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Aberrant structure of the statolith postnuclear zone in the squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae)

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Aberrant statolith microstructure was observed in an immature female of the squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) caught in the Moroccan shelf. The paralarval statolith, (a central part of adult statolith that developed at paralarval stage), showed the first 12 growth increments outside the nucleus was reversed to the posterior side of the adult statolith, and its main axis was turned perpendicularly to the main axis of the adult statolith. However, further statolith growth followed the common pattern, and the statolith acquired its normal shape at the level of 55–60 growth increments. Such aberrance in a direction of the paralarval statolith can be explained by its complete detachment from the *macula statica princeps* (MSP) during strong impact to the head of the paralarva (e.g. by a predator) and further occasional re-attachment of the statolith to the MSP again.

Statoliths (calcareous mineralized structures) are located in the equilibrium organs (statocysts) and are responsible for determining mainly linear accelerations during movement of coleoid cephalopods (Budelmann, 1988). The important role of the statoliths in cephalopod orientation was shown during cultivation of octopuses, squid and cuttlefish in recirculating water systems. A considerable number of their hatchlings had unusual behaviour which was characterized by spinning or somersaulting in water (Colmers et al., 1984). These 'spinners' either lack or have reduced statoliths. Thus, the absence or inappropriate development of the statoliths led to disorientation and subsequent death of such 'spinner' hatchlings (Hanlon et al., 1989).

Squid statoliths bear growth increments within their microstructure. The increments start radiating from a rounded nucleus, which is a 'protostatolith' (i.e. statolith of the hatchling) in ommastrephid squid and formed during embryogenesis in loliginid squid (for review see Lipinski et al., 1991). Since the statolith microstructure is translucent, it is possible to examine the shape of the paralarval statolith and its growth in the statoliths of adult animals. As a rule, orientation of the statolith remains unchanged between paralarval and adult stages, i.e. the rostrum is always on the ventral part, and the dorsal dome develops on the dorsal part of the statolith (Lipinski et al., 1991). Although the direction of the maximum statolith growth (seen as the widest growth increments) slightly changes during ontogenesis, the general pattern of growth (i.e. maximum growth of the dorsal dome is observed dorsalwards) does not change significantly (Lipinski et al., 1991).

The present study attempted to show how a very rare event in life of a squid paralarva (displacement and re-attachment of the statolith in the statocyst) was registered within the statolith microstructure.

The abnormal microstructure was described in the left statolith (the right one was lost during preparation) of an immature female of *Todarodes sagittatus* (182 mm mantle length, ML) which was caught on the West African shelf (south Morocco) during the experimental survey of the RV 'Bakhchisarai' on demersal fishes and cephalopods conducted by AtlantNIRO in September 1987. Terminology of the statolith parts and microstructure is after Clarke (1978) and Lipinski et al. (1991).

The statolith had a very particular development of the inner postnuclear zone (Figure 1A–C). The position of the statolith having the first 12 growth increments (referred here as 'paralarval statolith') was very different from the usual pattern (Figure 1D). This paralarval statolith was turned perpendicularly to the main axis of the statolith growth, and its growth increments were the widest in the direction to the tip of the rostral angle (Figure 1C). The tip of the rostral primordium of the paralarval statolith was pointed in the direction of the dorsal dome of the adult statolith, and its dorsal dome was already somewhat developed and inclined to the anterior part of the wing of the adult statolith. However, the rest of the growth increments (N=21) in the postnuclear zone had maximum width in the direction of the lateral dome of the adult statolith, as in the normal statolith of *T. sagittatus* (Figure 1D). As a result, the whole postnuclear zone had the shape of a wide oval, with the main growth axis still perpendicular to the main axis of the adult statolith growth (Figure 1A,B). The statolith acquired the normal shape after approximately 55–60 growth increments (=days) from the nucleus (Figure 1D). The adult statolith of this female looked absolutely normal and had the same parts as the normal statoliths of other *T. sagittatus* (Figure 1D).

It is possible to suggest an hypothesis explaining such a strange development of the statolith postnuclear zone. On one hand, the paralarval statolith could be displaced and turned at an angle of 90° on the *macula statica princeps* (MSP) (but did not detach from it). Statoliths of the ommastrephid paralarvae at this phase of development do not yet have the wing, which serves mainly to attach the statolith onto the MSP (Morris & Aldrich, 1984). Therefore, they could be easily displaced on the MSP during the sudden external impact to the head of the paralarva (for example, during predator attack) than the statoliths of adult squid. In this case, the anterior surface of the paralarval statolith should coincide with the anterior surface of the adult statolith, whereas the axes of maximum growth should be different.

However, positions of both the rostrum and dorsal dome of the paralarval statolith showed, that its anterior surface coincide with posterior surface of the adult statolith, i.e. paralarval statolith was over-turned on the MSP. This could have happened only

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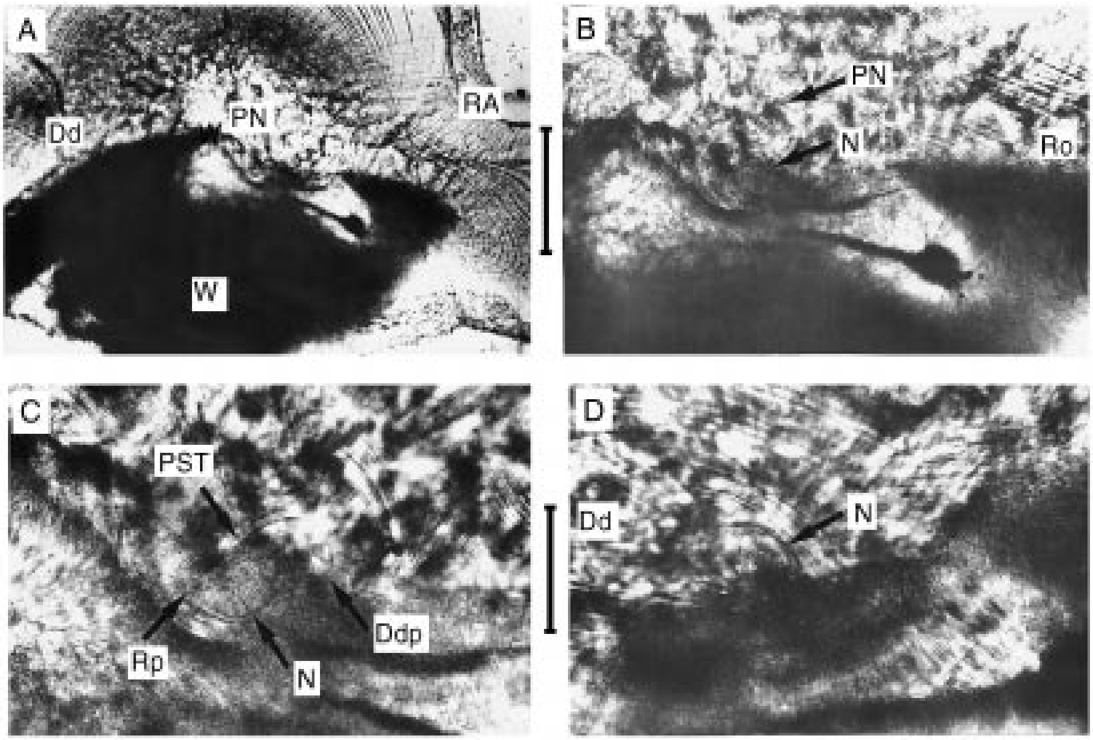

Figure 1. Statolith with aberrant postnuclear zone (A–C) from an immature female (182 mm ML) and statolith with common postnuclear zone (D) from another immature female (181 mm ML) of the squid *Todarodes sagittatus*. (A) General view of the aberrant statolith; (B) postnuclear zone of the aberrant statolith; (C) postlarval over-turned statolith within postnuclear zone; (D) postnuclear zone of common statolith. PN, postnuclear zone; N, nucleus; RA, rostral angle; Ro, rostrum; Dd, dorsal dome, W, wing; PST, paralarval statolith; Rp, rostrum of paralarval statolith; Ddp, dorsal dome of paralarval statolith. Scale bar: A, 200 μm; B, D, 100 μm; C, 50 μm.

in case of complete detachment of the paralarval statolith from the MSP and its re-attachment to the MSP, but in an incorrect position. Nevertheless, it is possible to see in the statolith section that such incorrect attachment did not interfere with further growth of the paralarval statolith. Moreover, further growth did not follow the growth axes of the re-attached statolith, but was in the correct direction, resulting in the gradual appearance of the normal statolith shape 40–50 d from the dramatic moment of detachment.

Aberrant development of the statolith microstructure has been shown previously in a specimen of *Loligo vulgaris*, which had two foci in the statolith nucleus as a result of subdivision of the statolith primordium in embryogenesis (Arkhipkin, 1995). Sometimes (but very seldom) there were observed additional centres of statolith growth outside the nucleus (*Dosidicus gigas*; Arkhipkin & Murzov, 1986). In all these cases (including that of the present report), the further statolith growth completely eliminated such aberrances in the statolith shape, which however remained registered within its microstructure enabling estimation of its occurrence. Results show that sometimes the ‘spinner’ paralarvae with detached statoliths (probably during unsuccessful predator attack) can recover themselves completely but only in cases where the statolith reattaches again to the MSP by an unknown mechanism. Occurrence of such an event is probably extraordinarily rare, as it is the first description of such an aberrance despite thousands of statoliths of various squid species already studied (Jackson, 1994; A.I.A. & A.N.G., unpublished data).

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