JAWS, RADULA, AND CROP OF *ARNIOCERAS* (AMMONOIDEA)

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ABSTRACT. Several specimens of the ammonite genus *Arnioceras* in nodules from the Lower Lias of the Yorkshire coast were sectioned. The 'anaptychi' found within their body chambers were the lower jaws of these ammonites. They were associated with the hitherto unknown upper jaws and with the radulae. In one specimen the oesophagus was found, leading from the radula into the crop which contained well-preserved shells of ostracods and possibly foraminifera.

WHILE searching for the radula of ammonoids, I investigated the 'anaptychus' of a specimen of *Pleuroceras* from Domerian strata exposed north of the Harz mountains (Germany). The 'anaptychus' was situated within the aperture of the shell. I discovered that it consisted of two unconnected parts, the smaller one closely similar to upper jaws of recent Coleoidea, the larger one (the 'anaptychus' itself) evidently the lower jaw. Further support for this conclusion was provided by a specimen of *Psiloceras* sp. from Nellingen near Stuttgart, Germany. The 'anaptychus' of this specimen was found in the same position within the aperture. It was sectioned and the sections used to build a three-dimensional model of the whole structure. Again, it consisted of an upper and a lower jaw. This is the basis of my theory that the so-called 'anaptychi' of Lower Jurassic ammonites are actually their lower jaws.

Acknowledgements. In my quest for further examples of ammonites with their 'anaptychi' in front of their body-chambers, I was aided by Dr. M. K. Howarth (British Museum, Natural History) and Mr. R. V. Melville (Geological Survey, London), who lent me two limestone nodules containing specimens of ammonites with 'anaptychi'.

DESCRIPTION OF THE MATERIAL

The nodule loaned by Mr. Melville is from the Obtusum Zone of the Lower Lias of Yorkshire (Geol. Surv. No. 2270) and contains small specimens labelled *Arnioceras* (*Eparnioceras*) *flavum* S.B. *Arnioceras* (*Eparnioceras*) *semicostatoides* Spath. The complete specimens and a small fragment of a living-chamber from this nodule were closely investigated and showed the features described below. The living-chambers contain only very little sediment and are filled with clear calcite. This allowed internal structures to be observed as soon as the outer shell was removed.

Specimen no. 1 (Pl. 61, fig. 2). This is a fragment of a body chamber containing the 'anaptychus' (lower jaw) and between its 'wings' the upper jaw. Both consist of black horny material which in the lower jaw is covered externally by a thin layer of calcite. The jaw apparatus is closely similar in shape to that of *Psiloceras* sp. (Lehmann 1970) and to those described below. The upper jaw consists of one piece. Anteriorly it is produced into two 'wings', the outer one forming a hood which rises only slightly

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above the inner wing. The beak is pointed. The lower jaw is the structure known as 'anaptychus' and is usually found flattened into a plane. As a consequence, cracks frequently extend from the margin towards the interior, a feature which may be expected in an originally curved jaw, but not in a plane operculum. Its outer 'wing' extends posteriorly but the inner 'wing' forms only a narrow brim. In its normal state of preservation, the 'anaptychus' does not look much like a jaw. This explains why 'anaptychi' of this type have previously been mistaken for opercula.

Specimen no. 2 (Pl. 61, figs. 1, 3–5). This is a complete specimen of *Arnioceras* with an 'anaptychus' visible in the ventral part of the body chamber. The 'anaptychus' was first ground in a plane parallel to the plane of symmetry of the ammonite shell. Soon it became evident that it consisted of the 'anaptychus' proper (lower jaw) and the upper jaw within it. The lower jaw was 4·7 mm long and the upper jaw 3·0 mm long. When the radula appeared (Pl. 61, fig. 3) the grinding process was stopped. The part containing the radula was then isolated and again ground, this time in two parallel planes perpendicular to the first grinding plane. The radula could then be seen from above and from below. Two successive stages in the grinding process seen from the upper side are shown in Plate 61 (figs. 4 and 5). This radula (1·65 mm long and 0·72 mm wide) is excellently preserved. It consists of seven longitudinal rows of denticles with one point each; the denticles of the five inner rows are short, those of the two marginal rows are much longer and converge towards the mid-line (text-fig. 1).

TEXT-FIG. 1. Diagram of a transverse row of denticles in the radula of *Arnioceras*. Not to scale.

There are about 24 transverse rows preserved in the specimen. Complete recent radulae at my disposal contain about 80 transverse rows of denticles in an *Octopus* sp., 60 in *Sepia* sp., and 45 in *Nautilus* sp. The same number of longitudinal rows of denticles was observed by Closs (1967) in *Eoasianites* of Upper Carboniferous age and by Lehmann (1967) in *Eleganticeras* of Toarcian age. In the radula of recent coleoids, however, the longitudinal rows may number nine, and the radula of recent *Nautilus* has thirteen rows of denticles and is relatively wider and shorter.

Specimen no. 3 (Pl. 61, figs. 6–8). This is also a complete specimen of *Arnioceras*. It was ground parallel to the plane of symmetry. The 'anaptychus' again included the upper jaw between its two 'wings'. Grinding deeper, the first signs of the radula were found. Most surprising, however, was a tube starting behind the radula and leading backwards for about 3·5 mm, where it widened to form a sac-like structure 2·5 mm wide. The latter possessed rather thick, almost spongy walls and in its interior numerous remains of ostracods and evidently foraminifera. The size of these shells was 0·15–0·20 mm. This structure is interpreted as the oesophagus and crop of the ammonite. In order to get a better view of the radula, grinding was continued, although the anterior part of the oesophagus had to be sacrificed. The radula is not preserved as well as that in specimen no. 2, but is clearly recognizable in the lateral aspect. Its total length is 2·4 mm. The upper jaw in this section measures 1·6 mm, the lower jaw 4·0 mm; the diameter of the ammonite shell is 13·6 mm. Since the ventral length of the living-chamber is 17 mm, the length of the original may have been 25 mm. Beyond the crop, no further identifiable organic remains were found.

DISCUSSION

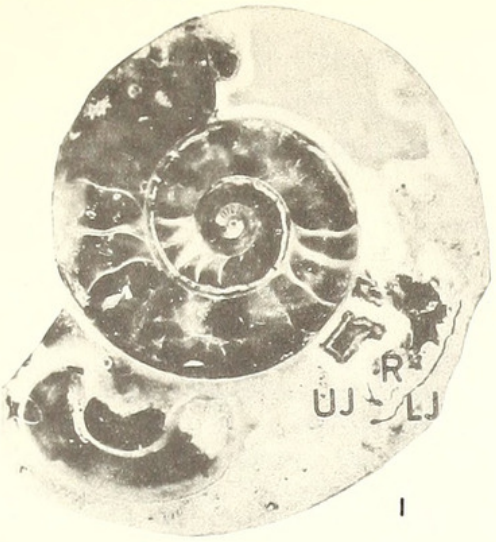
The nodule with the *Arnioceras* specimens described above is most unusual and must have formed rapidly at the bottom of the Liassic sea. The ammonites, of about equal size and individual age, seem to have perished together and to have become embedded at the same place, quickly enough to prevent decomposition of the more resistant parts of the body. The nodules, therefore, must have originated syngenetically.

The more resistant parts of ammonite bodies are, in the first place, the horny beaks and radulae. In living cephalopods they are enveloped by extremely strong and resistant muscles to form the buccal mass. All the fossil radulae hitherto found were situated between the upper and lower jaw in their life position. This demonstrates the high resistance of the jaw muscles to decomposition. Although the radula teeth may be preserved in an isolated state, they would then be hardly discernible and would offer no further information as to their *intra vitam* arrangement. Therefore, intact radulae can only be expected within the complete buccal mass. This is usually found within the body chamber, in the frontal third on the ventral side. A position met with so frequently that Trauth (1927–38) called it the *Normalstellung* (normal position) of 'anaptychi' and aptychi.

Other fairly resistant parts of the body seem to be the oesophagus and the crop. This is demonstrated in specimen no. 3, which contains these parts in a good state of preservation, whereas the parts of the gut behind the crop are not visible at all and seem to be completely decomposed. The oesophagus is resistant even in recent cephalopods. The structure interpreted as a crop has thick walls, and within it are a considerable number of ostracods and foraminiferan tests. Another crop found lately within a specimen of *Hildoceras* from near Hannover contained beaks of smaller ammonites. The fact that these tests and beaks are still intact indicates lack of chemical and mechanical wear. It shows that the crop was not a stomach. Also it seems evident that neither the jaws nor the radula did much damage to small and fragile shells. This agrees with Robson's (1929–31) opinion that in recent coleoids the radula assists in swallowing the prey but does not cut it to pieces, this being done by the jaws. In our specimen, the prey seems to have been too small even for the jaws to be applied.

EXPLANATION OF PLATE 61

Figs. 1–8. *Arnioceras* (*Eparnioceras*) *flavum* S.B. (*semicostatoides* Spath), Lower Lias, Yorkshire, from nodule no. 22703, Geological Survey Collection, London. 1, Median section of complete specimen no. 2. The entrance of the body chamber is barred by a small ammonite shell. Upper (UJ) and lower jaw (LJ) and radula (R) visible in the centre of the body chamber. ×3. 2, Transverse section of the body chamber of specimen no. 1 containing ventrally an upper (UJ) and lower jaw (LJ) in their normal position relative to each other. ×6. 3, Sagittal section through part of the body chamber of specimen no. 2, showing the radula (R) between the upper (UJ) and lower jaw (LJ) seen from the left side. ×30. 4–5. Serial sections of the same specimen at right angles to that in fig. 3, showing the radula seen from above, surrounded by the right 'wing' of the upper jaw (UJ). 4, long denticles of the two lateral rows of the radula bent towards the mid-line and covering the short denticles of the five central rows. ×36. 5, Lateral denticles mostly ground away to reveal the central denticles. ×36. 6–8. Section of specimen no. 3 parallel to the sagittal plane. 6, Radula (R) and jaw apparatus (UJ, LJ) passing into the oesophagus (Oe) and crop (Cr), seen from the right side. ×10. 7, Same seen from the left side. Contents of crop visible. ×10. 8, Enlarged view of crop with contents. ×20.



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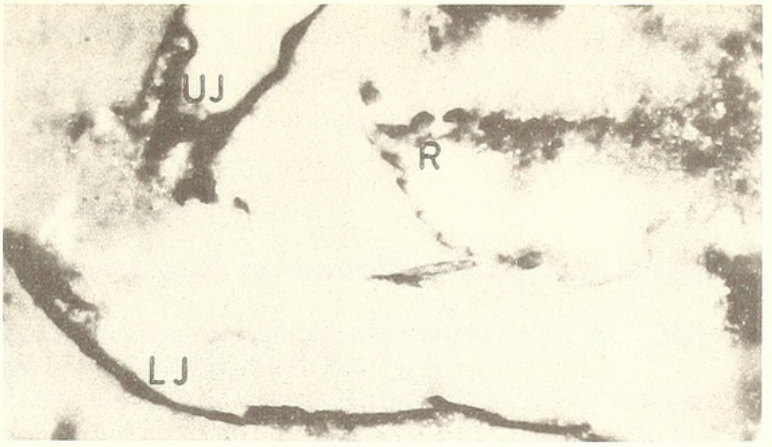

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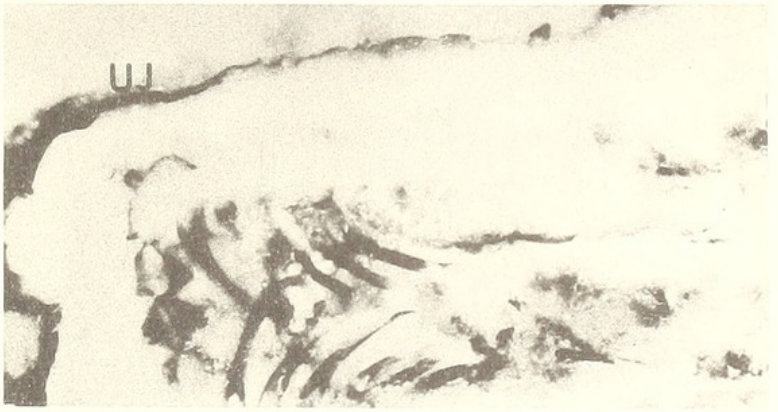

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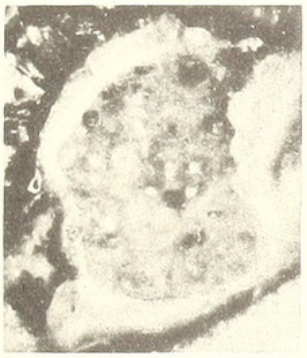

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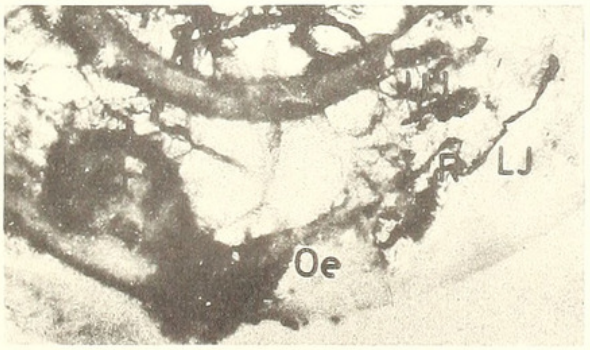

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LEHMANN, Jaws, radula and crop of *Arnioceras*