THE APTYCHI OF *SONNINIA* (AMMONITINA) FROM THE BAJOCIAN OF SCOTLAND

by N. MORTON

ABSTRACT. Aptychi found in the body chambers of four specimens of *Sonninia* (*Papilliceras*) from Skye, western Scotland, are described and figured. The aptychi do not exactly fit the aperture but it was not possible to establish conclusively whether they functioned as opercula or as part of the jaw apparatus.

FOUR specimens of the ammonite genus *Sonninia* (*Papilliceras*) were found to have aptychi preserved within the body chamber. Three of the specimens (HMS26394, HMS26396, BkC F329) belong to the species *S.* (*P.*) *arenata* (Quenstedt) and the fourth (HMS26395) to *S.* (*P.*) *mesacantha* (Waagen). Both species are macroconchs. The specimens are from the Massive Sandstone of the Bearreraig Sandstone (Morton 1965), i.e. Sauzei Subzone, Bajocian. They were all found in loose blocks at Rudha Sughar, Bearreraig, Skye, so that details of orientation relative to bedding are not available.

The descriptive terms used are as outlined by Arkell (1957, pp. L437–439, fig. 556). This terminology is not entirely satisfactory, because it refers to relationships of the aptychi as opercula and would be inappropriate if the aptychi had a different function. It is used herein only because explanation of it is readily accessible. The specimens are in the collections of the Hunterian Museum, University of Glasgow (HM), or the Department of Geology, Birkbeck College, University of London (BkC).

DESCRIPTION OF THE SPECIMENS

Position. In all four specimens under discussion the aptychi occur inside the body chambers of the ammonites. In one specimen (HMS26394, text-fig. 1B) the valves are separated and lying, one partly on top of the other, against the outer part of the whorl side near the back of the body chamber. That this side was the lower side during burial is confirmed by the partial infilling of the body chamber with sediment.

In the other three specimens (text-fig. 1A and 1C, Pl. 18, fig. 3) the aptychi are preserved with the two valves together in the ventral part of the body chamber much nearer the aperture, in a position varying from 44° to 63° from the aperture (see below for details). This is by far the most common position for the preservation of aptychi, and is the *Normalstellung* of Trauth (1927–1938). All three specimens have the apex and inner margin towards the aperture, and the harmonic margin against the ventral part of the whorl. In HMS26396 (Pl. 17, fig. 3) and HMS26395 (Pl. 17, fig. 4) the harmonic margins are in line with the middle of the venter (as defined by the keel) and the planes of bilateral symmetry coincide approximately with those of the ammonites, but in BkC F329 these are displaced slightly (1·5–3·5 mm) to one side.

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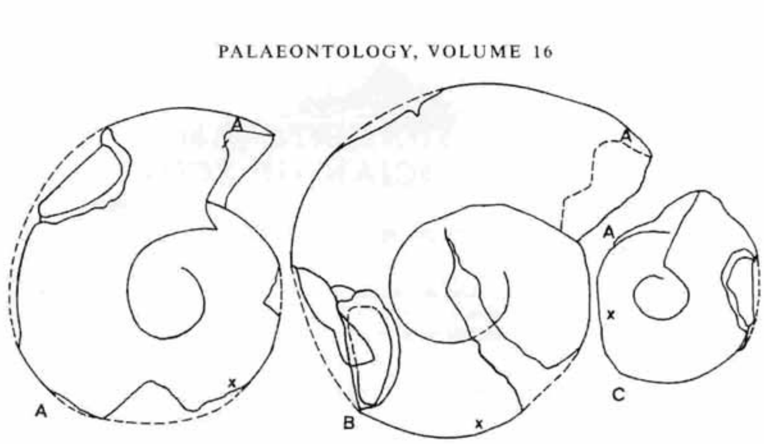

TEXT-FIG. 1. Outlines of ammonites (partly restored) showing positions of aptychi. 'A' marks the position of the aperture, 'X' marks the end of the phragmocone. All specimens ×0·33. A, *Sonninia* (*Papilliceras*) *arenata* (*Quenstedt*), HMS 26396; B, *Sonninia* (*Papilliceras*) *arenata* (Quenstedt), HMS 26394; C, *Sonninia* (*Papilliceras*) *mesacantha* (Waagen), HMS 26395.

Dimensions:

A. aptychus	HMS26396	BkC F329	HMS26394	HMS26395
1. maximum length	46·0	45·9	51·8	33·1
2. length of hinge line	44·6	c. 41·3	49·5	30·9
3. maximum width	20·5	19·7	21·7	14·2
4. convexity of right valve	5·9	3·8	—	5·0
5. convexity of left valve	5·2	—	4·6	—
6. thickness of pr. of valves[1]	16·4	—	—	c. 10·7
B. aperture[2]				
1. distance from keel to keel	44·9	c. 46·0	54·0	—
2. whorl height[3]	56·4	54·3	61·1	—
3. maximum whorl breadth	25·1	29·3	31·9	—
C. position of aptychus				
1. distance from aperture[4]	53°	44°	131° 152°	63°
2. length of body chamber[4]	245°	230°	235°	280°

Notes:

1. As preserved, not necessarily the same as in life.
2. Outside measurements, including shell.
3. From keel to umbilical seam.
4. Measured as angles subtended about protoconch (axis of coiling) by umbilical end of aperture and nearest part of aptychus, and by aperture and beginning of body chamber.

Description. The aptychi consist of a pair of valves showing approximate but not quite exact bilateral symmetry, with the plane of symmetry passing between the valves. In three specimens the valves are in contact along one margin (see Pl. 17, figs. 3, 4) and were presumably hinged along this margin (the harmonic margin), but no hinging structures are present and the specimens all show slight displacement of one valve relative to the other. In the fourth specimen (HMS26394, Pl. 17, fig. 5) the two valves have been separated. The valves are not in contact along the other margins, the separation being approximately 15·8 mm at the middle of the lateral margin in HMS26396.

The shape of each valve (Pls. 17 and 18) is subtrigonal, with the angle opposite the harmonic margin broadly rounded, the apical angle a fairly sharp right angle, and the ventral angle between 20° and 30° but rounded. The harmonic margin is straight, only very slightly shorter than the maximum length of the valve, and there is a distinct harmonic facet (visible as a furrow on the internal mould, but not evident on the exterior) which becomes gradually broader from the apex to the ventral angle (Pl. 17, figs. 4 and 5). The outer margin is rounded and is not distinct from the lateral margin which is curved. Outer and lateral facets are not present or only very slightly different in attitude from the rest of the outer surface of the valve (Pl. 17, figs. 1 and 2). There is no distinct umbilical projection but a broadly rounded angle, and the inner margin is practically straight or with very slight incurvature. The maximum width of the valves is developed at about 30% of the distance from the apex to the ventral angle, and the maximum convexity of the valve is in the area between this line and the inner margin.

The exterior (i.e. where the shell is present) does not differ in appearance from the rest of the ammonite shell and there is little surface ornamentation. Faint ridges radiating from the apex are present on the adharmonic slope of the outside surface (Pl. 18, fig. 1) and are even more faint on the inside surface. More prominent are growth lines, evident on both inside and outside surfaces. The growth lines on the aptychus of *S.* (*P.*) *mesacantha* (Waagen) (HMS26395) are more prominent than those of *S.* (*P.*) *arenata* (Quenstedt). Prominent growth rugae are developed near the outer and part of the lateral margins on two specimens (Pl. 17, fig. 2; Pl. 18, fig. 1). There is no keel, and the adharmonic slope is not distinct from the flank.

The shells of the aptychi have been recrystallized to coarsely crystalline calcite, so that evidence of shell structure is limited. A thin section through the ammonite shell and the aptychus shows confirmation of the recrystallization, but the recrystallization of the aptychus is very different from that of the ammonite shell. In the aptychus large crystals of calcite with highly irregular outlines extend across the whole thickness of the shell. The ammonite shell is recrystallized so that it retains a layered structure, with smaller crystals of calcite which never extend across the whole thickness of the shell. The difference in recrystallization is presumably related to the ammonite shell having been originally composed of aragonite and the aptychus of calcite. In spite of the recrystallization the aptychus shows relict lamination with the laminae oblique (about 20°) to the surface of the aptychus and extending from one surface to the other in just over 3 mm. It appears that growth was by adding new layers along the oblique growing edge but not over previously formed parts of the aptychus. Shell thickness varies up to approx. 0·5 mm, but generally the shell is thinner towards the apex and inner margin, so that the thickness of the calcareous layer of the aptychus increased with growth. On all specimens there is an inner layer of dark brown or black organic material which is generally dull and rather spongy in appearance.

DISCUSSION

Taxonomy. The occurrence and biological affinities of aptychi have been extensively discussed, and the literature on Mesozoic occurrences is summarized by Arkell (1957, pp. L99–100, L437–440). The Skye specimens provide still more evidence of close association between specimens of aptychi and ammonites, and there can be little doubt but that they belonged to the same animal.

There then arises a taxonomic problem such as has been discussed by Arkell (1957, pp. L438–439) and Moore and Sylvester-Bradley (1957, pp. L465–470). Arkell used a taxonomic procedure in which non-Linnaean form-genera were used, but Moore and Sylvester-Bradley used full Linnaean nomenclature. According to Arkell (1957, p. L267) the sonniniid aptychus is of the *Cornaptychus* type which is described (p. L439) as having a shiny black surface with coarse folds. The Skye aptychi do not possess either of these features and so cannot belong to this type. They are more similar in ornamentation to *Laevicornaptychus*, but again do not have the shiny black surface. However, this feature may have been misinterpreted, recalling the black inner layer under the calcareous layer. Of figured specimens of aptychi the Skye aptychi are not identical with any named types, but they are almost identical with the *Sonninia* aptychus figured, but not named, by Nicklès (1900).

Function. It has generally been assumed that aptychi were ammonite opercula, and a few specimens have been found with aptychi in a position apparently closing the aperture (e.g. a specimen figured by Arkell 1957, fig. 145, p. L99), but these are extremely rare and there is doubt as to whether Arkell's specimen is complete. Several authors have commented on the fact that many aptychi do not provide a good fit for the aperture of the ammonite with which they are associated. Many aptychi associated with lappet-bearing ammonites have been recorded and it is difficult to see how in at least some cases the aptychi could have functioned as opercula, especially with more specialized apertures such as that of *Normannites* (compare Westermann 1954, figs. 32 and 35 for example).

The length of the aptychi described herein is closely comparable with the whorl height (measured from the keel of the preceding whorl to the ventral part of the aperture), but the width of the two valves together (as preserved) is less than the whorl width (breadth) at the aperture (text-fig. 2). However, since the aptychi consist of two apparently hinged plates it is possible that by increasing the angle between the valves a better correspondence between apertural width and width of aptychus

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EXPLANATION OF PLATE 17

All stereo-pair photographs, separation 63·5 mm. Natural size unless otherwise stated.

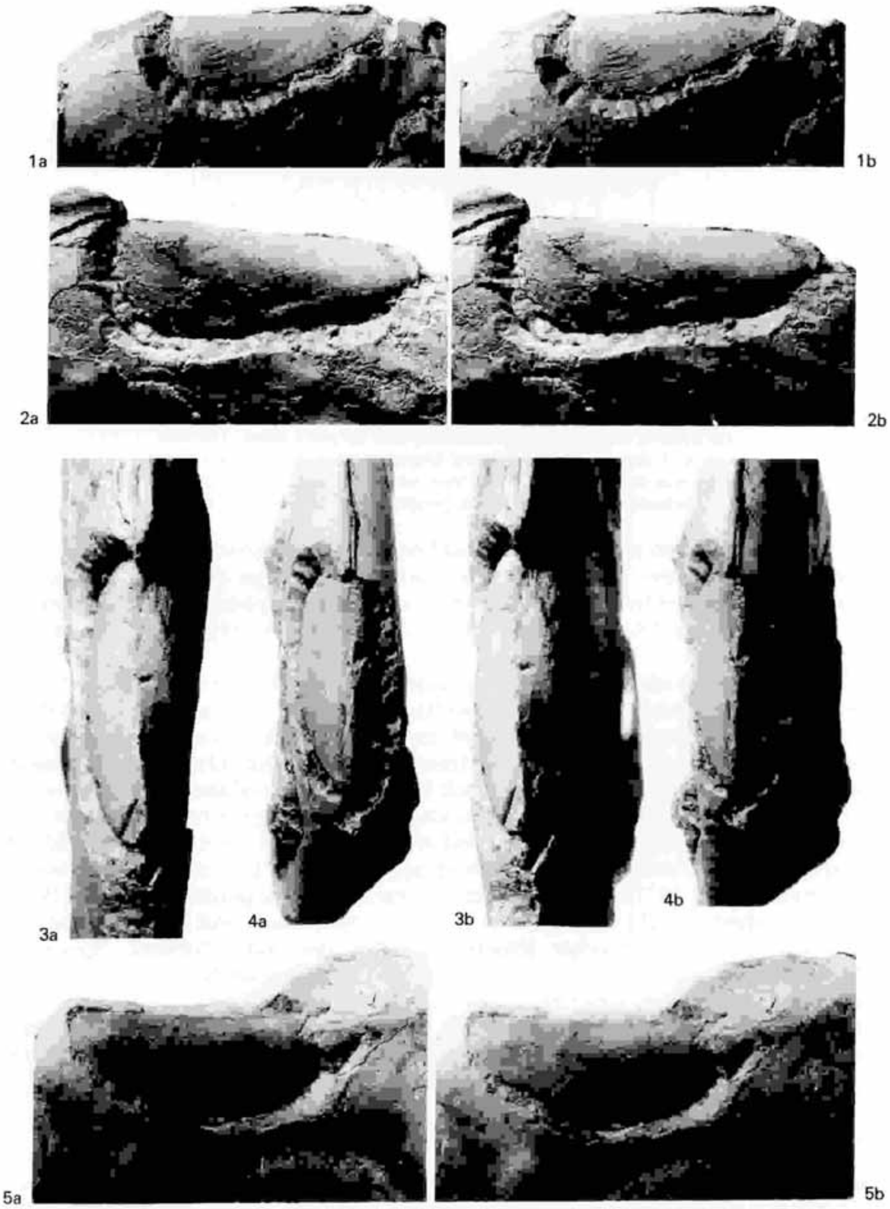
Figs. 1A, B. Right valve of aptychus of *Sonninia* (*Papilliceras*) *mesacantha* (Waagen), HMS26395. Mostly internal mould with little shell remaining.

Figs. 2A, B. Right valve of aptychus of *Sonninia* (*Papilliceras*) *arenata* (Quenstedt), HMS26396. Shell present except on inner part.

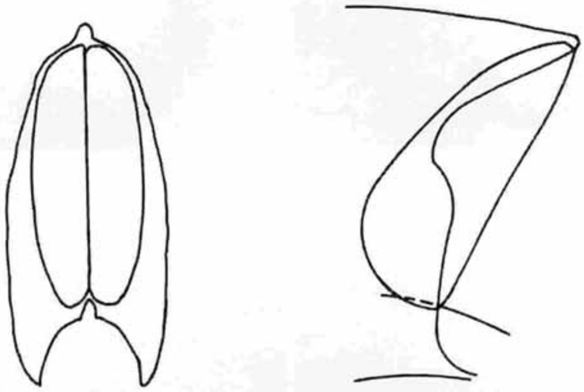
Figs. 3A, B. Harmonic/ventral view of fig. 2.

Figs. 4A, B. Harmonic/ventral view of fig. 1.

Figs. 5A, B. Left valve and part of right valve of aptychus of *Sonninia* (*Papilliceras*) *arenata* (Quenstedt), HMS26394. Internal mould to left valve, external mould of right valve. ×0·7.



MORTON, *Sonninia* aptychi



TEXT-FIG. 2. Aperture of HMS 26396, with aptychus fitted. The two valves of the aptychus are shown hinged at the angle at which they are preserved. In the apertural view note that the aptychus appears reduced in length because of perspective of drawing. ×1·0.

may be achieved. Even so the aptychi would not provide a perfect fit for the aperture, especially on the inner part of the whorl where it overlaps the preceding whorl. However, the hood of living *Nautilus* does not in itself completely close the aperture (see Stenzel 1964, fig. 68, p. K91), so that this does not necessarily preclude opercular function.

Change of shape with growth was investigated for one of the specimens (HMS26394) (text-fig. 3), and it was found that the width/height ratio decreases with growth in both whorl shape (measured as ratio of maximum width to height from keel of preceding whorl) and shape of aptychus (measuring one valve only at various growth lines). However, the rate of change is much less for the valve of the aptychus than for the whorl shape. This is not surprising since, even assuming opercular function, the length of the aptychus would correspond with the whorl height, but the width of the aptychus valve would correspond with approximately half of the whorl width.

Lehmann (1970, 1971) has reinterpreted some Liassic anaptychi, and later (1972) various bivalved aptychi, as the lower jaw of the ammonite, and has described the upper jaw, radula, and other structures within the body chamber. Specimen HMS26396 was sectioned through the aptychus approximately along the line of maximum convexity (see description above) and through the centre of the umbilicus. Within the aptychus various shreds of dark brown or black organic matter and some small black fragments were found. Some of the shreds appear to be derived from the

EXPLANATION OF PLATE 18

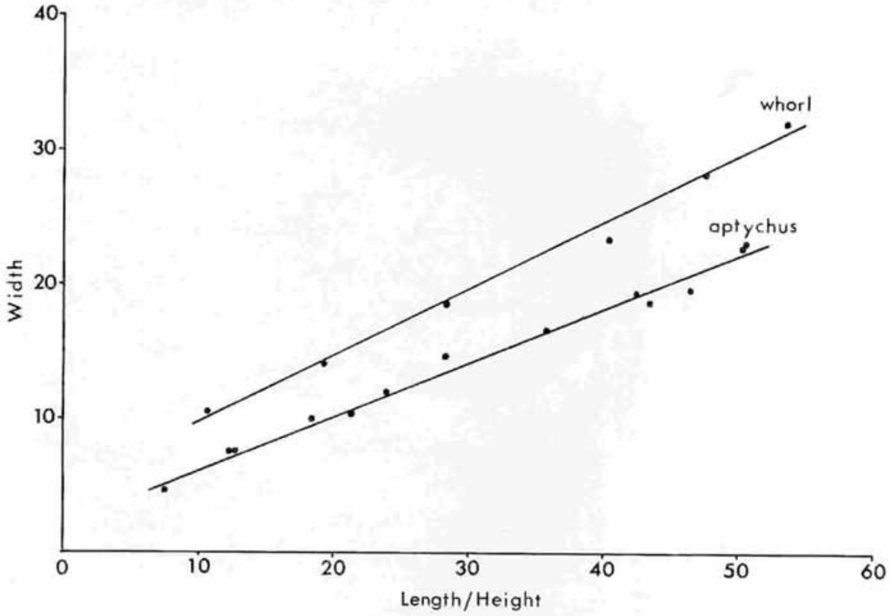
All figures natural size.

Figs. 1–3. *Sonninia* (*Papilliceras*) *arenata* (Quenstedt). 1, Left valve of aptychus, HMS26394. Internal cast with shell partly replaced. 2, Left valve of aptychus, HMS26396. Internal mould with shell partly preserved. 3, Complete conch with aptychus, BkC F329.

MORTON, *Sonninia* aptychi

organic layer of the aptychus, but no definitely identifiable structures such as those figured by Lehmann (1972, pl. 9, fig. 1) were found. The small black fragments may represent isolated radular teeth.

On the basis of the information available no definite conclusion can be arrived at regarding the function of the aptychi in the ammonite specimens from Skye. The possibility that they acted as rather badly fitting opercula cannot be rejected, although the fit is bad enough to suggest that this function is unlikely. The regularity in the position of the aptychi inside the body chamber in most of the Skye specimens (as in others) does suggest that this was close to their position in life. If this is so then the aptychi were situated well inside the body chamber, further away from the aperture than shown by Arkell (1957, fig. 124, p. L82). It is difficult to imagine a mechanism whereby the aptychus was pushed out of the body chamber into the aperture at the same time as the body was being retracted into the body chamber, especially if the mantle cavity (important in providing space for retraction) was between the aptychus and the aperture, a situation which would result from placing the aptychus 50° (see p. 196) from the aperture in Arkell's diagram. In gastropods and *Nautilus* the operculum or hood is on the part of the body which is last to be drawn into the shell —a very different situation. On the other hand the position of the aptychi does fit in well with the interpretation advanced by Lehmann that they were lower jaws, and this seems the more likely function.



TEXT-FIG. 3. Width plotted against height or length for whorl dimensions and one valve of aptychus of HMS 26394. The whorl height used is from keel to keel rather than umbilical seam to keel.

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ADDENDUM

Since the above was written another sonniniid ammonite from Bearreraig has been found to have the aptychus preserved within the body chamber. This is a specimen of *Euhoploceras fissilobatus* (Waagen) from the Sowerbyi Zone, Shaly Sandstones, cliff south of Bearreraig. The aptychus is in the normal position with the harmonic margin exactly in line with the keel (i.e. mid venter) and the plane of symmetry corresponding with that of the ammonite. The aptychus is 51° from the aperture, a position comparable with those of the specimens described above. The dimensions for this specimen (HMS26397) corresponding with those given above are:

A: 1	2	3	4	5	6	B*: 1	2	3	C: 1	2
60·2	54·1	30·0	5·0	5·3	30·6	*c*. 70·0	*c*. 88·0	*c*. 44·0	51°	217°

* The aperture is not completely preserved and one side is crushed so that apertural dimensions are estimated.

The shape and other features of this specimen are the same as for the other specimens described above. The main difference is in the surface ornamentation. The growth lines and growth rugae are very much more pronounced on both internal and external surfaces. Other, minor, differences include a more pronounced change of slope between the adharmonic slope and the flank, and a larger harmonic facet on the *Euhoploceras* specimen.