THE JAWS AND RADULA OF THE JURASSIC AMMONITE *DACTYLIOCERAS*

by ULRICH LEHMANN

ABSTRACT. Anaptychi (=lower jaws) and upper jaws of two specimens of *Dactylioceras* from the Yorkshire coast, found within their living chambers, are described and analysed. The corresponding lower and upper jaws are about equal in length and much shorter than the height of the living chambers. One of the ammonites contained numerous radular teeth between the lower and upper jaw. In addition, isolated lower and upper jaws attributed to *Dactylioceras* are reported from Reichenschwand (near Nürnberg, Federal Republic of Germany).

WHEN investigating specimens of *Dactylioceras* from the Yorkshire coast, several anaptychi were discovered within their living chambers. Two of them were sawed out of the surrounding matrix and subsequently ground down. Both were found to be associated with upper jaws. The sectioned anaptychi are here treated as Nos. 1 and 2.

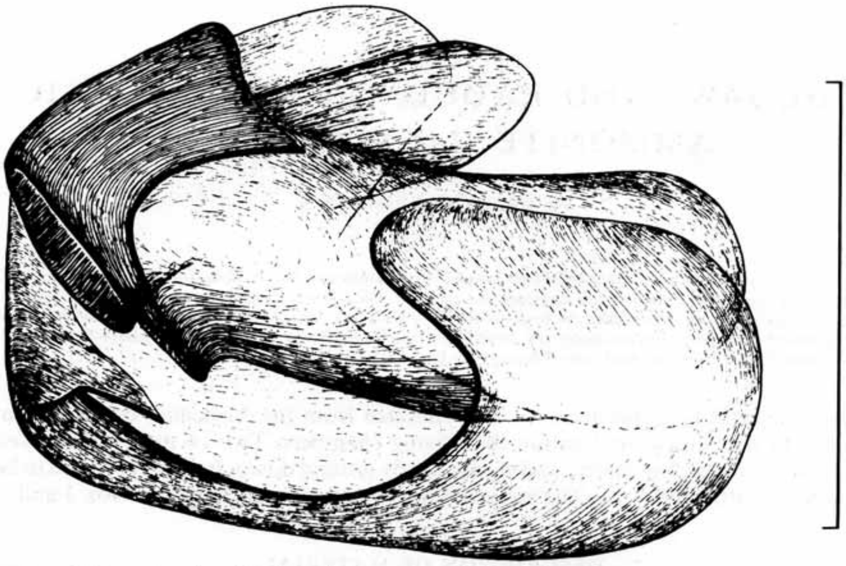
DESCRIPTION OF MATERIAL

Anaptychus No. 1 was located within the living chamber of an adult specimen of *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young and Bird) from bed 22 (Howarth 1973) at Port Mulgrave, lying about 90° behind the aperture. The diameter of the ammonite conch is 82 mm, and the apertural rim of the shell is thickened. The innermost whorls are pyritized; the septa of the outer part of the phragmocone are destroyed. The living chamber seems to be complete, but there may have been water movement within it prior to entombment, caused possibly by implosion of the septa and resulting in the anaptychus being oriented with its longitudinal axis at an angle of about 60–70° to the living chamber.

The anaptychus was found after the ammonite had been cut along its median plane. It was then ground and photographs and drawings made at intervals of about 0·05 mm, resulting in seventy-seven sections. The drawings were transferred to thick transparent plastic plates, and from them text-fig. 1 was drawn. This shows the relative position of the anaptychus with the upper jaw between its wings. The upper jaw is pressed rather closely against the right flank of the anaptychus, causing some difficulty with the reconstruction. There is no indication of a calcareous coating of the flanks of the anaptychus. The front part is quite straight; an inner lamella bends backwards, in the median part its length attains one-quarter of that of the outer lamella. In most previous illustrations of anaptychi the inner lamella is not represented.

The upper jaw is similar in shape to upper jaws of recent cephalopods; it consists of two wings joining anteriorly to form a wedge and then bending outwards and backwards as an outer lamella, the hood. There is no real beak as in recent forms. Between the anaptychus and the upper jaw remains of the radula were found.

[Palaeontology, Vol. 22, Part 1, pp. 265–271, pl. 27.]



TEXT-FIG. 1. Reconstruction of the lower jaw (= anaptychus) and of the upper jaw of a specimen of *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young and Bird) (= specimen No. 1) as found within the living chamber. The thick lines indicate the position of the first 'section', a small part of the left side of the structure beyond the lines being lost.

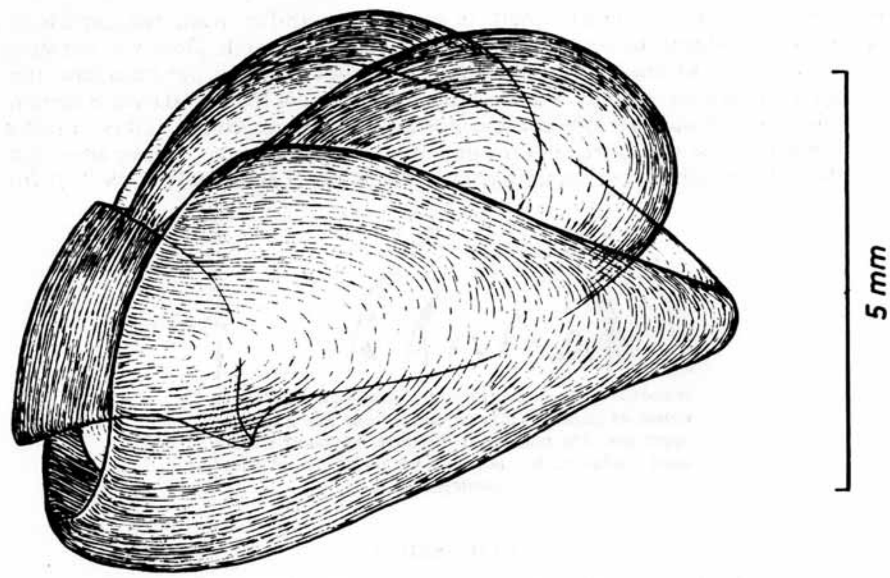
Anaptychus No. 2 was found in the living chamber of an adult specimen of *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) from bed 28 probably at Port Mulgrave (obliteration of locality sign during preparation leaves some doubt about locality). It lay about 90° behind the aperture of the ammonite.

The diameter measures 82 mm, and the apertural rim of the shell is thickened. The state of preservation is very good, all septa being preserved, and the last ones are more closely spaced than the preceding ones. The inner half of the living chamber is filled with clear calcite crystals, the outer half contains sediment and the anaptychus embedded in it. Its orientation is 'normal': front towards the aperture, base towards the exterior (ventrally) (Trauth 1927; Morton 1975).

As with No. 1, anaptychus No. 2 was found after the ammonite had been cut in the median plane. It was subsequently treated the same way as No. 1, but at intervals of about 0·1 mm, resulting in forty-two sections from which text-fig. 2 was drawn. Nothing is now left of the two anaptychi; the photographs and drawings are kept in the Hamburg collections.

The position of the upper jaw within the anaptychus was easier to analyse because they were not as closely pressed against each other. No radular teeth were found between the jaws.

The two text-figures are not identical, but they give the exact form and relative



TEXT-FIG. 2. Reconstruction of the lower jaw (= anaptychus) and of the upper jaw of a specimen of *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) (= specimen No. 2) as found within the living chamber.

position of each pair of structures as they were found. Differences between the figures are due to the kind of preservation and to different angles of view, so they should not be overemphasized. In text-fig. 1 the thick lines indicate the first section; the missing parts of the left side of anaptychus and upper jaw fell victims to the saw before they were detected.

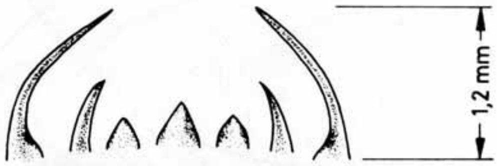
Measurements

	Diameter of ammonite	Length of anaptychus	Approximate height of anaptychus	Length of upper jaw	Height of upper jaw
Number 1	82 mm	8·2	5·5	8·1	3·7
Number 2	82 mm	8·6	5·9	8·7	3·8

Radula. In sections 38 to 62 of anaptychus No. 1, a considerable number of radular teeth were seen to be preserved between anaptychus and upper jaw. They are clearly visible on the photographs (Plate 27, fig. 1, 5). All are simple, thin-walled hollow cones. Although the individual teeth are well preserved, so many of them are detached that it is not possible to reconstruct the complete radular ribbon.

Three types of teeth are distinguishable (text-fig. 3). On each side of the radula one long marginal tooth (1·2 mm in length); the next towards the centre are half as long;

three short teeth, 0·2–0·3 mm in length, of which the central or rhachidian tooth is the largest, seem to form the centre of each transverse row of teeth. However, the short central teeth are so much disarranged that their exact number per transverse row cannot be given with certainty, whereas the arrangement of the lateral teeth is certain. Text-fig. 3, therefore, only indicates the most probable arrangement. If it is correct it corresponds to the arrangement of the transverse rows in the other known ammonite radulae, all of which have seven teeth per transverse row (Lehmann 1967, 1971, 1976).



TEXT-FIG. 3. Reconstruction of a transverse row of the radula as preserved between anaptychus No. 1 and the upper jaw. The number of the three innermost teeth is most probable, but not certain, owing to advanced disintegration.

DISCUSSION

Previous studies by the author (Lehmann 1970, 1971, 1976) have established that anaptychi and aptychi of ammonites are their lower jaws, in contrast to their former interpretation as opercula (Trauth 1927, 1935; Arkell 1957; Schindewolf 1958).

Up to now no aptychi or anaptychi of *Dactylioceras* have been known (Schmidt-Effing 1973, p. 29). This had led to the assumption that *Dactylioceras* may possibly not have possessed any jaws at all, and therefore may have been a plankton feeder. However, jaws of *Dactylioceras* are not as rare as it may seem. For example, a limestone slab from Ziegelei Reichenschwand, east of Nürnberg, W. Germany (shown on Plate 27, figs. 2–4) has the surface covered with several upper and lower jaws of the same shape as the ones described from the coast of Yorkshire. The strata exposed at Reichenschwand have so far produced ammonites of the genera *Harpoceras* and *Dactylioceras*, but only jaws of the type shown on Plate 27, figs. 2–4. The jaws of *Harpoceras* being well known it is highly probable that the jaws belong to *Dactylioceras*, particularly as they resemble the jaws from Yorkshire. Upper and lower jaws

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EXPLANATION OF PLATE 27

Fig. 1. Part of the living chamber of *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young and Bird) from bed 22, Port Mulgrave, Yorkshire, with the jaw apparatus and sections of radula teeth (white arrow) as seen in section No. 41, approx. ×15.

Fig. 2. Surface of a slab of limestone from Ziegelei Reichenschwand, near Nürnberg, Lias epsilon (lower Toarcian), with isolated upper and lower jaws presumably of *Dactylioceras* sp., ×3.

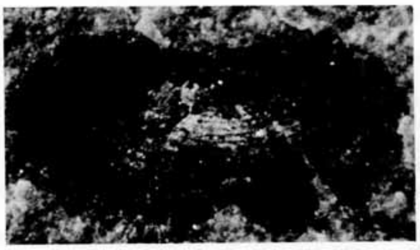
Fig. 3. Lower jaw (=anaptychus) presumably of *Dactylioceras* sp., ×14. Same locality as Fig. 2.

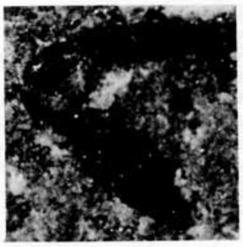
Fig. 4. Upper jaw presumably of *Dactylioceras* sp., ×17. Same locality as Fig. 2.

Fig. 5. Marginal radular tooth of same specimen as Fig. 1. Section 56, ×25.

1

2





3 4 5

LEHMANN, Jaws and radula of *Dactylioceras* are detached but they have not been transported very far. Their size is less than that of the jaws from Yorkshire. Due to compaction they are pressed into a plane and this has caused rupture of the outer margins of the lower jaw.

The jaws of recent cephalopods and of ammonoids are very similar: both have no articulation, their relative movements being effected only by muscles and both owe their cutting ability to a shearing effect (Kaiser and Lehmann 1971). This has been shown to apply for *Nautilus* jaws as well, in spite of the calcification of their mandibles which even produces prominent denticles (Saunders *et al.* 1978). Even thin and seemingly weak jaws of recent cephalopods may prove to be surprisingly powerful biting organs. '*Amphitretus*, an octopod, has flat, delicate jaws, which G. C. Robson considered incapable of biting, but a specimen was collected taking the bait off fish hooks' (A. Bidder, *in litteris*, Nov. 1977).

The fact that the radulae of recent cephalopods and of ammonoids are rather narrow and uniform, in contrast to radulae of prosobranch gastropods, seems to indicate rather similar use for all of them, which means more or less omnivorous or carnivorous diet. Plankton feeders would not need radulae either to seize or to swallow their food. That does not mean that ammonoids did not occasionally eat plankton, but that they did not depend on it.

Plankton and other soft-bodied organisms are not found in the stomachs of ammonoids, although they may very well have composed part of their diet. The presence of ostracods, foraminifers, crinoids, and other ammonites, etc. (Lehmann 1971, 1975, 1976) points to the diet of a scavenger and carnivore much like that of many recent octopods. 'However, ammonites are a diverse and variable group, and a single feeding strategy seems unlikely' (Kennedy and Cobban 1976).

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