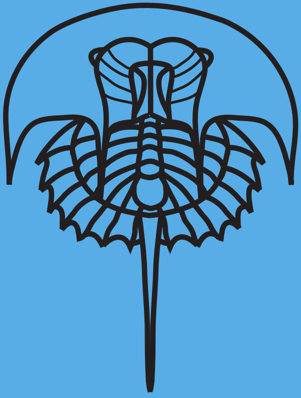

TREATISE ONLINE

Number 102

Part M, Chapter 11:
Statoliths and Coleoid Evolution

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2018

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART M, CHAPTER 11: STATOLITHS AND COLEOID EVOLUTION

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INTRODUCTION

Statoliths are the small, hard, aragonitic stones that lie, pair-wise, in the fluid-filled cavities, or statocysts, within the cartilaginous head capsules (cephalic cartilage) of all living—and probably all fossil—members of the Coleoidea (CLARKE, 1978) (see *Treatise Online,* Part M, Chapters 4, 13). The usefulness of these balance organs in taxonomy, systematics, and evolution has been explored by CLARKE and MADDOCK (1988a, 1988b); DOMMERGUES, NIEGE, and VON BOLETZKY (2000); NEIGE and DOMMERGUES (2002), and NEIGE (2006), among others. In particular, they have become important in the study of growth: fine layers in their structure have been shown to mark daily growth in several species (SPRATT, 1978; MARTINS, 1982; ARKHIPKIN, 1988, 2004, 2005; LIPINSKI, 1993, 2001; JACKSON, 1994, 2004). Many statoliths have been found in Cenozoic (CLARKE & FITCH, 1975, 1979; CLARKE, MADDOCK, & STEURBAUT, 1980; LEHMANN, 2010) and Mesozoic (CLARKE, 2003; HART & others, 2010, 2013, 2015, 2016; KLUG & others, 2016) sediments in North America and Europe. Many of these Jurassic records refer to the important Christian Malford Lagerstätte (Callovian, Jurassic) in Wiltshire, UK, where abundant statoliths and hooks are associated with soft-bodied preservation of the potential host animals.

STATOLITHS IN RECENT COLEOIDS

Statolith shape in the Octopoda (Incirrata, Cirrata) and Vampyromorpha differs markedly from that of the Decabrachia. Statoliths of the Vampyroteuthidae consist of loosely adhering, dumbbell-shaped crystals arranged to form a limpet shape. The Octopoda have statoliths varying from the limpet-shaped form of the largely inshore Octopodidae (e.g., *Eledone* LEACH, 1817) to the bar shape of the oceanic Bolitaenidae CHUN, 1911 (e.g., *Eledonella* VERRIL, 1884: Fig. 1). While fossil octopod statoliths have not yet been described, the hard, aragonitic nature of those from living forms suggests they may well be found in the future.

Decabrachian statoliths are quite variable in shape but have several parts that can generally be identified (Fig. 2). The four principal parts are the lateral dome, the dorsal dome, the rostrum, and the wing, which cups an area of randomly arranged, opaque crystals to which the soft tissues of the animal are attached in life. Most of the statolith consists of fairly transparent crystals radiating from one or two centers within the domes. The domes may have secondary lobes and are sometimes not separated from one another externally. On the lateral side of the attachment area, the lateral dome has an extension or spur. Viewed from the rostral or ventral end, the rostrum is seen to be oval in outline and is often at an angle to the

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[†]Deceased.

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FIG. 1. Various statoliths; *1–5, Eledone cirrhosa* (LAMARCK, 1798), anteriolateral (*1*), posterior (*2*), ventral (*3*), medial (*4*), and dorsal (*5*) views, length 1.74 mm; *6, Eledonella pygmaea* (VERRILL, 1884), view uncertain, length 0.42 mm; *7, Benthoctopus* sp., lateral view, length 0.31 mm (adapted from Clarke, 1978).

main axis of the lateral dome (Fig. 3). Variation in shape between the statoliths of nine living genera within six families is shown in Figure 4. Although some of the features described above are missing in some species or in some fossilized squid statoliths, there is usually no doubt that fossils are statoliths. Their aragonitic composition often leads to

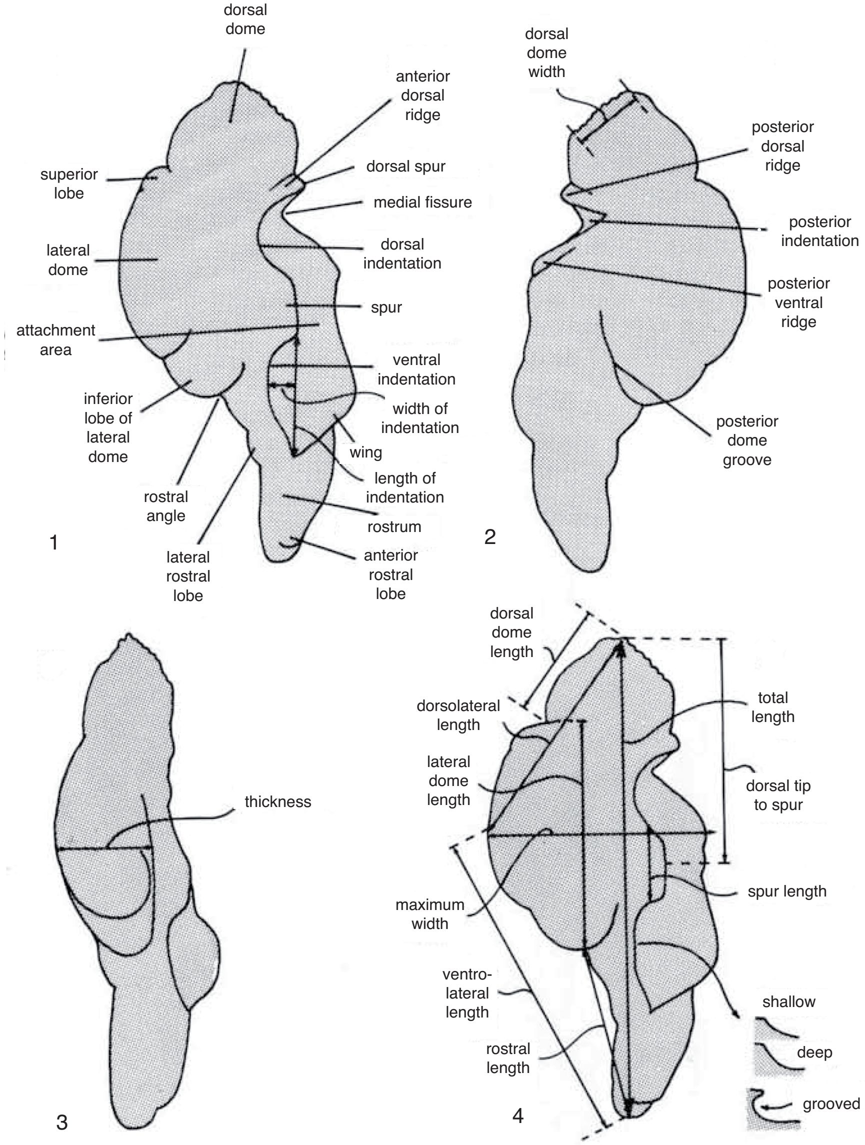

FIG. 2. Diagrams of a generalized teuthoid right statolith, showing dimensions and terms used in descriptions; view of anterior (*1*), posterior (*2*), lateral (*3*), and anterior (*4*) sides (adapted from Clarke, 1978).

their co-occurrence with fish otoliths, which have the same composition. Indeed, some papers on fish otoliths include descriptions of cephalopod statoliths, without recognizing their real identity (FROST, 1926, fig. 13–14; NETH & WEILER, 1953, pl. 8,*8;* MARTIN & WEILER, 1954, pl. 3,*116;* RUNDLE, 1967, fig. 4; ENGESER, 1990, p. 155), and LEHMANN (2010, pl. 1,*1,7*) identified some specimens as statoliths, although they are probably otoliths. The largest statoliths are about 3 mm in length, but fossil examples of less than 0.1 mm have been recognized. All fossil statoliths found so far are from continental-shelf, neritic, shallow-water deposits. It is, therefore, useful to review the extant

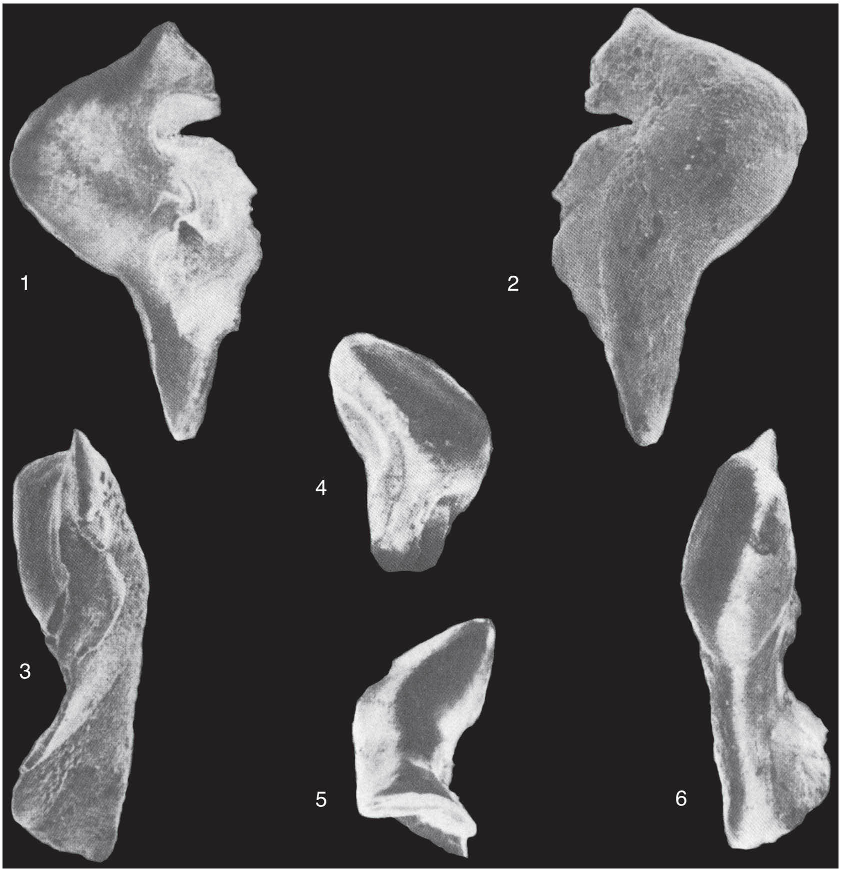

FIG. 3. Right statolith of *Loligo forbesii* STEENSTRUP, 1856; view of anterior (*1*), posterior (*2*), medial (*3*), dorsal (*4*), ventral (*5*), and lateral (*6*) sides, length 2.0 mm (adapted from Clarke, 1978).

coleoids that occur in shallow-water environments, since relatives of these are the most likely to be found in the more-recent fossil deposits. They are principally from the orders Octopoda (family Octopodidae ORBIGNY, 1840 in FÉRRUSAC & ORBIGNY, 1835–1848), Sepiida (families Sepiidae LEACH, 1817, and Sepiadariidae FISCHER, 1882 in 1880–1887), Sepiolida (families Sepiolidae LEACH, 1817, and Idiosepiidae APPELLÖF, 1898), and Loliginida (=Myopsida). A few species of the order Oegopsida (families Ommastrephidae STEENSTRUP, 1857; Onychoteuthidae GRAY, 1849; and Gonatidae HOYLE, 1886) move onto the continental shelf to feed at some stage in their lives (BRIERLEY, CLARKE, & THORPE, 1996).

From the distribution of living species, one might expect the most common Cenozoic statoliths to belong to the families Octopodidae, Sepiidae, Sepiolidae, and Loliginidae LESUEUR, 1821. That only the Loliginidae has been described so far is probably due to the early stage of the investigations. Intermediate forms between belemnoids, teuthoids, and spirulids have been described from the late Cretaceous of Canada, Greenland, and Chile (JELETZKY, 1966; FUCHS & others, 2012, 2013). The relationships of Cenozoic spirulids such as *Belemnosella* NAEF, 1922; *Spirulirostra* ORBIGNY, 1842; and *Belopterina* MUNIER-CHALMAS, 1872—all apparently intermediate between late Cretaceous forms and living *Spirula*—could be clarified were

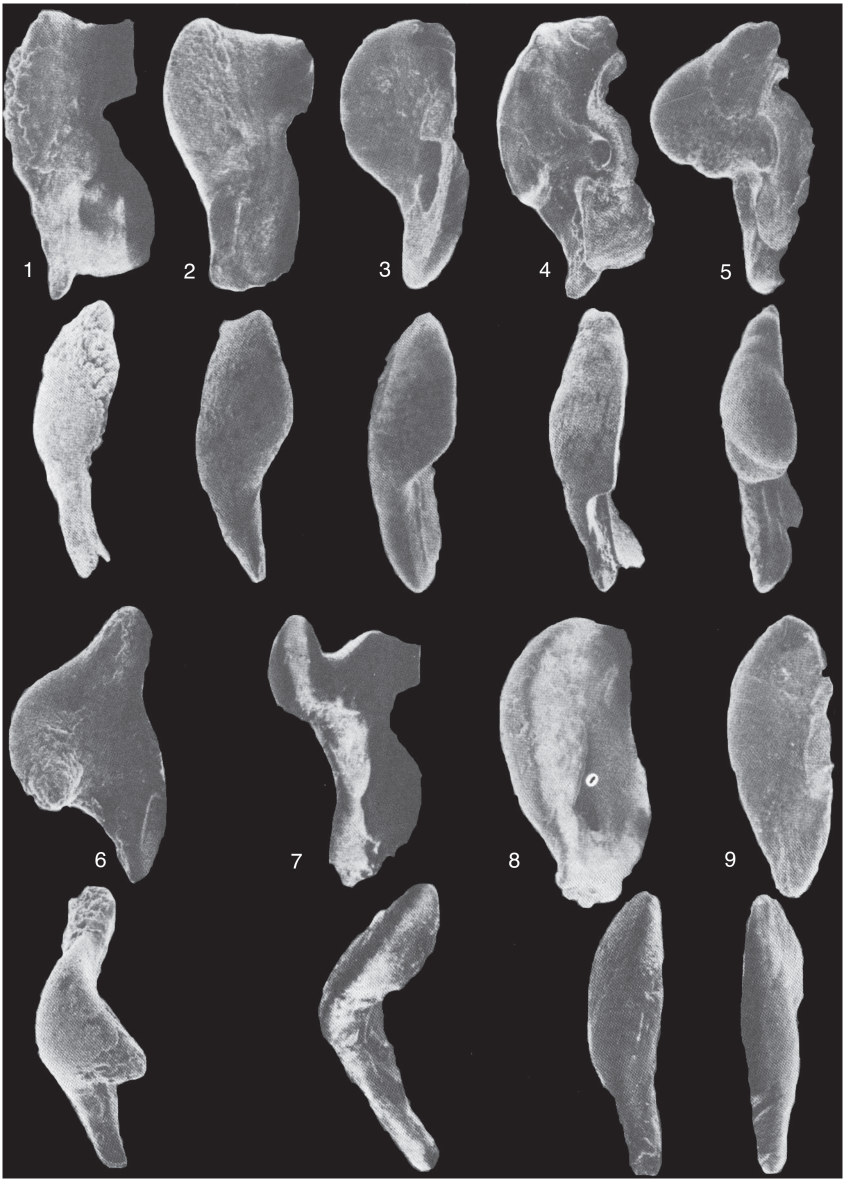

FIG. 4. Anterior (*upper*) and lateral (*lower*) views of statoliths of nine teuthoids; *1, Ommastrephes bartramii* (LESUEUR, 1821), length 1.37 mm; *2, Mastigoteuthis* sp., length 0.63 mm; *3, Teuthowenia megalops* (PROSCH, 1847), length 0.72 mm; *4, Nototodarus sloanii* (GRAY, 1849), length 1.26 mm; *5, Todarodes sagittatus* (LAMARCK, 1798), length 1.82 mm; *6, Pyroteuthis margaritifera* RÜPPELL, 1844, length 0.58 mm; *7, Histioteuthis bonnellii* FÉRUSSAC, 1834, length 0.97 mm; *8, Abraliopsis* sp., length 0.48 mm; *9, Helicocranchia pfefferi* MASSY, 1907, length 0.75 mm (adapted from Clarke, 1978).

statoliths to be found in the same strata. There is little doubt that more rigorous searching will eventually bring to light fossil statoliths of members of the Octopodidae, Sepiolidae, and Sepiidae in European and North American (Octopodidae and Sepiolidae only) rocks. This optimism is confirmed by recent records from the Eocene of France (NEIGE, LAPIERRE,

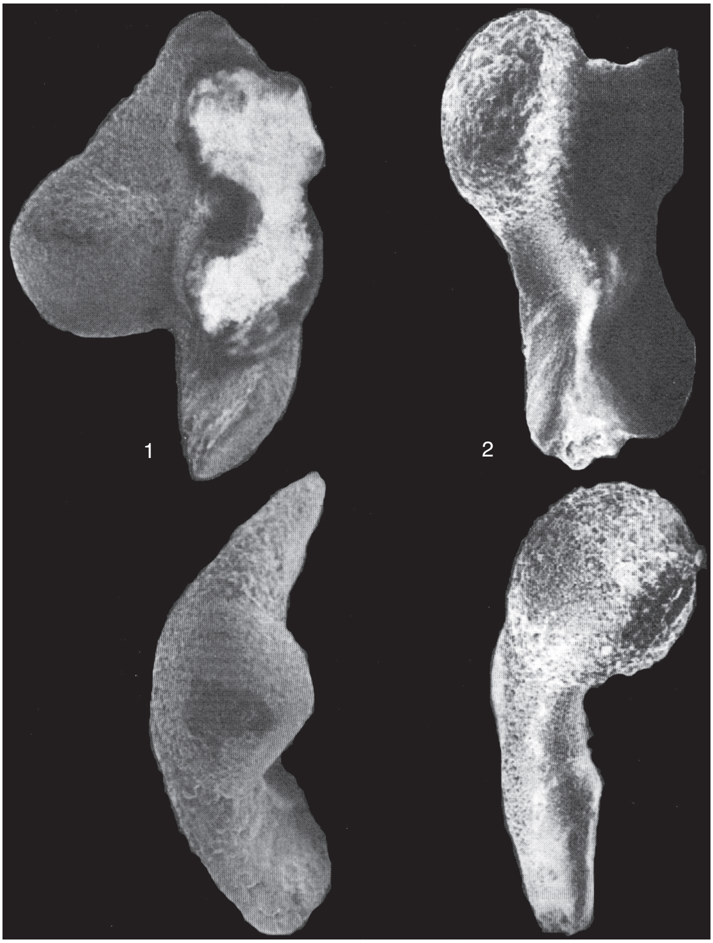

FIG. 5. Anterior (*upper*) and lateral (*lower*) views of statoliths; *1, Sepia elegans* BLAINVILLE, 1827, length 1.46 mm; *2, Spirula spirula* LINNAEUS, 1758, length 0.92 mm (adapted from Clarke, 1978).

& MERLE, 2016). The limpet shape of the octopodid statolith (Fig. 1), the globular form of the lateral dome in the sepiid (Fig. 5) and sepiolid, and the triangular or pointed form of the lateral dome in the loliginids make their identification to family level relatively straightforward (Fig. 3).

The oegopsids that regularly come onto the continental shelf of Europe are the ommastrephids, including *Todarodes sagittatus* (LAMARCK, 1798), *Todaropsis eblanae* (BALL, 1841), and *Illex coindeti* (VERANY, 1939). Fossil statoliths of these have not yet been found. In North America, the only oegopsid coming onto the shelf regularly on the east coast is the ommastrephid *Illex illecebrosus* (LESUEUR, 1821) and, on the west coast, the ommastrephid *Dosidicus gigas* (ORBIGNY, 1835 in 1834–1847) and the onychoteuthid *Moroteuthis robusta* (VERRILL, 1876). While fossil statoliths of the extant genus *Illex* STEENSTRUP, 1880, have not yet been recorded, fossil statoliths similar in form to those of *D. gigas* and *M. robusta* have been described and are considered to belong in the same genera (CLARKE & FITCH, 1979).

The gonatid squid *Berryteuthis magister* (BERRY, 1913) moves onto the North American continental shelf seasonally but is found farther north, as indeed are a few of the fish from the same deposit. A number of the fossils are certainly congeneric with this species but are not the same species. *Berryteuthis anonychus* Pearcy & Voss, 1963, is found off California today, but its statoliths have not become available for study. The ommastrephid *Sthenoteuthis* (formerly *Symplectoteuthis*) *oualaniensis* (Lesson, 1830) is normally entirely oceanic and does not stray onto the continental slope. It was, therefore, surprising to find a close relative of the same genus in the same fossil deposit as a species of *Loligo* Lamarck, 1798. Some fish in this deposit, however, were also mesopelagic and bathypelagic.

CENOZOIC STATOLITHS

NORTH AMERICA

Twelve of over thirty sedimentary successions in North America sampled by John Fitch have yielded fossil statoliths (Clarke & Fitch, 1975, 1979), and these comprised samples from mid-Eocene to early Pleistocene age. The great effort needed to make this collection can be imagined from the fact that more than 4500 kg of sediment were sieved to provide 467 statoliths: only ~0.1 statoliths per kg. The same samples, however, yielded more than 164,000 fish otoliths, which is a ratio of 352 otoliths to every statolith. This raises the question of whether these samples reflect a true numerical relationship between teleost fish and teuthoids in the seas around North America during the time intervals sampled. Two factors are probably involved in lowering the numbers of statoliths in the samples. Firstly, the finest sieve used to remove biological samples from the fossiliferous matrix had a mesh size of 0.5 mm, and there is little doubt that many statoliths would have passed through this sieve. Most of those collected had a width in excess of 0.5 mm and are probably at the larger end of the size spectrum. Secondly, living coleoids on the continental shelves often form large aggregations during spawning, which is followed by death; thus, unless a deposit encompassed such an area, the number of 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 sediments of the Christian Malford Lagerstätte described by Hart and others (2010, 2015, 2016) contain many more statoliths than otoliths and may represent such an environment.

FAMILY LOLIGINIDAE

The loliginid statoliths of the collections assembled by John Fitch are well differentiated back to the mid-Eocene and have all been included in the genus *Loligo. Loligo applegatei* Clarke & Fitch, 1979, from the Ypresian (Eocene) has an unusually large lateral dome (Fig. 6), which may have evolved into the Oligocene *Loligo mississippiensis* Clarke & Fitch, 1979, by becoming flattened on its inferior side. It may also have evolved into later *Loligo* sp. B, *Loligo* sp. D, and *Loligo valeriae* Clarke & Fitch, 1979, all of which are very similar in shape, by becoming much reduced and less pointed (Fig. 6–7). The inferior side of the lateral dome of *L. valeriae* is enlarged in a manner similar to the living *Doryteuthis pealei* (Lesueur, 1821) and *D. plei* (Blainville, 1823). The other living, east-coast loliginid, *Lolliguncula brevis* (Blainville, 1823), differs from *Loligo* statoliths in having a rounded lateral dome with no suggestion of a point at the superior end. On the west coast of North America, *Loligo* sp. A is completely different from the east coast *L. applegatei,* in having a more normally proportioned and less-pointed lateral dome. The lateral dome's inferior side is rather flat, as in some of the specimens of *Loligo barkeri* Clarke & Fitch, 1979, to which it may have given rise by becoming thicker and its rostrum becoming longer (Fig. 7–9). *Loligo stillmani* Clarke & Fitch, 1979, and the living *Doryteuthis opalescens* (Berry, 1911a) possibly developed from *L. barkeri* by extension of the dorsal dome, although *L. stillmani* has a more pointed

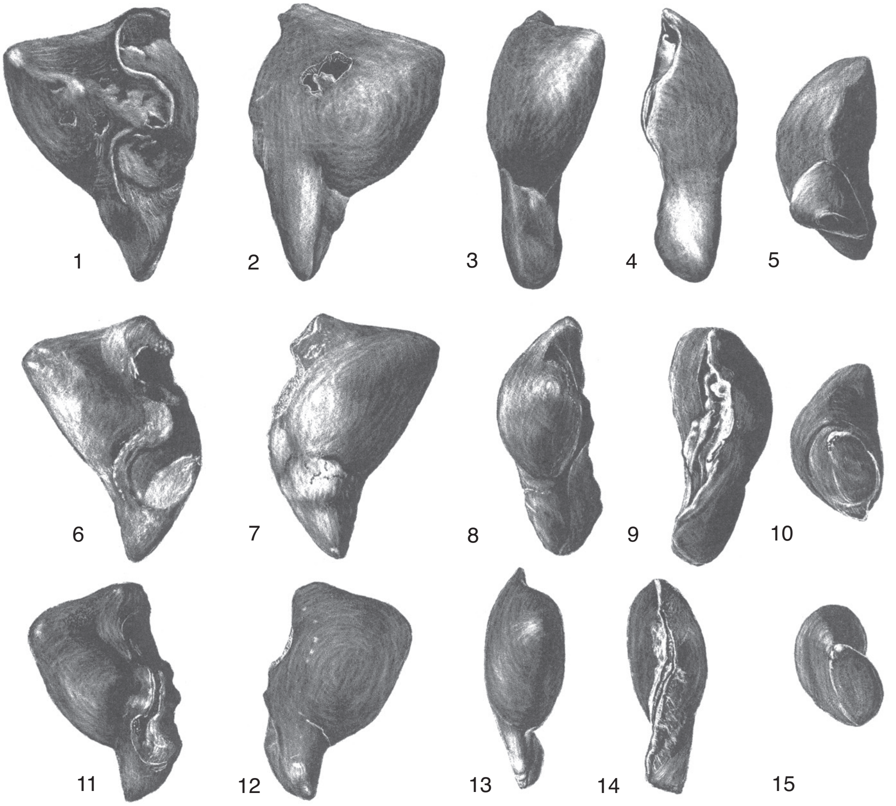

FIG. 6. Right statoliths of three fossil *Loligo* species. *1–5*, *Loligo applegatei* CLARKE & FITCH, 1979, Eocene, Nanjemoy Formation, Hanover County, Virgina, USA, length 1.45 mm; anterior (*1*), posterior (*2*), lateral (*3*), medial (*4*), and ventral (*5*) views. *6–10, L. mississippiensis* CLARKE & FITCH, 1979, Miocene, Chipola Formation, Calhoun County, Florida, USA, length 1.32 mm; anterior (*6*), posterior (*7*), lateral (*8*), medial (*9*), and ventral (*10*) views. *11–15, L. valeriae* CLARKE & FITCH, 1979, ?Miocene, Bowden Formation, Jamaica, 1.19 length mm; anterior (*11*), posterior (*12*), lateral (*13*), medial (*14*), and ventral (*15*) views (all adapted from Clarke & Fitch, 1979).

lateral dome than *D. opalescens* and is probably on a separate line of evolution. *Loligo* sp. C is distinct in having a very thick lateral dome and a large inferior lobe and may have developed on a different line from *L. barkeri.* Statoliths from the early Pleistocene are not distinguishable from the statoliths of living *D. opalescens.*

EUROPE

Based on the visual comparison of their shape, six similar *Loligo* statoliths from the early Miocene (CLARKE & others, 1980) could not be separated from the two living species of *Loligo* in Europe: *L. forbesii* STEENSTRUP, 1856, and *L. vulgaris* LAMARCK, 1798 (Fig. 10). LEHMANN (2010) reported on possible Eocene statoliths from the Paris Basin in France that had, for a long time, been confused with fish otoliths (*"Neobythitinarum" regularis*).

When compared with the North American statoliths, the European fossils appear to be closest to *L. mississippiensis,* which extended from the early-middle Oligocene into the early Miocene. They differ in having a less sharply pointed lateral dome, which is more rounded anteriorly and ventrolaterally and has a deeper medial fissure.

To investigate these relationships more closely, tracings of the five outlines shown in Figure 11 were drawn using a camera

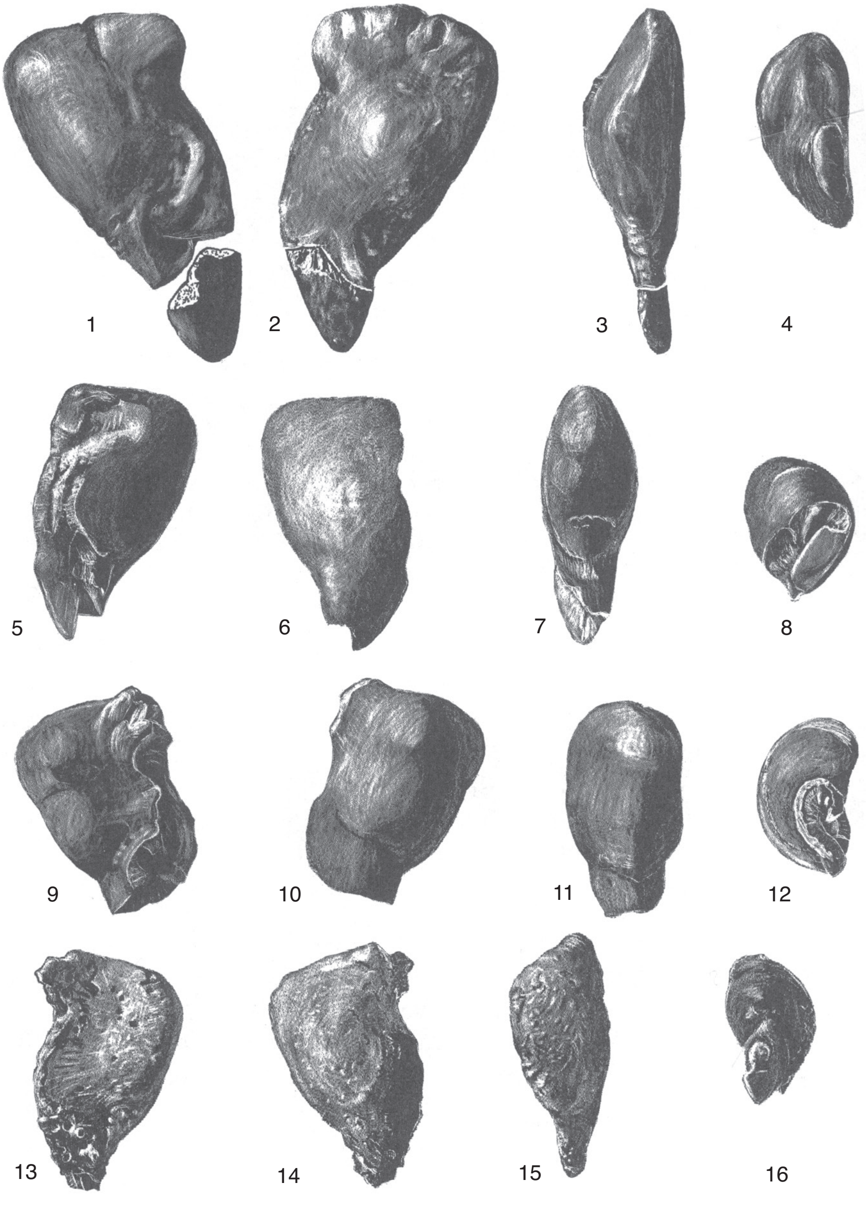

FIG. 7. Statoliths of four species of fossil *Loligo* LAMARCK, 1798. *1–4, Loligo* sp. A, right statolith, length 0.84 mm; anterior (*1*), posterior (*2*), lateral (*3*), and ventral (*4*) views. *5–8, Loligo* sp. B, left statolith, length 1.19 mm, anterior (*5*), posterior (*6*), lateral (*7*), and ventral (*8*) views. *9–16, Loligo* sp. D, right and left statolith, length 1.13 mm, anterior (*9, 13*), posterior (*10, 14*), lateral (*11, 15*), and ventral (*12, 16*) views (adapted from Clarke & Fitch, 1979).

lucida and stereoscopic microscope and then traced onto a digitizing tablet (CLARKE & MADDOCK, 1988a). Multiple discriminant analysis of the twenty-four resulting ratios was then computed, and the results are shown in Figure 12. All but two of the *Loligo* species are positive on axis 3, while all of the species of the other loliginid genera—*Alloteuthis* WÜLKER, 1920; *Lolliguncula* STEENSTRUP, 1881; and *Doryteuthis* NAEF, 1912—

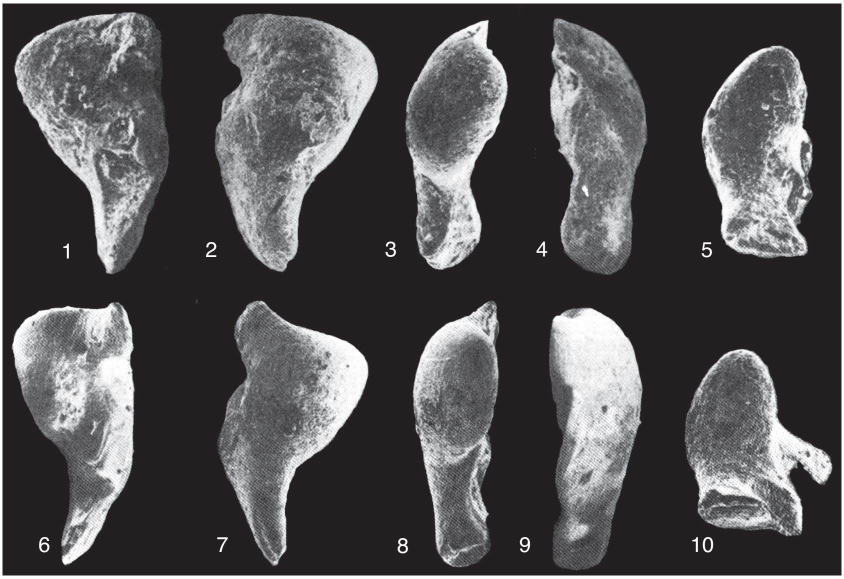

FIG. 8. Right statoliths. *1–5, Loligo barkeri* CLARKE & FITCH, 1979; anterior (*1*), posterior (*2*), lateral (*3*), medial (*4*), ventral (*5*) views, length 1.3 mm. *6–10, L. stillmani* CLARKE & FITCH, 1979, holotype; anterior (*6*), posterior (*7*), lateral (*8*), medial (*9*), ventral (*10*) views, length 1.42 mm (adapted from Clarke & Maddock, 1988a).

are negative on that axis (as indicated by the dashed line). The exceptions are *D. plei* and *L. forbesii,* which are distinguished from all species except *L. vulgaris.* The 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 there is the possibility that both species evolved from *L. mississippiensis.* Figure 12 shows the weightings, by the length of line, of the twenty-four respective measurements on the first two axes: a dashed line indicates a negative value on axis 3. The most important factors causing separation are the dome perimeter and length, which spread the groups to left and right; the rostral area and whole statolith width, which spread the groups diagonally from bottom left to top right; and the ventral statolith perimeter combined with the dome length, which spread the groups diagonally from bottom right to top left.

Some confidence can be attached to this analysis because of the grouping of congeneric species. All but two of the *Loligo* species are positive, and the members of the other genera are all negative. The European and the North American species are separate from one another and are separated from the fossils. On the other hand, species of *Alloteuthis, Lolliguncula,* and *Doryteuthis* are all negative, and each species forms 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 the analysis still indicates rational relationships in conformity to what is known from the living species. Comparison with a similar analysis of linear measurements taken with a microscope (CLARKE & MADDOCK, 1988a) clearly showed that to use a computer's analysis of area, perimeter, and other morphological features gave much better separation.

FAMILY GONATIDAE

In their detailed study of the statoliths of members of the Gonatidae, CLARKE and others (1980) showed that the Pliocene *Berryteuthis* (BERRY, 1913) statoliths are

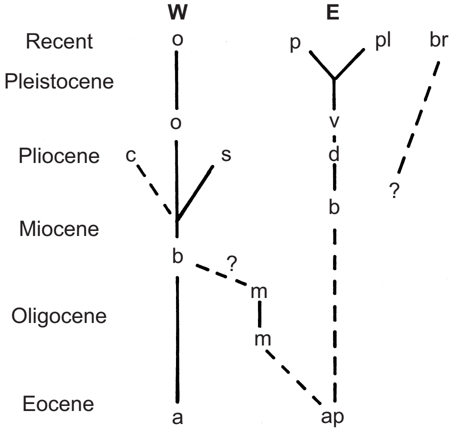

Fig. 9. The possible evolution of Cenozoic loliginids on the western (*W*) and eastern (*E*) sides of North America; *dashed lines* indicate very tentative lineages; *solid lines* indicate less tentative lineages; *a, Loligo* sp. A; *ap, Loligo applegatei* Clarke & Fitch, 1979; *b, Loligo sp.* B; *br, Lolliguncula brevis* (Blainville, 1823); *c, Loligo* sp. C; *d, Loligo* sp. D; *m, Loligo mississippiensis* Clarke & Fitch, 1979; *o, Doryteuthis opalescens* (Berry, 1911a); *p, D. pealeii* Lesueur, 1821; *pl, Doryteuthis plei* (Blainville, 1823); *s, Loligo stillmani* Clarke & Fitch, 1979; *v, Loligo valeriae* Clarke & Fitch, 1979 (adapted from Clarke & Maddock, 1988a).

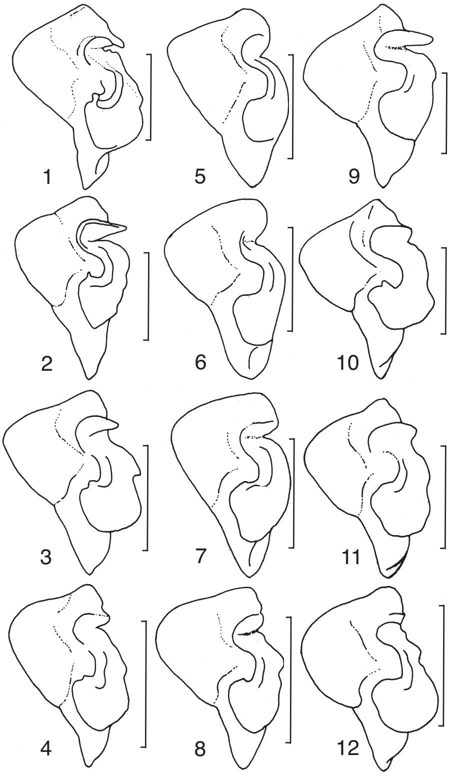

Fig. 10. Anterior views of *Loligo* statoliths. *1–4, L. vulgaris* Lamarck, 1798; *5–8,* Miocene fossils from Europe (Natural History Museum, London, UK, BMNH C46953–C469536); *9–12, L. forbesii* Steenstrup, 1856; scale bars, 1 mm (adapted from Clarke, Maddock, & Steurbaut, 1980, fig. 2).

certainly a different species from *B. magister,* but the Pliocene species was not named because of the existence of another species, *B. anonychus,* from which statoliths had not been examined. In view of the age of the fossils, at about two million years, and the fact that three other oegopsids from the same deposits had proved to be congeneric with living forms (albeit new species), it seemed reasonable and less confusing to name them even if they later turn out to belong to *B. anonychus.* Unfortunately, in their 1979 publication, Clarke and Fitch inadvertently left the manuscript name ("*Statiloteuthis enigmaticus* n. sp.") in the caption of their figure 10, instead of *Berryteuthis* sp., which should have been substituted for it before publication: the new name lacked formal definition and description and was, therefore, invalid.

To correct this taxonomic error, Malcolm Clarke had selected a holotype and a number of paratypes from a collection of 118 statoliths from Newport Mesa, Fernando Formation (7 statoliths) and the Lomita Marl Formation of California (26 statoliths). Although Clarke and Fitch (1979) regarded the sediments as uppermost Pliocene in age, they are currently viewed as lowermost Pleistocene. The statoliths are very similar in form (Fig. 13) to those of living *Berryteuthis magister,* but they differ in a number of ways, some of which may have been the result of their preservation.

A multiple discriminant analysis of linear measurements was done comparing the *Berryteuthis* fossil statoliths from the Plio-Pleistocene of California with four living species of the family collected from the northern North Pacific and North Atlantic (Clarke & others, 1980). This showed clearly that the fossil *Berryteuthis* sp. is a different species from the

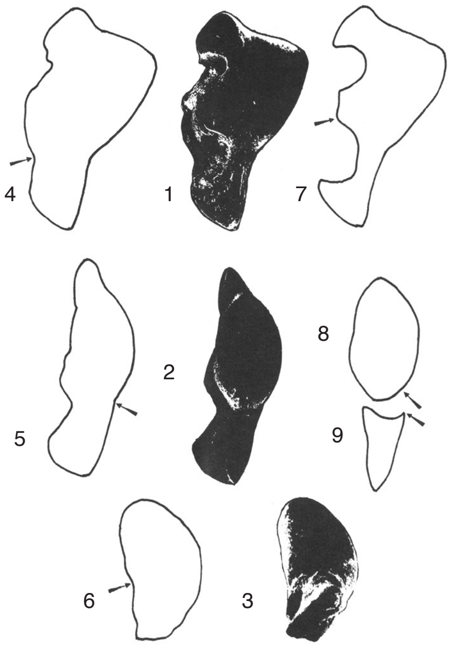

FIG. 11. Left statolith of a *Loligo* species; *1–3,* photographs of anterior (*1*), lateral (*2*), and ventral (*3*) views; *4–8,* tracings of anterior (*4, 7*), ventral (*6*), and lateral (*5, 8–9*) views used in digitizer analysis; *arrows* indicate the points at which tracings were started (adapted from Clarke & Maddock, 1988a).

living *B. magister* (Fig. 14–15). A taxonomic note on these differences is in preparation.

FAMILIES OMMASTREPHIDAE AND ONYCHOTEUTHIDAE

Statoliths of *Dosidicus lomita* CLARKE & FITCH, 1979, and *Sthenoteuthis pedroensis* (CLARKE & FITCH, 1979), both members of the Ommastrephidae, are illustrated in Figure 16. A statolith of *Moroteuthis addicotti* CLARKE & FITCH, 1979, belonging to the family Onycoteuthidae, is illustrated in Figure 17.

MESOZOIC STATOLITHS

The detailed description of several thousand statoliths from Jurassic successions across the Wessex Basin of southern England, compiled by Malcolm CLARKE, has not yet been published, except for a brief comparison (CLARKE & MADDOCK, 1988a) of a typical example with the statolith of a living myopsid, *Loligo forbesii.* This comparison, shown in Figure 18, demonstrates that the fossil is very different in shape from the statolith of *L. forbesii,* but it has the same component parts and it is much closer to that than to any fish otolith or to octopod or sepiid statoliths. The fossil possesses a very narrow, elongated spur; a rostrum that is shaped similarly to that of *Loligo,* particularly in its ventral view (compare Fig. 18.4 with Fig. 18.12); and a lateral dome. It differs in being thinner (compare Fig. 18.10 with Fig. 18.7) and having a ventrally curving edge where the dorsal dome (Fig. 18.4) is developed in many living teuthids. Jurassic statoliths presently group into at least four or five morphotypes (HART & others, 2015), using generic criteria established for living species. CLARKE assigned these Jurassic taxa to the paraphyletic order Teuthida because their shapes are much more like extant teuthoids than extant Sepiida. Although fragments of Belemnotheutidina are found in the same deposits as the statoliths, this phragmocone-bearing group is physiologically much closer to Sepiida than to gladius-bearing teuthoids that rely on other methods for buoyancy (CLARKE, 1988). Shape analysis (CLARKE & MADDOCK, 1988a; Fig. 18) and work on the physiological function of living statoliths (ARKHIPKIN & BIZIKOV, 1998, 2000) show that some aspects of statolith shape are related to methods of swimming and buoyancy. If these statoliths are indeed from teuthoid squids, they are clearly particularly significant for the study of the evolution of cephalopods; see ENGESER (1990) for an account of possible coleoid phylogeny. Any statoliths from the Cretaceous and Paleocene could record the changes from the Jurassic species to the Eocene species when, present-day, living families appeared.

The Jurassic material studied by CLARKE (2003) was provided by amateur fossil collectors who had processed many kilograms of sediment (mainly clays) from a number of Jurassic (Hettangian to Kimmeridgian) localities in the Wessex Basin, UK (HART & others, 2015, fig. 1); at the time, this was one of the largest collections of fossil statoliths. CLARKE (2003) preliminarily identified three new

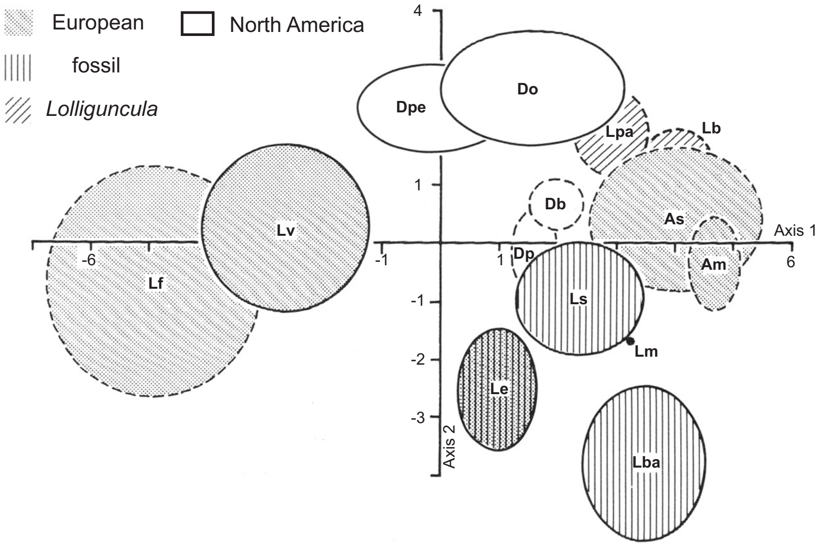

FIG. 12. Results of a multiple discriminant analysis of digitized dimensions of loliginid statoliths (see Fig. 11). The specimens were plotted on the first two axes in units of mean group standard deviation and each group was positioned at its centroid, and its standard deviation on each axis was used 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. The length of line indicates the weightings of the twenty-four respective measurements on the first two axes: *dashed line* indicates a negative value on axis 3. *Am, Alloteuthis media* (LINNAEUS, 1758): 6 specimens used; *As*, *Alloteuthis subulata* (LAMARCK, 1798): 61; *Db*, *Doryteuthis bleekeri* (KEFERSTEIN, 1866 in 1862–1866): 3; *Lb, Lolliguncula brevis* (BLAINVILLE, 1823): 12; *Lba, Loligo barkeri* CLARKE & FITCH, 1979: 30; *Le*, *Loligo* sp., European fossil: 6; *Lf, Loligo forbesii* STEENSTRUP, 1881: 77; *Do*, *Doryteuthis opalescens* (BERRY, 1911a): 14; *Dp*, *D. plei* (BLAINVILLE, 1823): 4; *Lpa*, *Lolliguncla panamensis* BERRY, 1911b: 3; *Dpe*, *D. pealeii* (LESUEUR, 1821): 45; *Lv, Loligo vulgaris* LAMARCK, 1798: 52; *Ls*, *Loligo stillmani* CLARKE & FITCH, 1979: 18; *Lm*, *Loligo mississippiensis* CLARKE & FITCH, 1979 (adapted from Clarke & Maddock, 1988a).

species (Jurassic sp. A, B, and C), and he was preparing a paper in which these taxa were to be formally designated. This work, unfortunately, was never published and remains in manuscript form. Just before his untimely death in 2013, CLARKE was made aware of new information on Jurassic statoliths being generated by HART and others (2009, 2010). This material also came from a range of locations in the Wessex Basin, but most of the statoliths were from the Phaeinum Subchronozone sediments of the Oxford Clay Formation (upper Callovian) of the Christian Malford Lagerstätte (WILBY & others, 2008), which had long been famous for their preservation of soft-bodied fossils of both coleoids and belemnoids (PEARCE, 1841; OWEN, 1844; MANTELL, 1848; DONOVAN, 1983; ALLISON, 1988; MARTILL & HUDSON, 1991; PAGE & DOYLE, 1991; DONOVAN & CRANE, 1992; TANG, 2002; WILBY & others, 2004, 2008). In this material, HART and others (2010, 2015) found large numbers of CLARKE's (2003) Jurassic sp. A (~95% of the assemblage) and Jurassic sp. C (~5% of the assemblage) (Fig. 19). There are three important factors to be noted: (1) the exceptionally large numbers of statoliths generally outnumbered the otoliths quite significantly; (2) the statoliths were associated with the soft-bodied remains of potential host animals (see WILBY & others, 2004 and references therein); and (3) the statoliths are associated with thousands of belemnoid hooks (see *Treatise Online,* Part M, Chapter 10), many of which could be identified by reference to KULICKI and SZANIAWSKI (1972), WIND, DINKELMAN, and WISE (1977), ENGESER (1987), ENGESER and CLARKE (1988), and KLUG and others (2010). This combination of soft-bodied preservation of potential host animals, statoliths and hooks makes the

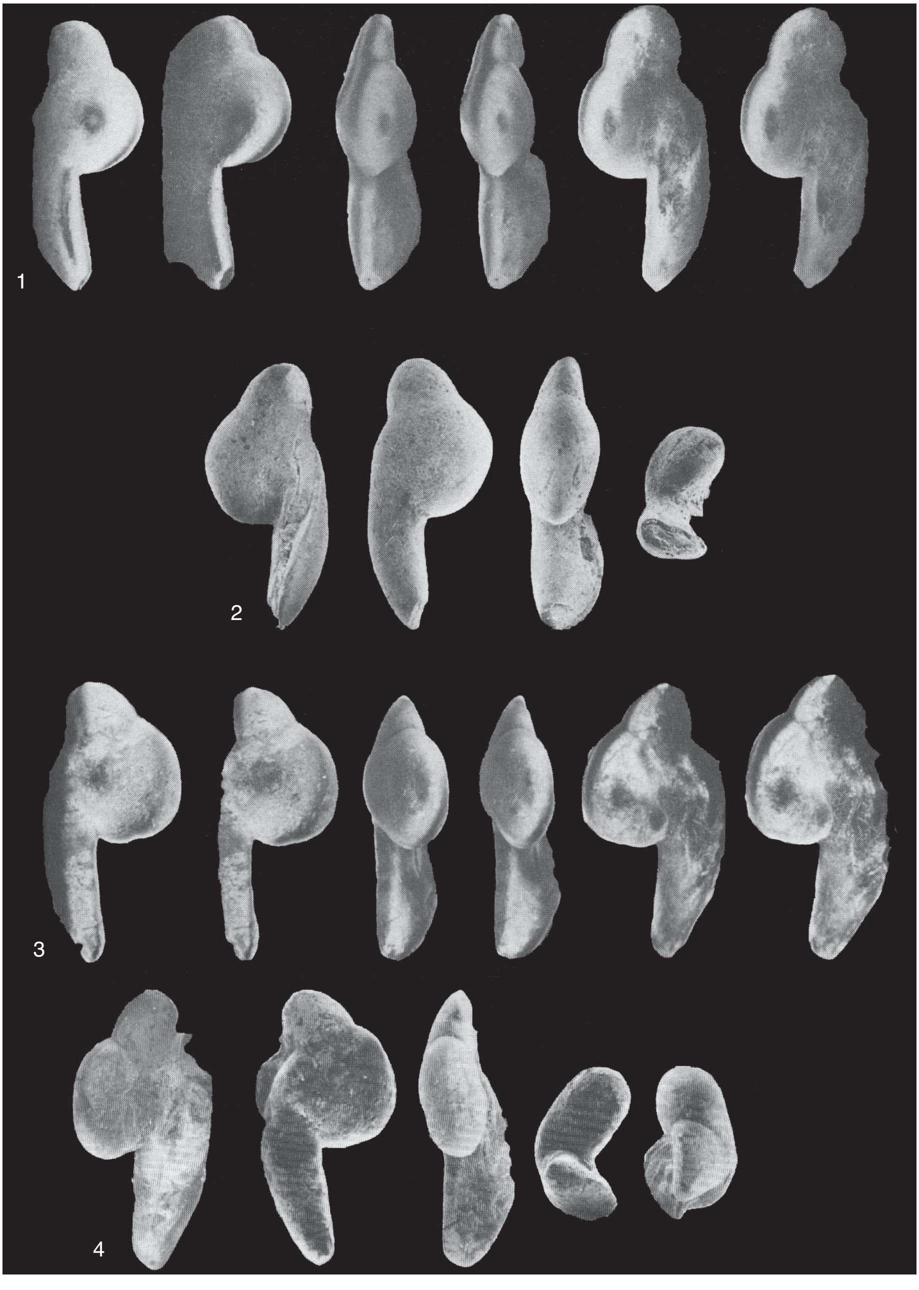

FIG. 13. Right statoliths of *Berryteuthis* (BERRY, 1913). *1–2, Berryteuthis* sp., lowermost Pleistocene, California, USA, length 2.88 mm; *1,* posterior (*left*) to anterior (*right*) views; *2,* anterior, posterior, lateral, ventral views (*left to right*). *3–4, Berryteuthis magister* (BERRY, 1913), length 2.44 mm; 3, posterior (*left*) to anterior (*right*) views; 4, anterior, posterior, lateral, ventral, and dorsal views (*left to right*); stereopairs in *1* and *3* can be viewed by copying and placing 63 mm apart (adapted from Clarke & others, 1980, fig. 5).

Christian Malford Lagerstätte a significant location for the study of coleoid evolution (HART & others, 2016).

In their account of Jurassic statoliths, HART and others (2015) confirmed the occurrence of CLARKE's (2003) Jurassic sp. B in the Hettangian (Fig. 20). This probably came from the same part of the Lias Group on the Dorset Coast, east of Charmouth, which is well known for the preservation of such belemnoids as *Phragmoteuthis huxleyi* (DONOVAN, 2006) and *Clarkeiteuthis* (formerly *Phragmoteuthis*) *montefiorei* (BUCKMAN, 1880). This location may also provide a link between a statolith and the host animal (see discussion in HART & HUTCHINSON, 2017). In the Lower Jurassic (Toarcian) of southern Germany, a different form of statolith has been confirmed (W. RIEGRAF, personal communication, 2013–2015), which might be associated with *Clarkeiteuthis conocauda* (QUENSTEDT, 1849 in 1845–1849). Similar statoliths to those described by RIEGRAF have been illustrated from the Toarcian and Aalenian by SCHWARZHANS (2018, fig. 8). In the lower part of the Middle Jurassic, HART and others (2009) described a different statolith in the Bathonian (Fig. 20). Work on linking all these taxa to the host animals is ongoing.

Despite intensive studies of Cretaceous marine successions (e.g., Speeton Clay and Gault Clay formations) by HART and his graduate students, no statoliths have been recorded. Both the Speeton Clay and the Gault Clay formations are well known for their assemblages of belemnites (SWINNERTON, 1936, 1937, 1948, 1952, 1955; MITCHELL & UNDERWOOD, 1999). The Chalk Group in northwestern Europe (including the UK), though containing well-known belemnite assemblages, does not allow for the preservation of aragonite fossils and, therefore, no statoliths have ever been recorded. This gap in the statolith record may well be problematic!

Although statoliths were probably dissolved, the oldest evidence of statocysts has been detected by FUCHS and LARSON (2011, fig. 4,*6*) in a gladius-bearing octobrachiate from the Cenomanian Plattenkalks of Hâkel, Lebanon. By contrast, KLUG and others (2016) have

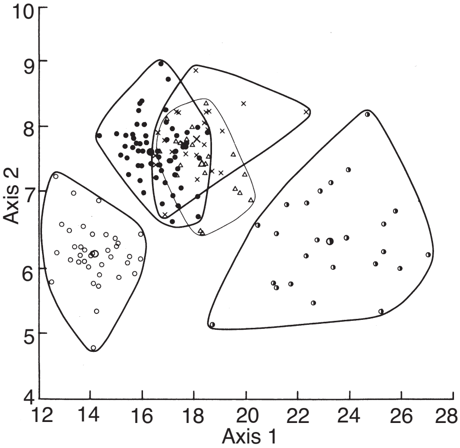

FIG. 14. Multiple discriminant analysis of five groups of *Berryteuthis* (BERRY, 1913): *Berryteuthis* sp., righthand group with half-filled circles; *B. magister* (BERRY, 1913), four remaining groups; axes are in arbitrary units; scores of individuals are plotted on first two axes and enclosed by a freehand line, with centroids indicated by larger symbol (adapted from Clarke & others, 1980).

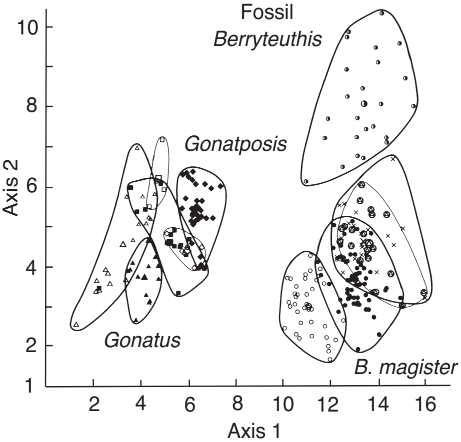

FIG. 15. Multiple discriminant analysis of eleven groups of four genera in the family Gonatidae; axes are in arbitrary units; scores of individuals are plotted on first two axes and enclosed by a freehand line, with centroids indicated by an enlarged symbol (adapted from Clarke & others, 1980).

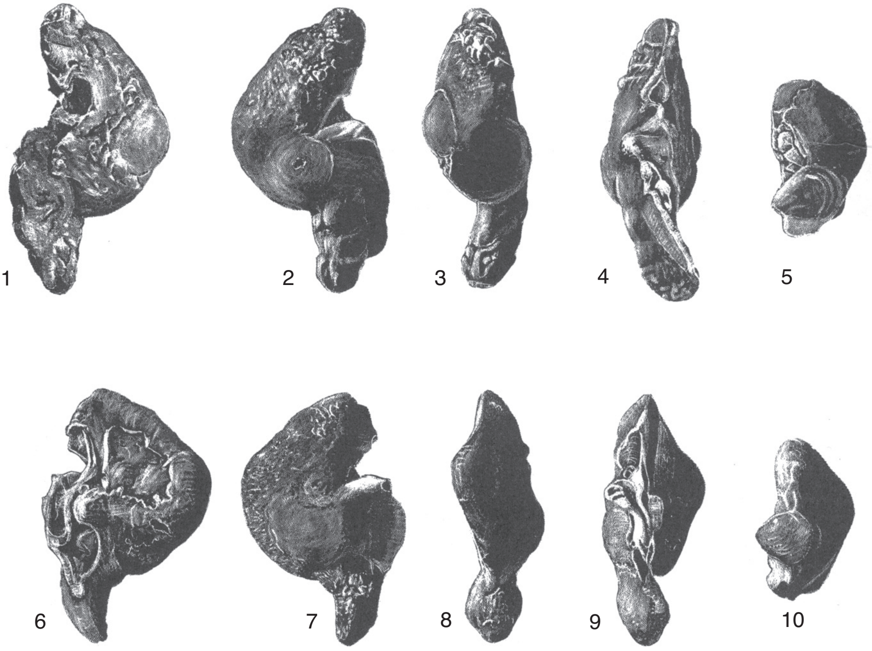

Fig. 16. Statoliths of two species of fossil ommastrephid squids. *1–5, Dosidicus lomita* Clarke & Fitch, 1979, length 2.52 mm; posterior (*1*), anterior (*2*), lateral (*3–4*), ventral (*5*) views; *6–10, Sthenoteuthis pedroensis* (Clarke & Fitch, 1979), length 2.26 mm; posterior (*6*), anterior (*7*), lateral (*8–9*), ventral (*10*) views (adapted from Clarke & Fitch, 1979).

recently found statocysts including statoliths in the head capsule of a belemnotheutid from the Tithonian Plattenkalks of Solnhofen, southern Germany. However, a detailed comparison with other statolith morphologies is not possible due to poor preservation.

BIOLOGICAL CONCLUSIONS FROM FOSSIL STATOLITHS

NUMBERS RELATIVE TO FISH

As discussed above, the relative numbers of statoliths and otoliths in the North American Cenozoic deposits could suggest that there were far fewer teuthids in the sea than teleost fish (with a mean statolith-otolith ratio of 1:279 and a range of 1:20 to 1:1,300). However, this is more likely to be a reflection of the smallest sieve used and the loliginid habit of assembling to spawn and die, which would greatly reduce the adults from all deposits except in places where spawning took place.

The relative numbers of statoliths in Jurassic beds compared with fish otoliths might be biased by their smaller size and less-robust nature, but they generally outnumber the fish otoliths (with a mean statolith-otolith ratio in six sites of 8:1 and a range of 1:2 to 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 belemnitid rostra than the number of statoliths leads one to expect if the statoliths came from belemnoids. Belemnoid shells, however, were buoyant and may have floated in surface currents to other localities (particularly those of belemnotheutids), while the more-dense statoliths would have fallen straight to the sea bottom when the flesh disintegrated after death. Although Kear, Briggs, and Donovan (1995) suggested that statoliths would not survive the decay process, on the basis of experimental work, the fossil record of Jurassic statoliths indicates that they are often preserved in good condition.

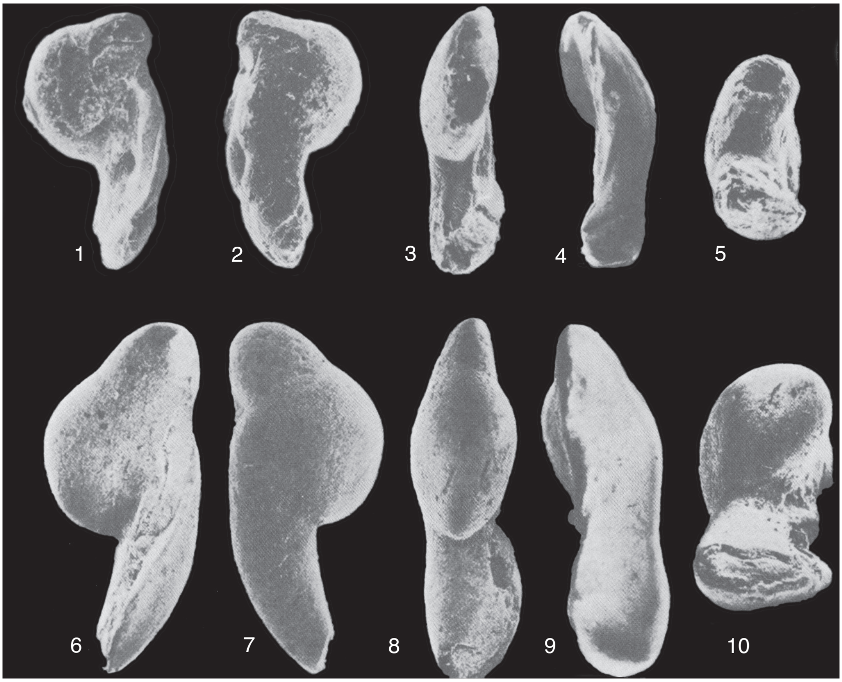

FIG. 17. Statoliths; *1–5, Moroteuthis addicotti* CLARKE & FITCH, 1979; posterior (*1*), anterior (*2*), lateral (*3–4*), ventral (*5*) views; length 1.48 mm. *6–10, Berryteuthis* sp.; posterior (*6*), anterior (*7*), lateral (*8–9*), ventral (*10*) views; length, 2.77 mm (adapted from Clarke & Fitch, 1979).

GROWTH

Statoliths of many living decabrachians lay down regular rings during growth, averaging one ring per day in several species (SPRATT, 1978; MARTINS, 1982; ARKHIPKIN, 2005 and references therein). Such daily rings have not yet been demonstrated in Cenozoic statoliths, although they are expected to be present. The Jurassic statoliths, however, easily break along a central fracture of the lateral dome (Fig. 18.7); the exposed surface is crossed by a series of minute growth ridges that run parallel to the lateral and dorsomedial rims of the lateral dome and the curved edge, where there is a dorsal dome in living species. These ridges seem to be analogous to the growth rings of living teuthoids. The largest fossil statoliths from the Jurassic sediments of the Wessex Basin have about 100 or more ridges, which would suggest a much-faster growth rate than is found in living squids of the same size, unless each ridge represents three to four days of growth.

SIZE OF TEUTHOIDS

In living cephalopods, the size of the statolith is often correlated with length and weight (GUERRA & SÁNCHEZ, 1985). For example, the total lengths of loliginid statoliths are positively correlated with the dorsal mantle lengths (M. R. Clarke, unpublished data), and it is therefore likely that the *Loligo* individuals providing the fossil statoliths examined so far had mantle lengths of 8–16 cm compared with the living *L. forbesii,* which can have mantle lengths exceeding 80 cm (MARTINS, 1982). Similarly, the statolith length of *Berryteuthis magister* is correlated with dorsal mantle length (CLARKE & others, 1980), and this suggests that the adults of the fossil *Berryteuthis* were larger than adults of *B. magister.* The fossils had a mean length of 2.8 mm (representing a mantle length of 300 mm) and a maximum length of 3.3 mm (representing a mantle of 370 mm), while the samples of *B. magister* had peak lengths of

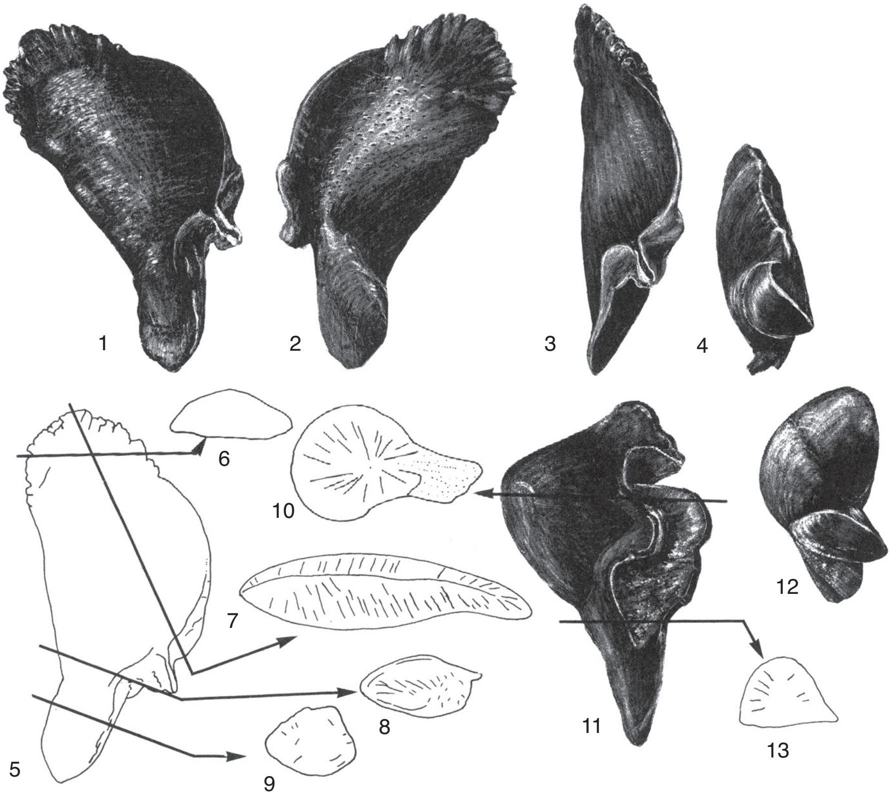

FIG. 18. Right statolith of a Jurassic species *(1–9)* compared with a right statolith from the extant *Loligo forbesii* STEENSTRUP, 1856 *(10–13);* anterior (*1, 5, 11*), posterior view (*2*), medial (*3*), and ventral (*4, 12*) views; *6–10, 13,* cross section views of the points indicated by *arrows,* no scale information available (adapted from Clarke & Maddock, 1988a).

2.4–2.65 mm (representing a dorsal mantle lengths of 160–220 mm) and a maximum length of 3.0 mm (representing a dorsal mantle length of 305 mm).

Although the size of statoliths within genera can be roughly related to the size of the animal, it varies markedly between genera and families. Members of the Cranchiidae PROSCH, 1847, for instance, have very small statoliths, while pterygioteuthids have large statoliths for their size. Thus, it is not possible to estimate the size of the Jurassic coleoids from the statoliths, but only to say that the statoliths are much the same size as those from living species.

BUOYANCY

All the Cenozoic statoliths examined so far, except for *Berryteuthis* sp., are from teuthoid squids having negative buoyancy and, therefore, needing to swim to stay in midwater (CLARKE, 1988). The neutral buoyancy of *Berryteuthis* is probably provided by special oils (CLARKE, DENTON, & GILPIN-BROWN, 1979), as in *Gonatus fabricii* (LICHTENSTEIN, 1818). The living species of coleoids with gas-filled shells (*Sepia* LINNAEUS, 1758, and *Spirula* LAMARCK, 1799) have globular lateral domes; large, broad spurs; and long rostra (Fig. 5). This 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 teuthids or Mesozoic gladius-bearing octobrachians with a squid-like appearance and lifestyle. This assumption is made more complicated by the similarity between *Berryteuthis* and *Sepia,* which was shown by both

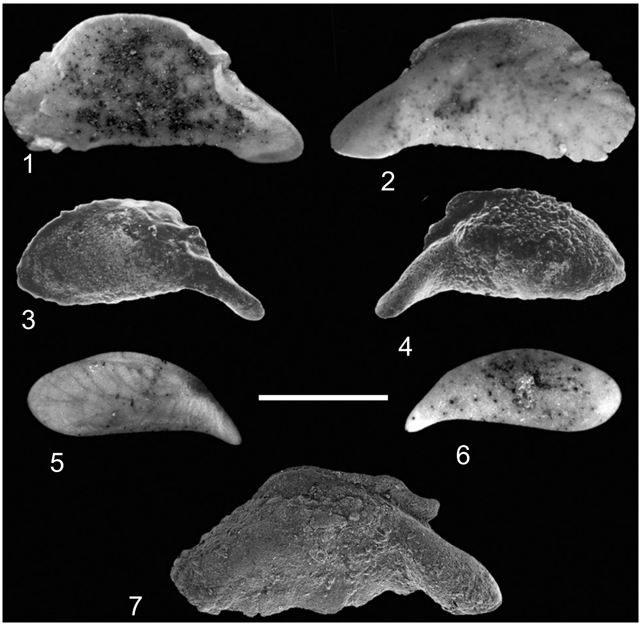

FIG. 19. Morphospecies of Jurassic statoliths. *1–2,* Jurassic sp. A, from the Oxford Clay Formation, Somerset, UK; morphospecies characterized by its large size, curved rostrum, and crenulated margin. *3–4,* Jurassic sp. B from the Lias Group mudstones, Dorset coast east of Charmouth, UK; morphospecies characterized by the distinctly hooked rostrum and wide, rounded, margin with no sign of any crenulation. *5–6,* Jurassic sp. C, from the Oxford Clay Formation, Somerset, UK; morphospecies characterized by the smooth outline, with no crenulations on the margin and markings that look like the veins of a leaf; the structure of these features, and their purpose, is completely unknown as they have not been seen in any of the other morphospecies; *7,* Jurassic sp. D, from the Wattonensis Beds, Frome Clay Formation, upper Bathonian, Rodden Hive Point section, UK (see Hart & others, 2009). Scale bar, 1 mm (adapted from Hart & others, 2015).

multiple discriminant analysis and principle component analysis (CLARKE & MADDOCK, 1988b). The similarity cannot be put down to neutral buoyancy since very different statolith shapes are present in other neutrally buoyant forms, including other members of the Gonatidae. As *Berryteuthis* is only very distantly related to *Sepia,* whether there is some feature in its way of life or behavior that suggests a cause for this similarity needs to be investigated. At present, it can only be observed that it has a similar lifestyle in living close to the bottom and on the continental shelf for some of its life, which may involve similar body movements to *Sepia.*

ENVIRONMENTS

From the deposits in which they occur, the fossil *Loligo* from Europe came from shallow seas with temperatures similar to those off the coast of Morocco today. Living species of *Loligo* mainly inhabit shelf seas less than 200 m in depth, but they also migrate down the slope to 500 m. *Berryteuthis, Dosidicus,* and *Moroteuthis* species seasonally move onto the upper slope and continental shelf along the western coast of North America, although they are predominantly oceanic genera. *Sthenoteuthis* VERRILL, 1880, is oceanic and occurs in deep seas off California.

DISCUSSION

Study of fossil statoliths is likely to prove to be a very valuable means of improving our knowledge of the evolution of the Coleoidea. So far, there are hints from studies of the complicated shape of statoliths that some features may be related to body form, way

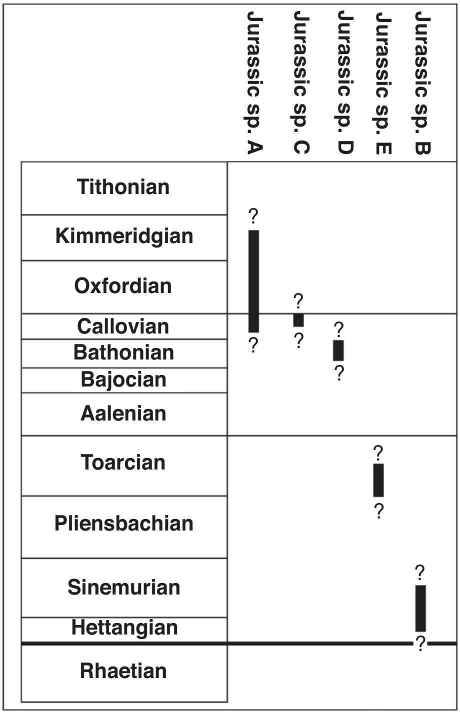

FIG. 20. Known ranges of the statolith morphospecies in the Jurassic of Europe. Ranges should be viewed as tentative, given the few records on which to establish linkages between the different forms (adapted from Hart & others, 2015).

of life, or behavior of the animals. If this can be established in detail for living species, it is possible that we may be able to reconstruct the likely shapes, movement, and perhaps way of life of some species of the Jurassic and perhaps the Cretaceous, of which we are never likely to collect more than a few remains, other than statoliths. Notwithstanding these possible developments, there is no doubt that many features of the statoliths are not related solely to their function and may show evolutionary relationships.

REFERENCES

Allison, P. A. 1988. Phosphatised soft-bodied squids from the Jurassic Oxford Clay. Lethaia 21:403–410.

Appellöf, J. J. A. 1898. Cephalopoden von Ternate, 2: Untersuchungen über Idiosepius, Sepiadarium und verwandte formen, ein Beitrag zur Beleuchtung der Heklokotylisation und ihrer systematischen Bedeutung. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 24(4):570–637.

Arkhipkin, A. I. 1988. Comparative analysis of subannual growth increments in squid statoliths and fish otoliths. Biologicheskie Nauki 11:5–16. In Russian with English abstract.

Arkhipkin, A. I. 2004. Diversity in growth and longevity in short-lived animals: Squid of the suborder Oegopsina. Marine and Freshwater Research 55:341–355.

Arkhipkin, A. I. 2005. Statoliths as ‘black boxes’ (life recorders) in squid. Marine and Freshwater Research 56:573–583.

Arkhipkin, A .I., & V. A. Bizikov. 1998. Statoliths in accelerometers of squids and cuttlefish. Ruthenica 8:81–84.

Arkhipkin, A. I., & V. A. Bizikov. 2000. Role of the statolith in functioning of the acceleration receptor system in squids and sepioids. Journal of Zoology 250:31–55.

Ball, R. 1841. On a species of *Loligo,* found on the shore of Dublin Bay. Proceedings of the Royal Irish Academy 1(19):362–364.

Berry, S. S. 1911a. Preliminary notices of some new Pacific cephalopods. Proceedings of the United States National Museum 40(1838):589–592.

Berry, S. S. 1911b. A note on the genus *Lolliguncula.* Proceedings of the Academy of Natural Science of Philadelphia 63(1):100–105.

Berry, S.W. 1913. A review of the cephalopods of western North America. Bulletin of the U.S. Bureau of Fisheries 30:267–336.

Blainville, H. M. D. d. 1823. Mémoire sur les espèces du genre Calmar (*Loligo,* Lamarck). Journal de Physique, de Chimie et d’Histoire Naturelle 96:116–135.

Blainville, M. H. D. d. 1827. Mémoire sur les Bélemnites. Levrault. Paris. 156 p.

Brierley, A. S., M. R. Clarke, & J. P. Thorpe. 1996. *Ctenopteryx sicula,* a bathypelagic loliginid squid? Symposium on the Evolution of Coleoid Cephalopods, Hilo, Hawaii, 11–12 June, 1995. American Malacological Bulletin 12:137–143.

Buckman, James. 1880. On the *Belemnoteuthis Montefiorei.* Proceedings of the Dorset Natural History and Antiquarian Field Club 3:141–143.

Chun, Carl. 1911. *Cirrothauma,* ein Blinder Cephalopode. Ph.D. dissertation. Leipzig. 22 p.

Clarke, M. R. 1978. The cephalopod statolith: An introduction to its form. Journal of the Marine Biological Association of the United Kingdom 58:701–712.

Clarke, M. R. 1988. Evolution of Buoyancy and Locomotion in Recent Cephalopods. *In* M. R. Clarke & E. R. Truman, eds., Palaeontology and Neontology of Cephalopods. The Mollusca. Vol. 12. Academic Press. London. p. 203–213. K. M. Wilbur was editor-in-chief of series.

Clarke, M. R. 2003. Potential of statoliths for interpreting coleoid evolution: A brief review. Berliner Paläobiologische Abhandlungen 3:37–47.

Clarke, M. R., E. J. Denton, & J. B. Gilpin-Brown. 1979. On the use of ammonium for buoyancy in squids. Journal of the Marine Biological Association of the United Kingdom 59:259–276.

Clarke, M. R., & J. E. Fitch. 1975. First fossil records of cephalopod statoliths. Nature 257:380–381.

Clarke, M. R., & J. E. Fitch. 1979. Statoliths of Cenozoic teuthoid cephalopods from North America. Palaeontology 22:479–511.

Clarke, M. R., J. E. Fitch, T. K. Kristensen, Tsunemi Kubodera, & Linda Maddock. 1980. Statoliths of one fossil and four living squids (Gonatidae: Cephalopoda). Journal of the Marine Biological Association of the United Kingdom 60:329–347.

Clarke, M. R., & Linda Maddock. 1988a. Statoliths of fossil coleoid cephalopods. *In* M. R. Clarke & E. R. Truman, eds., Palaeontology and Neontology of Cephalopods. The Mollusca. Vol. 12. Academic Press. London. p. 153–168, 11 fig.

Clarke, M. R., & Linda Maddock. 1988b. Statoliths from living species of cephalopods and evolution. *In* M. R. Clarke & E. R. Truman, eds., Palaeontology and Neontology of Cephalopods. The Mollusca. Vol. 12. Academic Press. London. p. 169–184.

Clarke, M. R., Linda Maddock, & Etienne Steurbaut. 1980. The first fossil cephalopod statoliths to be described from Europe. Nature 287:628–630.

Dommergues, J.-L., Pascal Neige, & Sigurd von Boletzky. 2000. Exploration of morphospace using Procrustes analysis in statoliths of cuttlefish and squids (Cephalopoda: Decabrachia): Evolutionary aspects of form disparity. The Veliger 43(3):265–276.

Donovan, D. T. 1983. *Mastigophora* 1856: A little-known genus of Jurassic coleoids. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 165:484–495.

Donovan, D. T. 2006. Phragmoteuthida (Cephalopoda: Coleoidea) from the Lower Jurassic of Dorset, England. Palaeontology 49:673–684.

Donovan, D. T., & M. D. Crane. 1992. The type material of the Jurassic cephalopod *Belemnotheutis*. Palaeontology 35:273–296.

Engeser, Theo. 1987. Belemnoid arm hooks ('onychites') from the Swabian Jurassic: A review. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 176:5–14.

Engeser, Theo. 1990. Phylogeny of the fossil coleoid Cephalopoda (Mollusca). Berliner Geowissenschaftliche Abhandlungen (A) 124:123–191.

Engeser, Theo, & M. R. Clarke. 1988. Cephalopod hooks, both recent and fossil. *In* M. R. Clarke & E. R. Truman, eds., Palaeontology and Neontology of Cephalopods, vol. 12, K. M. Wilbur, ed., The Mollusca. Academic Press, Inc. London. p. 133–151.

Férussac, A. É. J. P. F. d'A. de A. 1834. Notice sur deux nouvelles espèces des Céphalopodes appartenant aux genres Calmaret (*Loligopsis veranii*) et Cranchie (*Cranchia bonnellii*). L 'Institut 2(77):355.

Férussac, A. É. J. P. F. d'A. de A., and Alcide d'Orbigny. 1835–1848. Histoire Naturelle Générale et Particulière des Céphalopodes Acétabulifères Vivants et Fossiles. J.-B. Baillière. Paris. lvi + 361 p., 144 pl.

Fischer, Paul. 1880–1887. Manuel de Conchyliologie et de Palaéontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossilles. Savy. Paris. 1369 p.

Frost, G. A. 1926. Otoliths of fishes from the Jurassic of Buckinghamshire and Dorset. Annals and Magazine of Natural History 18:81–85.

Fuchs, Dirk, Yasuhiro Iba, Christina Ifrim, Tomohiro Nishimura, Jim Kennedy, Helmut Keupp, Wolfgang Stinnesbeck, & Kazushige Tanabe. 2013. *Longibelus* gen. nov., a new Cretaceous coleoid genus linking Belemnoidea and Decabrachia. Palaeontology 56(5):1081–1106.

Fuchs, Dirk, Helmut Keupp, Pat Trask, & Kazushige Tanabe. 2012. Taxonomy, morphology and phylogeny of Late Cretaceous spirulid coleoids (Cephalopoda) from Greenland and Canada. Palaeontology 55(2):285–303.

Fuchs, Dirk, & N. L. Larson. 2011. Diversity, morphology, and phylogeny of coleoid cephalopods from the Upper Cretaceous Plattenkalks of Lebanon—Part I: Prototeuthidina. Journal of Paleontology 85(2):234–249.

Gray, J. E. 1849. Catalogue of the Mollusca in the Collection of the British Museum. Part 1. Cephalopoda Antepedia. British Museum (Natural History). London. 614 p.

Guerra, Angel, & Pilar Sánchez. 1985. Crecimiento relitavo del estatolito de *Sepia officianalis* (Cephalopoda, Sepioidea) de la Ria de Vigo. Scientia Marina: Investigación Pesquera 49:545–557.

Hart, M. B., M. R. Clarke, Alex De Jonghe, G. D. Price, K. N. Page, & C. W. Smart. 2015. Statoliths from the Jurassic succession of south-west England, United Kingdom. Swiss Journal of Palaeontology 134:199–205.

Hart, M. B., Alex De Jonghe, Keith Duff, K. N. Page, G. D. Price, C. W. Smart, & Philip Wilby. 2010. Microfossil evidence for a mid-Jurassic squid egg-laying area in association with the Christian Malford Lagerstätte. Geophysical Research Abstracts 12:EGU2010–4415.

Hart, M. B., Alex De Jonghe, Grimes, S. T., B. Metcalfe, G. D. Price, & C. Teece. 2009. Microfaunal analysis of the Wattonensis Beds (Upper Bathonian) of South Dorset. Geoscience in South-West England 12:134–139.

Hart, M. B., Alex De Jonghe, K. N. Page, G. D. Price, & C. W. Smart. 2016. Exceptional accumulations of statoliths in association with the Christian Malford lagerstätte (Callovian, Jurassic) in Wiltshire, United Kingdom. Palaios 31:203–220.

Hart, M. B., Alex De Jonghe, A. J. Rundle, & C. W. Smart. 2013. Statoliths: Neglected microfossils. Journal of Micropalaeontology 32:219–220.

Hart, M. B., & Deborah Hutchinson. 2017. A newly described Jurassic 'squid-like cephalopod' from the Lias Group of Dorset. Geoscience in South-West England 14:35–38.

Hoyle, W. E. 1886. Report on the Cephalopoda Collected by H.M.S. Challenger during the Years 1873–1876. The Voyage of H.M.S. Challenger, Zoology 16(44):1–245.

Jackson, G. D. 1994. Application and future potential of statolith increment analysis in squid and sepioids. Canadian Journal of Fisheries and Aquatic Sciences 51:2612–2625.

Jackson, G. D. 2004. Advances in defining the life histories of myopsid squid. Marine and Freshwater Research 55:357–365.

Jeletzky, J. A. 1966. Comparative morphology, phylogeny and classification of fossil Coleoidea (Mollusca 7). The University of Kansas Paleontological Contributions 42:1–166, 25 pl., 15 fig.

Kear, A. J., D. E. G. Briggs, & D. T. Donovan. 1995. Decay and fossilization of non-mineralized tissues in coleoid cephalopods. Palaeontology 38:105–131.

Keferstein, W. M. 1862–1866. Kopftragende Weichtiere (Malacozoa cephalopophora). *In* H. G. Bronn, ed., Dr. H. G. Bronn's Klassen und Ordnungen der Weichthiere (Malacozoa). C. F. Winter. Leipzig & Heidelberg. p. 1307–1464.

Klug, Christian, Günther Schweigert, Dirk Fuchs, & Gerd Dietl. 2010. First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany). Lethaia 43(4):445–456.

Klug, Christian, Günther Schweigert, Dirk Fuchs, Isabelle Kruta, & Helmut Tischlinger. 2016. Adaptations to squid-style high-speed swimming in Jurassic belemnitids. Biology letters 12(1):DOI:10.1098/rsbl.2015.0877.

Kulicki, Cyprian, & H. Szaniawski. 1972. Cephalopod arm hooks from the Jurassic of Poland. Acta Palaeontologica Polonica 17:379–419.

Lamarck, J. B. 1798. Extrait d'un mémoire sur le genre de la Séche, du Calmar et du Poulpe, vulgairement nommés, Polypes de Mer. Bulletin des Sciences par la Société Philomatique 2(5):129–131.

Lamarck, J. B. 1799. Prodome d'une nouvelle classification des coquilles. Mémoires de la Société d'Histoire Naturelle de Paris 1:63–91.

Leach, W. E. 1817. Synopsis of the orders, families, and genera of the class Cephalopoda. *In* W. E. Leach, The Zoological Miscellany: Being Descriptions of New or Interesting Animals, Vol. 3. B. McMillan & E. Nodder & Son. London. 137–141.

Lehmann, Jens. 2010. Statolithen: Kleine Fossilien ganz groß. Fossilien 27(6):359–366.

Lesson, R. P. 1830. Mollusques, Annelides et Vers. Voyage Autour du Monde, sur la Corvette de la Majeste, La Coquille, Pendant les Annees 1822, 1823, 1824 et 1825, 2(1):239–471.

Lesueur, C. A. 1821. Descriptions of several new species of cuttlefish. Journal of the Academy of Natural Sciences of Philadelphia 2(1):86–101.

Lichtenstein, H. C. 1818. Von den Sepien mit Krallen. Isis über Encyclopadische Zeitung 1818(9):1591–1592.

Linneaus, Carolus. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, diferentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentius Salvius. Stockholm. 824 p.

Lipinski, M. R. 1993. The deposition of statoliths: A working hypothesis. *In* T. Okutani, T., R. K. O'Dor, & Tsunemi Kubodera, eds., Recent Advances in Cephalopod Fisheries Biology. Tokai University Press. Tokyo. p. 241–262.

Lipinski, M. R. 2001. Statoliths as archives of cephalopod life cycle: A search for universal rules. Folia Malacologica 9:115–123.

Mantell, G. A. 1848. Observations on some belemnites and other fossil remains of Cephalopoda, discovered by Mr Reginald Neville Mantell in the Oxford Clay near Trowbridge, in Wiltshire. Philosophical Transactions of the Royal Society 138:171–182.

Martill, D. M., & J. D. Hudson, eds. 1991. Fossils of the Oxford Clay. Palaeontological Association, Field Guide to Fossils, No. 4. The Palaeontological Association. London. 283 p.

Martin, G. P. R., & Wilhelm Weiler. 1954. Fisch-Otolithen aus dem deutschen Mesozoikum (Dogger bis Wealden). Senckenbergiana Lethaea 35:119–192.

Martins, H. R. 1982. Biological studies of the exploited stock of *Loligo forbesi* (Mollusca: Cephalopoda) in the Azores. Journal of the Marine Biological Association of the United Kingdom 62:799–808.

Massy, A. L. 1907. Preliminary notice of new and remarkable cephalopods from the south-west coast of Ireland. Annals and Magazine of Natural History (series 7) 20:377–384.

Mitchell, S. F., & C. J. Underwood. 1999. Lithological and faunal stratigraphy of the Aptian and Albian (Lower Cretaceous) of the Type Speeton Clay, Speeton, N.E. England. Proceedings of the Yorkshire Geological Society 52(3):277–296.

Munier-Chalmas, E. 1872. Sur les genres *Bayanoteuthis* et *Belopterina.* Bulletin de Société Géologique de France, 2 (serie 29):530–531.

Naef, Adolf. 1912. Teuthologische Notizen. 4. Die Gattungen der Loliginidae. Zoologischer Anzeiger 39(25):741–745.

Naef, Adolf. 1922. Die fossilen Tintenfische: Eine Paläozoologische Monographie. Gustav Fischer. Jena. 322 p.

Neige, Pascal. 2006. Morphometrics of hard parts in cuttlefish. Vie et Millieu 56(2):121–127.

Neige, Pascal, & J.-L. Dommergues. 2002. Disparity of beaks and statoliths of some Coleoids: A morphometric approach to depict shape differentiation. Abhandlungen der Geologischen Bundesanstalt 57:393–399.

Neige, Pascal, Herve Lapierre, & Didier Merle. 2016. New Eocene coleoid (Cephalopoda) diversity from statolith remains: Taxonomic assignation, fossil record analysis, and new data for calibrating molecular phylogenies. Plos One 11(5):e0154062.

Neth, Ursula, & Wilhelm Weiler. 1953. Untersuchungen an Fischotolithen aus dem deutschen Dogger. Paläontologische Zeitschrift 27:113–121.

Orbigny, Alcide d'. 1834–1847. Mollusques. Voyage dans l'Amerique Méridionale 5(3):1–758.

Orbigny, Alcide d'. 1842. Mémoire sur deux genres nouveaux céphalopodes fossiles (les *Conoteuthis* et *Spirulirostra*) offrant des passages, d'un côte entre la spirule et la sèche, de l'autre des bélemnites et les Ommastrephes. Annales de la Société des Sciences Naturelles (2, Zoologie) 17:362–379.

Owen, R. A. 1844. Description of certain belemnites, preserved, with a great proportion of their soft parts, in the Oxford Clay at Christian Malford, Wilts. Philosophical Transactions of the Royal Society 125:65–85.

Page, K. N., & Peter Doyle. 1991. Other cephalopods. *In* D. M. Martill & J. D. Hudson eds., Fossils of the Oxford Clay. Palaeontological Association, Field Guide to Fossils, No. 4. The Palaeontological Association. London. p. 144–162.

Pearce, J. C. 1841. On the mouths of ammonites and on fossils contained in laminated beds of the Oxford Clay, discovered in cutting the Great Western Railway, near Christian Malford in Wiltshire. Proceedings of the Geological Society, London 3:592–594.

Pearcy, W. G., & G. L. Voss. 1963. A new species of gonatid squid from the northeastern Pacific. Proceedings of the Biological Society, Washington 76:105–112.

Prosch, Victor. 1847. Nogle nye Cephalopoder, beskrevne og anatomisk undersogte. Kongelige Danske Videnskabernes Selskabs Skrifter (series 5) 1:53–72.

Quenstedt, F. A. 1845–1849. Petrefactenkunde Deutschlands, 1. Abteilung, 1. Band, Cephalopoden. Verlag Fues. Tübingen. 581 p.

Rundle, A. J. 1967. The occurrence of Upper Liassic otoliths at Holwell, Leicestershire. Mercian Geologist 2:63–72.

Rüppell, Eduard. 1844. Intorno ad alcuni cefalopodi del mare di Messina. Lettera del Dr. Eduardo Rüppell di Frankfort sul Meno al Prof. Anastasio Cocco. Giornale del Gabinetto Letterario di Messina 5(27–28):129–135.

Schwarzhans, Werner. 2018. A review of Jurassic and Early Cretaceous otoliths and the development of early morphological diversity in otoliths. Neues Jahrbuch der Geologie und Paläontologie, Abhandlungen 287(1):75–121.

Spratt, J. D. 1978. Age and growth of the market squid, *Loligo opalescens* Berry, from statoliths. Californian Cooperative in Oceanic Fisheries Investigations, Results 20:58–64.

Steenstrup, Japetus. 1856. Hectoctyldannelsen hos Octopodslaegterne Argonauta og Tremoctopus, oplyst ved Iagttagelse af lignende Dannelser hos Blacksprutterne i Almindelighed. Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke. Naturvidenskabelig og Mathematisk 4:185–216.

Steenstrup, Japetus. 1857. Prof. Steenstrup foreviste og beskrev nogle nye Blaeksprutter, *Dosidicus Eschrichtii* Stp. og *Onychoteuthis*(?). Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjöbenhavn 1856–1857:120–121.

Steenstrup, Japetus. 1880. De Ommatostrephagtige Blaeksprutter indbyrdes Forhold, en Oreintering. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger 1880:73–110.

Steenstrup, Japetus. 1881. Sepiadarium og Idiosepius to nye Slaegter af Sepiernes Familie. Med Bemaerknin ger om de to beslaegted e former Sepioloide a D'Orb. og Spirula Lmk. Det Kongelige Dansk Videnskabernes Selskabs Skrifter (series 6) 1:213–242.

Swinnerton, H. H. 1936. The Cretaceous belemnites. Part 1. Monograph of the Palaeontographical Society, London 89(403):1–16.

Swinnerton, H. H. 1937. The Cretaceous belemnites. Part 2. Monograph of the Palaeontographical Society, London 90(407):17–30.

Swinnerton, H. H. 1948. The Cretaceous belemnites. Part 3. Monograph of the Palaeontographical Society, London 102(446):31–52.

Swinnerton, H. H. 1952. The Cretaceous belemnites. Part 4. Monograph of the Palaeontographical Society, London 106(461):53–62.

Swinnerton, H. H. 1955. The Lower Cretaceous belemnites. Part 5. Monograph of the Palaeontographical Society, London 108(469):63–86.

Tang, C. M. 2002. Oxford Clay: England's Jurassic Marine Park. *In* D. J. Bottjer, Walter Etter, J. W. Hagadorn, & C. M. Tang, eds., Exceptional Fossil Preservation: A Unique View on the Evolution of Marine Life. Columbia University Press. New York. p. 307–325.

Verany, J. B. 1839. Mémoire Sur Six Nouvelles Espéces de Céphalopodes Trouvées dans la Méditerranée à Nice. Mémoire della Reale Accademia della Scienza di Torino (series 2) 1:91–98.

Verrill, A. E. 1876. Note on Gigantic Cephalopods: A Correction. American Journal of Science and Arts 12:236–237.

Verrill, A. E. 1880. The cephalopods of the northeastern coast of America. Part I: The gigantic squids (*Architeuthis*) and their allies; with observations on similar large species from foreign localities. Transactions of the Connecticut Academy of Sciences 5(5):177–257.

Verrill, A. E. 1884. Second catalogue of the Mollusca, recently added to the fauna of the New England Coast and the adjacent parts of the Atlantic, consisting mostly of deepsea species, with notes on others previously recorded. Transactions of the Connecticut Academy of Sciences 6(1):139–294.

Wilby, P. R., Keith Duff, Kevin Page, & Susan Martin. 2008. Preserving the unpreservable: A lost world rediscovered at Christian Malford, UK. Geology Today 24(3):95–98.

Wilby, P. R., J. D. Hudson, R. G. Clements, & N. T. J. Hollingworth. 2004. Taphonomy and origin of an accumulate of soft-bodied cephalopods in the Oxford Clay Formation (Jurassic, England). Palaeontology 47:1159–1180.

Wind, F. H., M. G. Dinkelman, & S. W. Wise Jr. 1977. Jurassic scolecodont-like microfossils from the Falkland Plateau (Deep Sea Drilling Project Site 330). *In* P. F. Barker, I. W. D. Dalziel, & S. W. Wise, Jr., eds., Initial Reports of the Deep Sea Drilling Project, Vol. 36. U.S. Government Printing Office. Washington DC. p. 829–843, 6 pl.

Wülker, Gerhard. 1920. Über Cephalopoden des Roten Meeres. Senckenbergiana 2(1):48–58.