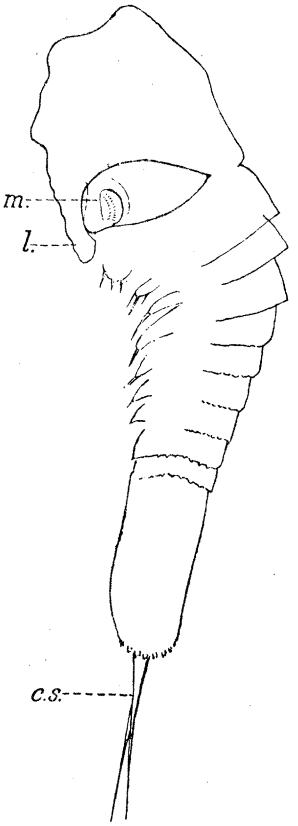

FIG. 39.—Young with ten somites. × 150. (In. 25712.)

that similar setæ were also present in the earlier stages, although not preserved in the specimens so far found. With the exception of the mandibles, the appendages are not very clear in this specimen. The ventral view of the tail of another specimen at about this stage of development is shown in fig. 40. This shows the forked termination of the caudal segment and the two peculiar conical setæ very plainly.

Later Stages in Development.—The stages so far referred to, while showing steady increase in the number of somites and in the development of the appendages, have not shown any essential alteration of the caudal segment. At a stage, however, not very far beyond the last described, the beginning of an important series of changes in the form and armature of the caudal segment took place. The first indication of this is shown in fig. 41, in which it will be seen that a little lateral process terminated by a single short spine has appeared just in front of the caudal fork. At the stage reached by the specimen

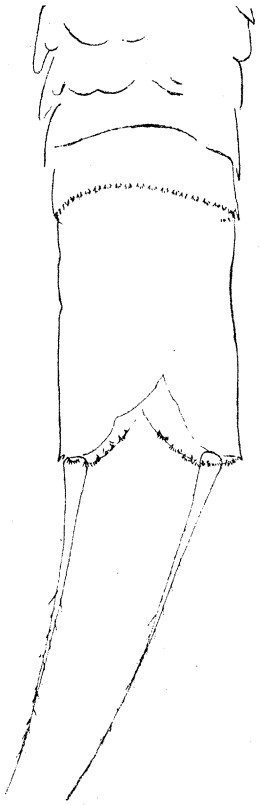

Fig. 40.—Posterior part of young (probably at about the same stage as last), showing the primary caudal furca with its characteristic conical setæ. × 210. (In. 25724.)

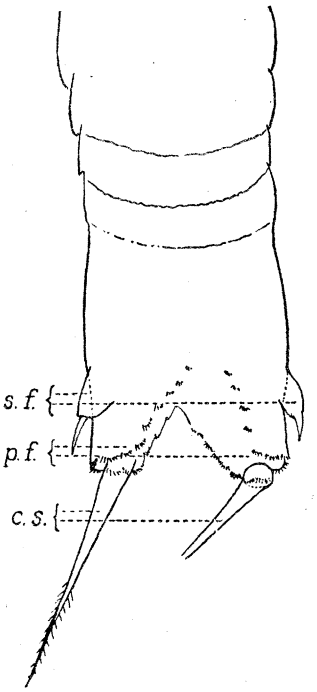

Fig. 41.—Posterior part of young showing primary caudal furca with its conical setæ, and the first rudiments of the secondary furca appearing as little lateral processes. × 210. (In. 25713.)

represented in fig. 42 this lateral outgrowth had considerably enlarged, had come to lie parallel to and almost reaching the end of the furca, and was furnished with two setæ. A still later stage (fig. 43) shows this process reaching to the end of the furca and furnished with three spines, two being quite long. It also shows the budding out of another little lateral process, armed with a single spine, at a point about half-way along the caudal segment.

The rudiments for the development of the long caudal processes forming such a marked feature of the adult, already referred to as the secondary furca, and of the smaller lateral caudal processes of the adult, are thus already clearly indicated. Although a complete series of changes from the last stage mentioned above to the adult has not yet been obtained, a number of examples of secondary furcal processes shorter than those characteristic of the full grown adult have been seen, so that there is every reason to assume that such changes took place. While the caudal processes constituting the secondary furca were gradually becoming larger and larger, and the caudal segment increasing in width and depth to accommodate them, the primary furca was remaining stationary or even receding somewhat, so that in the adult it was relatively of small size, consisting of two little knobs, bearing the conical setæ, pushed up into a dorsal position as already mentioned.

In addition to the changes in the caudal segment, there were naturally changes taking place in other parts of the body during development. The large bifid seta arising from

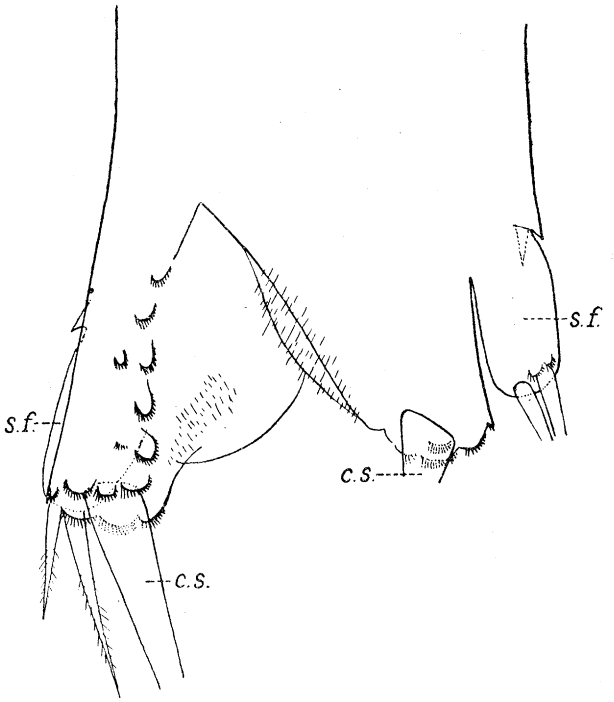

Fig. 42.—Dorsal view of end of caudal segment of specimen represented in fig. 3, showing the rudimentary secondary furca more developed than in the preceding figure, fimbriated scales, very fine hairs on inner sides of furca, &c. × 440. (In. 24493.)

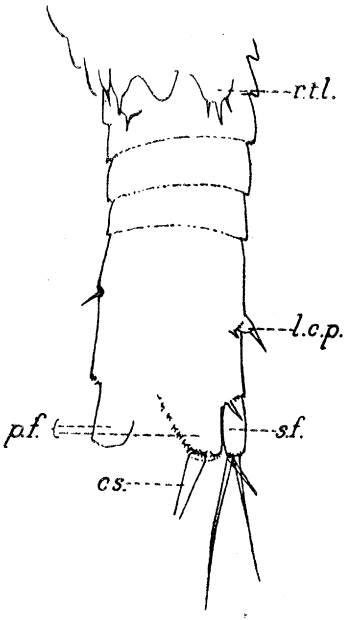

Fig. 43.—Posterior part of body of immature individual, showing developing appendages, increasing secondary furca, first rudiments of lateral caudal processes, &c. × 150. (In. 25727.)

the base of the second antenna alluded to in connection with the youngest forms found, and also shown in figs. 44 & 45 (see also figs. 46 & 51), was apparently absent in the adult,

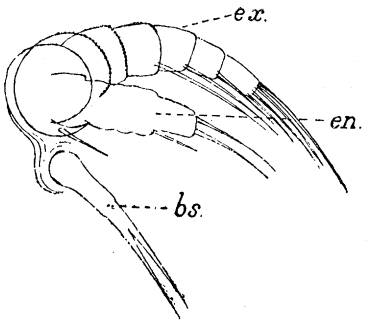

Fig. 44.—Second antenna of a young individual, showing bifid seta (masticatory process) in position at base. × 240. (In. 25714.)

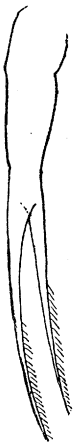

Fig. 45.—Detached specimen of bifid seta of second antenna. × 400. (In. 25715.)

but it persisted at least as far as the stage represented by the specimen shown in figs. 3 & 4, which was about half the adult size.

Although many scores—probably hundreds—of mandibles of all sizes have been seen,

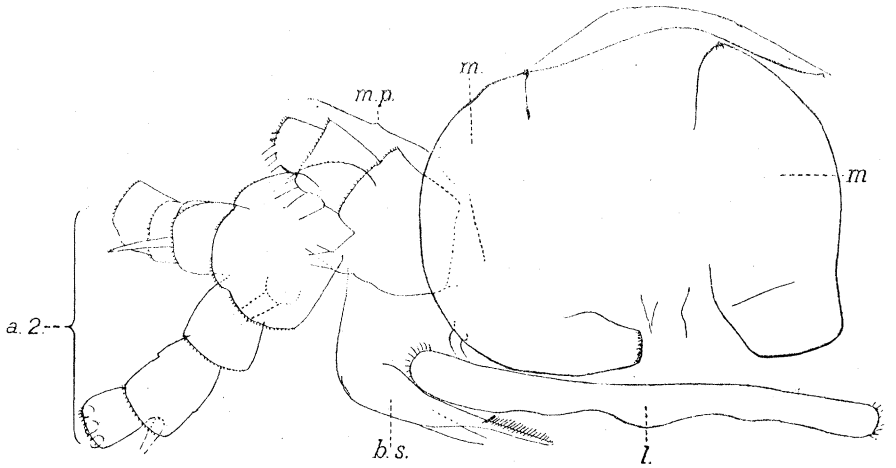

Fig. 46.—Transverse section through head of a very young individual (probably same stage as specimen shown in fig. 36), showing on one side the second antenna, with its two branches and large bifid seta, and also the mandibular palp. × 440. (In. 24657.)

both connected with other parts of the animal and isolated, the only definite evidences obtained of the existence of a palp are those shown in figs. 46, 47 & 51, and one other case not figured. All these are parts of very young forms, those shown in fig. 46 belonging, as is evident from the small size, to an individual in about the same stage of development as shown in fig. 36, and those shown in figs. 47 & 51 to individuals not much older. It will be seen from figs. 46 & 47 that the palp was three-jointed, with two setæ from the basal segment, two from the second segment (one with a swollen base) and three from the last segment. This is exactly as in the young forms of *Chirocephalus*, and no doubt most other Branchiopods. That a palp must have been present in all cases in the earlier stages is certain, and its almost uniform absence in the specimens is rather remarkable, but it may, of course, have been unusually delicate and in any case probably atrophied quite early. The structure marked *m.p.?* in fig. 4 was very probably the last remnant of a palp. As already mentioned, this animal was about half-grown.

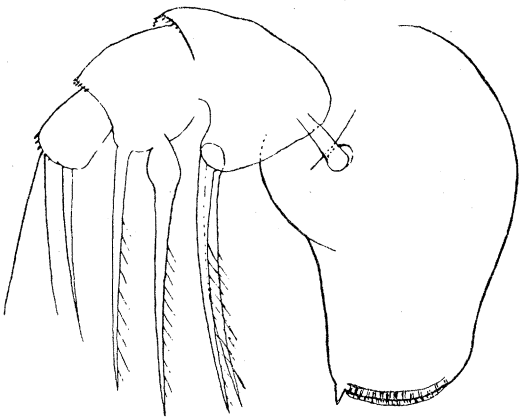

Fig. 47.—Portion of a mandible of a slightly older individual, showing palp in more perfect condition. × 500. (In. 24657.)

The first rudiments of the trunk limbs—at least, of the posterior members of the series—were apparently in the form of paired lobes projecting but a very short distance

from the segments (see fig. 48). Later, the lobes increased in length and became distinctly bifid, as shown in fig. 49. Later still, the bifurcation extended so as to produce two distinct branches, more or less separated from the basal portion of the original lobe and provided with setæ on the distal margin (see fig. 50).

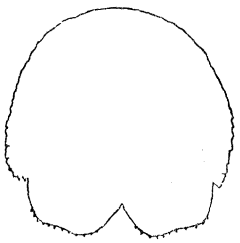

FIG. 48.—Section through a body ring, showing an early stage in the development of the posterior trunk limbs. × 240. (In. 25716.)

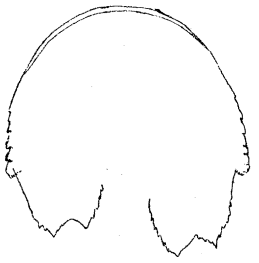

FIG. 49.—Ditto, showing a somewhat later stage. × 240. (In. 25716.)

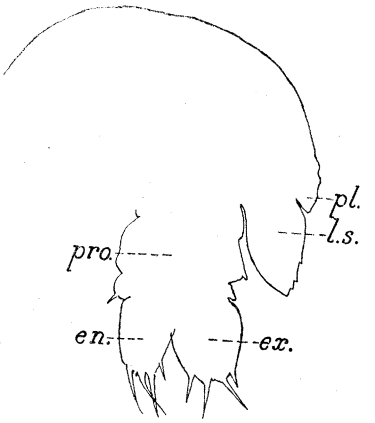

FIG. 50.—A still later stage in the development of a copepodoid trunk limb. × 240. (In. 25717.)

The development of the large clasping organs of the male would no doubt, if it could be followed, form a very interesting study. The only stage in this development, however, that has so far been found is that shown in fig. 51. In this the basal and terminal joints are already well formed, though the latter is evidently not so specialised as in the adult,

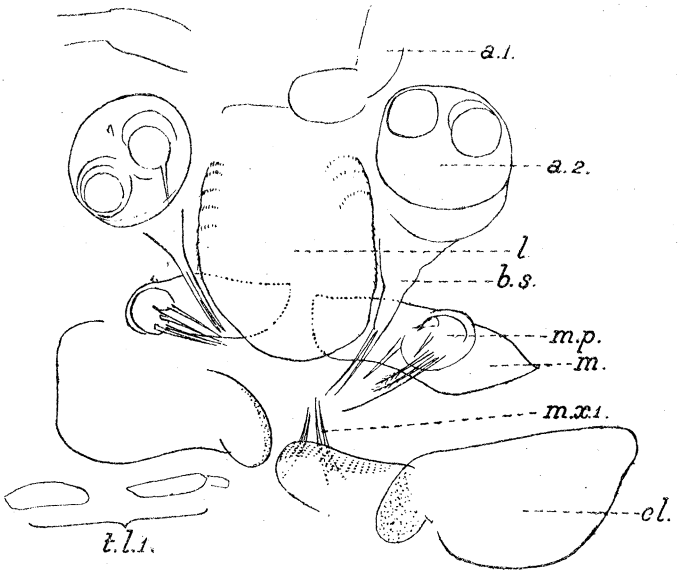

FIG. 51.—Anterior part (ventral) of a young male, showing palps on mandibles, developing claspers, &c. × 240. (In. 25718.)

being little more apparently than a simple cylindrical outgrowth, with some rows of minute teeth on part of its surface. Between the basal and terminal joints there occurs a little rounded pad covered with very minute papillæ. What the significance of this may be is uncertain. No vestige of such a structure has been seen in the adult male.*

3. Classification.

From the foregoing description of the Rhynie Chert Crustacean, it is evident that the animal exhibited a very curious combination of characters. In many respects it was undoubtedly very similar to an Anostracan, and it will be useful, perhaps, to enumerate, in the first instance, the characters in which this resemblance was most marked.

Points of Agreement with the Anostraca.

1. Elongated form and general appearance.
2. Absence of dorsal shield or bivalve shell.
3. Structure of the mandibles and absence—at least, in the later stages—of mandibular palp (in this agreeing with the Branchiopoda in general).
4. Reduced size and simple structure of the first pair of maxillæ (in this agreeing with the Branchiopoda in general).
5. First three pairs of trunk limbs, although modified, of unmistakably foliaceous type (in this agreeing with the Branchiopoda in general).
6. Presence of gnathobases on the anterior trunk limbs, at least as far as the fifth or sixth pair (and in so far agreeing with the Branchiopoda in general).

On the other hand, the differences between the Crustacean here described and any recent Anostracan are very numerous, and it even differs, in some characters, from

* *Some other Small Fossil Crustacea showing Structure.*—Although the foregoing account of *L. rhyniensis* is believed to be more detailed and more complete than that of any small fossil Crustacean hitherto recorded —possibly even than that of any other fossil animal of similar size—there are two previous descriptions of small fossil Crustaceans which also give very many structural details.

The earliest of these is the description of the Ostracod *Palæocypris edwardsii* by C. Brongniart (1876). Fourteen specimens of this minute species, the shells of which are only about $\frac{1}{50}$ inch ($\frac{1}{2}$ mm.) long, were found in a section of a silicified fruit of *Cardiocarpus* from the Coal Measures of St. Étienne. The animals had evidently obtained access to the interior through a crack while the fruit was floating in the water. The state of preservation was extremely good, for Brongniart was able to make out many of the appendages, and even shows in one of his figures the feathering on some of the setæ with a magnification, apparently, of about 300.

The second is that of the Conchostracan *Limnestheria ardra* by Mabel C. Wright (1920). The specimens of this species were found in material from a boring in the Kilkenny Coal Measures, and the shells measured $\frac{1}{6}$ inch to $\frac{1}{4}$ inch (5–6 mm.) in length. In spite of the fact that the rock in which these animals were found was a dark, opaque shale, many important details of structure—*e.g.*, antennæ, mandibles, claspers of the male, furca, &c.—could be made out quite clearly.

any known member of the Branchiopoda. The principal of these differences may be stated as follows :—

Points of Difference from the Anostraca.

1. Absence of stalked eyes.

2. First antennæ distinctly three-jointed (in this differing also from the majority of the Branchiopoda).

3. Second antennæ in the adult of both sexes forming large biramous swimming organs, retaining, in fact, the chief characteristics of the second antennæ as found in the larval forms of the Anostraca and most Branchiopods.

4. The adult male provided with a pair of powerful clasping organs, which were not modifications of the second antennæ as in the Anostraca, but arose just behind the mandibles and were probably developed from the maxillulæ.

5. Trunk limbs rather sharply separated into two series (in this differing also from the majority of the Branchiopoda).

6. The first three pairs of trunk limbs, although of the foliaceous type, having the terminal part much modified to form scraping or rasping organs.

7. The fourth to eleventh pairs of trunk limbs in the form of biramous copepodoid swimming feet (in this differing not only from the Anostraca but from all known Branchiopoda).

8. Structure of the gnathobase, which more closely resembled what is found in the Notostraca than in the Anostraca.

9. Presence of an egg-pouch cover, probably consisting of a pair of modified trunk limbs.

10. Presence in adult female of a pair of rudimentary uniramous appendages posterior to the egg-pouch.

11. The two last pair of appendages in the adult male somewhat modified as compared with the preceding copepodoid swimming feet.

12. Probable absence of a branchial exite (bract or epipodite) on the trunk limbs (in this differing, also, from the majority of the Branchiopoda).

13. Caudal segment with a small articulated process projecting on each side from about the middle of the segment.

14. Caudal segment with two long articulated processes, each with four long terminal setæ, projecting backwards from each of the posterior outer angles, forming what has been alluded to as the secondary furca.

15. Caudal segment terminating in two short knobs placed somewhat dorsally, each carrying a characteristic seta. These knobs represent the primitive division of the posterior end of the last body segment, and have been referred to as the primary furca.

Although probably not a point of difference of any systematic value, it must not be forgotten that the Rhynie Chert Crustacean is very decidedly smaller (only about 3 mm.) than any known Anostracan. Further, the fusion with the head of the segment

carrying the first pair of trunk limbs is probably yet another point of difference from the Anostraca, but the value to be attached to this is somewhat uncertain.

A careful consideration of the above statements makes it quite clear, I think, that the differences from the Anostraca far outweigh the resemblances, and that it would be impossible so to modify the definition of the order as to allow of *Lepidocaris rhyniensis* being placed within it. It might even seem to be a matter for consideration whether it can be regarded as coming within the sub-class Branchiopoda—at least, as usually defined. But my own opinion is that, in spite of the distinctly jointed first antennæ, the separation of the trunk limbs into two series, the remarkable copepodoid nature of the posterior series, the apparent absence of branchial exites, and the double furca, it is not necessary to look upon *Lepidocaris rhyniensis* as other than a somewhat peculiar Branchiopod. There certainly seems no ground for thinking that it in any way forms a link between the Branchiopoda and the Copepoda, although it does show very clearly how the typical Copepod swimming foot is related to the foliaceous type of appendage.

The conclusion, therefore, follows that *Lepidocaris rhyniensis* represents the type of a new order of the Branchiopoda, taking its place side by side with the Anostraca, Notostraca, Conchostraca and Cladocera, though showing a closer approach to the first named than to the others. It is proposed to call the new order the *Lipostraca*, and, in correspondence with the definitions of the other orders as given in Dr. Calman's "Crustacea" (1909), and subject to the reservations mentioned in the body of the paper, it may be formally defined as follows :—

Sub-Class Branchiopoda. Order *Lipostraca*, nov.

Carapace absent; paired eyes (if present) not pedunculate; antennæ biramous, natatory; maxillulæ forming claspers in male; trunk-limbs, about eleven pairs in two series, the first three pairs foliaceous and lobed, the posterior eight pairs biramous, none post-genital (or one vestigial pair in female); bases of trunk-limbs protected by scale-like plates (? exites or pleura); furcal rami (secondary furca) unsegmented, styliform, preceded by another smaller pair of styliform appendages on the terminal somite; development with metamorphosis.

Family *Lepidocarididæ*, nov. Genus Lepidocaris, nov. Genotype *L. rhyniensis*, sp. nov.

Holotype, the immature female specimen figured in text—figs. 3 and 4 and photographs 1, 2 and 3 (Plate 21) of this paper, now in the Geological Department of the British Museum (Reg. No., In. 24493) from Chert Bed of Old Red Sandstone, Rhynie, Aberdeenshire. Collected and presented to the Museum by the Rev. W. Cran, of Skene, Aberdeenshire.

4. Summary.

1. Only one species of Crustacean, described as *Lepidocaris rhyniensis*, gen. et sp. nov., has so far been found in the Rhynie Chert.

2. It is a microscopic form, only reaching about 3 mm. in length in the fully grown adult.

3. It is represented by both sexes in various stages of development, from a minute larva with only four somites and only 0·3 mm. in length onwards.

4. Owing to the semi-transparent nature of the Chert and the excellent preservation of minute structures therein, it has been possible, notwithstanding the fragmentary condition of most of the remains, to reconstruct the animal in practically all its external details, and to a considerable extent to follow its development during growth, this being probably the first time that a fossil animal of such small size has been so fully described.

5. Although looking superficially like a diminutive member of the Anostraca, and possessing many features in common with that order, it exhibits several very peculiar features (*e.g.*, absence of stalked eyes, natatory second antennæ, division of the trunk limbs into two series of which the posterior consists of Copepodoid natatory feet, claspers in the male developed from the maxillulæ, double furca, &c.), which necessitate the erection of a new order of the Branchiopoda, the *Lipostraca*, to receive it.

6. Considered as a whole, *L. rhyniensis* does not seem to have led to any subsequent development so far as our knowledge of recent and fossil Crustacea goes. Although retaining some primitive characters in the adult stage (*e.g.*, biramous second antennæ), it was in many ways more specialised than any living Anostracan, and probably fitted into a very peculiar environment.

7. Some of its details, however, seem to throw important light on the evolution of Crustacean appendages, *e.g.*, the transition, proceeding backwards, from a foliaceous type of limb to a biramous Copepodoid type, and the conversion of the "flabellum" into the exopodite; the development of a caudal furca from what were probably primitive appendages, &c.

8. The absence of all certain traces of "pond-life" organisms other than *L. rhyniensis* seems to confirm the theory that the water in which the Rhynie Chert Bed was deposited may have been hot and highly charged with silica.

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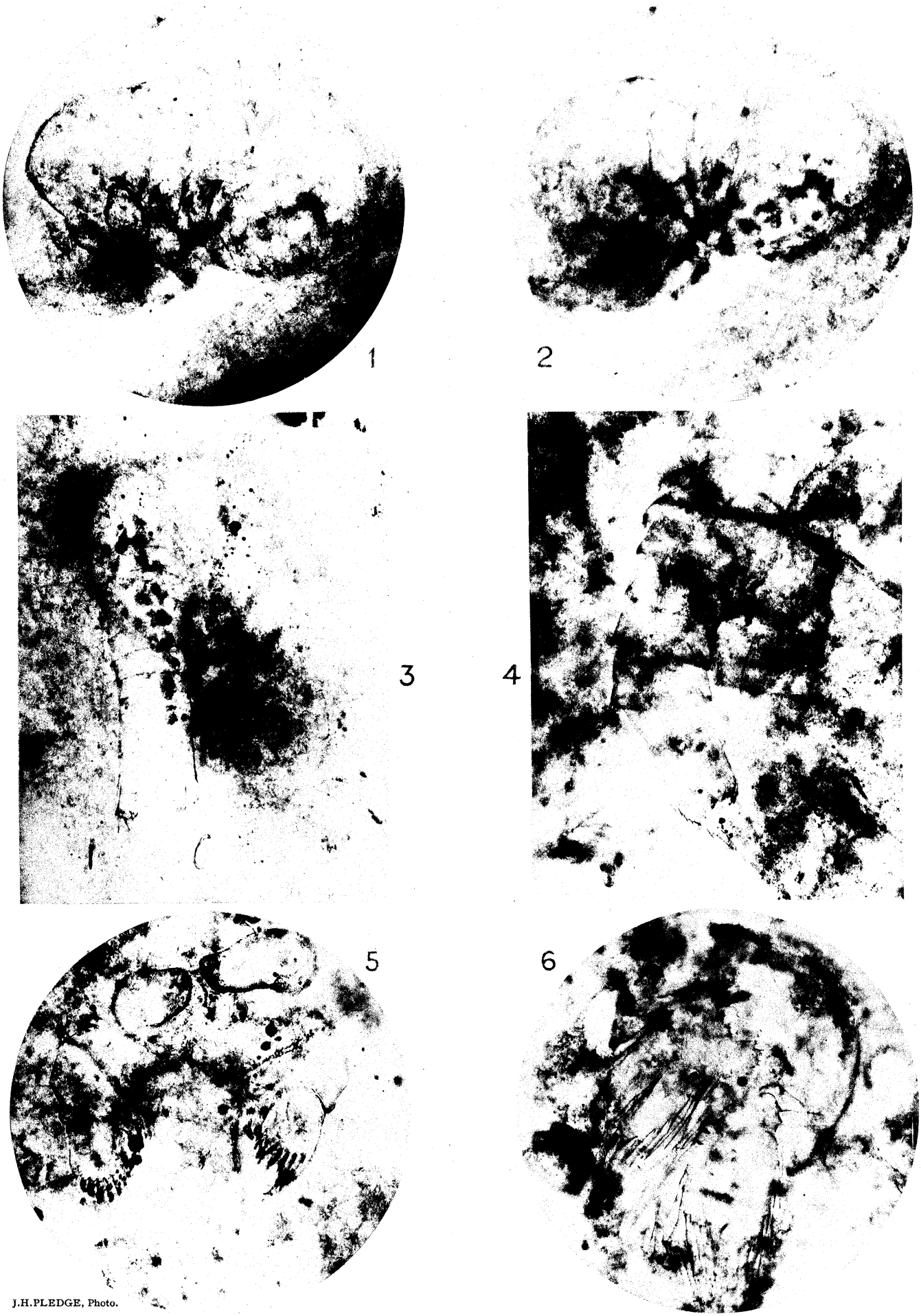
EXPLANATION OF THE LETTERING OF THE TEXT-FIGURES.

a. 1 = Antenna of first pair (Antennule).
a. 2 = Antenna of second pair.
b.s. = Bifid seta (masticatory process) of second antenna.
c.g. = Cervical (mandibular) groove.
cl. = Clasper (of male).
c.s. = Conical seta of primary furca.
en. = Endopodite.
end. = Endite (end. 1 = gnathobase).
e.p. = Egg-pouch.
e.p.c. = Egg-pouch cover.
ex. = Exopodite.
fl. = Flabellum.
gn. = Gnathobase.
l. = Labrum.
l.c.p. = Lateral caudal process.
l.s. = Lateral scale.
l.t.l. = Last trunk limb (of male).
m. = Mandible.
m.p. = Mandible palp.
mx. 1 = Maxilla of first pair (maxillula).
mx. 2 = Maxilla of second pair (maxilla).
o.s. = Olfactory setæ ?
p.f. = Primary caudal furca.
p.a.l. = Palmate apical lobe of anterior trunk limbs.
pl. = Pleuron.
pro. = Protopodite.
p.s. = Pectinate spines on anterior trunk limbs.
r.a. = Rudimentary appendage posterior to egg-pouch.
r.t.l. = Rudimentary trunk limb.
s.f. = Secondary caudal furca.
t.l. 1, &c. = Trunk limb 1, &c.



LEPIDOCARIS RHYNIENSIS gen. et sp. nov.

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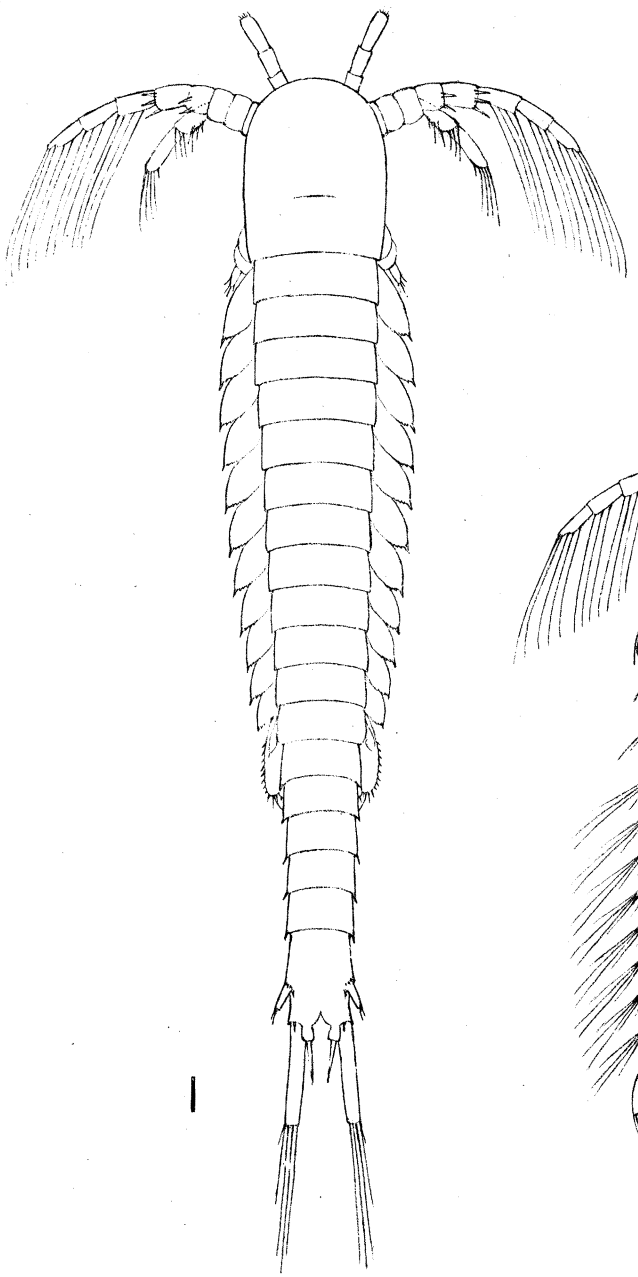
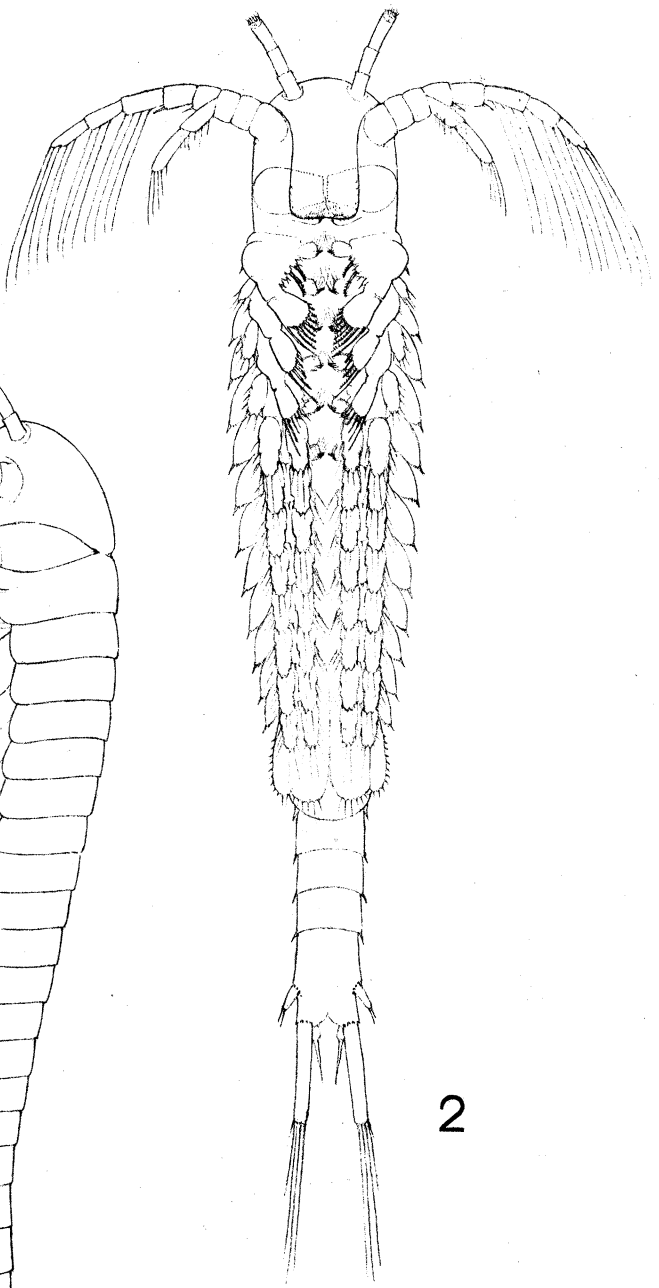
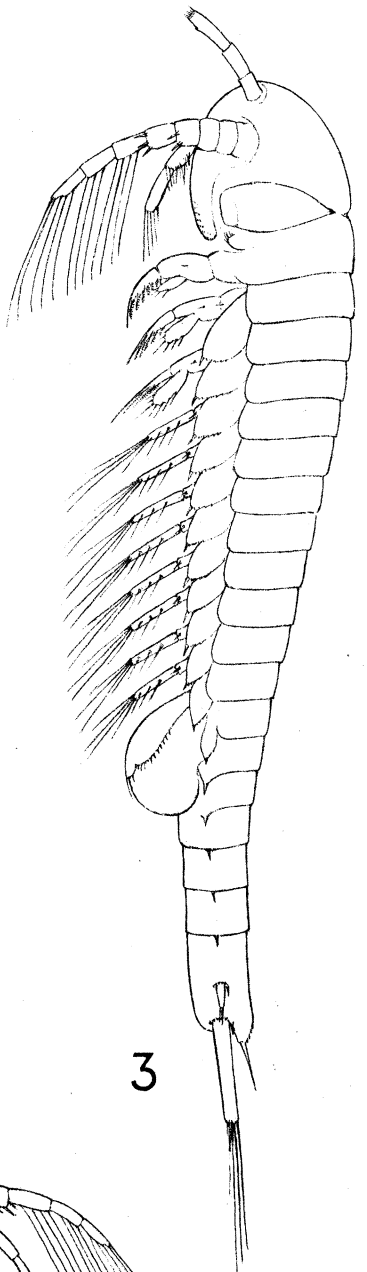
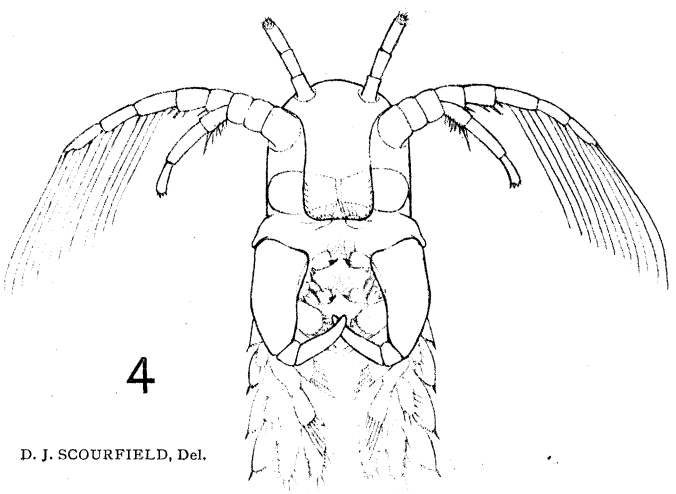
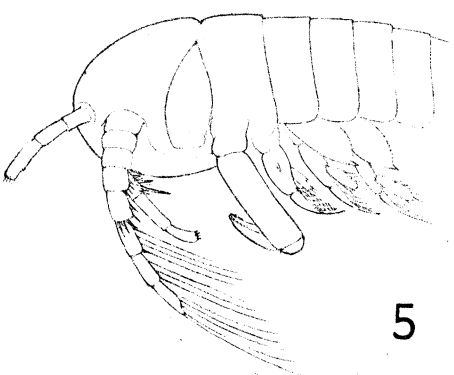






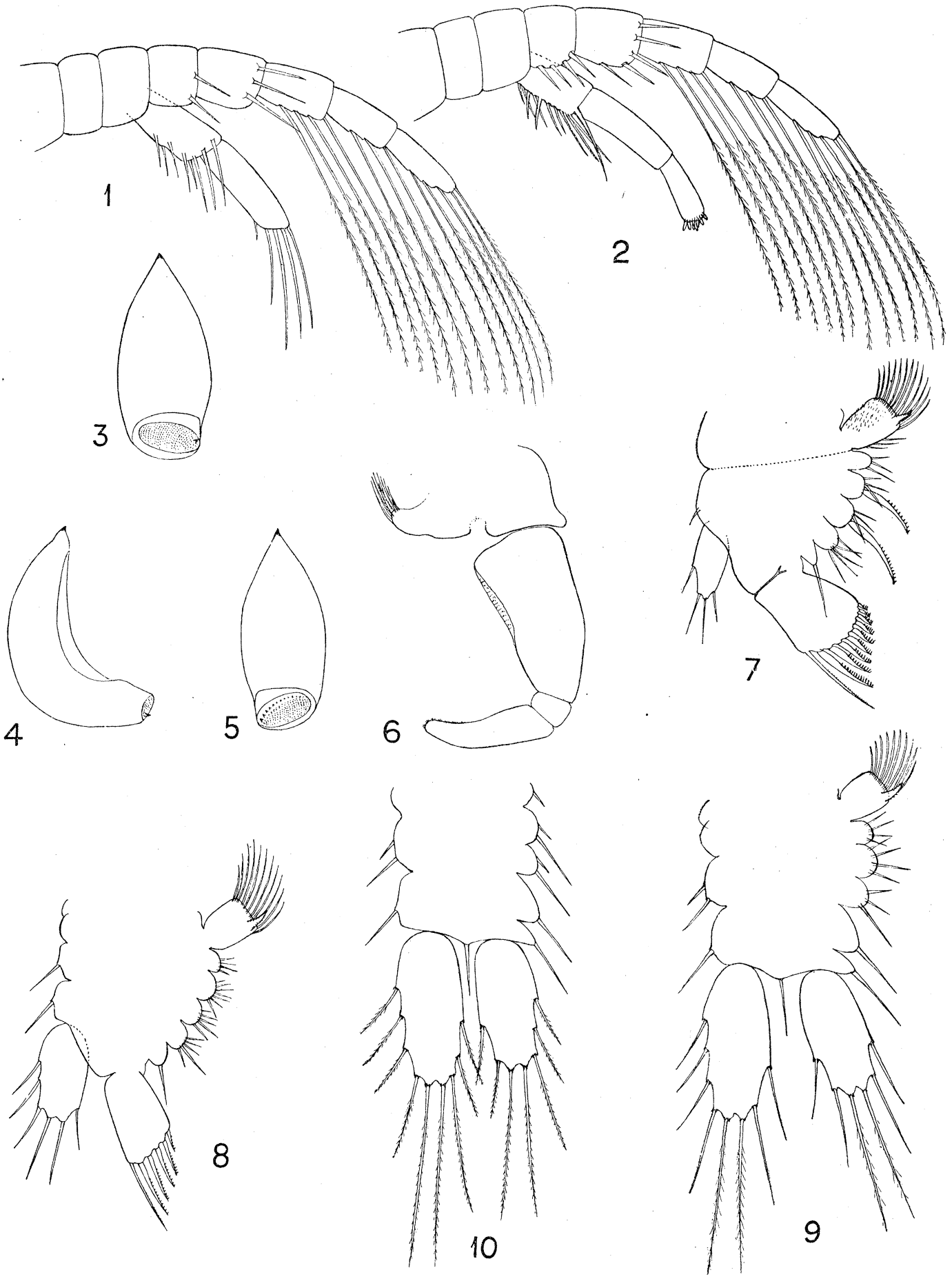




D. J. SCOURFIELD, Del.

LEPIDOCARIS RHYNIENSIS gen. et sp. nov.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

DESCRIPTION OF PLATES.

Plate 21.

Photographs of *Lepidocaris rhyniensis*, direct from the specimens.

1. Anterior part of specimen shown in text-figs. 3 & 4. (For references to parts, see text-fig. 4.) × 100. (In. 24493.)
2. Anterior part of specimen shown in text-figs. 3 & 4, at a slightly deeper focus. × 100. (In. 24493.)
3. Posterior part of same specimen. (For references to parts, see text-fig. 3.) × 100. (In. 24493.)
4. Lateral view of posterior part of another specimen. One of the rami of the " primary " furca with its characteristic conical seta is plainly shown. × 100. (In. 25719.)
5. Transverse section through head region, showing mandibles, maxillulæ and first pair of trunk limbs. × 150 (In. 25725.)
6. Transverse section through middle part of body, showing Copepodoid appendages. (For references to parts, see text-fig. 19.) × 150. (In. 25726.)

Plate 22.

(Restorations of *Lepidocaris rhyniensis*.)

1. Female, dorsal view. × about 45.
2. Female, ventral view. × about 45.
3. Female, side view. × about 45.
4. Anterior part of male, ventral view. × about 45.
5. Anterior part of male, side view. × about 45.

Plate 23.

(Restorations of Appendages of *Lepidocaris rhyniensis*.)

1. Second antenna of female. × about 150.
2. Second antenna of male. × about 150.
3. Right mandible from inner side. × about 120.
4. Right mandible from front. × about 120.
5. Left mandible from inner side. × about 120.
6. Clasper of male. × about 120.
7. First trunk limb. × about 150.
8. Trunk limb of second (and third) pair. × about 150.
9. Trunk limb of fourth to ? sixth pairs. × about 180.
10. Trunk limb of ? seventh to eleventh pairs. × about 180.

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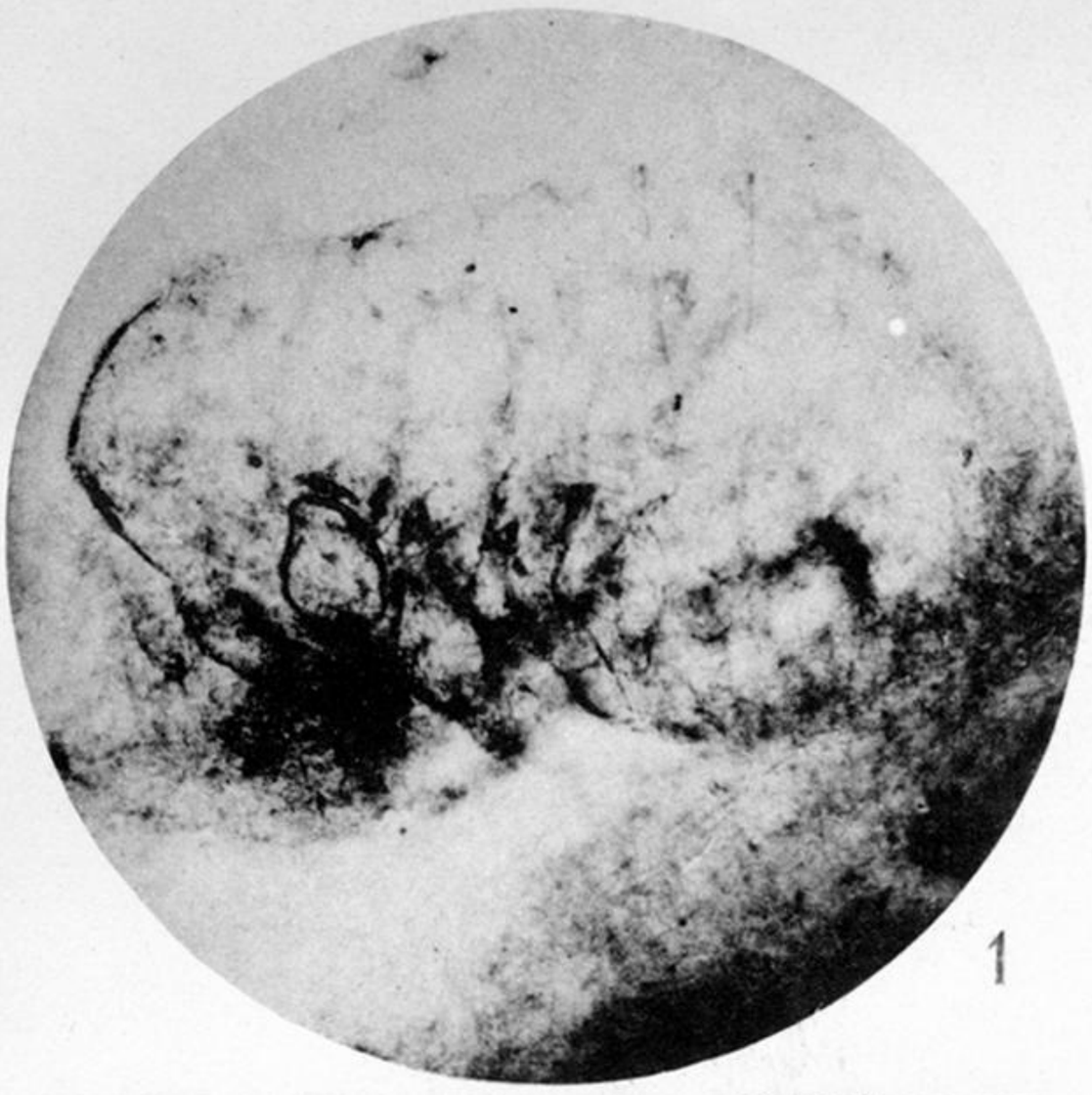

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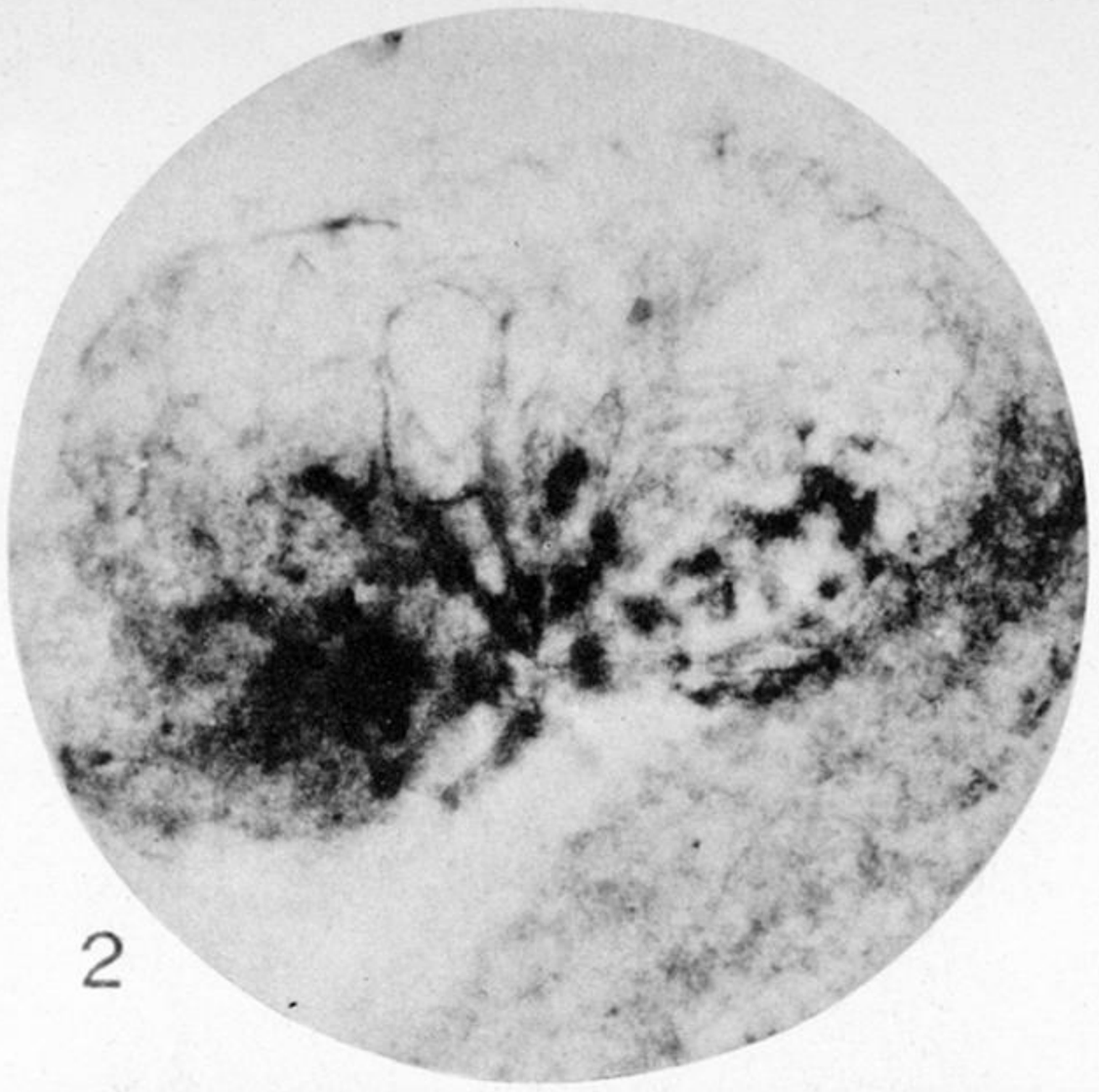

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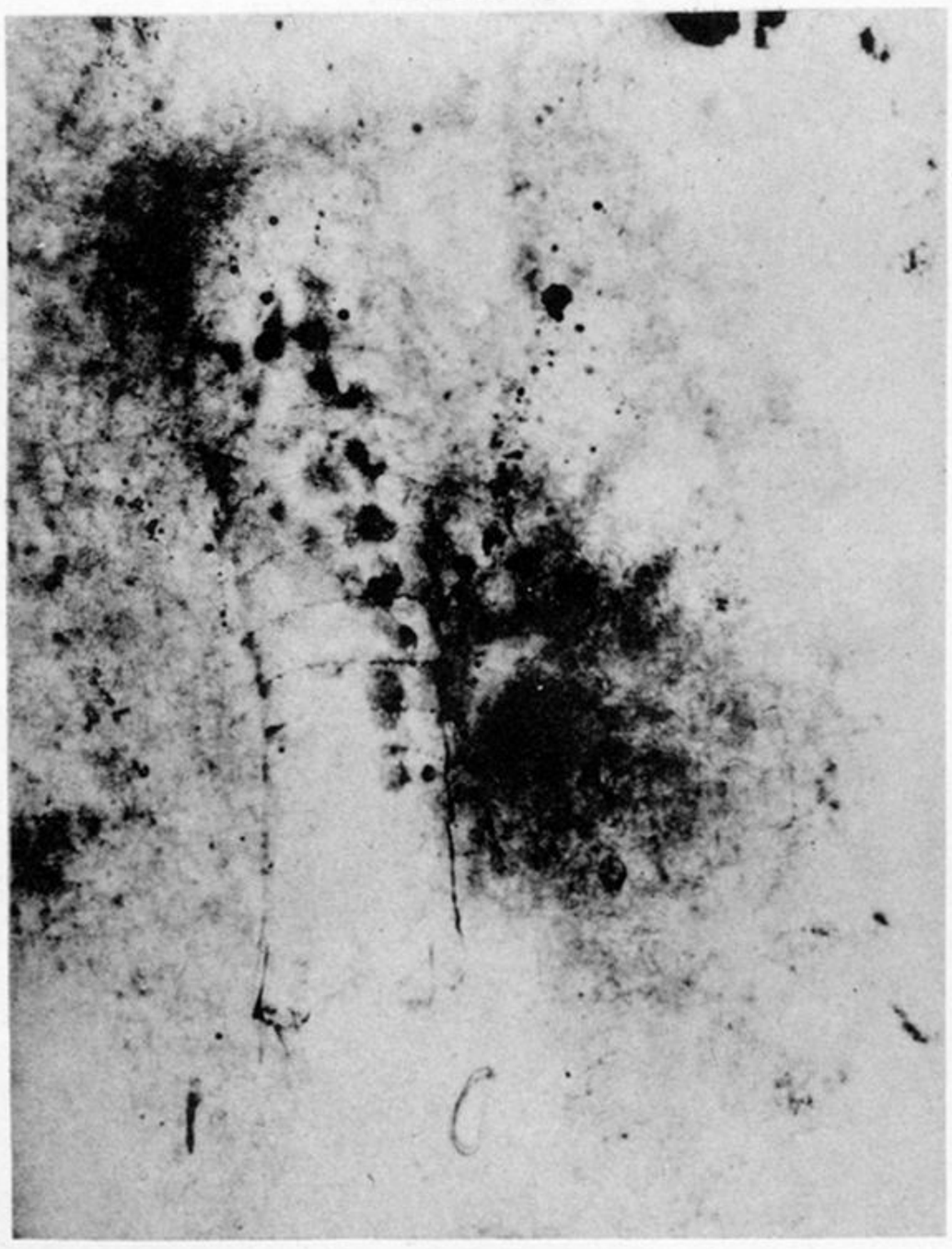

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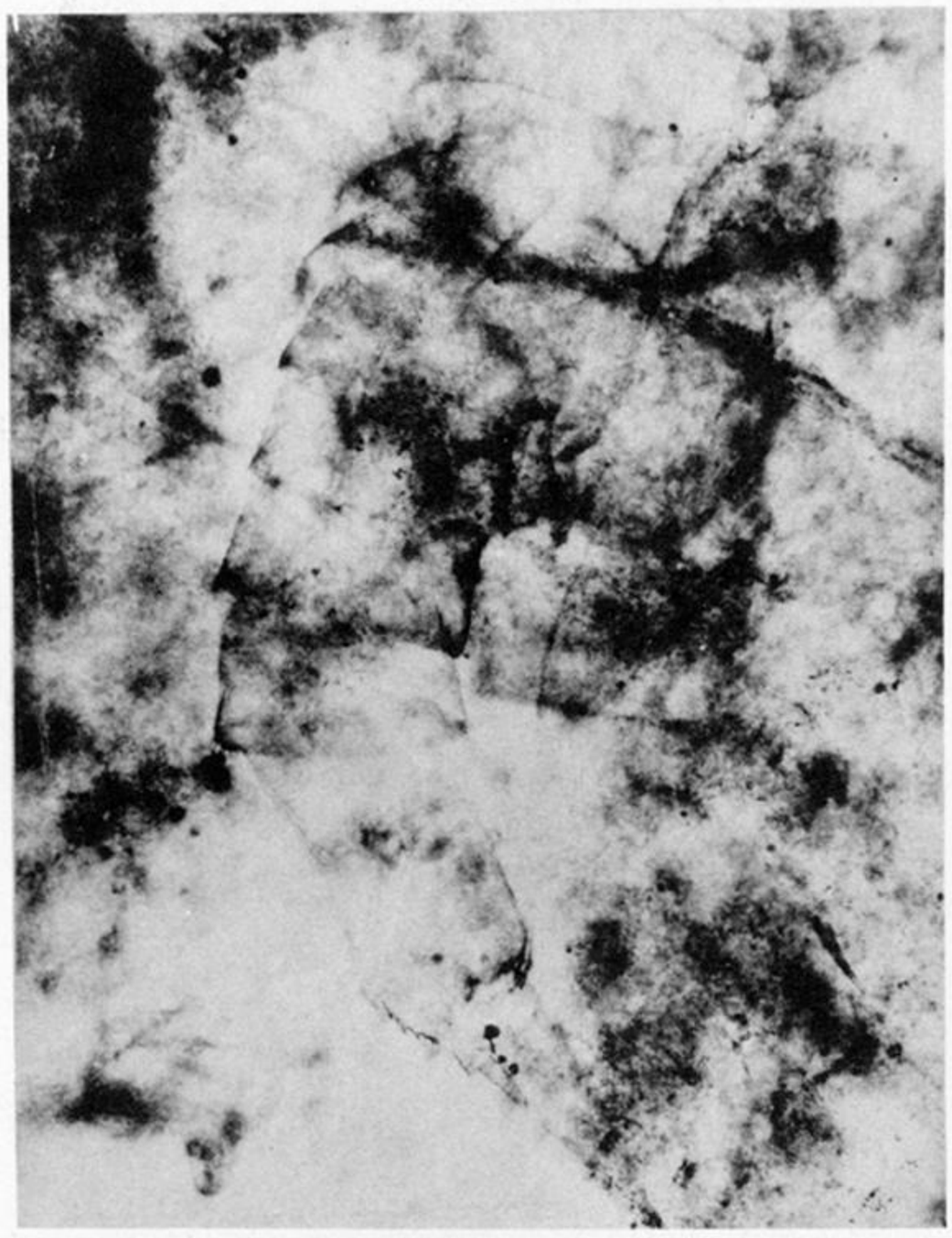

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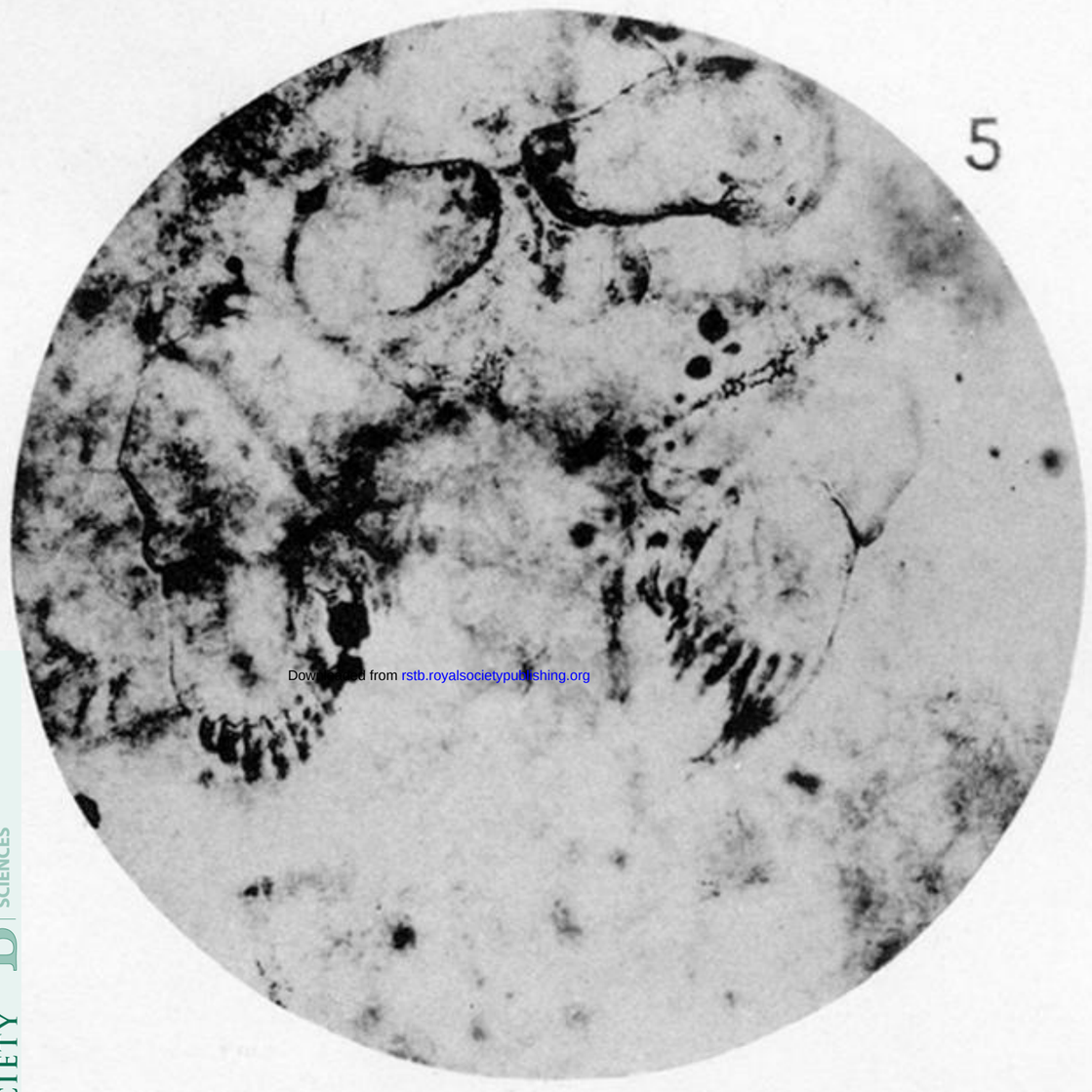

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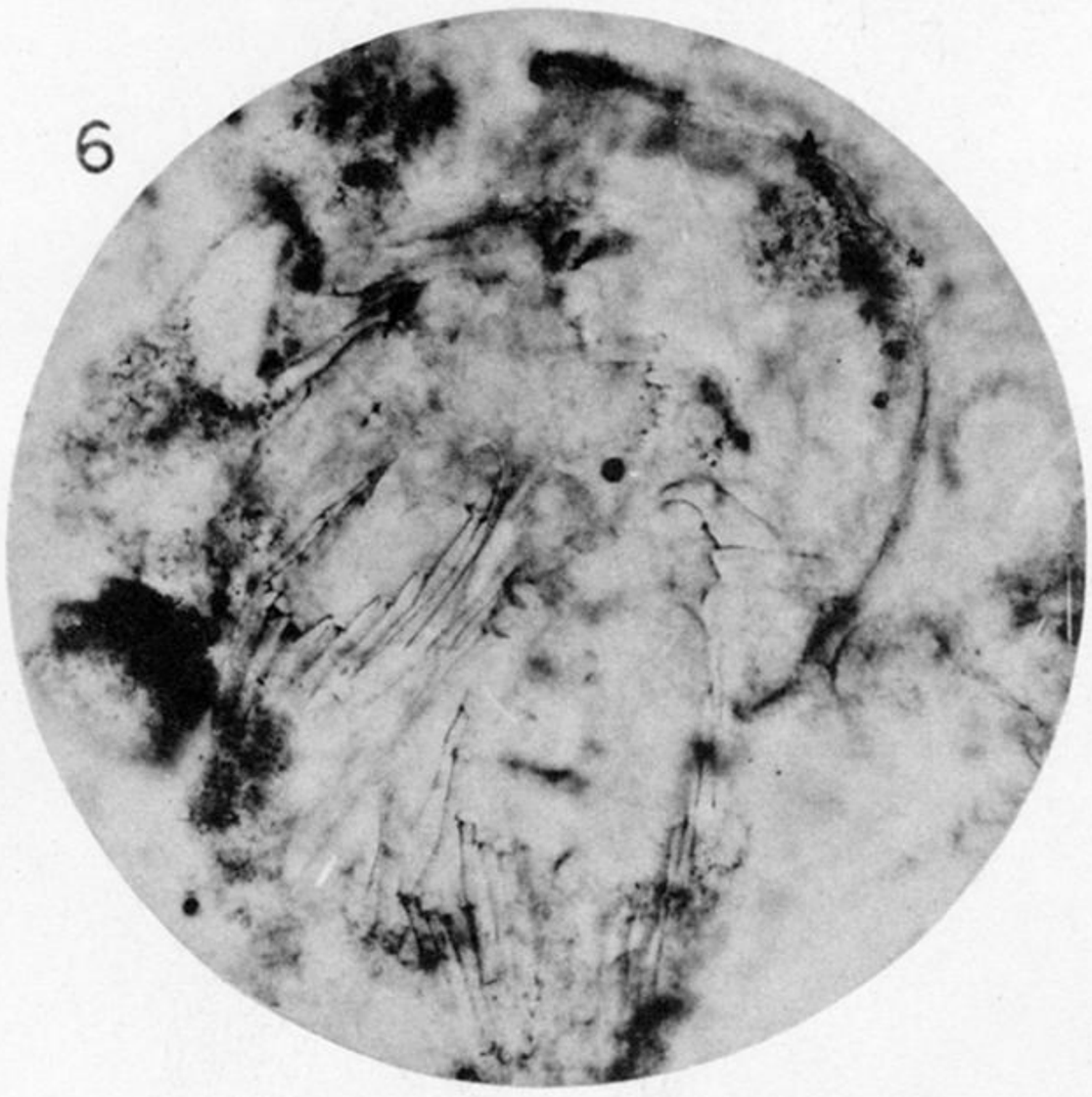

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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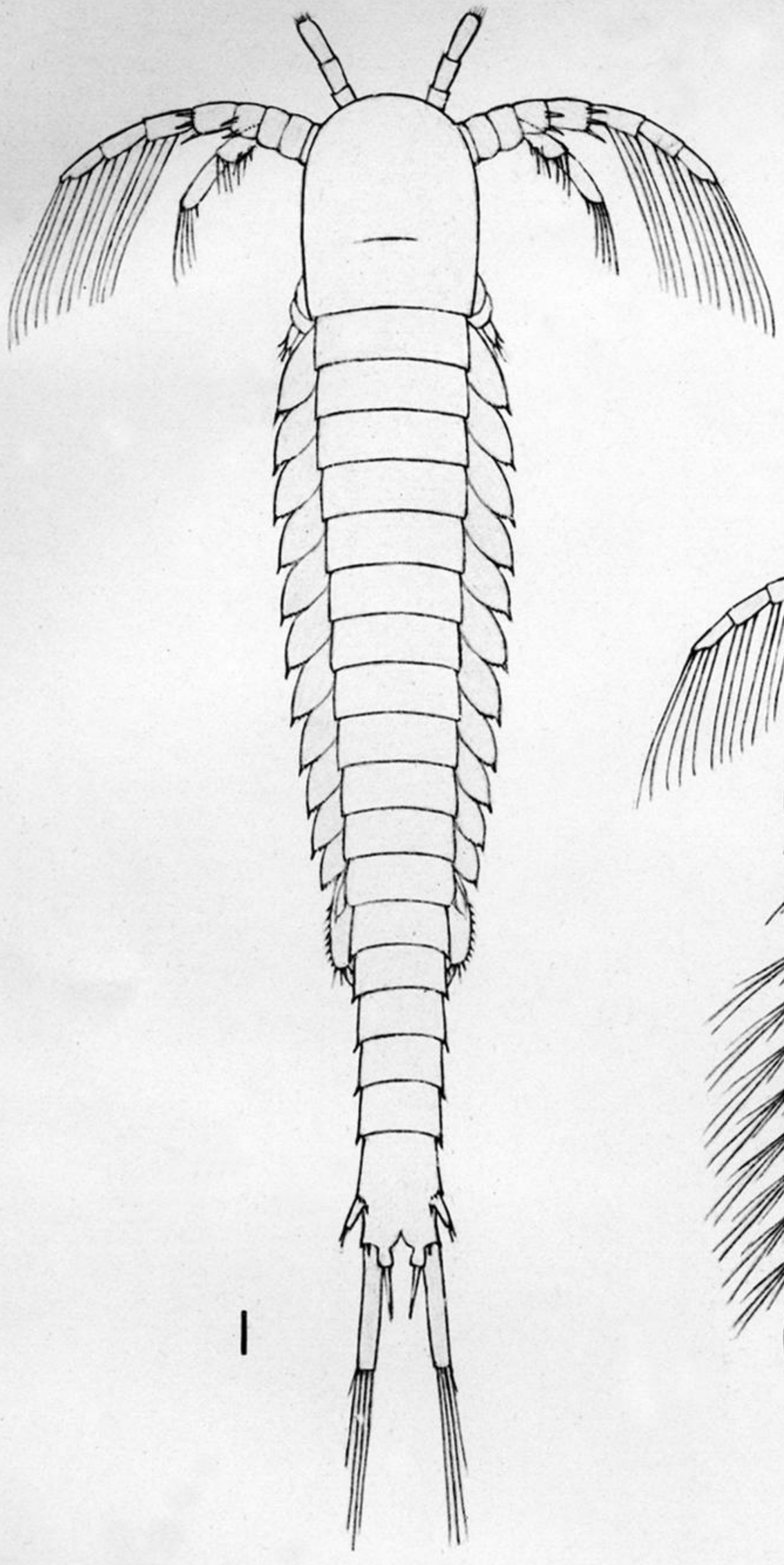

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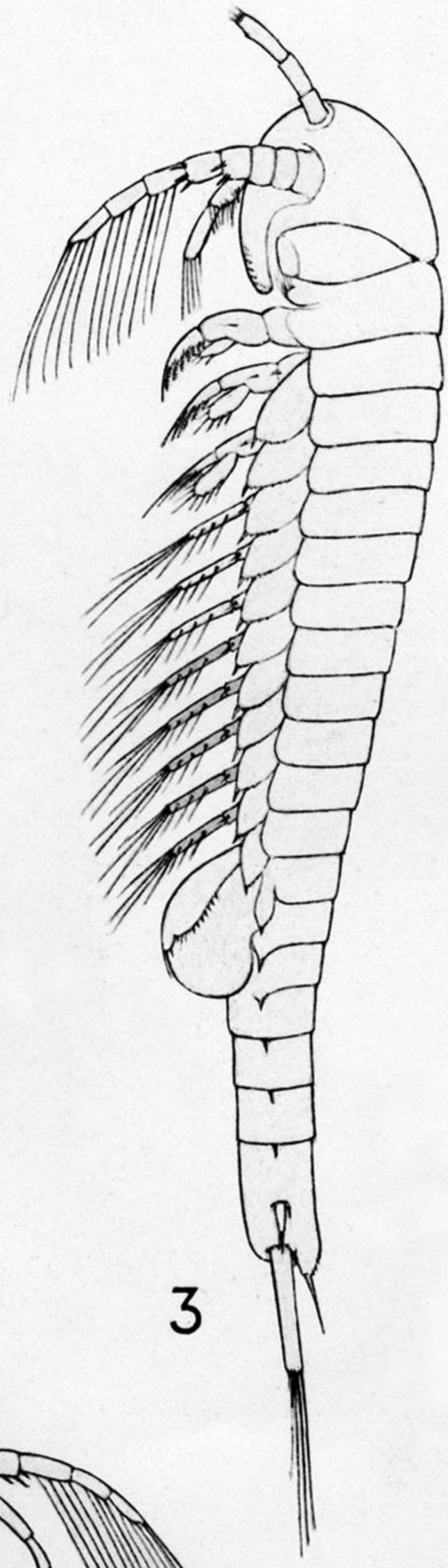

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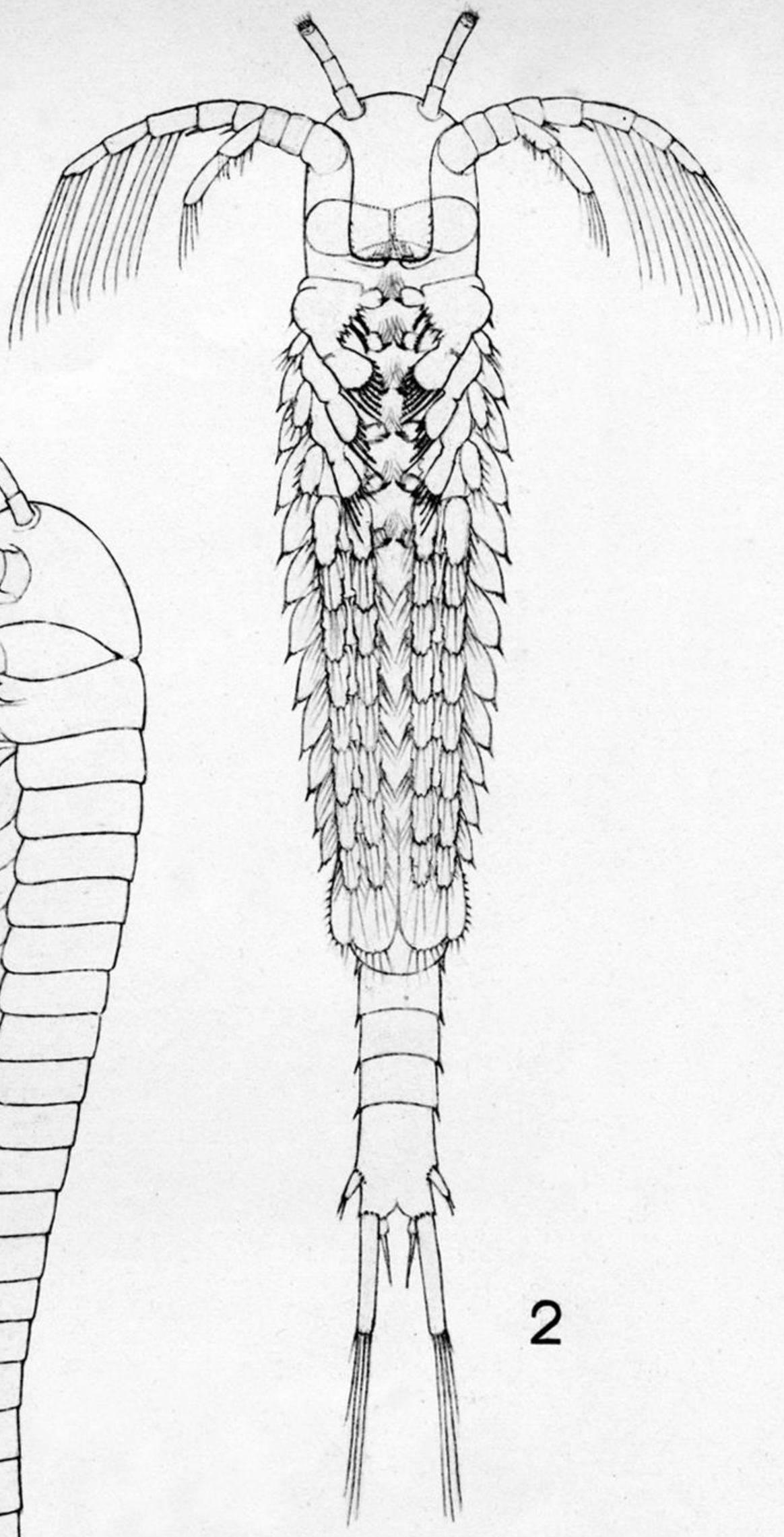

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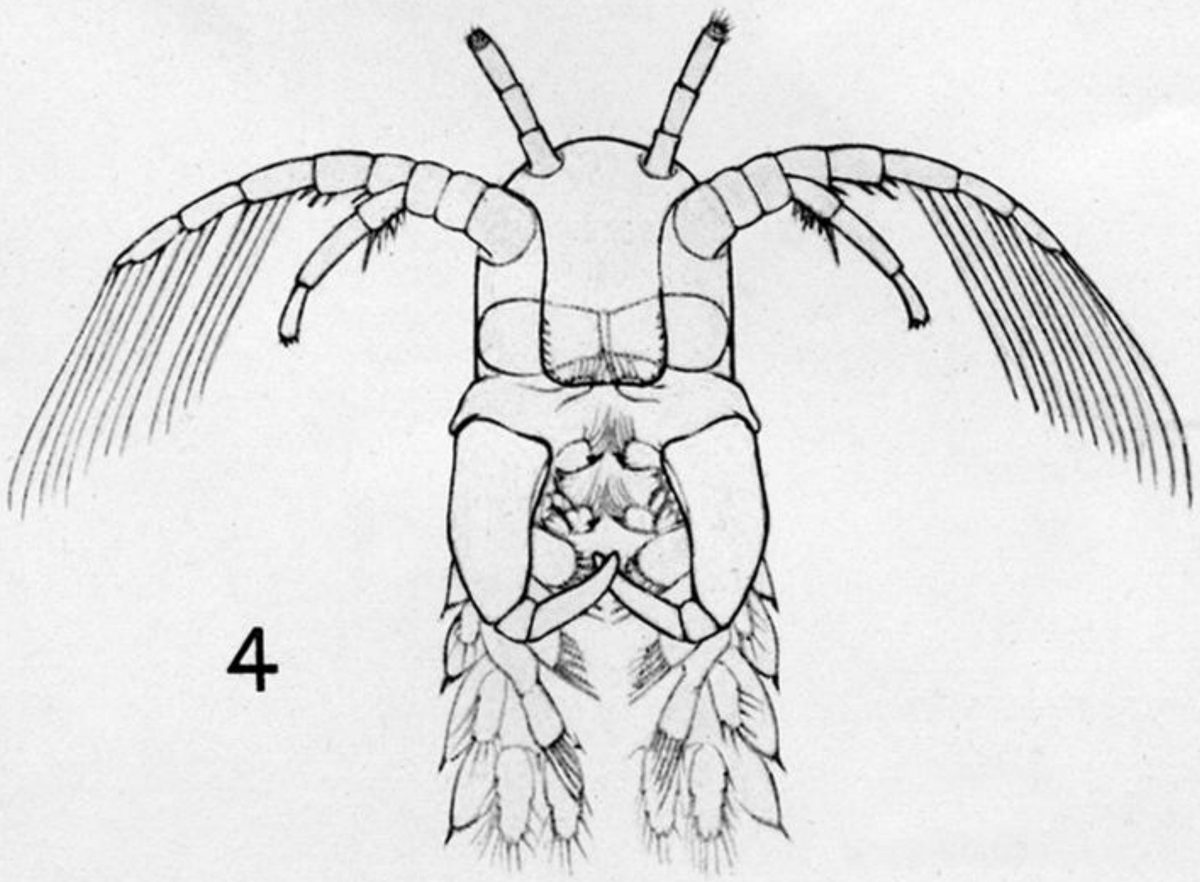

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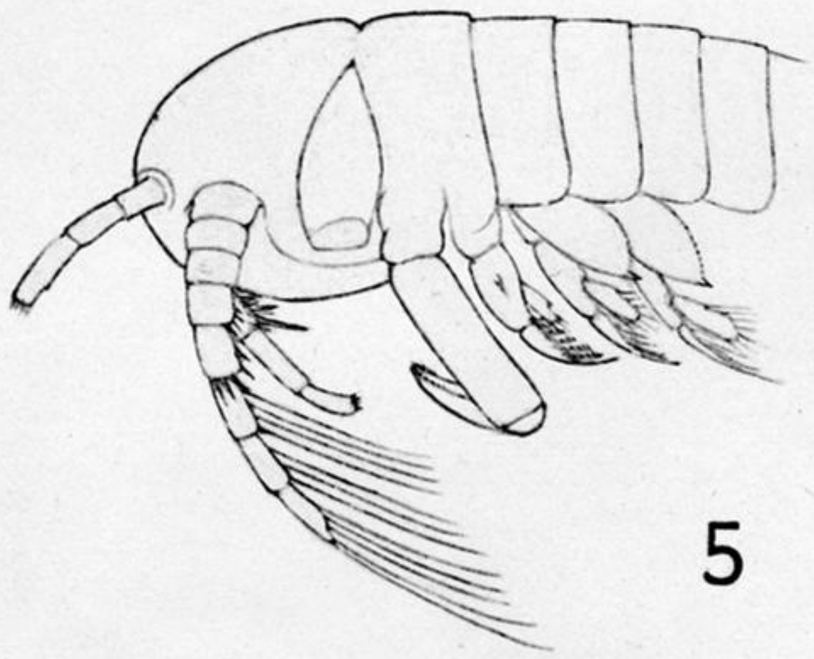

5

PLATE 22.

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