The Rhynie Crustacean.

By Dr. W. T. CALMAN, F.R.S.

MR. D. J. SCOURFIELD'S memoir "On a new Type of Crustacean from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire), *Lepidocaris rhyniensis*, gen. et sp. nov." (*Phil. Trans.* B, 415, 1926), which has already been noticed in NATURE (April 3, 1926, p. 498), is so important a contribution to arthropod morphology that no excuse is needed for directing further attention to some of the problems suggested by it.

In the first place, it should be emphasised that no other fossil crustacean is known with anything approaching the completeness with which Lepidocaris has been described by Mr. Scourfield. The only fossil arthropod, and in fact the only fossil invertebrate, which comes near it in this respect is the well-known *Eurypterus fischeri* as described by Holm. In the second place, in spite of its antiquity, Lepidocaris is far from being a primitive crustacean. In some respects (notably in retaining the biramous swimming antennæ of the nauplius) it is indeed more primitive than the existing Anostraca, but it shares with them many characters that are by no means primitive, such as the simplified mouth-parts, which are much more specialised than those of many Copepods. The development of male claspers, of Anostracan type, from the maxillulæ instead of the antennæ, is a surprising feature, the significance of which remains obscure. It may indicate that Lepidocaris is off the main line of Anostracan descent. It is doubtful also whether the absence of eye-stalks can be regarded as a primitive character.

One of the most difficult problems of crustacean morphology has been the correlation of the biramous type of limb found in so many Crustacea with the 'phyllopod' type seen in the Branchiopoda. Since Ray Lankester, in his classical memoir on Apus, showed that the Branchiopoda (or Phyllopoda) are the most archaic of living Crustacea, it has been generally accepted that the biramous has been derived from the phyllopod type. Lankester argued that the two branches of the biramous limb, the endopod and exopod, were derived from the two distal 'endites' or lobes of the inner edge of the phyllopodium. Huxley had earlier identified the exopod with the flabellum' of the Phyllopod and the endopod with the distal part of the stem or 'corm,' and this interpretation has been adopted by others, notably by Dr. Borradaile in a recent paper.[1] Lepidocaris would seem to provide the answer to this question, for while the first three pairs of its trunk appendages are phyllopodia, comparable without much difficulty with those of recent Branchiopoda, the following limbs are biramous; and it is perfectly clear that the exopod of the posterior limbs is equivalent to the flabellum of those in front, the endopod being the distal endite.

Dr. Borradaile inclines to the opinion that, in the

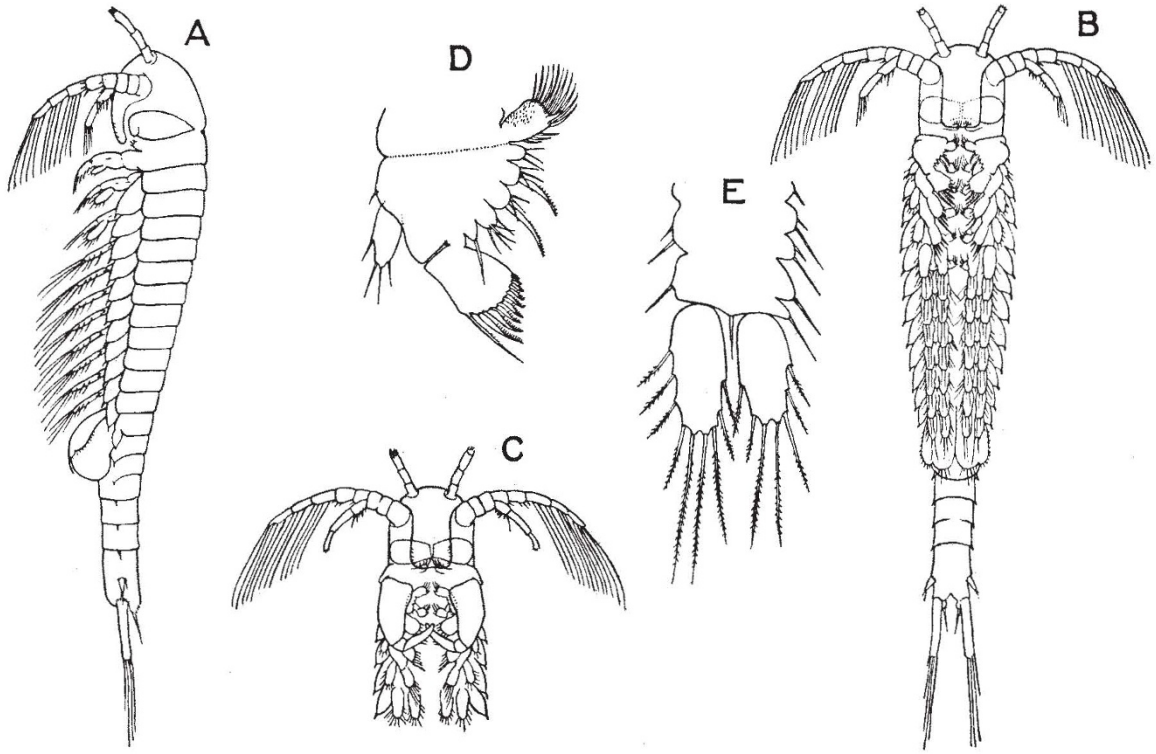

FIG. 1.—Restorations of *Lepidocaris rhyniensis*, Scourfield. A. Female, from the side. B. Female, from below. C. Male, anterior part of body from below. D. One of the first pair of trunk limbs. E. One of the trunk limbs of the posterior (? seventh to eleventh) pairs. Approximate magnification, A, B, and C×27, D×9, E×10. (After Scourfield.)

[1] "Notes upon Crustacean Limbs," *Ann. and Mag. Nat. Hist.* (9), **17**, p. 193, 1926.

evolution of the Crustacea, the biramous form of limb has been arrived at more than once by different modifications of the phyllopod type. In view, however, of the simple biramous form of the limbs in the nauplius larva and in the Trilobites (the close relationship of which to the Crustacea cannot now be doubted), and of the persistency with which the same type emerges in the most diverse groups of Crustacea, it seems more reasonable to assume that it represents the deep-seated plan of symmetry on which all crustacean limbs are built. It is indeed possible that the phyllopod type preceded the biramous and that Lepidocaris preserves the transition from one to the other. This would seem to be the view taken by Mr. Scourfield, who, although he gives us little in the way of speculation, does imply that the biramous hinder limbs of Lepidocaris are derived from the phyllopodous type of those in front. It is, however, a very general rule among Arthropoda that specialisation begins anteriorly and works backwards; we should expect the posterior limbs to be the more primitive; and Lepidocaris gives the impression of having had primitively biramous limbs of which the more anterior pairs have been specialised in adaptation, no doubt, for some special method of collecting food.

A minor problem is presented by the lateral row of large scales (to which the generic name alludes) covering the bases of the trunk limbs. These suggest the small scales at the base of the outer edge of the limbs in Anostraca which are generally interpreted as the proximal exites of the limbs. In Lepidocaris, however, at the posterior end of the series, the scales are seen to be merely the pinched-off pleura of the somites. It is a matter for further inquiry whether the proximal exites of the Anostraca may not also be of pleural origin.

Perhaps the most unexpected feature of Lepidocaris, however, is the structure of the last segment of the body. In many Crustacea, in the larva if not in the adult, the termination of the body is forked. Very often this fork is nothing more than a notch in the hinder edge of the telson, but sometimes the two prongs of the fork are movable rods jointed to the segment, and in a few cases (Notostraca, Cirripedia) they are long, many-jointed filaments. In Lepidocaris we see clearly, for the first time, that these movable appendages are not, as has been generally supposed homologous with the two branches of the notched telson. In the earliest larva found the telson is notched, and this notch persists in the adult to form what Mr. Scourfield calls the "primary furca." In the later larvæ, however, a pair of rod-like appendages grow out at the sides of the primary furca and become separated by articulation from the body of the telson, forming a "secondary furca" which is evidently the homologue of the articulated furca of Anostraca, Copepoda and Phyllocarida. In still later larvæ a second smaller pair of appendages appear at the sides of the telson in front of the secondary furca. Just above the articulation of each of these two pairs of appendages is set a small spine. The somites immediately in front of the telson bear no appendages, but each has, on either side, a similar spine, and as these spines are traced forwards they are plainly seen to be in series with the spines which tip the lateral scales already mentioned above the insertion of the limbs.

It seems impossible to avoid the conclusion that the appendages of the telson in Lepidocaris and the furcal rami of the groups mentioned above are serially homologous with the true limbs of the anterior part of the body. Now it is the general rule in the development of Arthropoda that the somites and their appendages appear and become differentiated in regular order from before backwards, new somites being added from a 'formative zone' in front of the telsonic region. In Lepidocaris alone do we find evidence of true appendages on the telson itself, *behind* the formative zone; and, emphasising the singularity of their position, the order of their development is the reverse of that of the pretelsonic appendages, the hinder pair appearing first.

It must be borne in mind that, at the time when Lepidocaris lived, the Crustacea had already behind them a long evolutionary history. It is now known from Walcott's remarkable discoveries that, so early as the Middle Cambrian period, a varied crustacean fauna existed and that several of the forms had at least a superficial resemblance to Anostraca. Unless some chance discovery, as fortunate as that at Rhynie, and an investigator with Mr. Scourfield's indefatigable patience and skill, combine to reveal a great deal more than we know at present about the structure of these early forms, speculations on phylogeny must go very cautiously.

Obituary.

Dr. Edward J. Bles.

BY the recent death of Edward J. Bles, zoological science has lost a devoted worker whose qualities of mind and character were of the highest. It is the faith of many of his friends that, but for factors of temperament, and health, he would have become a leader of thought in the subject of his choice. His publications, though of high merit, were relatively few; but his intimates know that they were far from representing all that he accomplished, and are aware of the temperamental restraints but for which he could and would have published much more. He was one of those investigators—deserving sympathy from colleagues with easier standards—who would fain allow publication to wait for perfection, and yet realise even better than others that perfection never arrives. In spite of such inhibitions, or perhaps because of them, his published output is of high value and stamped with the quality of absolute reliability.

For elementary teaching, or, at any rate, for the shackles of departmental teaching and organisation, Bles had some distaste. On the other hand, he was the ideal colleague and one of the most educative influences for the young research worker. He would give his time and ingenuity for days to devise methods for another's work; he was a most sincere and painstaking critic and there never was any one with whom it was more delightful to share the joys of discovery or the fruits of victory. Yet he greatly prized independence, and the freedom to work out his own ideas on his own