Coleoid cephalopods through time (Warnke K., Keupp H., Boletzky S. v., eds)

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POTENTIAL OF STATOLITHS FOR INTERPRETING COLEOID EVOLUTION: A BRIEF REVIEW

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ABSTRACT

The occurrence of statoliths of cephalopods from both living and fossil species shows great promise for future studies on coleoid evolution. The possible relationship between statolith shape and body movements of living species is discussed and may enable prediction of form and way of life of those early coleoids which have no other fossilised remains. An objective method for comparing statolith and body form by computer is described. Presence of growth rings in fossil statoliths are probably equivalent to those in living species and may reasonably be interpreted to have been laid down daily. The extent of variation in shape in living species permits an evaluation of variation in Jurassic statoliths and three clearly different species are illustrated.

INTRODUCTION

Statoliths are small, hard, aragonitic stones which lie in the fluid filled cavities or *statocysts* within the cartilaginous skulls of all living and probably all fossil members of the Coleoidea (Figs 1, 2; Clarke 1978). Although some of the features described are missing in some species or in some fossilised statoliths, there is usually no doubt from the detailed shape, if fossils are statoliths. Their aragonitic nature makes their occurrence with fish otoliths, of the same composition, most likely. The largest statoliths are about 3.5 mm in length but fossil examples of less than 0.1mm have easily been recognised.

In living coleoids they have become important in the study of growth. Many statoliths have been found in North American and European fossil deposits (Clarke & Fitch 1979, Clarke & Maddock 1988 a, b, Clarke *et al.* 1980b). Here, the potential of statoliths for the study of fossil coleoids is outlined and discussed.

MATERIAL AND METHODS

Statoliths vary in shape considerably between species of teuthoids (Fig. 3). Octopods also have a variation on a limpet-like form (Fig. 4). As there is some intraspecific variation in the form of statoliths, comparisons between species were, at first, described by making numerous linear measurements (Fig. 5. Clarke & Fitch 1979, Clarke *et al.* 1980a). For more detailed comparisons between 'living' and fossil statoliths the measurements were subjected to principal component analysis (PCA) and multiple discriminant analysis (MDA) (Fig. 6; Clarke *et al.* 1980a, Clarke & Maddock 1988 a, b). Linear measurements of a small, three-dimensional object like a statolith can involve subjective decisions in choosing the 'end points' and in manipulating the microscope. This possible source of inaccuracies were later overcome by making tracings of several outlines of different views and parts of views (lateral, anterior, ventral, lateral dome, dorsal dome, wing) with a camera lucida (Fig. 7). The tracings were then placed in a carefully defined orientation on a computer digitising tablet and each view, or part of view, was traced round so that the tablet, for each view, measured area, perimeter length, the greatest length from the starting point and the length and width relative to the axis of the tablet. Thus, 30 objectively selected points were measured for each statolith.

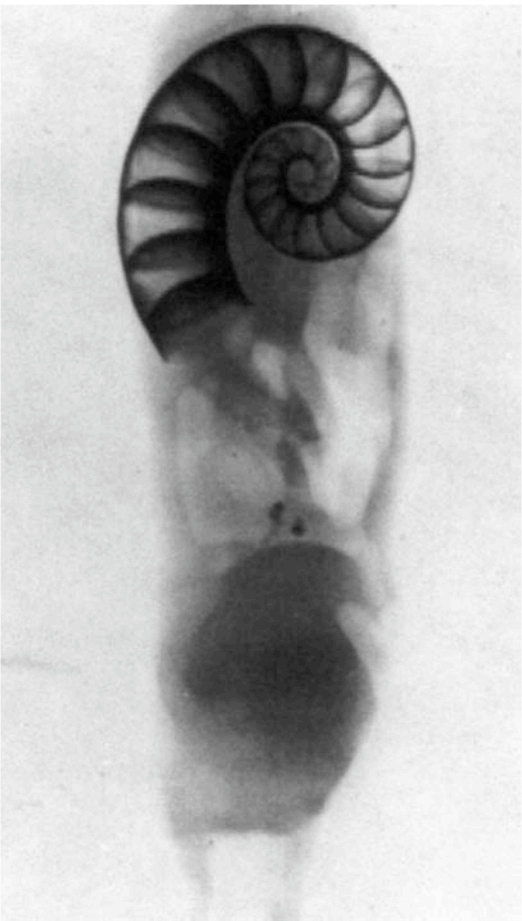


Fig. 1 *Spirula spirula*. X-ray showing the paired statoliths in the cephalic cartilage. Dorsal mantle length = 4 cm

Measurements were 'normalised' for size by division by the total length, the results were subjected to PCA and MDA (Clarke *et al.* 1980a, Clarke & Maddock 1988) and then plotted as in the analysis of loliginid statoliths in Fig. 8. Each group is positioned at its centroid and its standard deviation on each axis is used to plot an ellipse. An indication of the position on the third axis is given by the overlap of the ellipses, which are viewed as if from the positive side of axis 3, with a dashed outline signifying a negative score. In order to test the method a comparison was made between the MDA results obtained from using the linear measurements and those obtained from using the digitised tracings of loliginid species, both living and fossil. This showed clearly that discrimination of different species was much better when the digitised method was used.

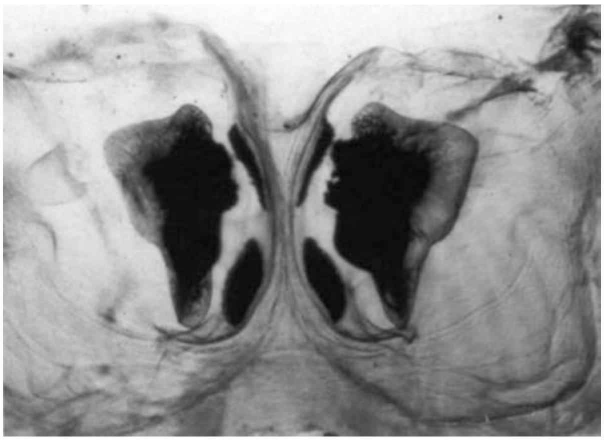


Fig. 2 Anterior view of statoliths of *Loligo forbesi* in situ within the cephalic cartilage. Statolith length = 2.5 mm

Inshore Coleoidea

All fossil statoliths found so far are from continental shelf, neritic, shallow water deposits. From the distribution of living species one might expect the commonest fossil statoliths to belong to the families Octopodidae, Sepiidae, Sepiolidae and Loliginidae. It is probably only an indication of the early stage in such investigations that only the Loliginidae of these four families have been described so far. Another contributory factor is that more fossil statoliths have been described from North America than from Europe and one would not expect sepiid statoliths in North American collections, to judge from present day distributions. There is little doubt that more rigourous searching will eventually bring to light fossil statoliths of members of the Octopodidae, Sepiolidae and Sepiidae in European seas and the former two in North American seas. The limpet shape of the octopodid statolith (Fig. 4), the globular form of the lateral dome in the sepiids (Fig. 9) and sepiolids and the triangular or pointed form of the lateral dome in the loliginids (Fig. 10) make their identification to family relatively easy.

The oegopsids which regularly come onto the continental shelf in Europe are the ommastrephids *Todarodes sagittatus*, *Todaropsis eblanae* and *Illex coindeti.* Fossil statoliths of these have not yet been found in North America. The only oegopsid coming on to the shelf regularly on the East coast is the ommastrephid *Illex illecebrosus* and, on the West coast, are the ommastrephid *Dosidicus gigas* and the onychoteuthid *Moroteuthis robusta.* While fossil *Illex*

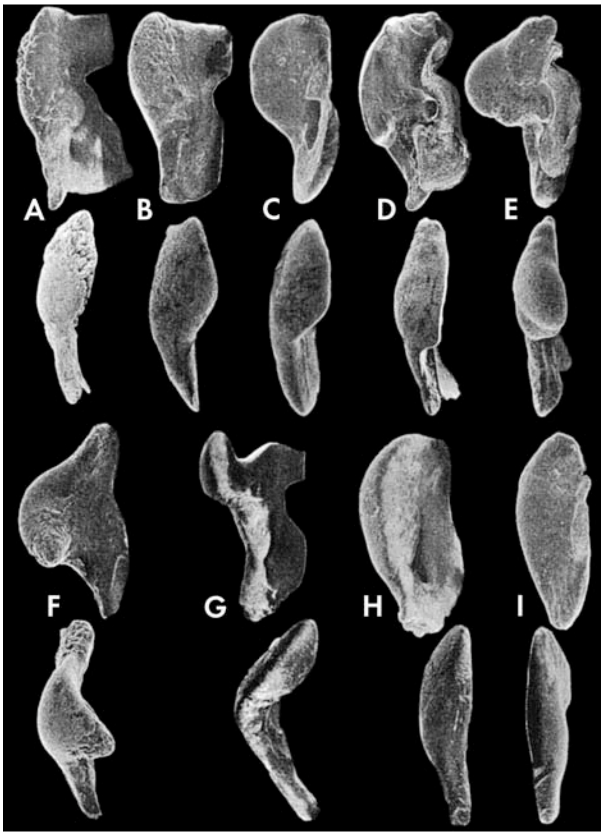
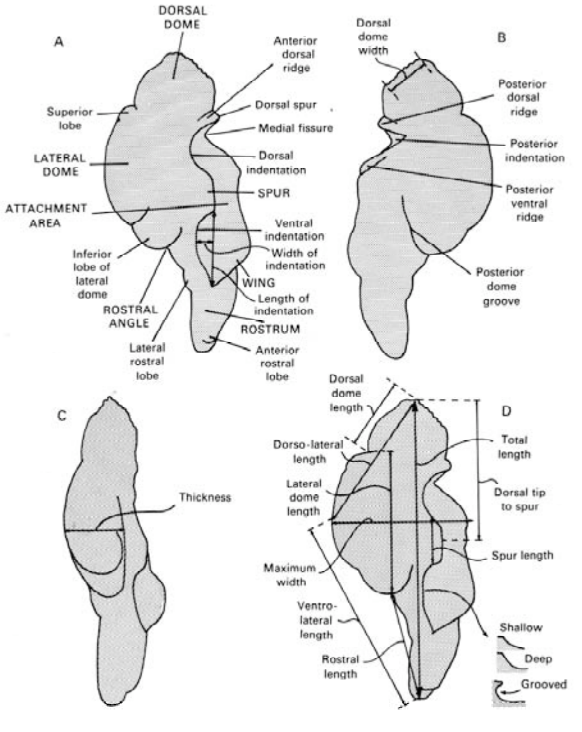


Fig. 3 Anterior (upper) and lateral (lower) views of statoliths of nine teuthoids (from Clarke 1978). **A**, *Ommastrephes caroli* (Furtado), statolith total length (STL) = 1.37 mm; **B**, *Mastigotheutis* sp., STL = 0.63 mm; **C**, *Taonius megalops* (Prosch), STL = 0.72 mm; **D**, *Nototodarus sloani* (Gray), STL = 1.26 mm; **E**, *Todarodes sagittatus* (Lamarck), STL = 1.82 mm; **F**, *Pyrotheutis margaritifera* (Rüppell), STL = 0.58 mm; **G**, *Histiotheutis bonellii* Férussac, STL = 0.97 mm; **H**, *Abraliopsis* sp., STL = 0.48 mm; **I**, Helicocranchia pfefferi Massy, STL = 0.75 mm.



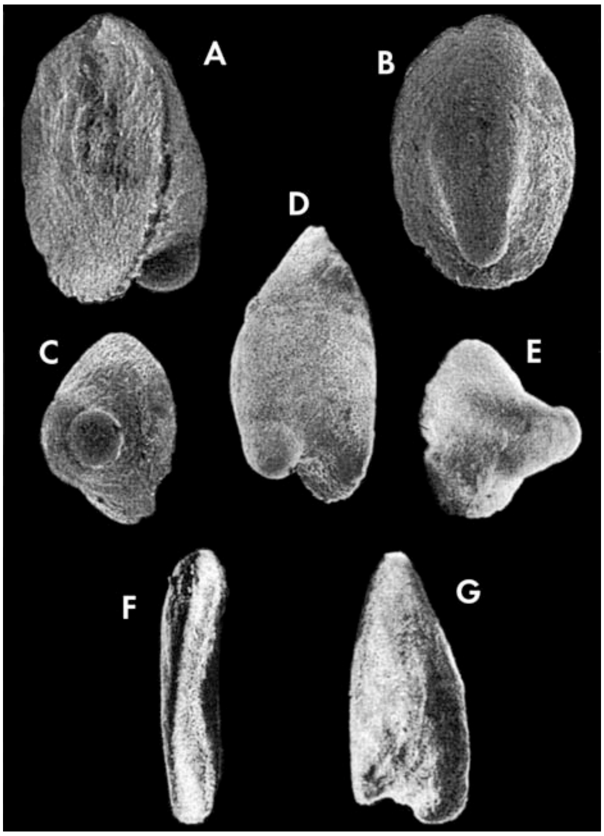


Fig. 4 *A - E*, statoliths of *Eledone cirrosa* (length = 1.74 mm), *F*, *Eledonella pygmaea* (length = 0,42 mm)*; G*, *Benthoctopus* sp. (length = 0.31 mm). **A**, Anterolateral view; **B**, posterior view; **C**, ventral view; **D**, medial view. **E**, dorsal view. **F**, view uncertain. **G**, lateral view (from Clarke 1978)

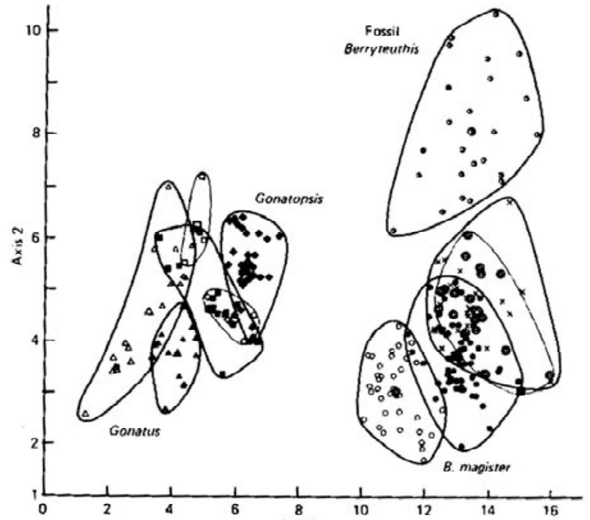


Fig. 6 Multiple discriminant analysis of 11 groups of four genera in the family Gonatidae (from Clarke *et al.* 1980)

Fig. 5 Diagrams of a generalised teuthoid right statolith showing dimensions and terms used in descriptions. **A**, view of anterior side, **B**, view of posterior side. **C**, view of lateral side. **D**, view of anterior side (from Clarke 1978)

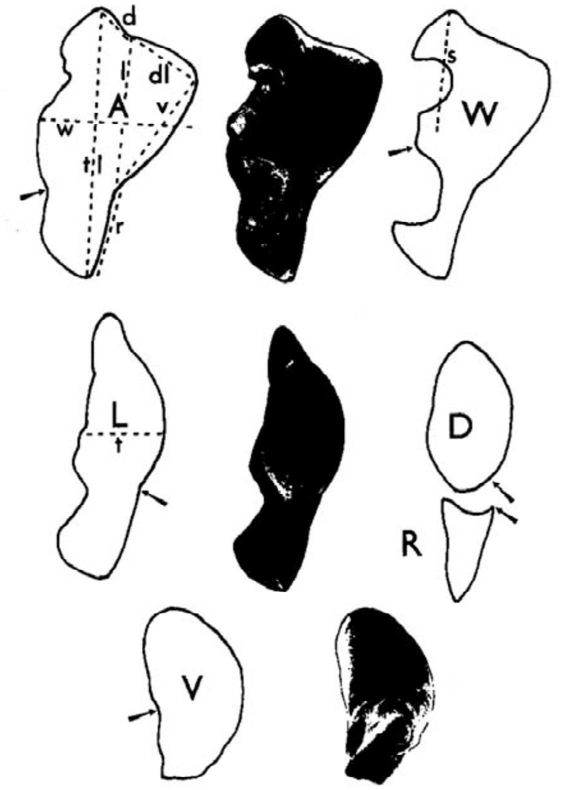


Fig. 7 Left statolith of a *Loligo* species showing photographs of three views and the five tracings used in the digitizer analysis. Arrows indicate the points at which tracings were started, (A, W) anterior views; (L, D, R) lateral views; (V) ventral (from Clarke 1978)

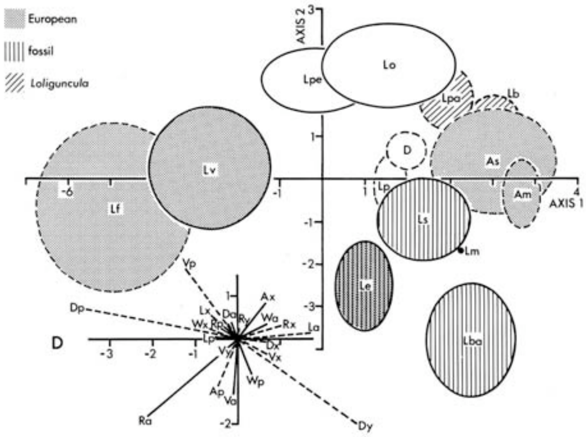


Fig. 8 Results of a multiple discriminant analysis of digitized dimensions of loliginid statoliths. See text for explanation. A. As, *Alloteuthis subulata* (No, of statoliths used = 61); Am, *Alloteuthis media* (6); Lb, *Lolliguncula brevis* (12); Lpa, *Lolliguncula panamensis* (3); Lv, *Loligo vulgaris* (52); Lf, *Loligo forbesi* (77); Lpe, *Loligo pealei* (45); L.p, *Loligo plei* (4); Lo, *Loligo opalescens* (14); Lba, Loligo *barkeri* (30); Ls, *Loligo stillmani* (18); Ie, *Loligo* sp. European fossil (6); Lm, *Loligo mississippiensis* (1); D, *Doryteuthis bleekeri* (3) (from Clarke & Maddock 1988a)

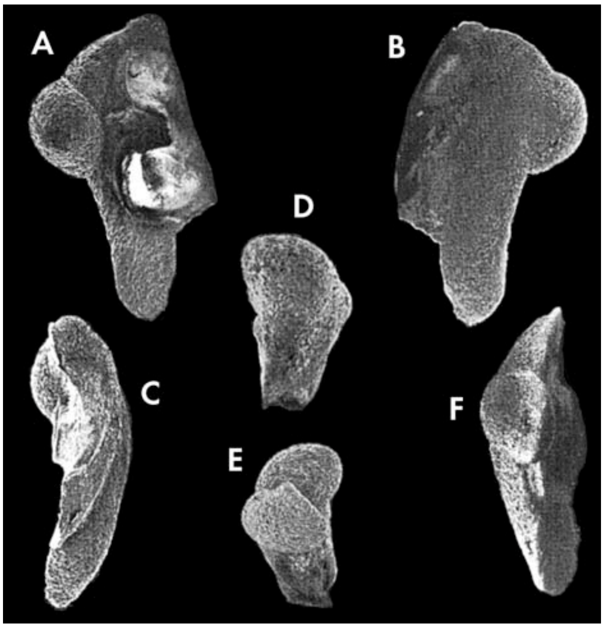


Fig. 9 Right statolith of *Sepia officinalis*, views of (**A**) anterior side, (**B**) posterior side. (**C**) medial side. (**D**) dorsal side. (**E**) ventral side, (**F**) lateral side (from Clarke 1978)

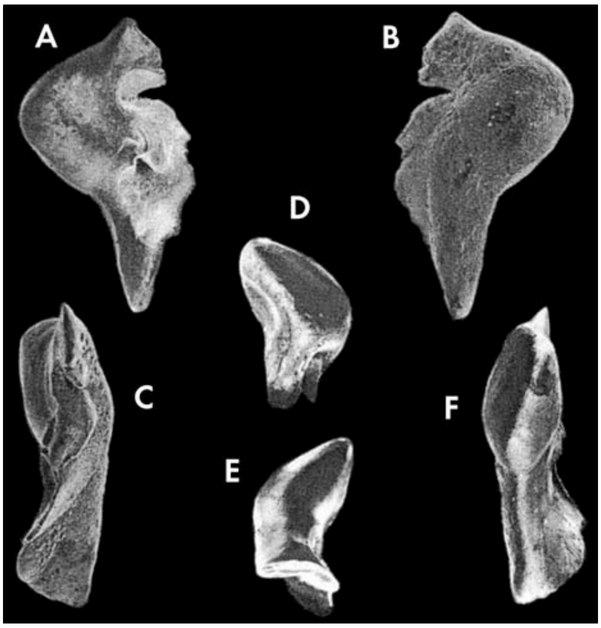


Fig. 10 Right statolith of *Loligo forbesi* (length = 2.0mm) views of (**A**) anterior side, (**B**) posterior side. (**C**) medial side. (**D**) dorsal side. (**E**) ventral side, (**F**) lateral side (from Clarke 1978)

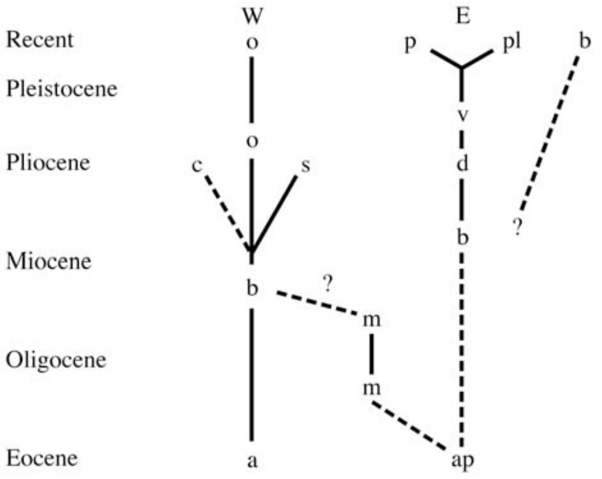


Fig. 11 The possible evolution of Cenozoic loliginids on the western (W) and eastern (E) sides of North America. Dashed lines are very tentative; solid lines are less tentative. (L, M, E indicate late, middle and early). a, *Loligo* sp.A; ap, *L.applegatei*.; m, *L.mississippiensis*; o, *L.opalescens*; p. *L.pealei*; b, *Lolliguncula brevis*; c, *Loligo* sp.C; s, *L.stillmani*; v, *L.valeriae*; d, *Loligo* sp.D; b, *Loligo* sp.B (from Clarke & Maddock 1988a)

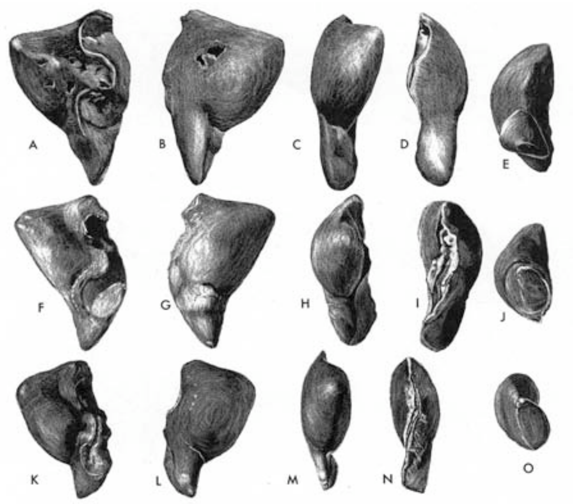


Fig. 12 Right statoliths of three species of fossil *Loligo*. **A - E** *Loligo applegatei* (length= 1.45mm); **A**, anterior view; **B**, posterior ; **C**, lateral ; **D**, medial; **E**, ventral; **F - J**, the same views of *L.mississippiensis* from Chipola farm (= 1.32 mm); **K-O**, same views of *L.valeriae* (=1.19 mm) (from Clarke & Fitch 1979)

statoliths have not yet been recorded, fossil statoliths close in form to *Dosidicus gigas* and to *Moroteuthis robusta* have been described and are considered to belong in the same genera (Clarke & Fitch 1979). Fossil statoliths of two other genera were found in californian deposits which would not be expected from present day distributions. The gonatid *Berryteuthis magister* is a squid which moves on to the continental shelf seasonally but is found further North. The fossils are certainly cogeneric. The ommastrephid *Sthenoteuthis (= Symplectoteuthis) oualaniensis* is normally entirely oceanic and does not stray on to the continental slope and it was surprising to find a close relative, probably of the same genus, in the same fossil deposit as a *Loligo* species.

Cenozoic Statoliths

North America

Twelve of over thirty deposits in North America sampled by John Fitch yielded fossil statoliths (Clarke & Fitch 1979) and these comprised samples from the Middle Eocene to the Early Pleistocene. The loliginid statoliths of the collection are well differentiated back to the Middle Eocene and have all been included in the genus *Loligo*. Eleven probable *Loligo* species were recognised and something of their possible evolutionary relationships could be concluded from their overall shape (Fig. 11). For example, *Loligo applegatei* from the Middle Eocene has an unusually large lateral dome (Fig. 12) which may have become flattened on its inferior side to give rise to *L. mississippiensis* and become much reduced and less pointed to give rise to *L. valeriae* and two other *Loligo* species very similar in shape. *L. valeriae* has the inferior side of the lateral dome enlarged in a manner similar to the living *L. pealei* and *L. plei*.

Comparison of loliginids of North America and Europe

To investigate relationships between fossil and living loliginid statoliths of North America and Europe, digitised camera lucida drawings analysed by MDA proved invaluable (Fig. 8). This showed that the fossil *Loligo* of Europe is closer to the living european species than to the american species and the fossils of North America are closer to the living species of that continent than to the european species (Fig. 10).

From this figure it is seen that all but one of the *Loligo* species are positive on axis three while the other loliginid genera, *Alloteuthis, Lolliguncula* and *Doryteuthis* are all negative on that axis. The exception

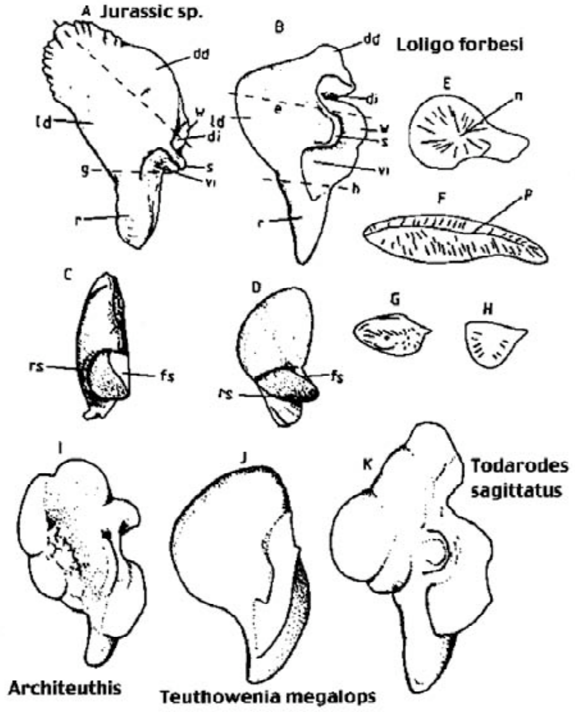


Fig. 13 A Jurassic right statolith (**A**, **C**, **F**, **H**) compared with a right statolith from *Loligo forbesi* (**B**, **D**, **E**, **G**) and three other species. (**A**, **B**, **I-K**) anterior views; (**E**, **F, G - K**) ventral views. (**E**, **F**) views of sections at points indicated by arrows (from Clarke *et al.* 1980a**)**

is *L. plei*, which has until recently, been considered as *Doryteuthis* and whose closeness to the genus is established. The fossil European Early Miocene *Loligo* lies between the North American fossil species and the living European *Loligo* species. It appears to be closest to *L. stillmani* and it is interesting that this is from the West Coast. *L. stillmani* however, lived later and possibly both species came from *L. mississippiensis*.

Figure 8D shows the weightings, by the length of line, of the 24 respective measurements on the first two axes (again a dashed line indicates a negative value on axis 3). Lower case letters refer to the measurement and capital letters to the view. From this the most important factors causing separation are the dome perimeter (Dp) and dome length (Dy) which spread the groups to left and right, the rostral area (Ra) and whole statolith width (Ax) which spread the groups diagonally from bottom left to top right and the ventral statolith perimeter (Vp) combined with the dome length (Dy) which spread the groups diagonally from bottom right to top left.

Some confidence can be attached to this analysis because of the grouping of cogeneric species. All but two *Loligo* species are positive and the members of the other genera are all negative. One of the exceptions (*L. plei*) is known to be very close to *Doryteuthis*. The European and the North American species are separate and separated from the fossils. On the other hand, *Alloteuthis* species, *Lolliguncula* species and *Doryteuthis* species (assuming *D. plei* should be grouped here) are all negative and each form groups. The value of such an analysis of such complicated shapes is shown by the fact that the standard deviation ellipses reflect a very big and overlapping variation in form but still the analysis indicates rational relationships in conformity to what is known from the living species.

Comparison of Berryteuthis *fossils with* B. magister

An MDA of the linear measurements of the statoliths of members of the Gonatidae (Fig. 6, Clarke *et al.* 1980a) showed that the Pliocene *Berryteuthis* statoliths are congeneric with but a different species from *B. magister* (Berry, 1913); it was not named because of the existance of another species, *B. anonychus* Pearcy and Voss, 1963 from which statoliths had not been examined. [**Note**. In Clarke and Fitch (1979) a manuscript name, *Statiloteuthis enigmaticus*, was inadvertently left on plate 55 and on Textfig. 10 instead of *Berryteuthis* sp. which should have been substituted for it.]. As was pointed out, *Berryteuthis* statoliths bore some strong resemblances to those of *Sepia* and it was suggested that these might have functional significance, in view of the distant relationship of the two genera. New light has recently been thrown on this similarity and will be discussed below.

Jurassic Statoliths

The detailed description of several thousand statoliths, which have been identified from Jurassic deposits of Southern England by the author, has not yet been published except for a brief comparison of a typical example with the statolith of a living teuthoid, *Loligo forbesi* (Clarke & Maddock 1988). These fossils are very different in shape from the statoliths of other living teuthoids (Fig. 13) but have the same component parts and are much closer to them than to any fish otolith or to octopod or sepioid statoliths. The fossil

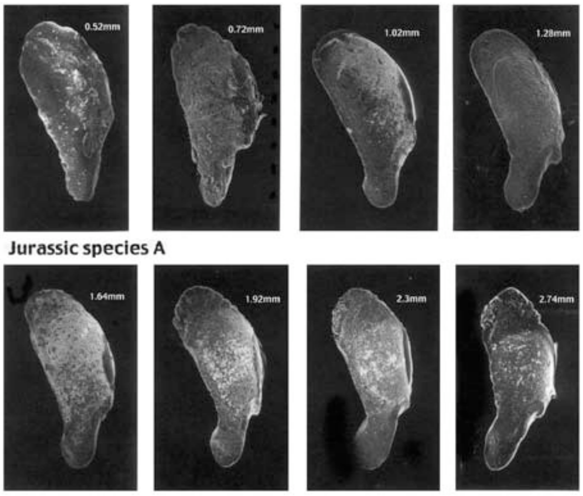


Fig. 14 Jurassic species A. Change in shape during growth showing Total lengths

possesses a very narrow, elongated spur, a rostrum which is shaped similarly to that of *Loligo*, particularly in its ventral view (cf. Fig. 13 C with D) and a lateral dome (ld). It differs largely in being thinner (cf. E, F) and having a ventrally curving edge where the dorsal dome (dd) is developed in many living teuthoids. Jurassic statoliths group into at least three types, which are separated, to judge from the differences between statoliths of living species, by differences of generic or family rank. Type A, which possibly contains more than one genus changes in shape as it grows (Fig. 14) and the largest have folds or crenelations round the rim of the lateral dome (Fig. 13). Type B (Fig. 15) has a more pointed lateral dome and a much narrower rostrum. Type C is much smoother and the rostrum is at less of an angle to and less clearly separate from the lateral dome.

At present, although not certain, it seems likely that these are statoliths of early teuthoids which have left no other fossilised remains and not statoliths of belemnites which have left guards in the same strata. This can only be disproved by finding a statolith in association with a Jurassic belemnite in good condition. Unfortunately examination of most of the belemnoids from the Oxford Clay has not produced a single statolith.

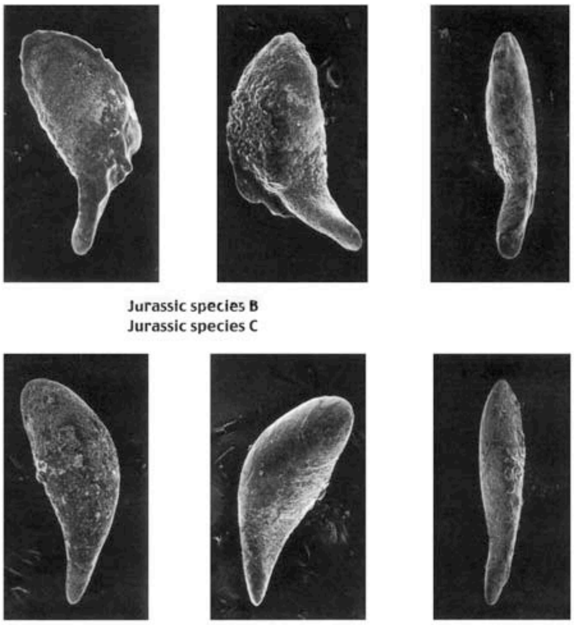


Fig. 15 Three views of Jurassic species B and C

Biological conclusions from fossilised statoliths

Numbers relative to fish

The great effort needed to make this collection can be imagined from the fact that over 4500 kg. of deposit were sifted to provide only 467 statoliths - only 0.1 statoliths per kg. However, the same samples yielded over 164,000 fish otoliths, a ratio of 351 otoliths to every statolith (with a mean for the samples of 1:279 and a range of ratios of 1:20 to 1:1300). The question arises whether this reflects a true numerical relationship between fish and teuthoids in the sea at the North American sites during the times sampled. Two factors are probably involved in lowering the numbers of statoliths in the samples. First, the statoliths are much smaller than many otoliths and the 0.5 mm square mesh used for sieving them from the mud would have allowed statoliths but not many otoliths to pass through this mesh. Secondly, living cephalopods on the continental shelves often form large aggregations during spawning followed by death and, unless a deposit encompassed such an area, most of the mature sized cephalopods might well seem sparse compared to fish. If spawning areas come to light in fossil deposits, far more statoliths than otoliths should be found.

The relative numbers in Jurassic beds compared with teleost otoliths might be biassed by their smaller size and less robust nature but they do generally outnumber the fish otoliths (mean for 6 sites = 7.8:1

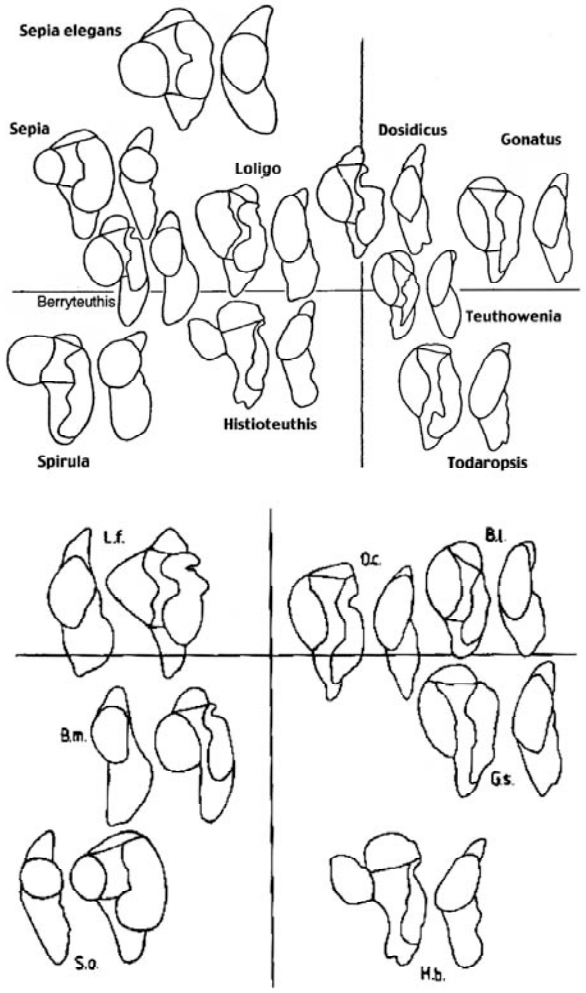


Fig. 16 Outlines of species placed in approximate relative positions according to MDA (top) and PCA (bottom) analyses of digitised tracings of their component parts and views

and range 1:2 - 45:1). This could reflect a change since the Jurassic from the numerical dominance of cephalopods to the dominance of teleost fish in the continental shelf seas.

Although the Jurassic beds contained numerous cephalopod hooks, they contained fewer guards than the number of statoliths would lead one to expect if the statoliths came from belemnoids. However, belemnoid shells were buoyant and may have floated in surface currents to other localities, while the dense statoliths would fall straight to the sea bottom when the flesh disintegrated after death.

Growth

During growth, statoliths of many living teuthoids and sepioids have been shown to lay down regular rings which, in several species, are known to average one a day. Such daily rings have not yet been demonstrated in Cenozoic statoliths although they might be expected. The Jurassic statoliths, however, easily break along a central fracture of the lateral dome (Fig. 17 middle), and the surface exposed is crossed by a series of minute growth ridges which run parallel to the lateral and dorso-medial rims of the lateral dome and the curved edge where there is a dorsal dome in living species. These ridges are in a fracture zone analogous to the more restricted nucleus of a living statolith and may not be analogous to the growth rings in living teuthoids. The largest fossil statoliths have about 100 ridges which would suggest a much faster growth than found in living squids of the same size, unless each ridge represents 3 - 4 days of growth. Other growth rings, which are more likely to be analogous to those in living statoliths, are present in the crystals radiating from the fracture zone (Fig. 17 top and bottom).

Size of teuthoids

In living cephalopod species size of the statolith is often correlated with length and weight (Guerra & Sanchez 1985). Similarly, the statolith length of *Berryteuthis magister* is correlated with dorsal mantle length (Clarke *et al.* 1980a) and *B. magister* had peaks of 2.4 - 2.65 mm representing dorsal mantle lengths of 160-220 mm and a maximum of 3.0 mm representing a DML of 305 mm. The adults of the fossil *Berryteuthis* were larger than adults of *B. magister*. The fossils had a peak at 2.8 mm possibly representing a mantle length of 300 mm and a maximum of 3.3 mm representing a mantle of 370 mm. Although size of statoliths within genera can be roughly related to size of the animal it varies markedly between genera and families, members of the Cranchiidae, for instance, have very small statoliths while Pterygioteuthidae have large statoliths for their size. Thus, it is not possible to estimate the size of the Jurassic coleoids, for example, from the statoliths except to say that they are much the same size as those from living species.

Buoyancy

All the Cenozoic statoliths examined so far, except for *Berryteuthis* sp., are from squids having negative buoyancy and therefore needing to swim to stay in midwater. *Berryteuthis* is probably neutrally buoyant provided by special oils as in *Gonatus fabricii* (Clarke *et al.* 1979). The living species of coleoids with gas-filled shells (*Sepia* and *Spirula*) have globular lateral domes, large, broad spurs and long rostra (Figs 9, 16) which may suggest that the fossil Jurassic statoliths do not come from animals with gas-filled shells like the belemnoids but are more likely to be from early teuthoids. This reasoning is made more complicated by the similarity between *Berryteuthis* and *Sepia* which was shown by both multiple discriminant analysis and principle components analysis (Clarke & Maddock 1988b). The similarity cannot be put down to neutral buoyancy since very diverse statolith shapes are present in other neutrally buoyant forms including other members of the Gonatidae. As *Berryteuthis* is only very distant in relationship to *Sepia*, the question must arise whether there is some feature in its way of life or behaviour which might suggest a cause for this similarity. Until recently, the only suggestion which could be made is that it has a similar life style in living close to the bottom and on the Continental shelf for some of its life and it has long fins which may provide similar body movements to *Sepia*.

DISCUSSION

Recent work by Arkhipkin and Bizikov (1998, 2000) on living teuthoids, including *Berryteuthis*, strongly suggests, counter to previous physiological conclusions, that statoliths are involved in detection of body movements in different planes as well as being just a sensor of gravitational forces along the long axis of the animal. Their experiments showed convincingly that movements of the animal squeezes liquid from in front of the statolith into the canals, or partly formed canals, in which sensory cells detect movements and provide a basis for their three dimensional analysis by the brain. They propose that the shape of statoliths influences the amount of water displaced to ‘canals’ concerned with each dimension so helping detection of rolling, pitching and yawing as well as the longitudinal acceleration their mass would detect. This breakthrough in understanding provides the missing link between statolith shape and requirements for monitoring swimming movements and methods. Arkhipkin and Bizikov pointed out that certain parameters of the statolith were more developed if greater sensitivity was required in the planes of pitch or roll. Such greater sensitivity might be more important to animals living close to the sea bottom than to animals living in midwater. They then attributed such developments to the similarities between *Berryteuthis, Loligo gahi* and *Todarodes sagittatus* compared with pelagic *Gonatus fabricii, Gonatopsis borealis* and *Moroteuthis ingens.* Further, they defined the bottom group and the pelagic group by indices; members of the bottom group have a greater distance between the wing and rostral tip, a shorter and narrower wing and a wider rostrum.

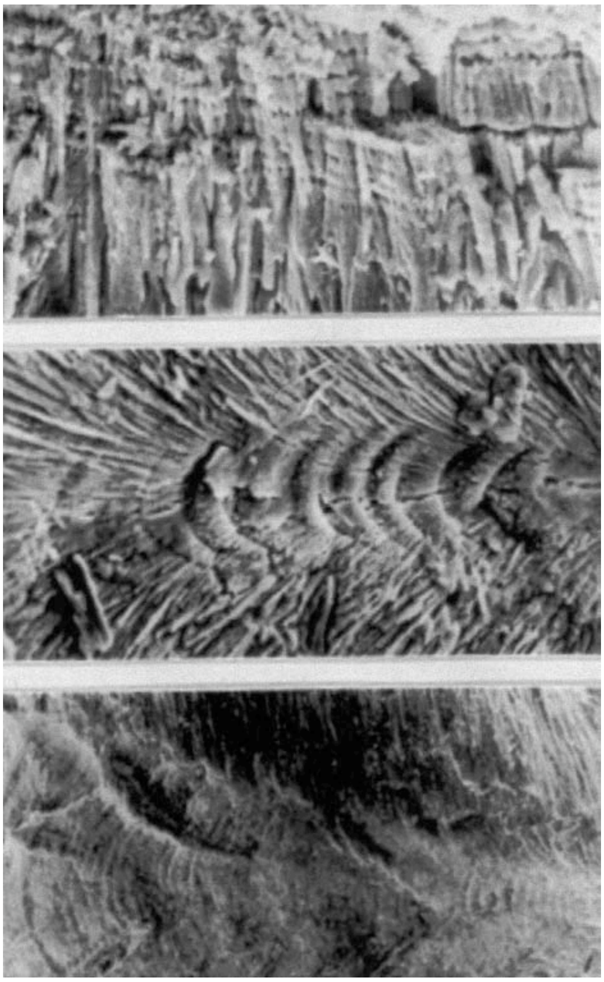


Fig. 17 Jurassic species A. Growth lines in the nucleus zone (middle) and in the radiating crystals of the lateral dome

While this work shows great potential it leaves many questions unanswered. First, the criteria for placing *Loligo gahi* and *Todarodes sagittatus* with *Berryteuthis* spp in the bottom group is not clear. They do not seem as easy to fit in that group as *Sepia* which was initially seen to resemble *Berryteuthis* most closely

(Clarke & Fitch 1979) and gave rise to the suggestion that living on the shelf might cause the similarity. The difficulty here is that *Spirula spirula*, a clear midwater species also shows close similarities to *Berryteuthis* (Fig. 16). Conversely, *Todaropsis eblanae*, which lives near the bottom for more of its life than *Todarodes sagittatus* is further in shape from *Berryteuthis* than is *Todarodes* (Figs 13, 16).

Clearly many functional possibilities of parts of the statolith need to be investigated. Fig. 3 shows the many intricate developments in different species. Why does the small, fast *Pyroteuthis* have an anteriorly extended lateral dome, similar to the slow, neutrally buoyant *Histioteuthis bonnellii?* What is the significance of the position of the spur in relation to the centre of gravity of the lateral dome or whole statolith? We may have to wait for a greater understanding of swimming and manoeuvring performance before understanding details of the statolith but Arkhipkin and Bizikov's work has certainly raised hope that, one day, statolith shape may well give us great insights into swimming and the way of life of extinct species which have left no fossils other than statoliths.

If we accept Arkhipkin and Bizikov's thesis regarding the significance of the width of the rostrum we might conclude that the Jurassic statolith species A is a bottom living form while species B and C have narrower rostra and live in midwater. On the other hand, it is interesting to see some resemblance between the Jurassic statoliths and *Architeuthis* (Fig. 13) although the very narrow spur separates the Jurassic from all living species.

Not withstanding functional forces acting to shape statoliths there is little doubt that details of their form are shaped by evolution. Evidence for this can be seen, for example, by similarities shown between loliginid genera and species (Fig. 8) although they have marked differences in body length and manoeuvrability and by similarities between *Sepia* and *Spirula* (Fig. 16) although they have very different swimming methods and ways of life.

In summary, study of fossil statoliths is likely to prove a very valuable means of improving our knowledge of the evolution of the Coleoidea. Many features of statoliths show relationships which are not just related to functional aspects.

In addition, recent physiological discovery suggests that shapes and some features of statoliths may relate to body form and way of life or behaviour of the animals. If this can be established in detail on living species it is possible that we shall be able to reconstruct the likely shapes, movement and way of life of some Jurassic, Cretaceous and possibly earlier species, of which other remains have not been fossilised.

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