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AMMONITE APTYCHI: HOW TO TRANSFORM A JAW INTO AN OPERCULUM?

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ABSTRACT. As in the evolutionary transition from a reptile front leg into a bird wing, the functions of a cephalopod lower jaw and a calcified opercular aptychus are too disparate for direct linkage. A hypothesized stepping-stone function of the anaptychus, as a spring in the feeding process, bridges the gap and explains why ligamental flexibility was maintained in mineralized aptychi.

Although I have known John Ostrom since 1955, when he was E. Colbert's field assistant in Arizona, and now for six years at Yale, he cannot expect me to celebrate him in his own field, vertebrate paleontology. However, communication between paleontologists, thank goodness, does not depend on taxonomic party lines! In all John's work, I have been most impressed by his postulate of a pre-*Archaeopteryx*—not yet flying, but with feathers and wings evolving in another functional context (Ostrom, 1979). Whether or not this hypothetical ancestor was a fly catcher is of less importance. What counts is the insight that some evolutionary transformations simply cannot be accomplished in one step. Rather, they depend upon functions that happen to lead adaptation in the general direction of a future breakthrough, allowing to coopt with the new function. I will elaborate on such a stepping stone by discussing another dramatic change in the function of an organ, the ammonite aptychus.

1. THE APTYCHUS PROBLEM (FIG. 1)

The association of aptychi with ammonite shells is a long recognized fact. But since no obvious counterparts exist in modern *Nautilus,* their nature has been the matter of a hot debate, in which issues of homology, function, and fabrication were not always clearly separated.

The major turning point in aptychus research came when Ulrich Lehmann discovered, by careful serial sectioning, that the aptychus is in fact a transformed lower jaw. In his latest publication on the subject (Lehmann and Kulicki, 1990, and references therein) he admits that the aptychus could have served a double function as a jaw *and* an operculum. I agree with this interpretation except for a caveat:

A. From a Darwinistic point of view, the direct transformation of a jaw into an operculum is almost as problematic as that from a reptile limb to an *Archaeopteryx* wing. A third function, bridging the gap between the two endmembers, would add credibility to Lehmann's assessment.

B. The ten muscular arms in Lehmann's reconstruction are based on the assumed sister-group relationship of ammonoids to coleoid cephalopods (for example, squids) rather than on fossil evidence. Since arms

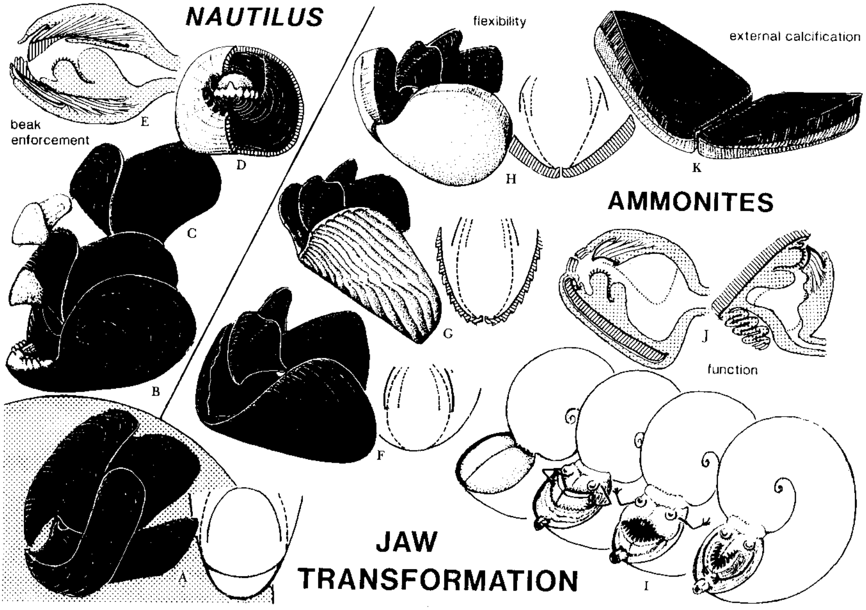

Fig. 1. Standard cephalopod jaws (A) are horny two-element exoskeletons that articulate along gliding edges rather than at a fixed joint. In *Nautilus* (B) the construction is similar; only that the chitinous beaks are much less pointed to accommodate calcitic caps (white in drawings; rhyncholite removed in (C)). Their arrangement in the buccal mass (removed on right side of front view, (D)) suggests that the jaws are closed by ring muscles in the surrounding epithelial fold (E).

In ammonites, the upper jaw retained a pointed horny tip, while its inner lamella developed a deep sinus between two lateral wings, possibly to accommodate an enlarged gut. The lower jaw may be hypertrophied into a broad *Anaptychus* (G); but the lack of a strengthened front edge, reduction of the inner lamella, and loss of the gliding joint suggest that it no longer acted as a biting antagonist to the upper jaw. It had probably become an elastic spring that assisted in a kind of suction feeding. At this stage the anaptychus could also coopt for the function of an operculum. This new role was enhanced in aptychi (G, H) by mineralization and concentration of the flexible zone into a median ligament. Note that new calcite layers were added from the outside (K). As in the operculum of *Turbo* (fig. 2), sliding out from an epithelial pocket (J) would have only temporarily interfered with the calcification process.

Admittedly, the arms shown in the cartoons (I) are unrealistic, but little more so than the arms in standard ammonite reconstructions.

would have been difficult to stow away when the lid closed the shell aperture, I suspect a case of anatomical shoehorning.

2. STRATINOMIC EVIDENCE FOR THE JAW HOMOLOGY

Statistical mapping of double-valved aptychi relative to associated flat-lying ammonite shells in the Jurassic Fossil-Lagerstätten of Holzmaden and Solnhofen (Uwe Decker, 1988, unpublished internal report, SFB 230) fully supports Lehmann's interpretation of these structures as homologues of lower jaws. The data suggest that the "normal position" (in which the aptychus is preserved at the bottom of the body chamber) is a taphonomic artifact caused by incipient decay of the soft parts within a shell floating upright in the water. In the "life position" (prevailing at Solnhofen, where burial was more rapid) the aptychus lies just in front of the aperture with an inclination to the spiral axis like that of a lower jaw. "Closing positions" are surprisingly rare in this material.

Decker's survey also shows that the thick *Laevaptychus* of *Aspidoceras* always has the two valves spread open. This "butterfly preservation" is rarer in *Lamellaptychus* (associated with oxycone shells) and in the thin *Punctaptychus* of perisphinctids, where the majority of specimens has the aptychus folded like a closed book ("folio preservation"). This indicates that the two halves gaped with an angle of less than 90° in the relaxed state and were therefore more likely to be squashed shut than opened during compaction of the tilted shell. In contrast, isolated pairs of aptychi—no matter what type—are mostly found in butterfly preservation, perhaps because they sank freely to the bottom with their convex sides facing downward, rather than coming to rest in a lateral position.

3. FABRICATIONAL ASPECTS: COMPARISON WITH GASTROPOD OPERCULA

A. Inside-out Structure of Aptychi

At first glimpse, aptychi resemble bivalve shells having two equal valves with a straight hinge and concentric growth lines. A closer look reveals basic differences:

1. Normal mollusc shells show periostracal growth lines on the convex outer side and a smooth calcareous lining on the concave inner surface. In aptychi the relationship is reversed: they were mineralized from outside (fig. 1,K), like a belemnite rostrum.

2. Nevertheless the calcareous outer layer of the aptychi may bear distinct sculpture patterns which one would normally associate with a surface covered by periostracum (fig. 1,G).

This inside-out world reflects a fabricational mode unlike the one of ordinary mollusc shells. Does it mean that aptychi were internal structures comparable to the cuttlebone of *Sepia,* which may also bear tubercular calcifications on its dorsal surface? This is probably what made Schindewolf (1958) think of the aptychus as an internal skeleton within a hood similar to the fleshy cap of modern *Nautilus.* After all, the *Nautilus* cap is bipartite and does serve as an operculum when the animal withdraws into its shell! Nevertheless there are great difficulties in making these two structures homologous. First, the hood of *Nautilus* consists of two transformed arms. If they were to produce shelly structures, we would not expect a ligamentary connection between them. Second, the "life position" of the aptychi discussed in the last chapter corresponds to that of a lower jaw, which is also an internal structure. But how can a jaw serve as an operculum?

B. *Inside-out Structure in Gastropod Opercula* (fig. 2)

In order to find a modern analogy, we must leave the cephalopods and turn to the opercula of gastropods. These are mostly horny plates, attached to the postero-dorsal side of the foot, that seal the aperture like a manhole cover as the animal withdraws into its shell. In *Strombus,* the horny operculum also has on its rear side a free umbonal spike that serves as a stick used in fast locomotion.

Some gastropod opercula are calcified but not always in the same style. The operculum of the Ordovician genus *Teiichispira,* for instance, is a horn-shaped, but massive structure (Yochelson and Jones, 1968) that may have served both as a lid and as an anchor for sedentary life on muddy bottoms. In the *Teiichispira* operculum calcareous fibers were added on the inside of the organic template, so that it could grow into a high cone coiling in the opposite sense of the shell—rudist style.

More relevant for our purpose is the modern genus *Turbo* (fig. 2), because its solid calcareous operculum has an inside-out structure similar

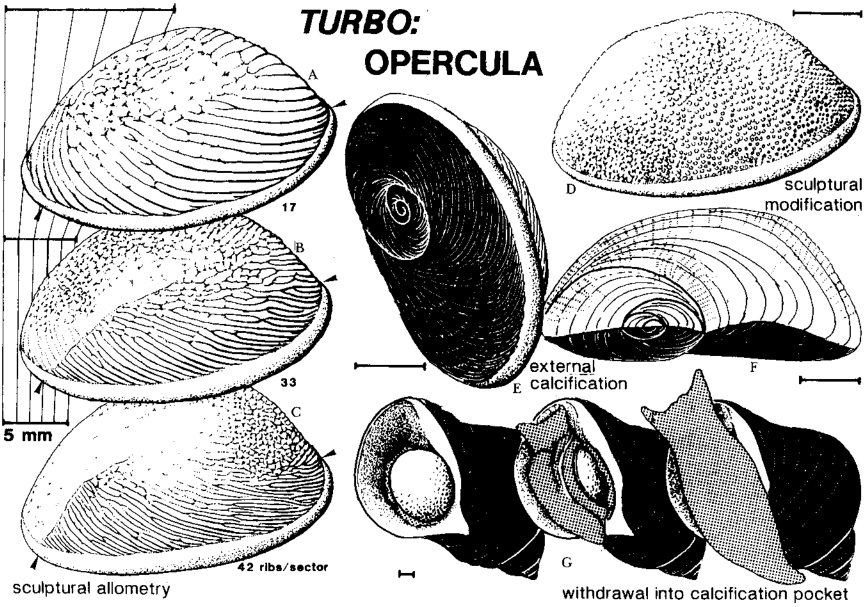

Fig. 2. The opercula of turbinid gastropods provide a functional and fabricational analogue to ammonite aptychi. They become calcified from the outside while withdrawn into an epithelial pocket. The "periostracal" surface (black, with growth lines; (E, F)) faces the body and serves for the attachment of retractor muscles. External sculptures show characteristics of self-organization: (1) pattern variability (D) and (2) constant distancing of elements (=negative allometry; A–C). Once established, these patterns are maintained in subsequent laminae (tracks in cross section; (F)), although epithelial contact is lost every time the operculum closes (G). (Drawn from specimens of *Turbo argyrostomus* collected in W. Samoa; GPIT 1705/1.)

to that of the aptychi. On the flat side there is a dark layer that at first sight looks like a periostracum. Its delicate growth lines are arranged in a flat spiral, but instead of being a mirror image of the shell spiral, it coils in the same dextral sense. In reality, the "periostracum" is on the inner, bodyward side of the lid, and the evenly vaulted porcellaneous side faces outward in closed position. Since this surface is not covered by living tissue when the lid is shut, how can calcareous layers be deposited on it?

The explanation comes when we see the animal emerge from its shell. As the head and foot unfold, the lid not only tilts toward the columellar side, it also slides snugly into a pocket formed by a soft epithelial fold. Thus we may assume that increments of the organic layer are secreted by the foot when the operculum is in closing position (thus copying the shape of the aperture), while calcareous layers become deposited when it is stowed away. As growth goes on, the operculum must also rotate relative to the foot in order to avoid twisting of the retractor muscles.

C. External Sculptures

The *Turbo* operculum resembles an aptychus not only by its inside-out structure, but also by the sculpture on its outer surface. While being perfectly smooth in some species, this side bears regular ornaments in others (fig. 2A,B). Specifically, there are minute round tubercles that disappear toward the apertural margin and merge into meandric ridges reminiscent of human finger prints on the trailing side of the growing operculum (fig. 2A). In another species (*T. fluctuosus*), the tubercles align into spiral (=normal) ribs. These ornamentations have no obvious functional value. Rather, unpredictability at the local and regularity at the global level suggest that these patterns arise primarily as fabricational noise, like so many self-organizing biological structures (Seilacher, 1991). Also, the spacing of the ornaments hardly changes as the operculum grows larger. This is another common feature among self-organized patterns expressed on rigid skeletons.

Aptychus ornaments have similar characteristics. The tubercles of *Granulaptychus* are arranged in concentric rings but otherwise show little regularity. The ribs of *Lamellaptychus* are divaricate, including occasional zig-zag repair patterns (fig. 1G). Divaricate patterns result from a combination of the zebra principle with marginal growth and are therefore common in mollusc shells. Thus their occurrence in *Lamellaptychus* suggests that the calcareous layer did accrete with a stronger marginal component than in the *Turbo* operculum.

D. Calcitic Composition

In contrast to the aragonitic ammonite shells, aptychi are calcitic. This is clearly an original feature, as shown by Holzmaden and Solnhofen ammonites: their shells were plastically deformed after diagenetic aragonite dissolution, while associated aptychi remained undeformed. Mineralogical divergence is also expressed in the preferred—or exclusive—

preservation of disarticulated aptychi in pelagic limestones deposited below the aragonite compensation depth, or in coquinas reworked from beds in which aragonite had been lost by early diagenesis. Such divergence is not uncommon among mollusc skeletons. Land snails seal their aragonitic shells for hibernation with a calcitic lid secreted by the foot. More directly relevant to our case: nautilid jaws, if mineralized, are always calcitic. So, it should not surprise us that aptychi show the same pattern.

E. Calcification in Nautilus Jaws

Calcitic reinforcements in the jaws of living *Nautilus* species (fig. 1B, C) mark the adaptation of horny cephalopod beaks to a more durophagous mode of nutrition. While their inside-out fabrication resembles that of aptychi, basic differences in design indicate a different functional context:

1. In *Nautilus,* calcification affects both upper and lower jaw elements, while in ammonites only the lower jaw became mineralized. The conflict between external calcification and jaw function is another problem that appears not to have been addressed previously (Saunders and others, 1978).
2. Calcification of nautiloid jaws is centered at the cutting edge with tapering extensions onto the horny inner and outer lamellae. Even in the most heavily calcified beaks, the larger part of the jaw lamellae remains uncalcified. This is consistent with jaw function. In an aptychus, the calcitic reinforcement does not taper away from the beak. To the contrary, it becomes thicker toward the growing margin, where only a narrow rim remained uncalcified to improve opercular sealing and provide a fitting matrix for mineralization.
3. While each nautiloid beak is calcified as one piece, aptychi remain uncalcified along the midline, which weakens the structure at the very point where a beak should be strongest.

F. General Modes of Shell Formation

In contrast to the skeletons of most arthropods, which are molted in their entirety, those of molluscs grow marginally. Their organic cuticle must be secreted continuously (or rather in small steps) in an epithelial fold comparable to the nail beds of our fingers. Accretionary growth of the skeleton along this fold is the basis for molluscan shell geometries, varying from flat plates to straight cones and logarithmically coiled structures. Growth lines record this rhythmical process even in environments where there are no diurnal or seasonal fluctuations.

A similar divergence regards the modes in which the organic matrix is mineralized in the two phyla. In arthropods, it is the same epithelium that must, in succession, produce organic and mineralized layers. In molluscs, different epithelial zones are responsible for mineralization as the growing organic shell layer passes over them like an assembly line. This mode is, in turn, different from shell fabrication in brachiopods, where mantle cells firmly adhere to the shell and "secrete" calcareous prisms in place, without lateral shift.

Among mollusc exoskeletons, different spatial relationships of shell layers result from the varying arrangement of the "nail bed" with regard to the calcifying epithelia or from stationary versus shifting modes of calcification:

1. *Beak skeletons.*—Here the "nail bed" produces a stiff organic shell that remains smooth except for growth lines. Notably, beak skeletons also lack the radial (=normal) ribs or spines so common in shell skeletons. The inside of beak skeletons serves for muscle attachment over the whole surface. As in shells, geometries vary from flat plates to straight or logarithmically coiled conical bodies, but because of their innate stiffness, beak skeletons commonly remain unmineralized. If mineralized layers are deposited on the organic template for additional strength or weight, two possibilities exist:

A *Internal calcification* from an epithelium at sites of muscle attachment. The resulting shell consists of parallel prisms running in growth direction and bears no sculptures on the calcifying surface. The horn-shaped opercula of *Teiichispira* belong in this category.

B *Outside calcification* requires that an epidermal fold or duplicature develop at the distal side of the nail bed. It is brought in contact with the skeleton's outer surface intermittently—either by the fold creeping over it (as presumably in the *Nautilus* jaws) or by retraction of the whole structure into an epithelial pocket (*Turbo* operculum and aptychi). In either case the calcareous layers may bear regular sculptures in standard self-organizing patterns (teeth and ridges in nautilid conchorhynchs and rhyncholites; ribs in *Lamellaptychus;* tubercles in *Granulaptychus;* fingerprint patterns in *Turbo* opercula). The continuity of these patterns is maintained by the structure previously laid down in the shell rather than by the epithelial tissue (see legend to fig. 2).

2. *Shell skeletons.*—The typical mollusc shell is the product of an epithelial duplicature, the mantle, with which it forms a fabricational and functional unit. For this system to work, some modifications of the beak model are necessary.

- The nail bed must be placed at the tip of the epithelial fold (mantle), rather than at its base. This arrangement allows fold and shell to be connected at their free ends, so that calcification can proceed without interruption (but nevertheless rhythmically) in the fluid-filled extrapallial cavity between the fold and the internal shell surface.
- Being placed at the margin of a very soft fold, the leading mantle edge alone can no longer control the regular shape of the shell. This problem is solved by making the organic layer (periostracum) so thin and flexible that it forms the skin of a marginal tube stiffened hydrostatically until it has been reinforced by the calcareous ectostracum. The rounded margins of mollusc shells express this hydrostatic control.

- With general shape control being transferred to the marginal pneu, the soft periostracum can be secondarily modeled into smaller-scale sculptures in the zone of calcification.
- Secondary thickening of the calcareous shell (endostracum) is accomplished by zones of the mantle inside the pallial line of attachment, where contact with the shell is less intimate. Therefore this inner layer generally has a smooth surface (which is not true for brachiopods!).
- A beak mode of internal calcification continues in areas of muscle attachment. The resulting myostracum differs from the surrounding layer by its fibrous structure and sometimes in mineralogy (oysters).

In summary, the inside-out position of organic and calcareous layers suggests that aptychi are beak skeletons that became externally mineralized while being stowed away in an epithelial pocket. From this pocket they could intermittently slide out to function as a nacked lid, not unlike the opercula of modern gastropods. Regular ornamentation of their outer surfaces need not have been functional in the strict sense but can be interpreted as fabricational noise related to the mineralization process.

4. APTYCHUS BIVALVEDNESS

Our interpretation has so far left open one important question: Why are mineralized aptychi always two-valved, whereas a single plate would have better served both a jaw and an opercular function? Accommodation within the shell is no argument, because in "life position" the aptychus remained in the widest part of the body chamber—so it did not have to be folded. Only after death could it fall into the narrow space inside the ventral keel ("normal position").

There can be no doubt that the organic base layer of the aptychus originally extended across the hinge. Otherwise it would be hard to understand why the two elements of isolated aptychi, falling out of drifting shells, remained articulated as they settled on a stagnant sea bottom. It is also likely that the connecting band of conchyolin had the elastic and energy-storing properties of a *diducting* ligament, because (1) isolated aptychi are always sprung open (butterfly preservation) and (2) since muscles inside and in the surrounding buccal sheath could only adduct, so that an antagonistic ligament would have to be an opener, as in bivalves.

The analogy between bivalves and aptychi has its limits, of course. In bivalves the ligament is a non-calcified facies of the calcareous shell and thickens, like the shell, by addition of new layers from inside. In an aptychus, the ligament would primarily thicken from inside, while calcification occurred only on the outside. But does this mean that a cleft remained open between the symphysial facets, or were they also connected by a resilium-like ligament added from the outer side? The abrupt ending of growth layers at the edge of the facet (cross section, fig. 1,K) speaks for the second assumption.

5. FUNCTION OF THE ANAPTYCHUS

So far, our focus has been on the final stage of the evolutionary transformation, the mineralized aptychi. They fit the paradigm of a stiff operculum except for their bivalvedness and probable ligamentary connection. In a formal sense they are also homologous to lower jaws, although the functions of a jaw and an operculum are too far apart to be directly linked by gradual Darwinian transformation. However, in contrast to the transformation of the reptile foreleg into an *Archaeopteryx* wing, the intermediate structure, the *Anaptychus,* is well known (Lehmann 1970, 1990).

Before tackling the crucial question about anaptychus function, we should remember that, in biological context, "function" is always a relative term. In contrast to the parts of a machine, most biological structures play more than one role. Therefore, "change in function" never means radical redesigning, but the gradual gain in relative importance of one function over another in a multifunctional dynamic system. The claws in the *Archaeopteryx* wing tell us that it still served as a foreleg in climbing. I propose that the hinge of a mineralized aptychus corresponds to these claws and that the anaptychus holds the clues to the whole problem.

Anaptychus function can be approached from the two endmembers, the operculum and the jaw. As shown above, the aptychus resembles the *Turbo* operculum with regard to function as well as fabrication but is neither flat on the inside, nor does it become calcified as one piece. Even in the role of an operculum, the outer lamina of the ex-jaw had to conform to the bulbous body of the enclosing buccal mass or pocket. This explains why the aptychi are vaulted; but bivalvedness agrees neither with the jaw nor the operculum model.

Approaching anaptychus function from the other end, the comparison of cephalopod jaws with birds' bills proves to be more than a descriptive metaphor. In fact, the two structures are comparable in many respects. Functionally, both reinforce the opposing sides of the mouth by rigid dermal sheaths. Fabricationally, both consist of nonliving horny material that grows by marginal accretion and are therefore confined to the morphospace of logarithmic spiral growth (Raup, 1966). Also, both have convex outer and concave inner flanks anchored in a "nail bed," where new growth rings are being added.

Biomechanically, however, birds' bills and cephalopod jaws work differently. Bills are parts of bony jaws with joints and lever muscles. In contrast, cephalopod jaws are embedded into the buccal mass, a hollow muscle without rigid purchase or hydrostatic core to work against. Even more strangely, cephalopod jaws have no pivot joints but glide past each other along their wing edges. Assuming that the muscles attached on the inside can open them—where are the closing masseters, strong enough to crush a fish skull? Presumably the masseter function is taken over by circular muscles within the epithelial fold that encloses the whole buccal mass (fig. 1D). If this is the case, adduction may also imply a deformation of the flexible jaw wings.

In standard cephalopod jaws (fig. 1A), the growing margin (that is, the "generating curve" in Raup's terms) is three-dimensional. On the two sides of the beak, corners extend into wings that primarily enhance anchorage within the buccal mass. These wings are longer on the side of the gut, while the outer lamella forms only a short "hood." Also, lateral parts of the hood in the lower jaw are relatively longer, so that they can glide over the outer edges of the upper jaw. As already mentioned, jaws in modern *Nautilus* and in some of its Mesozoic relatives are reinforced by calcite caps (fig. 1B–D), each of which mineralizes as a single piece centered on the jaw tip (Saunders and others, 1978).

In functional beaks, external calcification poses a fabricational problem, since the calcifying tissue would be destroyed in the biting action. The only possibility is that tissue extends over the beak for growth or repair and that the animal cannot bite during these periods. The calcification of *Nautilus* beaks also extends some distance over the horny lamellae—particularly on the gut side—but the shape of the horny parts remains essentially the same as in standard cephalopod jaws.

The horny anaptychus, in contrast, departs so far from the standard cephalopod design that the functional discontinuity must be sought here, rather than at the transition between anaptychi and aptychi.

Interestingly the change from jaw to anaptychus served neither the jaw nor the opercular function:

1. The transformation affects only the lower element, unlike calcification of nautilid beaks.
2. The whole gut part of an anaptychus—that is, the side that would be more directly involved in any kind of biting activity—becomes reduced to a short and soft lamella.
3. At the same time, the outer hood lamella transforms into a broadly curved blade that made Lehmann originally (1972) believe in a shovel function.
4. Hypertrophy of the outer lamella to a size larger than the whole upper jaw was certainly not to strengthen the anchorage of a shovel, whose cutting edge would have been too weak to resist any point force.
5. In fact, the hypertrophied outer lamella (the true anaptychus) was so broad that it could not have been accommodated within the body chamber unless bent into a gutter—the shape in which it was found when preserved in conjunction with the upper jaw and the radula (Lehmann, 1970). On the other hand, the oversized anaptychus is also far from the paradigm of a pure lid fitting the aperture.
6. In jaw pairs, which upon burial were probably still held together by the muscular buccal mass, the lower jaw protrudes rather than occluding.

Lehmann's reconstruction of the ammonite body truly reflects all this. But how could such an animal feed or rather feed better than its ancestors?

A preservational detail may provide the clue to this riddle: isolated anaptychi are never gutter-shaped or laterally compressed but always completely flat! Thus the anaptychus, now being a single lamella of elastic horny material, opened like a spring when it was released from the buccal mass. Accordingly it could also serve as an energy-storing antagonist to the adducting muscles while it was still within the buccal sheath.

Here the argument converges on our previous consideration about the kinetics of calcified aptychi, where the energy-storing elastomere had become concentrated into a narrow ligament. In order to conclude the whole story, we must now consider the other organs involved in cephalopod feeding.

6. OTHER AMMONITE FEEDING STRUCTURES

Presumably the transformation of the lower jaw implied a reduction of aggressive power and the necessity to improve on defensive strategies, such as an operculum. But what happened to the upper jaw? It had lost its antagonist but nevertheless maintained its original size and shape. What was the pincer good for when reduced to only the upper half?

A. Role of the Radula

The transformation described somewhat resembles the bill of a parrot, in which the upper element is greatly enlarged, and the tongue has to some extent taken over the role of the lower beak. Is it possible that the "tongue" of the ammonites, the radula, acted as a similar replacement? From the work of Closs (1967) and Lehmann (1967, 1990) the radula is known in various ammonoid genera. It differs little from the radulae of other cephalopods, but at least it had suffered no reduction and was therefore available as a substitute antagonist to the upper beak.

B. What Kind of Tentacles?

Textbooks are full of lively ammonite reconstructions, but most are little more than an ammonite shell with either a squid, an *Octopus,* or a *Nautilus* stuffed into it. The critical question concerns the function of the arms in food-gathering.

Here we are thrown back on speculation. Reported arm impressions have turned out to be either radial worm burrows, roll marks of broken shells (Kolb, 1967; Trusheim, 1934; see Seilacher, 1963) or compactional fracture patterns of body chambers (Zeiss, 1969). The expectation has always been that ammonites had fleshy arms, rather than numerous small tentacles as in *Nautilus.* Small tentacles would solve the preservational dilemma, however, as they would have been too delicate to leave recognizable impressions even in the Solnhofen lime muds, where coleoid arms are clearly recorded.

If ammonites could afford to reduce their biting equipment, why should they retain muscular arms like their predatory relatives? Several indirect arguments speak for their microphagous habit: (1) incapability of fast swimming, but specialization of the diving apparatus (including fluted septa); (2) large population densities compared with associated nautiloid species; (3) lappets in adult shell apertures; (4) the tendency of heteromorphs to turn their aperture *up;* (5) the dramatic demise of the whole group during the end-Cretaceous extinction.

In their latest reconstruction, Lehmann and Kulicki (1990) assumed an arrangement of the ammonite arms not as a closed ring around the mouth but as a ventral horse shoe. I would add that this half-ring was retractible and fringed by delicate tentacles (perhaps homologous to buccal papillae rather than arms), which were not only supported, but also passively moved, by the now flexible lower jaw. This would mean that in the expanded animal the edge of the anaptychus "shovel" was completely covered by soft parts and did emerge only when the fringe of tentacles was retracted for protection. From this arrangement, the opercular function of the aptychus with all necessary improvements (rotation of buccal mass, calcification in a shape fitting the aperture; Lehmann and Kulicki, 1990) could naturally follow.

In this model, the anaptychus had already lost the jaw function. Its elastic deformability did not only allow accommodation of the oversized structure into the shell but enabled the former jaw to take over a new, distinctive role in the processes of food catching. Whether the antagonistic interaction of adducting muscles and anaptychus spring has been used as a continuous pump or for spontaneous suction-feeding must remain an open question, but the fact that flexibility was maintained also in the calcareous aptychus attests for the continued importance of this feeding apparatus, along with its emerging secondary function as an operculum.

EPILOGUE

In the last century, evolutionary theory freed paleontologists from being the stratigraphic handmaidens of applied geology (for which they are still useful, as I happily realize on occasion) and the chroniclers of creation. After paleontology became more biological, however, we have for too long continued to adhere to an unnecessarily narrow uniformitarianism. As Stephen J. Gould (1989) has eloquently shown, the history of life on this planet is not only a prelude to our present world. It abounds in evolutionary experiments that failed not for their inadequateness but for bad luck in the face of extinction.

In this paper I have tried to analyze one such lost construction without shoehorning it into the anatomy of surviving relatives. This is a risky approach, but it gains rigor if we keep testing our tentative models against the rules of biomechanics, constructional morphology, structural transformation, and taphonomy. In every corner of paleontology we may thus discover things like dinosaurs, the strange creatures that once attracted John and yours sincerely to this fascinating field!

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