

# Aptychi: the myth of the ammonite operculum

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Re-examination of ammonite specimens with the aptychus apparently in place closing the aperture has shown that these are accidents of preservation and have been misinterpreted as indicating that aptychi functioned as opercula. There remain no convincing grounds for doubting that aptychi functioned only as lower jaws of ammonites, not as opercula. Chance preservation of exceptional specimens can sometimes be misleading. □ *Ammonoidea*. *aptychi*, *anaptychi*. *functional morphology*.

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Aptychi are single or paired structures sometimes found associated with ammonite shells, but more frequently occurring in isolation. There seem to be remnants of doubt about the function of bivalved aptychi in particular, in spite of the elegant studies by Lehmann (1970, 1971, 1972, 1976, 1978, 1979) showing both anaptychi (single) and aptychi (paired) to have been the lower jaws of ammonites. The myth of the function of aptychi as opercula closing the aperture appears to persist not only among non-specialists, but also among some ammonite specialists. For example Kennedy & Cobban (1976:13) still entertained doubts and noted a possible secondary function as opercula. No doubt this is partly due to the unequivocal discussions by Arkell (1957) in the *Treatise* and by Schindewolf (1958) and the figuring by Arkell (1957, Fig. 145, p. L99) and by Schindewolf (1958, esp. Pl. 1:1a and b) of ammonites with the aptychus apparently in place, closing the aperture. The improbability of the aptychus functioning as Arkell (1957:L99–100) suggested has already been pointed out (Morton 1973:202).

There are probably two main reasons for the persistence of the myth of opercular function for aptychi:

- (1) Coincidence of shape between aptychus and aperture (more precisely body chamber cross-section).
- (2) The Arkell and Schindewolf specimens showing the aptychus in place as operculum closing the aperture.

Both reasons merit further investigation.

## Aptychus shape and body chamber cross-section

The general similarity of aptychus and aperture shape has been commented on by several authors (e.g. in the classic studies by Trauth 1927–1938), and Arkell (1957:L99) mentioned almost exact fits for bivalved aptychi. Size similarity was shown by Morton (1973, esp. Fig. 3). However, as shown by Arkell (1957, Fig. 146) and Schindewolf (1958, Fig. 1), the shape of the anaptychus in particular is often a considerable misfit, and the same can be shown to be true for at least some bivalved aptychi (e.g. Morton 1973, Fig. 2). Other authors have noted that the shape of the aptychus being compared with that of the aperture does not allow for complexities of apertural shape such as where lappets are present, e.g., in the stephanoceratid microconch *Normannites* (Westermann 1954:124–127).

It has to be conceded that there is general similarity of shape, despite misfits, between aptychi and the ammonite they are normally associated with. The similarity, though, is with the cross-sectional shape of the body chamber, not necessarily the apertural shape. It can be argued that this is no more than predictable coincidence, since both are secreted by parts of the soft body and are likely to be indirectly related in size and shape.

The evidence of shape and size similarity of aptychus and ammonite body chamber cross-section is by itself inconclusive about aptychus function, but the frequency of at least partial misfit makes opercular function less likely. However, the large size of the aptychus in

relation to the size of the ammonite body makes one wonder about an animal so apparently dominated by its mouth!

### Specimens showing aptychus in place as operculum

More striking than just shape similarity is the preservation of a very few specimens with the aptychus apparently in place, closing off the end of the body chamber. It should be emphasised that this type of preservation is very exceptional – where the aptychus and the ammonite shell are preserved together, it is very much more common for the aptychus to be in a ventral position some way behind the aperture (the *Normalstellung* of Trauth 1927–1938). The majority of known ammonite–aptychus associations occur where both are flattened in the bedding plane, as in the Lower Jurassic *Posidonienschiefer* or the Upper Jurassic Malm of southern Germany. Where three-dimensional preservation is available, as in Lower Jurassic *Arnioceras* described by Lehmann (1971) or Middle Jurassic *Sonninia* and *Euhoplaceras* described by Morton (1973, 1975a), the coincidence of plane of symmetry between aptychus and ammonite shell suggests that there has been minimal post-mortem disturbance of the aptychus relative to the shell. In such cases the aptychus is always in the ventral position well behind the aperture. Following up this line of evidence, and using also crushed material where the aptychus was apparently not displaced, Morton (1975b) showed that for 24 specimens of Lower–Middle Jurassic Hildoceratacea the mean angular distance from the aperture to the aptychus is 52°. The angular distance to the aptychus divided by the angular length of the body chamber for 12 specimens in which both could be determined (Morton 1975b, Fig. 2) gave a mean of 0.23, with standard deviation 0.07. It is difficult to imagine a mechanism whereby the aptychus could be pushed out towards the aperture then angled across the body chamber at the same time as the animal was withdrawing the rest of the body into the shell. The more extreme possibility of withdrawal of the body behind the aptychus position into only three quarters of the body chamber seems unlikely, especially in view of the narrowness of many ammonite shells and the fact that retractor muscle scars are not prominent.

The only exceptions to ventral preservation of aptychus inside the body chamber that I know of (there may well be others unknown to me) are specimens of *Physodoceras* from the Upper Jurassic described and figured by Schindewolf (1958) and a specimen of '*Oppelia*' from the Middle Jurassic figured by Arkell (1957, Fig. 145). Further study of these specimens has shown that their preservation is not only exceptional but also capriciously misleading.

#### *The Schindewolf PHYSODOCERAS*

Schindewolf (1958) gave a detailed account of the morphology, structure and occurrence of aptychi, based largely on material from the Upper Jurassic Malm gamma of southern Germany, and elaborated on some problems (notably taxonomy) discussed in the *Treatise*. In particular Schindewolf described and figured several specimens of *Physodoceras* with associated aptychus. One specimen especially, a *Physodoceras* cf. *altenense* (d'Orbigny) with *Laevaptychus longus* (von Meyer), led him to the conclusion that the apertural position (*Verschlußstellung*), though extremely rare, proved without doubt that aptychi functioned as opercula. The normal position (*Normalstellung*) was interpreted as largely a preservational accident. As figured by Schindewolf (1958, Pl. 1:1a and b) in apertural and *oblique* side views the specimen seems convincing. However, examination of the specimen (Ce 1129/1 in Tübingen University) shows that it is partially crushed in a dorsoventral direction and must have been vertically embedded. True apertural and side views are given in Fig. 1A and B. Other specimens studied by Schindewolf show this even more clearly with more extreme crushing, for example as shown by Ce 1129/33 figured in Fig. 1C and D.

In all these specimens discussed by Schindewolf the position of the aptychus is clearly a preservational artefact, with the specimens being vertically entombed, the aptychus simply falling onto the sediment within the body chamber and then the whole being compressed vertically. Most specimens from the same rocks which have the more usual preservation of the ammonite plane of symmetry parallel to the bedding show the aptychus in the normal ventral position.

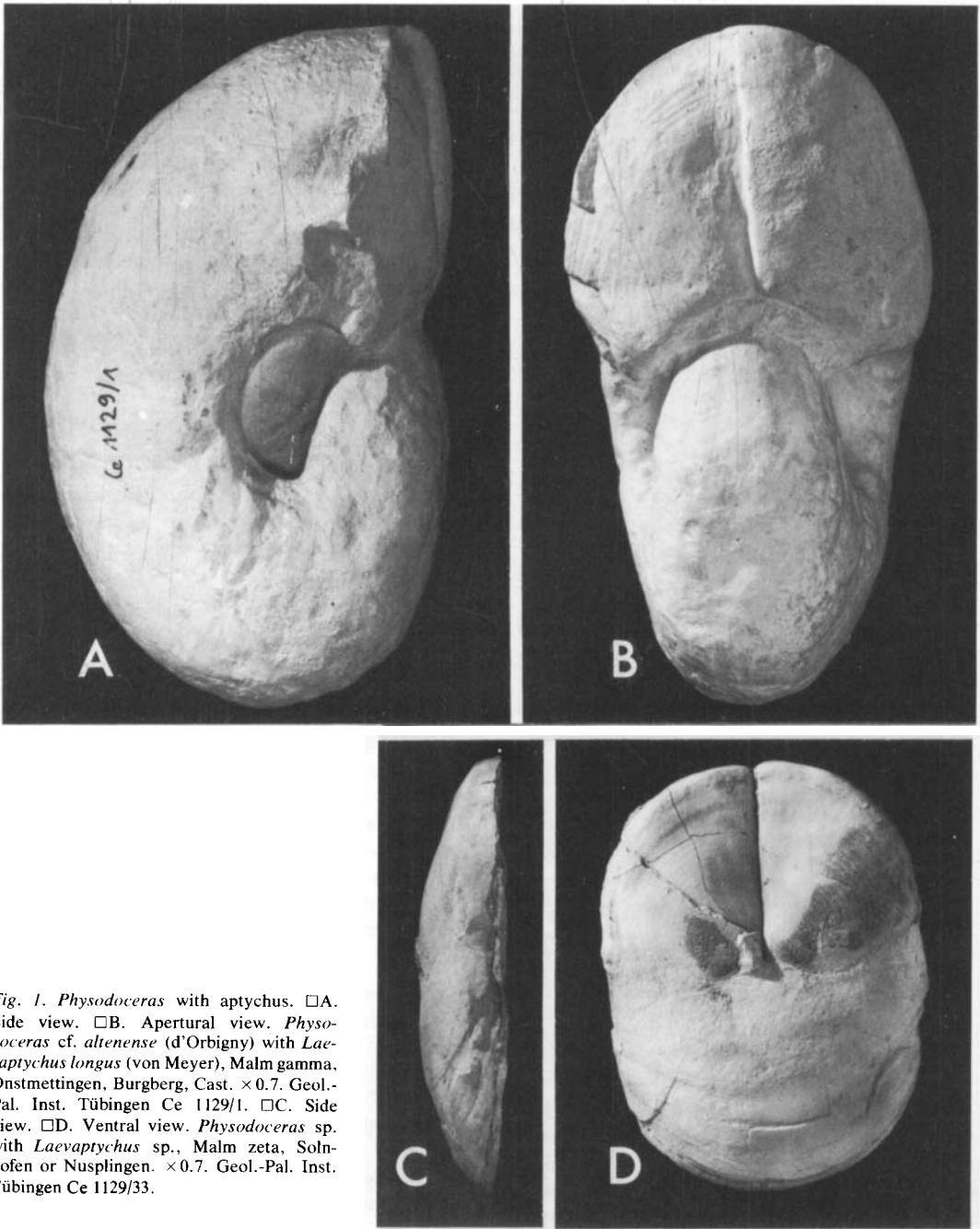


Fig. 1. *Physodoceras* with aptychus. □A. Side view. □B. Apertural view. *Physodoceras* cf. *altenense* (d'Orbigny) with *Laevaptychus longus* (von Meyer), Malm gamma, Onstmettingen, Burgberg, Cast.  $\times 0.7$ . Geol.-Pal. Inst. Tübingen Ce 1129/1. □C. Side view. □D. Ventral view. *Physodoceras* sp. with *Laevaptychus* sp., Malm zeta, Solnhofen or Nusplingen.  $\times 0.7$ . Geol.-Pal. Inst. Tübingen Ce 1129/33.

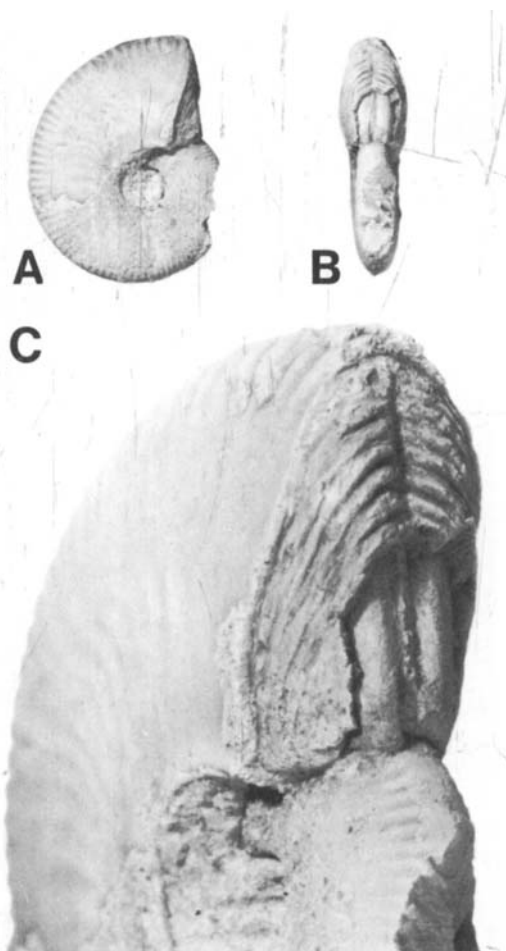


Fig. 2. *Bradfordia* with aptychus. □ A. Side view.  $\times 1$ . □ B. Apertural view.  $\times 1$ . □ C. Oblique apertural view.  $\times 4$ . *Bradfordia liomphala* Buckman with *Lamellaptychus* sp., Inferior Oolite, Dundry, British Museum (Nat. Hist.) 39627.

### The Arkell 'OPPELIA'

Arkell (1957, Fig. 145, p. L99) discussed and figured a specimen of 'Oppelia' (recte *Bradfordia liomphala* Buckman) with *Lamellaptychus* from the Middle Jurassic (Bajocian) Inferior Oolite of Dundry, England. The specimen was also described by Trauth (1927-1938). The function of the aptychus as an operculum was stated without much discussion, and no indication was given that the illustrated specimen was exceptional. Again ventral and oblique side views were given.

This specimen (Fig. 2) is in the British

Museum (Natural History, No. 39627) and shows no obvious signs of unusual preservation. There are, however, three lines of evidence to suggest that the position of the aptychus may be misleading:

(1) The phragmocone and a small part of the body chamber are filled with crystalline calcite, the rest of the body chamber being filled with sediment. On closer examination it becomes possible to estimate that the specimen must have been at an angle of approximately  $45^\circ$  to the horizontal (if the usual geopetal infill criterion of horizontal sediment surface is applied). The aptychus was in the lowest part of the body chamber and could have fallen there from higher up in the body chamber. It has remained at right angles to the horizontal, and across the width of the body chamber because it was jammed there and could not be turned round because of its shape and the 'wrapping-round' of the previous whorl. This must have happened during burial, but not before, otherwise the body chamber would not have been largely filled with sediment.

(2) The folds on the surface of the aptychus are in *Lamellaptychus* parallel to the edge of the valve or converge with the outer margin (see Arkell 1957:L439, Figs. 557, 558). In this specimen the folds converge with the edge of the aptychus towards the lateral margins, suggesting that the valves are broken where they are in contact with the mid part of the sides of the ammonite whorl (see Fig. 2C). This breakage must be a post-mortem effect and fits in with my interpretation of the position of the aptychus as being jammed across the body chamber during burial.

(3) The end of the phragmocone can be more or less accurately determined in this specimen, and from this to the aptychus is  $150^\circ$ . I have been unable to determine the normal body chamber length of other *Bradfordia* from Dundry, but even on this specimen there is the trace of the umbilical seam for approximately a further  $30^\circ$ . It is evident that in this specimen the aptychus was not at the aperture but well inside the body chamber.

Preservation of the aptychus in an apertural position as an operculum is more difficult to disprove for this specimen of *Bradfordia* than for the *Physodoceras*, but the combined evidence is enough to suggest that here also the position of the aptychus is a preservational accident.

## Conclusions

With reinterpretation of the *Bradfordia* and *Physodoceras* specimens described by Arkell and Schindewolf respectively, the evidence for an opercular function for aptychi (and anaptychi) becomes at best circumstantial, and the arguments to justify continuation of the myth unconvincing. It is much more likely, though of course as yet unproved, that all aptychi functioned as lower jaws (as demonstrated for some by Lehmann) and that no even secondary opercular role was adopted. Lack of resistant material attaching the aptychus to the shell has resulted in them being preserved in a wide variety of positions, but the ventral position inside the body chamber is likely to have been closest to the position in life.

Some problems do remain, however, concerning the functional interpretation of aptychi: the extremely large size of the aptychus as a jaw apparatus in relation to the size of the rest of the animal; calcification of the aptychus; the presumed evolution from anaptychus to bivalved aptychus.

Chance preservation of exceptional specimens frequently in palaeontology gives otherwise unavailable insights about the morphology, function, taxonomic affinities, etc., of an extinct fossil group. It is interesting to record that in these examples of ammonites with aptychi two of the most eminent ammonite specialists were misled by such chance preservations to wrong conclusions about the function of aptychi in ammonites.

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