STATOLITHS OF CENOZOIC TEUTHOID CEPHALOPODS FROM NORTH AMERICA

by MALCOLM R. CLARKE *and* JOHN E. FITCH

ABSTRACT. Statoliths of fossil teuthoids are described in detail for the first time. Several hundred statoliths collected at eleven North American sites including Eocene, Oligocene, Miocene, Pliocene, and Pleistocene deposits are from fourteen kinds of teuthoid. These include six species of the family Loliginidae. Five new species, *Loligo applegatei* n. sp., *L. mississippiensis* n. sp., *L. barkeri* n. sp., *L. valeriae* n. sp., and *L. stillmani* n. sp. are extinct; *L. opalescens* is still living off California. The new ommastrephid species *Dosidicus lomita* n. sp. and *Symplectoteuthis pedroensis* n. sp. and the new onychoteuthid species *Moroteuthis addicotti* n. sp. are extinct species of genera which include species now living off California. Fossils of *Berryteuthis* differ from *B. magister* but have not been given a specific name. Four other kinds of *Loligo* statoliths are described but are immature or damaged and are not named. The genus *Loligo* is found as early as the Eocene while squids of the genera *Dosidicus*, *Symplectoteuthis*, *Berryteuthis*, and *Moroteuthis* were living in the Pliocene. The evolution of *Loligo* and the ecology of the species are discussed.

STATOLITHS of cephalopods are small, hard, calcareous stones which lie in fluid-filled cavities or statocysts within the cartilaginous skull of members of the Octopoda, Sepioidea, and Teuthoidea. While the internal shapes of the statocysts have been described for many species (Ishikawa 1924; Dilly *et al.* 1975), very little attention has been paid to the form of the statolith (Clarke and Fitch 1975; Dilly 1976). As pointed out previously (Clarke and Fitch 1975) statoliths have shapes which are often characteristic for species and description of statoliths from living cephalopods is currently under way (Clarke 1978 and in preparation) to form a basis for a detailed study of fossil ancestors of the living Teuthoidea and Sepioidea. The present work is the first description of fossil statoliths and includes specimens from ten North American Tertiary formations of Eocene, Oligocene, Miocene, Pliocene, and Pleistocene age.

All the species represented in the present collection belong to the Teuthoidea and the majority belong to the Loliginidae. Loliginid squids are neritic, living exclusively on or near continental shelves in near coastal waters. No loliginid is known to live exclusively in oceanic waters and, near the edge of the continental shelf, their numbers may change from extreme abundance to total absence within a few kilometres although they can extend down the continental slope, near the sea bottom, to about 500–600 m. As all the formations described here contain loliginid squid statoliths and there is no evidence to suggest that extinct loliginids had different habits from the living forms, the formations are almost certainly derived from shallow, coastal seas.

The majority of oceanic species of teuthoid, generally grouped in the Oegopsida, do not enter shallow coastal seas and only a few species are regularly found on the continental shelf (Clarke 1966); species that do, nearly all belong to the family Ommastrephidae. In the present collection four species of oegopsid are represented and of these, two belong to this family. The close relationship of these four oegopsids is not certainly established and this must await further work on oegopsid statoliths.

[Palaeontology, Vol. 22, Part 2, 1979, pp. 479–511, pls. 53–55.]

However, sufficient is known to make it likely that three species are new to science and they have therefore been given specific names and provisional generic names.

Sepioids are also neritic, shelf-living cephalopods but are not represented in the present collection. *Sepia* does not live in waters around North America but the genus is known in fossil deposits (Jeletzky 1966).

Fourteen distinct types of cephalopod are present in this collection. While there is individual variation and changes of form due to growth, the samples are large enough and experience with living species is great enough to be sure that at least ten species are represented and nine of these are different from living species whose statoliths have been examined (Clarke 1978 and in preparation). Statoliths of all living species have not been examined since they dissolve in the most commonly used preservatives and fresh specimens need to be collected for statoliths to become available. However, over fifty species including more than forty genera and twenty families have now been examined by one of the authors (M. R. C.). Several hundred specimens of several species have been examined to ascertain changes during growth and the extent of individual variation. This basic work, while not exhaustive, gives sufficient confidence to name eight new fossil species of teuthoid on the basis of the statolith alone. While the creation of names based upon a small part of the animals is usually inadvisable, in the present instance it is justified by the almost total lack of other remains of teuthoids and Octopods in the fossil record and the not inconsiderable number of features of the statolith which can be used as criteria for identification (Clarke 1978). Thus, the description and naming of statoliths will not conflict with names based upon other parts of the same cephalopods (unless members of the Ammonoidea and Belemnitida are also found to have possessed statoliths; living *Nautilus* does not possess similar calcareous statoliths).

MATERIALS AND METHODS

Since squid statoliths, fish otoliths, and shells of most marine molluscs are composed of one polymorph of calcium carbonate (i.e. aragonite), one can assume that a fossil deposit containing an assortment of sea shells will probably contain statoliths and earstones also. By using this philosophy as a working hypothesis, one of us (J. E. F.) routinely sampled every shelly fossil exposure that he encountered in North America if it was friable or could be broken down without destroying or dissolving the aragonitic components. Not all such beds produced statoliths, but twelve of more than thirty deposits that were sampled yielded one or more of these tiny artifacts.

When a potentially productive fossiliferous exposure was observed in a road cut, cliff, stream bank, or at a construction site, a field sample comprising 5 to 50 kg or more of fossiliferous matrix was collected. At the first opportunity, the field sample was allowed to soak in a tub of water and then screened through a series of three sieves with mesh sizes of 2, 1, and 0·5 mm (approximately 10, 20, and 30 openings per inch). To start the process, several handfuls of the saturated 'dirt' solution would be placed in the largest-mesh sieve which was then partially submerged in a second tub of water where the mixture was filtered by gently rotating and shaking the screen. The retained residue was then dumped on to several layers of newspaper and allowed to dry in the sun. This process was continued until the entire field sample had been sieved with the 2 mm screen. At that time, the residue which had passed through the 2 mm mesh, was processed with the 1 mm sieve in the same manner, and finally with the 0·5 mm screen.

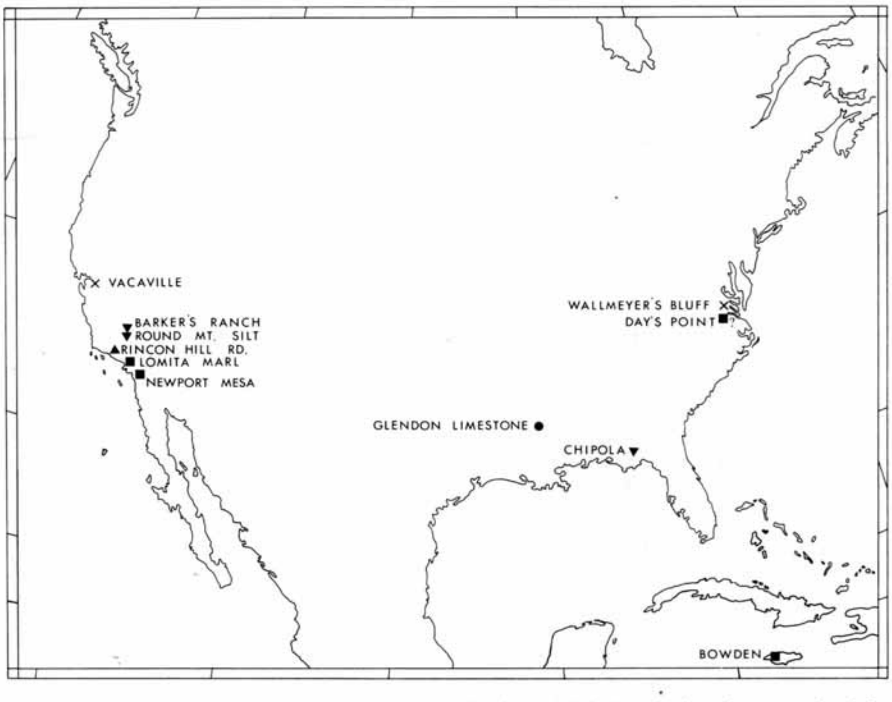
When the samples were dry, the coarsest fraction was screened through 6·3 mm (¼-inch) mesh to remove large shells, rocks, bone fragments, etc. The residue retained by the ¼-inch mesh would be checked by eye, but all other residue was examined by spreading a spoonful at a time in a flat dish with raised edges, and systematically searching through this residue with a pair of forceps while viewing through a binocular microscope at six magnifications. By having washed the samples through three sieves, the particles were graded by size and the task of searching through the material under the microscope was greatly simplified.

If a particular exposure proved highly productive of the types of fossils desired, additional matrix, sometimes in excess of one ton, would be removed and processed. To date, no squid statoliths have been found in the residue retained by the 2 mm sieve, but both the 1 and 0·5 mm fractions have yielded statoliths. Unfortunately, only recently did we determine that statoliths of meso- and bathypelagic cephalopods will pass through the finest-mesh sieves (0·5 mm) that we used.

Field samples which would not break down by soaking in water (e.g. siltstone, heavy clay, etc.), were successfully processed by first drying the sample thoroughly and then submerging a bucketful at a time in paraffin (kerosene) for 24 hours. When removed from the kerosene and placed in water, even rock-hard pieces of siltstone would crumble quite rapidly so that sieving was easily accomplished.

The geographical positions of the eleven locations where samples contained statoliths of teuthoids are given in text-fig. 1. Description of the statoliths is based upon criteria for identification and the method outlined elsewhere (Clarke 1978).

The living species whose statoliths have been examined and are most pertinent to the present work are *Loligo opalescens* Berry, 1911, *L. pealei* Lesueur, 1821, *L. vulgaris* Lamarck, *L. forbesi* Steenstrup, 1856, *L. plei* Blainville, 1823, *Lolliguncula panamensis* Berry, *L. brevis* (Blainville, 1823), *Alloteuthis subulata* (Lamarck, 1798), *Symplectoteuths oualaniensis* (Lesson, 1830), *Dosidicus gigas* (d'Orbigny, 1835), *Todarodes*



TEXT-FIG. 1. Geographical positions and age of the sites from which deposits have been examined for cephalopod statoliths. ×= Eocene; ● = Oligocene; ▼= Miocene; ■ = Pliocene; ▲= Pleistocene.

saqittatus (Lamarck, 1799), *Berryteuthis magister* (Berry, 1913), and *Moroteuthis robusta* (Verrill, 1876). For each fossil species, a drawing or, if several specimens are available, a scanning electron micrograph, measurements, and a verbal description mentioning criteria important for its identification are given. Where a sufficient number of statoliths represent a species, regressions for measurements have been calculated, plotted, and compared statistically. SEM photographs of a size range of two species are given to show the usual variation seen within a species. Terms and dimensions used in the descriptions are shown in text-fig. 2. Measurements were made with a Wild M5 microscope with an eyepiece micrometer.

Holotypes have been deposited in the Natural History Museum of Los Angeles County (LACM) and, where numbers of specimens allow, representatives will also be deposited in the U.S. National Museum of Natural History (USNM) Washington and the British Museum (Natural History) London (BMNH).

DESCRIPTION OF FORMATIONS AND CONTAINED STATOLITHS

WALLMEYER'S BLUFF, VIRGINIA

Age. Middle Eocene (or Lower?).

Location. Wallmeyer's Bluff, Hanover County, Virginia. South Bank of Pamunkey River on property owned by Mr. Wallmeyer. 1·6 km (1·0 miles) north of state road 732 from intersection with state road 629 then 0·3 km (0·2 miles) on private road to River Nanjemoy Formation.

Previous reports and associated fauna. Approximately 90 kg (200 lbs) of fossiliferous matrix were sampled from this site, but only the residue retained by 1·0 mm and larger mesh was examined very carefully. The residue retained by the 0·5 mm sieve consisted mostly of rounded, water-worn quartz sand and contained very few otoliths, so less than a pint (0·47 l) of it was examined under the microscope. Since the single squid statolith from this site turned up in this small amount of fine residue, a considerably greater number of statoliths probably could be obtained with additional sampling.

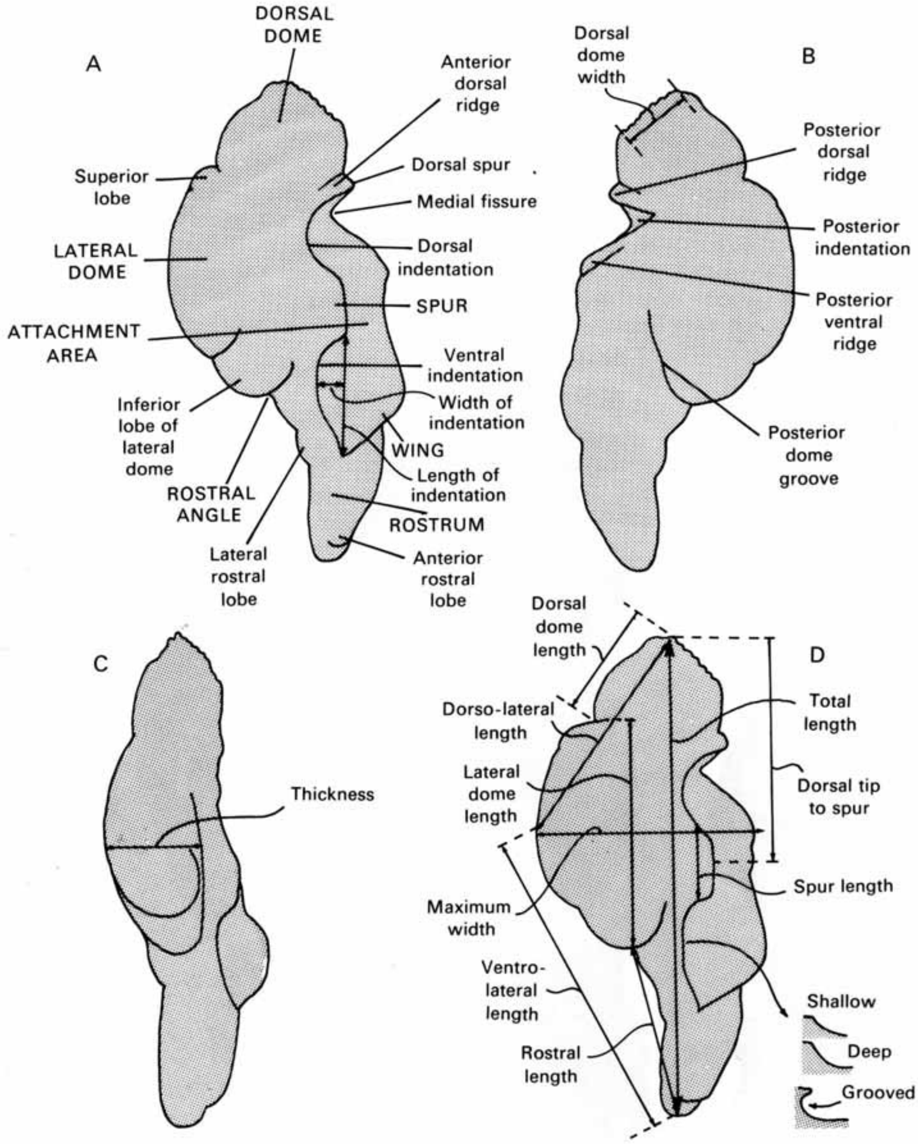
The residue that was examined yielded several hundred otoliths and teeth representing about thirty-five species of sharks, rays, and bony fishes belonging to at least twenty families. Otoliths of cusk-eels (Ophidiidae), eels (Congridae), flatfishes (Bothidae), and croakers and drums (Sciaenidae) were most abundant. Other shallow-water forms included salt-water catfish (Ariidae), pearlfish (Carapidae), pterothrissids (Pterothrissidae), and herrings (Clupeidae). Extant boarfishes (*Antigonia* spp.) and berycids (Berycidae) are mostly deep-water forms, but their remains were not common in this deposit. Based only upon the fish remains at this one locality, the Nanjemoy Formation represents deposition at sea depths no greater than about 100 m.

CEPHALOPODA, TEUTHOIDEA
Family LOLIGINIDAE d'Orbigny, 1835
Loligo applegatei n. sp.

Text-fig. 3A–E

Material. The single right statolith found in this deposit is clearly distinct from any species of living loliginids examined previously (Clarke, in preparation) or fossil loliginids described here. Its condition is good except for a few deeply pitted areas which are probably caused by some organism capable of dissolving aragonite. Holotype LACMIP 5756.

Diagnosis. This statolith (the holotype) may be distinguished by the following diagnostic features (text-fig. 3A–E): The lateral dome is broadest at its dorsal end, i.e. it is pointed in the manner typical of *Loligo* (Clarke, in preparation); it is more sharply pointed than most other species examined. The lateral dome represents a large area in anterior and posterior aspects and is both broad and long in comparison with the rostrum. In outline, the lateral margin of the dome is smoothly curved and there is no inferior lobe to the dome. There is no distinct posterior dome groove. The dorsal dome is deflected anteriorly and extends dorsal to the point of the lateral dome.



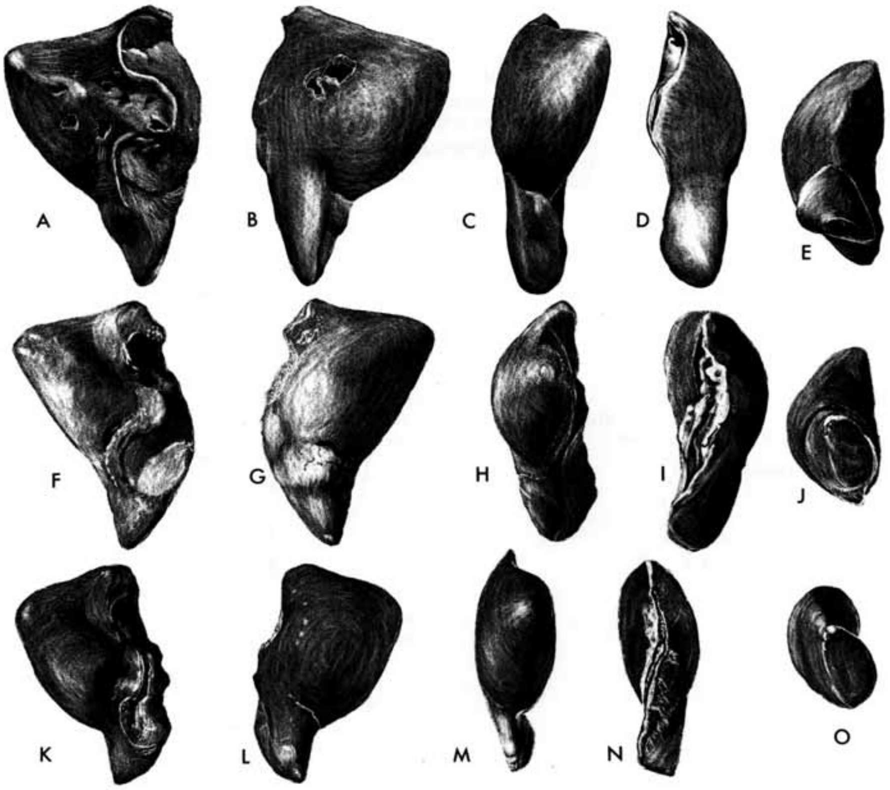
TEXT-FIG. 2. Diagrams of a generalized teuthoid right statolith to show dimensions and terms used in descriptions. A, view of anterior side; B, view of posterior side; C, view of lateral side; D, view of anterior side to show the principal measurements used and terms used to describe the form of the indentations. W = width; L = length.

The well-defined spur has an eroded ventral margin but was probably fairly wide. The dorsal and ventral indentations are approximately the same size. There is a very small dorsal spur and no posterior indentation.

Remarks. Dimensions of this statolith are given in Table 1. As will be seen from text-figs. 4–6 the only dimension which clearly distinguishes the species from the other ones plotted is the maximum width (text-fig. 4). This dimension also clearly distinguishes the specimen from the living loliginids so far examined (Clarke, in preparation). *L. plei* is closest to it in this respect.

The very unusual dome of this specimen clearly separates it from other species and justifies the erection of the species based upon one specimen only.

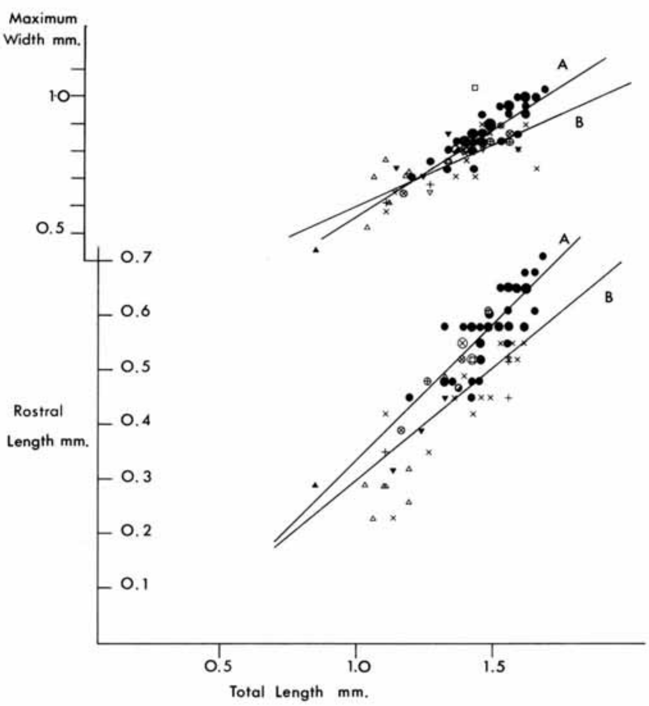
This is named after Shelton P. Applegate who first collected at this site and gave us directions for locating it.



TEXT-FIG. 3. Right statoliths of three species of fossil *Loligo*. A–E, *Loligo applegatei* n. sp., holotype (total L = 1·45 mm); A, anterior view; B, posterior view; C, lateral view; D, medial; E, ventral view; F–J, the same views of the statolith of *L. mississippiensis* from Chipola Fm. (total L = 1·32 mm); K–O, the same views of the statolith of *L. valeriae* n. sp. Paratype, total L = 1·19 mm.

TABLE 1. Dimensions of holotypes, some paratypes, and some figured specimens of the species described here.

	Total length	Dorso-lateral length	Ventro-lateral length	Lateral dome length	Rostral length	Dorsal tip to spur	Spur length	Maximum width	Thickness	Dorsal dome length	
Loligo applegatei n. sp.	1·45	0·77	1·42	0·89	0·52	0·58	0·26	1·03	0·52	0·29	Text-fig. 3A–E
Loligo sp. A	0·84	0·29	0·81	0·61	0·29	0·42	0·19	0·44	0·23	—	
L. mississippiensis n. sp.											
Paratype 1	1·55	0·74	1·52	1·03	0·45	0·65	0·23	0·84	0·48	0·19	
Paratype 2	1·26	0·58	1·06	0·94	0·48	0·52	0·23	0·68	0·39	0·16	
Paratype 3	1·10	0·58	0·97	0·74	0·35	—	—	0·61	0·32	0·10	
Holotype 4	1·48	0·61	1·42	0·90	0·61	0·68	0·26	0·84	—	0·13	Pl. 54, figs. 11–15
Chipola	1·32	0·71	1·26	0·87	0·47	0·61	0·26	0·82	0·48	0·23	Text-fig. 3F–J
L. barkeri n. sp.											
Paratype	1·52	0·94	1·32	1·03	0·48	0·65	0·29	1·00	0·58	0·29	Pl. 54, figs. 1–5
Holotype	1·55	0·58	1·35	0·94	0·61	0·68	0·23	0·90	0·52	0·26	
L. valeriae n. sp.											
Holotype	1·32	0·65	1·32	0·89	0·48	0·61	0·32	0·77	0·45	—	
Paratype 1	1·19	0·61	1·06	0·87	0·32	0·58	0·29	0·71	0·40	—	Text-fig. 3K–O
Paratype 2	1·03	0·58	1·03	0·79	0·29	0·52	—	0·58	0·39	—	
Loligo sp. C	—	0·61	—	0·84	—	0·61	0·32	0·81	0·48	—	Text-fig. 7I–L
Loligo sp. D	1·13	0·55	1·00	0·81	0·26	0·61	0·26	0·68	0·42	—	
L. stillmani n. sp.											
Holotype	1·42	0·68	1·16	0·74	0·48	0·68	0·26	0·84	0·42	0·29	Pl. 54, figs. 6–10
Berryteuthis sp.	2·77	1·48	1·87	1·19	1·10	1·39	0·48	1·48	0·77	0·81	Text-fig. 11, figs. 1–5
Dosidicus lomita n. sp.	2·52	1·58	1·52	1·61	0·71	1·39	0·29	1·26	0·81	0·26	Text-fig. 8A–E
Symplectoteuthis pedroensis n. sp.	2·26	1·23	1·55	1·45	0·48	1·13	0·29	1·35	0·68	0·52	Text-fig. 8F–J
Moroteuthis addicotti n. sp.	1·48	0·71	1·03	0·77	0·65	—	—	0·81	0·39	0·32	Pl. 54, figs. 16–20
Paratype 1	1·26	0·68	1·00	0·71	0·52	—	—	0·65	0·32	0·35	
Paratype 2	1·58	0·77	1·16	0·84	0·68	—	—	0·81	0·42	0·29	



TEXT-FIG. 4. Statolith dimensions. Maximum width and rostral length plotted against the total length of the statolith. Regressions for A, *Loligo barkeri* n. sp. and B, *L. stillmani* n. sp. are included (see Table 2). □ *L. applegatei* n. sp.; ▲ *Loligo* sp. A; + *L. mississippiensis* n. sp. from Glendon Limestone; ◑ *L. mississippiensis* n. sp. from Chipola Formation; ○ ● *L. barkeri* n. sp. from Barker's Ranch. Larger symbols for two and three specimens; ▼ *L. barkeri* n. sp. from Round Mount silt; △ *L. valeriae* n. sp.; ▽ *Loligo* sp. C; × *L. stillmani* n. sp.

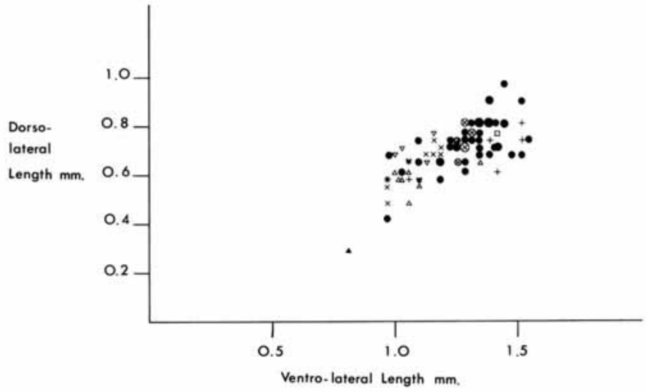
VACAVILLE SHALE—CALIFORNIA

Age. The Vacaville Shale correlates with the Lutetian Stage of Europe, and thus is younger than the London Clay and older than the Barton Beds (Bartonian) of England.

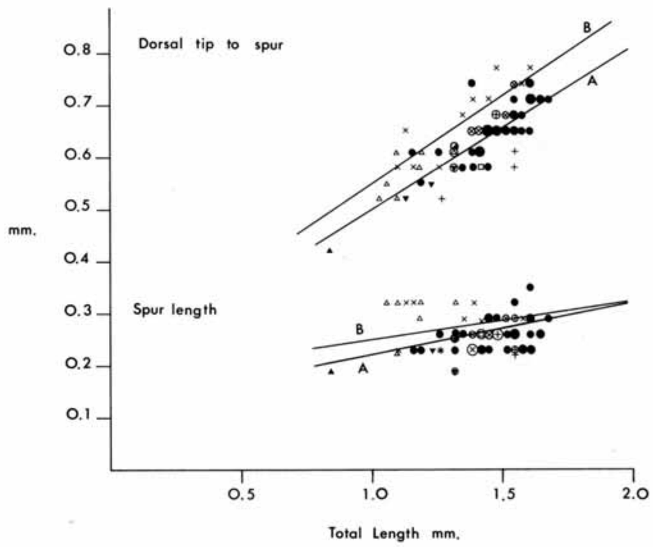
Location. 6·4 km (4 miles) north of Vacaville, California, in the vicinity of Dunn's Peak along Vlatis Creek (township 6 N., range 1 W., Vaca Valley Quadrangle, U.S. Geological Survey topographic map).

Previous reports and associated fauna. Approximately 18 kg (40 lbs) of fossiliferous matrix were collected. This material, when screened with 50-mesh sieves, yielded about twenty otoliths and otolith fragments (four or five species), a few shark teeth (one species), and a single tiny squid statolith (Welton, pers. comm.).

Foraminifers from this locality indicate a deep-water coastal embayment, warm subtropical to tropical waters, and normal oceanic circulation. Although few in numbers, vertebrate remains tend to substantiate these conclusions regarding depth and temperature at time of deposition. Previous reports on the site were published by Palmer (1923) and Mallory (1959).



TEXT-FIG. 5. Statolith dimensions. Dorso-lateral length plotted against ventro-lateral length. Symbols as in text-fig. 4.



TEXT-FIG. 6. Statolith dimensions. Dorsal tip to spur and spur length plotted against total length of statolith. Symbols as in text-fig. 4. Regressions for A, *Loligo barkeri*, n. sp. and B, *L. stillmani* n. sp. are included (see Table 2).

CEPHALOPODA, TEUTHOIDEA

Family LOLIGINIDAE d'Orbigny, 1835

Loligo sp. A

Text-fig. 7A–D

Material. One right statolith was collected in good condition but was unfortunately broken into two fragments when transferred between containers.

Remarks. This is probably from a young squid since it is the smallest collected and only has a total length of 0·84 mm. It has the narrow rounded lateral dome characteristic of young loliginids (Pl. 53 and Clarke, in preparation). Because it is juvenile, has a rather uncharacteristic shape, and there is only one, this specimen has not been named but is probably distinct from our other Eocene species *Loligo applegatei* n. sp. It almost certainly belongs to the genus *Loligo* since the lateral dome is widest dorsally, the dorsal dome is small and does not protrude dorsally more than the lateral dome and the spur and indentations are very distinct.

Distinctive features of this statolith are as follows (text-fig. 7A–D): The lateral dome is widest near its dorsal end but is not pointed as in *L. applegatei* n. sp. There is no clear posterior dome groove. The rostral angle is very obtuse. The dorsal dome barely protrudes dorsally further than the lateral dome. The distinct spur is longer than wide.

Dimensions of this statolith are given in Table 1. Comparing these measurements with the other fossil loliginids described here, the dorso-lateral length (text-fig. 5), the dorsal tip to spur and the spur length (text-fig. 6) all seem rather lower than expected in smaller specimens of other available species. The dorso-lateral length is relatively smaller than in living *L. opalescens* of the same size from California (Clarke, in preparation).

This specimen certainly suggests that more samples from this deposit will yield a west coast Eocene species distinct from the east coast *L. applegatei* n. sp.

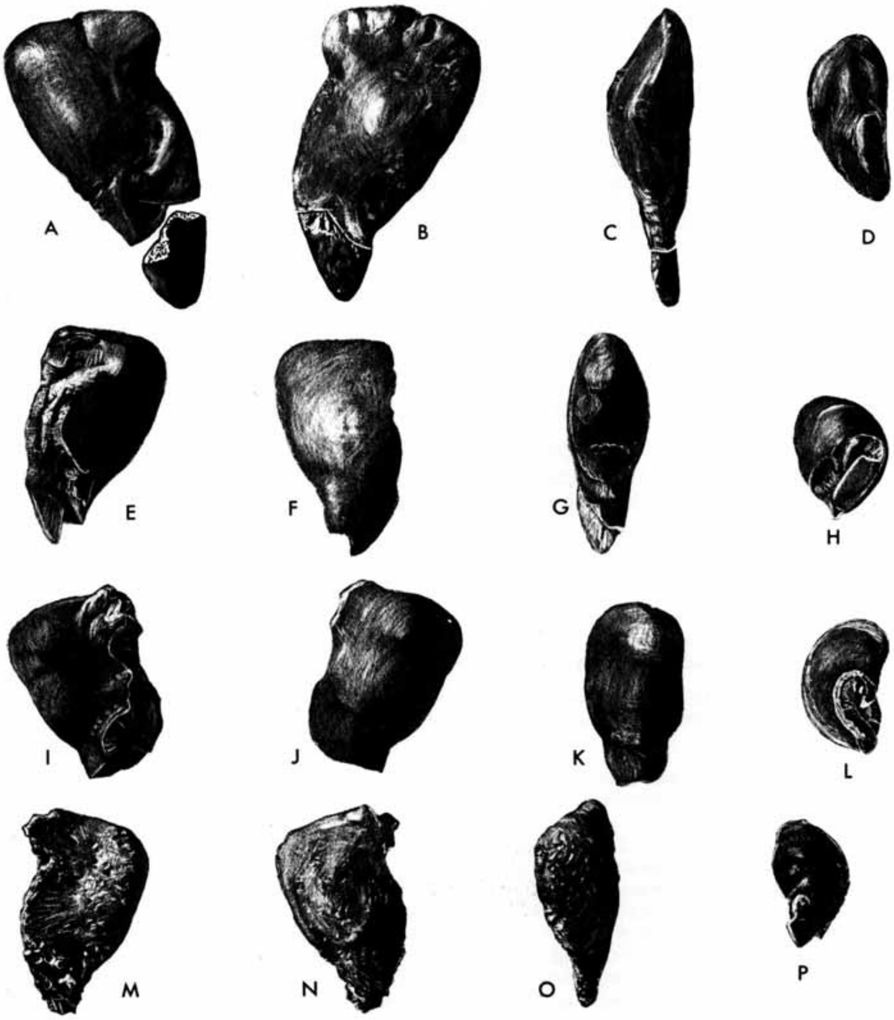
GLENDON LIMESTONE—MISSISSIPPI

Age. Lower–Middle Oligocene.

Location. Road cut on east side of US-61 just north of intersection of US-61 bypass from Interstate-20 (Vicksburg, Mississippi).

Previous reports and associated fauna. Approximately 18 kg (40 lbs) of fossiliferous matrix yielded nearly 4000 otoliths representing at least twenty-five kinds of fish belonging to twenty or more families. Teeth from sharks, rays, and a triggerfish added a half-dozen other species. Nearly 90% of the otoliths were from two kinds of flatfish (Bothidae and/or Pleuronectidae), five kinds of eels (mostly Congridae), and one kind of codlet (Bregmacerotidae). Although some species of *Bregmaceros* are inhabitants of the pelagic realm, others are known to enter very shallow water including estuaries. If one assumes the *Bregmaceros* otoliths in this deposit were from a shallow-water form, it would not be unreasonable to speculate that the entire fish fauna represented a shallow, near-shore environment.

Previously Frizzell and Dante (1965) reported upon the otoliths of two species of sciaenids they found in Glendon Limestone.



TEXT-FIG. 7. Statoliths of four species of fossil *Loligo*. A–D, right statolith of *Loligo* sp. A, total L = 0·84 mm; A, anterior view; B, posterior view; C, lateral view; D, ventral view; E–H, the same views of the left statolith of *Loligo* sp. B, Length = 1·19 mm; I–L, the same views of the right statolith of *Loligo* sp. C, Length = 1·06 mm; M–P, the same views of the left statolith of *Loligo* sp. D, Length = 1·13 mm.

CEPHALOPODA, TEUTHOIDEA
Family LOLIGINIDAE
Loligo mississippiensis n. sp.

Plate 54, figs. 11-15

Material. Of ten statoliths belonging to this species five are in good condition and are taken as types. All but one of the rest are almost complete. They all have the shape of adult loliginids except for two which are smaller than the others. Holotype LACMIP 5757, paratypes LACMIP 5758-5760.

Diagnosis. Diagnostic features of this species based upon the holotype are as follows (Pl. 54, figs. 11-15): The lateral dome is widest and rather pointed at its dorsal end. The lateral dome is not divided into superior and inferior lobes and it has a distinctly flattened ventro-lateral side. The lateral dome is thin from anterior to posterior. The dorsal dome extends dorsally further than the lateral dome. There is a prominent spur which is square in shape. The ventral indentation is longer than the dorsal indentation (and often wider in paratypes). There is no distinct antero-inferior lobe of the lateral dome in the holotype or larger statoliths.

Remarks. Dimensions of the types are given in Table 1, and are plotted in text-figs. 4-6. Compared with other fossil species of the same length described here, the rostral length (text-fig. 4) and the dorsal tip to spur (text-fig. 6) tend to be smaller.

CHIPOLA FORMATION—FLORIDA

Age. Lower Miocene. Stratigraphically, the Chipola Formation is the lowest (oldest) of three deposits which are generally conceded as comprising the Alum Bluff Group (Vernon 1942). At the Ten Mile Creek locality, the fossiliferous portion of the Chipola Formation is approximately 4 m (12 ft) thick, although total thickness of the formation ranges from about 6 m to 17 m (20-56 ft) (Cooke 1945).

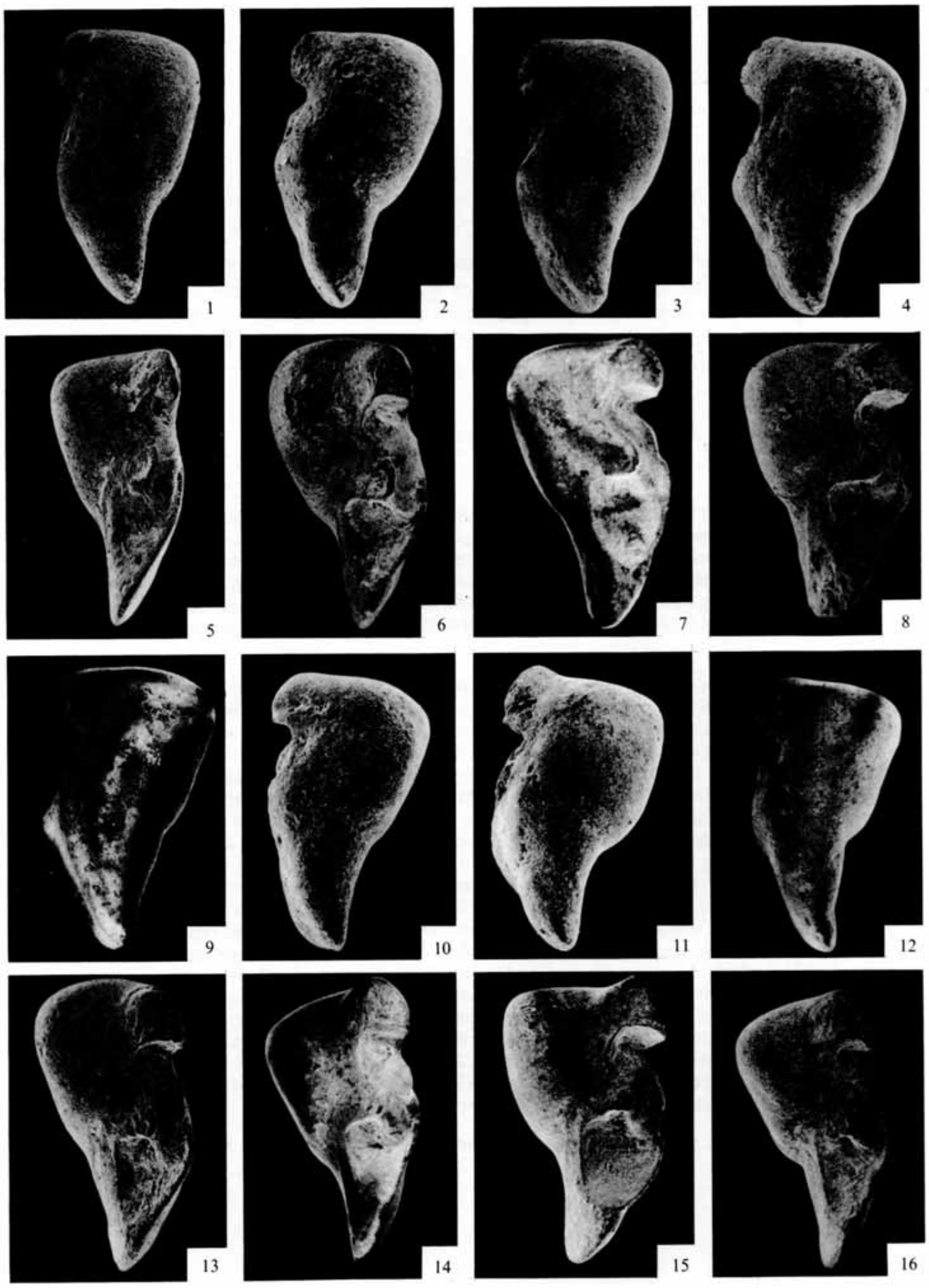
Location. Chipola Formation, Calhoun Co., Florida. North bank of Ten Mile Creek east of bridge on state highway 73, about 8 km (5 miles) north of Clarksville. Sites sampled are immediately below bridge and 100 m downstream.

Previous reports and associated fauna. Approximately 300 kg (700 lbs) of fossiliferous matrix from this deposit yielded several thousand otoliths from at least forty-five species belonging to more than twenty-five familes. In addition, there were teeth from two kinds of sharks, two rays, and a skate plus two other kinds of bony fishes. Almost all of the fish remains were from shallow-water forms with those from gobies (Gobiidae), grunts (Pomadasyidae), flatfish (Bothidae), and sparids (Sparidae) being most abundant. Bonefish (*Albula*), croaker (Sciaenidae), cardinalfish (*Apogon*), herring (Clupeidae), dactyloscopid, and mojarra (Gerreidae) otoliths were also present in considerable numbers. The outcrop at this site is a fine blue-grey to yellowish sandy clay which when thoroughly dry, breaks down readily after soaking in paraffin. The aragonitic components (molluscs, otoliths, statoliths, etc.) are in an excellent state of preservation.

Cushman and Ponton (1932) reported upon the Foraminifera which occur in the Chipola Formation, while the molluscan fauna has been reported upon by Gardner (1926-1950, 1936) and Vernon (1942).

EXPLANATION OF PLATE 53

Figs. 1-16. Eight statoliths of *Loligo barkeri* n. sp. to show variation in shape. 1-4, 9-12, posterior views of right statoliths. 5-8, 13-16, anterior views of the same statoliths. Total lengths: 1 and 5 = 1·30 mm; 2 and 6 = 1·44 mm; 3 and 7 = 1·50 mm; 4 and 8 = 1·56 mm; 9 and 13 = 1·60 mm; 10 and 14 = 1·64 mm; 11 and 15 = 1·70 mm; 12 and 16 = 1·76 mm.



CLARKE and FITCH, *Loligo barkeri* n.sp.

CEPHALOPODA, TEUTHOIDEA

Family LOLIGINIDAE d'Orbigny, 1835

Loligo mississippiensis

Text-fig. 3F–J

Material. This species is represented by one right statolith which is in very good condition and has the form of an adult *Loligo*.

Remarks. Dimensions of the specimen are given in Table 1, and text-figs. 4–6. They do not separate this specimen from other species described here.

The specimen cannot be distinguished from *L. mississippiensis* n. sp. from the Glendon Limestone. It has a slightly more pointed and thicker lateral dome but these differences are insufficient to erect a new species.

BARKER'S RANCH—CALIFORNIA

Age. Middle Miocene.

Location. Barkers Ranch. Olcese Sand—Temblor Formation. Numerous localities east of Bakersfield, Kern Co., California, and north of Kern River. The 221 squid statoliths found in Barker's Ranch strata came from nearly every exposure sampled, but most of them came from two outcrops, dubbed 'Ledge Site' and 'Clupeid Site', which were sampled more extensively than the others. These two sites and five other beds that were sampled rather heavily were exposed in several north–south trending canyons in the north-west corner of section 33, township 28 S., range 29 E., Rio Bravo Ranch quadrangle (U.S. Geological Survey topographic map).

Previous reports and associated fauna. Addicott (1970) in a monumental report upon the gastropods and biostratigraphy of the Kern River area of California said that the Barker's Ranch beds contained 'a gastropod-rich sublittoral molluscan fauna that has proved to be the largest, most diverse pre-Pliocene faunal unit of the Pacific Coast States'. He further stated that 'This fauna serves as the standard of reference . . . for the "Temblor Stage" of the Pacific coast megafossil chronology, a provincial time-stratigraphic unit regarded as middle Miocene.' He noted that the Middle Miocene fauna of the Olcese Sand and Round Mountain Silt, including the Barker's Ranch fauna, consisted of 157 species of gastropods.

The upper part of the Olcese Sand consists of fossiliferous fine to very fine sand and siltstone that are weathered to light grey to tan. In places it is 21 m to 35 m (70–116 ft) thick and included in the upper part of the Olcese Sand is the Barker's Ranch assemblage. Over a several-year period, Fitch removed and processed approximately 2 tons (1800 kg; 4000 lbs) of fossiliferous matrix from perhaps a dozen exposures of Barker's Ranch beds. This material has yielded more than 100 000 fish otoliths representing upwards of sixty-five species belonging to thirty or more families. Additional species are represented among several thousand shark, skate, and ray teeth, and basking shark (*Cetorhinus*) gill rakers.

Among the fish remains there is nothing to refute Addicott's (1970) conclusion that it represents sublittoral deposition. There are a dozen species of drums and croakers (Sciaenidae), seven kinds of right- and left-eyed flatfishes (Pleuronectidae and Bothidae), several basses (Serranidae), plus silversides (Atherinidae), mullets (Mugilidae), gobies (Gobiidae), herrings (Clupeidae), and several other families which are typical inhabitants of nearshore waters. Deep-water forms (Melamphaidae, Moridae, Myctophidae, Macrouridae, etc.) are present, but are relatively scarce (Fitch, unpublished data).

Statoliths. These were indistinguishable from those of the Round Mountain Silt and these are treated together below.

ROUND MOUNTAIN SILT—CALIFORNIA

Age. Middle Miocene.

Location. All of the Round Mountain Silt squid statoliths came from the canyon containing LSJU locality 2121 reported upon by Keen (1943), and from an adjacent north–south trending canyon that drains into the Kern River. The Round Mountain Silt rests conformably upon the Olcese Sand in most localities and is overlain by the Miocene Santa Margarita Formation.

Previous reports and associated fauna. Keen (1943) described nineteen new species of molluscs from the Round Mountain Silt and noted that seventy-seven molluscan species had been found at a single locality (i.e. LSJU no. 2121) east of Bakersfield, California. Although Addicott (1970) reviewed previous reports of Round Mountain Silt assemblages and recognized that Round Mountain Silt was distinguishable stratigraphically from Barker's Ranch strata, he did not give separate listings for the gastropods from the two. Addicott (1970) included the bone beds of Sharktooth Hill in the Round Mountain Silt.

Approximately 320 kg (700 lbs) of fossiliferous matrix were processed by Fitch and examined for identifiable fish remains. In all, approximately 3000 otoliths were found which represented more than forty-five species belonging to at least twenty-five families. Croakers and drums (Sciaenidae) and left- and right-eyed flatfishes (Bothidae and Pleuronectidae) comprised about 60% of the total otoliths. Lanternfishes (Myctophidae), morids (Moridae), and a few other deep-water forms were more abundant than in Barker's Ranch deposits, and probably reflect a slightly deeper environment than the 'sublittoral' assignment of Addicott (1970) for the Barker's Ranch molluscan assemblage.

CEPHALOPODA, TEUTHOIDEA
Family LOLIGINIDAE d'Orbigny, 1835
Loligo barkeri n. sp.

Plate 53, figs. 1–16; Plate 54, figs. 1–5

Material. This species is represented by 221 statoliths in good condition and thirty-four fragments provisionally identified as this species. The holotype is a left statolith having the characteristics of a mature loliginid (LACMIP 5761). Paratypes LACMIP 5762–5812, together with material in the U.S. National Museum of Natural History and the British Museum (Natural History).

Diagnosis. Distinctive features of this species based on the holotype are as follows (Pl. 54, figs. 1–5): The lateral dome is broadest at the dorsal end which has no sharp point and is rounded on the dorsal side. There is no indication of an inferior lobe of the lateral dome. The ventral border of the lateral dome may be rounded as in the holotype or almost flat as in a few paratypes. Posteriorly, the lateral dome is prominent and there is a distinct posterior dome groove (not present in a few paratypes). The rostral angle is obtuse but distinct (not distinct in a few paratypes). The dorsal dome extends dorsally slightly more than the lateral dome and is wider than long. It is not distinctly separated from the lateral dome except anteriorly. The spur is very distinct and is either 'square' as in the holotype or wider than long. The ventral indentation is longer and wider than the dorsal indentation.

Remarks. Dimensions of the holotype and the paratype in Plate 54, figs. 1–5 are given in Table 1 and are plotted for other specimens in text-figs. 4–6. This west coast species mainly differs from the Florida Miocene *Loligo mississippiensis* n. sp. by having a dorsally more rounded and thicker lateral dome. While some dimensions

TABLE 2. Coefficients in mm and standard errors of regressions plotted in text-figs. 4, 5, 6 of *Loligo barkeri* n. sp. and *L. stillmani* n. sp. and text-fig. 9 of *Berryteuthis* sp.

	n	a	b	sy.x	s_a	s_b
Maximum width						
Loligo barkeri	50	−0·09	0·66	0·04	0·07	0·05
L. stillmani	16	0·15	0·45	0·07	0·14	0·10
Berryteuthis sp.	15	0·51	0·32	0·09	0·28	0·10
Lateral dome length						
Berryteuthis sp.	16	0·80	0·14	0·06	0·16	0·06
Thickness						
Berryteuthis sp.	16	−0·01	0·29	0·06	0·18	0·06
Rostral length						
L. barkeri	50	−0·16	0·50	0·04	0·07	0·05
L. stillmani	16	−0·11	0·41	0·06	0·12	0·09
Berryteuthis sp.	15	−0·18	0·49	0·07	0·21	0·07
Dorsal dome length						
Berryteuthis sp.	15	−0·12	0·29	0·07	0·22	0·08
Dorsal tip to spur						
L. barkeri	48	0·19	0·31	0·03	0·06	0·04
L. stillmani	15	0·21	0·34	0·04	0·09	0·06
Spur length						
L. barkeri	49	0·10	0·11	0·03	0·05	0·07
L. stillmani	14	0·18	0·07	0·04	0·09	0·06

show a different distribution to those of *L. stillmani* n. sp. differences between their regressions are not statistically significant (Table 2).

The species is named after Mr. Lloyd W. Barker, a student helper who showed great promise as a palaeontologist before his untimely death.

DAY'S POINT—VIRGINIA

Age. Upper Miocene or possibly old Pliocene. McLean (1956) reviewed most of the palaeontologic research on the formation, and assigned it to the Miocene as had been done historically to that date. Recent research with planktonic foraminifera (Blow 1969; Akers 1972), echinoids (Kier 1972), ostracods (Hazel 1971, 1977), and fish remains (R. L. Meyer, pers. comm.; J. Fitch, unpublished data) has shown that its age ranges upwards, from late Miocene into early Pliocene, at least. Gardner (1943, 1948) included Yorktown Formation mollusca in her extensive reports on Miocene and Lower Pliocene pelecypods, gastropods, and scaphopods of Virginia and North Carolina. The beds from which our squid statolith was gleaned fit almost in the centre of Hazel's (1971) *Orionina vaughani* assemblage and thus would be middle early Pliocene in age.

Location. Day's Point, Yorktown Formation on Edward's Ranch 1·2 km (0·7 miles) down river from FFA-FHA camp on south bank of James River which is 4·5 km (2·8 miles) on state highway 673 from its junction with state highway 674 north of Smithfield Va on highway 10.

Previous reports and associated fauna. The Yorktown Formation and equivalents comprise a widespread transgressive unit over much of the Atlantic Coastal Plain. In Virginia and North Carolina there are numerous surface outcrops which are composed of silty sands, clays, shell marl, and coquinas. Greatest thickness of the Yorktown Formation is reported to exceed 150 m (500 ft) (Gernant *et al.* 1971).

Approximately 140 kg (300 lbs) of fossiliferous matrix from this deposit yielded more than 1300 otoliths from more than twenty-five species belonging to sixteen families. In addition, there were teeth from six sharks, skates and rays, and a single squid statolith. Otoliths of *Ammodytes* sp., two kinds of bothid flatfishes, and three kinds of cusk-eels (Ophidiidae) comprised nearly 85% of the total otolith yield. Similar or identical fish species live in the western Atlantic at that latitude today, and all can be taken at depths shallower than 91 m (50 fathoms). The fauna identified from bottom sediments off Massachusetts (Wigley and Stinton 1973), although several hundred miles farther north, had many similar components, especially at the shallower depths.

CEPHALOPODA, TEUTHOIDEA

Family LOLIGINIDAE d'Orbigny

Loligo sp. B

Text-fig. 7E–H

Material and remarks. The single statolith from this formation has the tip of its rostrum broken off, is small, and has the typically rounded lateral dome and indistinct rostral angle of an immature loliginid (text-fig. 7E–H). It closely resembles *Loligo stillmani* n. sp. specimens of the same size.

BOWDEN, JAMAICA

Age. Lower Pliocene? Historically, the Bowden Formation has been reported as late Miocene, but recent investigations of planktonic foraminifera (Blow 1969) and a critical evaluation of the fish fauna (J. Fitch, unpublished data) indicate that the Bowden ranges upwards from late Miocene into early Pliocene, at least. The outcrops from which our squid statoliths were gleaned appear to be equivalent to Blow's (1969) Zones N 19 and N 20, and thus would be early Pliocene in age.

Location. Road cut on property of Bowden Estates Ltd., approximately 1·3 km (0·8 miles) on Bowden Parochial road limits junction with main road. Exposures are at fork in road and approximately 1·2 m and 2·5 m (4–8 ft) above the road bed.

Previous reports and associated fauna. Approximately 225 kg (500 lbs) of fossiliferous matrix from this site yielded some 25 000 otoliths representing more than 110 kinds of fish belonging to fifty to sixty families. In addition, upwards of 100 teeth gleaned from this material are from at least three kinds of sharks and rays and three families of bony fish. Obviously, the fish assemblage of the Bowden Formation is extremely rich, a situation previously noted for the invertebrate faunas. Foraminifera, corals, bryozoans, and molluscs have been reported upon (Woodring 1925, 1928; Blow 1969) and these as well as crustacean, echinoderm, sponge, barnacle, and gorgonian remains were abundant in the material examined by Fitch. What was reported as a needlefish jaw fragment from the Bowden Formation by Caldwell (1965) is actually part of a claw from the shrimp *Ctenocheles* sp., family Callianassidae (W. C. Blow, pers. comm.).

Caldwell (1965) speculated that the 'marine species from Bowden seem to represent a drifted (mixed) assemblage from several ecological environments, as both bottom and pelagic types are represented, including forms from the intertidal zone to a maximum depth of some 600 feet'. The fish fauna too is comprised of both shallow- and deep-water forms, but if drift occurred, it was before the fishes deteriorated and their otoliths fell out. One suspects that this deposit represents a mass mortality similar to those resulting from dinoflagellate blooms (red tide organisms) off the Florida coast within the past thirty years.

Among the otoliths from this locality there were such shallow-water forms as bonefish (*Albula*), croakers (*Micropogon*, *Larimus*, and *Equetus*), soldierfish (*Myripristis* and *Holocentrus*), cardinalfish (*Apogon*), jawfish (*Opisthognathus*), pearlfish (*Carapus*), plus herrings, anchovies, gobies, goatfish, gurnards, cusk-eels, catfish, and a host of others. Fitch (1969*b*) reported upon a laternfish found in this deposit, but deep-water forms which are unreported include several other kinds of lanternfish, a morid (*Physiculus*), a berycid (*Diretmus*), codlets (*Bregmaceros* spp.), a lightfish (*Polyipnus*), a pelagic cardinal-fish (*Synagrops*), plus eels, gonostomatids, brotulids, macrourids, melamphaids, and others. A majority of the otoliths have crisp, uneroded margins, usually with delicate spinules and other ornamentation still intact.

CEPHALOPODA, TEUTHOIDEA
LOLIGINIDAE d'Orbigny, 1835
Loligo valeriae n. sp.

Text-fig. 3K–O

Material. This species is represented by nine statoliths, seven of which are in good condition. Eight have features such as long domes and short rostra which suggest the squids were not fully mature. Holotype LACMIP 5813, paratypes LACMIP 5814–5815.

Diagnosis. The holotype is a right statolith having the following diagnostic features (paratype in text-fig. 3 K–O is slightly less mature). The lateral dome smooth, is widest and pointed at its dorsal end, the ventro-lateral side rounded. The lateral dome is oval in lateral aspect. The dorsal dome extends dorsally very little further than the 'peak' of the lateral dome and is not separated from the lateral dome on the dorsal side. The spur is distinct and is longer than wide. A rather prominent antero-inferior lobe of the lateral dome extends on to the spur. The ventral indentation is much wider and longer than the dorsal indentation. If a posterior dome groove is present it is indistinct.

Remarks. Dimensions of the three types are given in Table 1 and those for all seven types are plotted in text-figs. 4–6. The species is distinguished from the other fossil species described here by the shape of the lateral dome and the spur.

The species is named in honour of Mrs. Maurice W. Facey (Valerie), Kingston, Jamaica without whose help the Bowden beds could not have been sampled.

NEWPORT MESA—FERNANDO FORMATION—CALIFORNIA

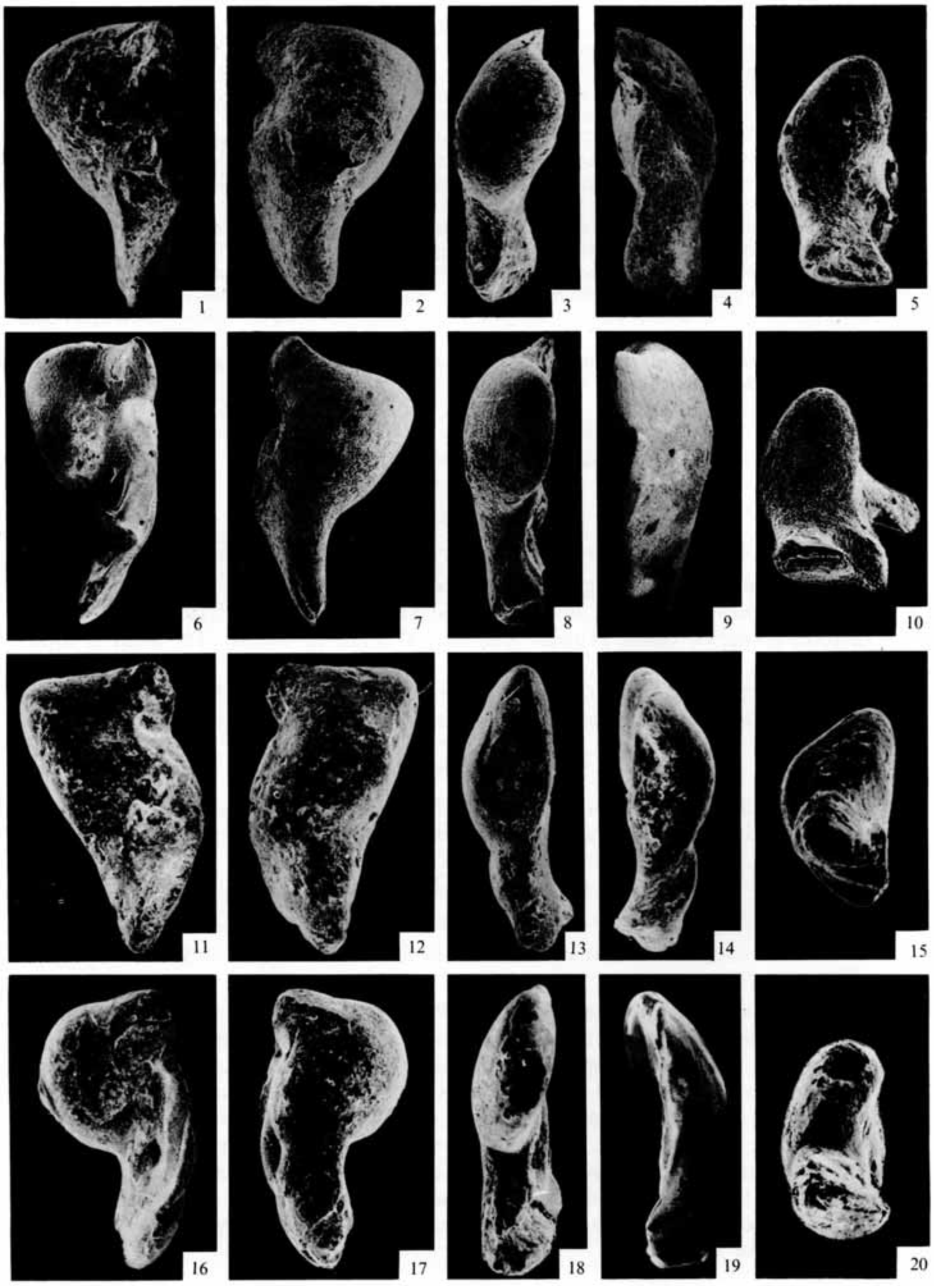
Age. Late Pliocene.

Location. Fernando Formation. 240 m (800 ft) south and 15 m (50 ft) west of north-east corner section 24, township 65, range 10 W., Newport Mesa south of Upper Newport Bay, Orange Co., California. This deposit (LACMIP 471) was reported by Mount (1970) as being a '6 foot thick lens of sandy cobble conglomerate which occurs approximately 425 feet stratigraphically above the base of the formation'. It lies at lat. 33° 38′ 21″ N., long. 117° 53′ 02″ W. and at the present time 'is located under the residence at 2161 Vista Entrada, Newport Beach, California'.

Previous reports and associated fauna. Mount (1970) noted that he and associates had recovered over 200 species of larger invertebrates from the site, and listed four bivalve molluscs and three gastropods which were characteristic of the fauna. He described a new species of *Neadmete*, and reported the age of the deposit as late Pliocene. He did not offer a suggestion as to depth of deposition.

EXPLANATION OF PLATE 54

Figs. 1–20. Right statoliths of four species of fossil teuthoids. 1–5, *Loligo barkeri* n. sp., total L = 1·52 mm. 1, anterior view. 2, posterior view. 3, lateral view. 4 medial view. 5, ventral view. 6–10, the same views of the statolith of *L. stillmani* n. sp., holotype, total L = 1·42 mm. 11–15, the same views of the statolith of *L. mississippiensis* n. sp., holotype, total L = 1·48 mm. 16–20, the same views of *Moroteuthis addicotti* n. sp., holotype, total L = 1·48 mm.



CLARKE and FITCH, Cenozoic teuthoid statoliths

Zinsmeister (1970) listed thirty-one species of bivalve molluscs, forty-eight of gastropods, two scaphopods, one brachiopod, three sharks, and thirteen bony fishes from LACMIP 471. He noted that the fauna was comprised of forms which typically inhabit shallow as well as moderately deep water, and speculated that the recovered fossils reflected 'a depth between 20 and 100 fathoms'.

Fitch (1969*a*, 1969*b*) reported finding over 5100 fish otoliths and 1200 elasmobranch teeth in approximately 230 kg (500 lbs) of fossiliferous matrix that he dug from this site (noted as possibly being Pico Formation). Although the 5100 otoloths represented more than fifty-five species belonging to thirty families, twenty-five species belonging to six families (i.e. Moridae, Myctophidae, Pleuronectidae, Scorpaenidae, Cottidae, and Merlucciidae) contributed 90% of these (Fitch, unpublished data). Twenty-two of these twenty-five species are still living off California today, and most can be found where water depths range between 110 and 183 m (60 and 100 fathoms). Today, two of the more than fifty-five fish species are extinct, one does not approach within approximately 1600 km of California (offshore), and the southern limit of range for four others does not approach within 480 to 1600 km the latitude of Newport Beach (Fitch, unpublished data).

The 230 kg (500 lbs) of matrix sampled by Fitch from this site also yielded the twenty-one squid statoliths and fragments (three species) being reported upon in this paper.

CEPHALOPODA, TEUTHOIDEA

Family LOLIGINIDAE d'Orbigny

Loligo sp. C

Text-fig. 7I–L

Material. This is only represented by one left statolith with the tip of the rostrum missing.

Remarks. It has the following diagnostic features (text-fig. 7I–L): The lateral dome is widest at its dorsal end but is not pointed and there is an inferior lobe. There is a distinct posterior dome groove. The rostral angle is obtuse. The spur is longer than wide.

This species seems close to *Loligo valeriae* n. sp. from the Pliocene of Jamaica (p. 496), but is thicker and has a more distinct inferior lobe of the lateral dome.

Family ONYCHOTEUTHIDAE

Living species of this family are oceanic but *Moroteuthis robusta* (Verrill) is sometimes caught in bays on the west coast of North America (Clarke 1966).

Moroteuthis addicotti n. sp.

Plate 54, figs. 16–20

Material. Three complete statoliths and three broken statoliths. Holotype LACMIP 5816, paratypes LACMIP 5817–5821.

Diagnosis. The most important features (Plate 54, figs. 16–20) are as follows: The shape of the lateral dome is almost semi-circular in outline in anterior aspect in the holotype and three largest specimens. In the two smallest specimens it is broadest at its dorsal end. The dorsal dome is very small, antero-posteriorly flattened, and is not distinctly separated from the lateral dome except on the anterior surface. There is no distinct medial fissure. The spur is very ill-defined or absent. The rostrum is rather thick in comparison with its length and has a well-defined lateral lobe closer to its ventral tip than to its dorsal end. The lateral dome has a smoother outline in anterior aspect than in *Moroteuthis robusta*. The rostrum is relatively longer and thinner than in *M. robusta*.

Remarks. The holotype (Plate 54, figs. 16–20) is a right statolith having the size and appearance of a mature oegopsid and showing greater affinities to the Onychoteuthidae and to *Moroteuthis* than to other families and genera (unpublished data of M. R. C.). The first five features listed in the diagnosis indicate the generic relationship. Dimensions of the complete types are given in Table 1.

It is named in honour of W. O. Addicott, U.S. Geological Survey, Menlo Park, California who has been instrumental in bringing numerous fossil sites to our attention and has been helpful in numerous other ways.

Family GONATIDAE
Berryteuthis sp.

Remarks. Seven statoliths in good condition and seven broken statoliths represent this species which is described below from more numerous specimens found in the Lomita Marl.

FERNANDO FORMATION—LACMIP 466—CALIFORNIA

Age. Late Pliocene.

Location. During excavation of a sub-basement for the Crocker Citizens plaza building to the south side of 6th Street between Hope and Grand, Los Angeles, a lens of the fossiliferous Fernando Formation was exposed.

Previous reports and associated fauna. From approximately 140 kg (300 lbs) of matrix that was salvaged by personnel from the Natural History Museum of Los Angeles County, Fitch was able to glean more than 4200 fish otoliths representing at least fifty-six species belonging to twenty-eight families. Teeth from sharks, skates, and rays represented an additional ten species in eight families.

This deposit (LACMIP 466) was mentioned briefly (as Pico Formation) by Fitch (1969*a*) who reported that hake, *Merluccius productus*, otoliths comprised more than 13% of the total otolith yield. The seven kinds of lanternfish (Myctophidae) otoliths found in this deposit also were reported upon by Fitch (1969*b*). Four fish families (fourteen species) contributed 77% of the 4285 otoliths found in this deposit: Bothidae (three species, 28%), Gobiidae (three species, 23%), Merlucciidae (one species, 13%), and Scorpaenidae (seven species, 10%). Three of the fish species found in this deposit (a goby, a morid, and a cottid) are extinct, four others (*Ammodytes*, *Microgadus*, *Lyconectes*, and *Malacocottus*) are locally extinct northern forms, and one (*Benthosema*) is a locally extinct offshore species (Fitch, unpublished data). Only a single broken squid statolith was found in LACMIP 466.

LOMITA MARL—CALIFORNIA

Age. Late Pliocene. Based upon the molluscan assemblage, Woodring *et al.* (1946) assigned the Lomita Marl to Lower Pleistocene as did both Kennedy (1975) and Langenwalter (1975).

Kanakoff and McLean (1966) described a new species of *Neadmete* from LACMIP 435, and interpreted the Lomita Marl as being Late Pliocene in age although 'previously reported in the literature as Early Pleistocene'. They also reported that extensive excavations of these outcrops had yielded a large and unique fauna with new fossil records of molluscs, but did not elaborate. They speculated that LACMIP 425 probably corresponded to U.S. Geological Survey locality no. 12222 of Woodring *et al.* (1946).

Zinsmeister (1970) in reporting upon a Pliocene faunal assemblage at Newport Beach stated that he made comparisons with material from Lomita Marl and found numerous similarities; whereas, Hertlein (1970) in describing a new species of *Kelletia* from LACMIP 435 noted that the Lomita Marl was 'Late Pliocene or Early Pleistocene'.

Based upon his work with fossil fish otoliths, and intensive sampling of the Lomita Marl by personnel from the Natural History Museum of Los Angeles County, Fitch (1969*a*) concluded there was substantial evidence that the Lomita Marl was in fact the youngest marine Pliocene unit in southern California.

Location. LACMIP 435. 12 m (40 ft) long exposure on south side of gully north-west of intersection of Park Western Drive and Host Place, San Pedro, California. Exposure is 10·7 m (35 ft) below Host Place road bed.

Previous reports and associated fauna. Woodring *et al.* (1946) noted that the Lomita Marl consists of a variety of calcareous rocks, principally marl and calcareous sand. They used the term 'calcareous sand' to include 'unconsolidated calcareous material of sand or granule size composed chiefly of calcareous organic remains—calcareous algae, Foraminifera, Bryozoa, small shells, and shell fragments'. Their investigations led them to believe that the Lomita Marl included several faunal associations which they interpreted as being different depth associations ranging from 'shallow water to about 100 fathoms'. In a listing of 'Pleistocene mollusks locally extinct in the latitude of San Pedro but now living farther north or south, including forms that are not known to be living but that are closely related to living forms', they note four gastropods and three pelecypods having northern affinities and four gastropods and one pelecypod with southern ties.

Kennedy (1975) gave a relatively complete bibliography for faunal assemblages reported from Lomita Marl. Included were references to publications on foraminifera, ostracods, molluscs, and vertebrates. Langenwalter (1975) reported fish species, from a list supplied by Fitch, that had been identified from Lomita Marl.

Over one tonne (2000 lbs) of fossiliferous matrix from LACMIP 435 yielded nearly 25 000 fish otoliths representing more than eighty-seven species belonging to thirty families (Fitch 1969*a*, and unpublished data). In addition, teeth and other remains from seventeen kinds of sharks, skates, and rays belonging to twelve families have been found at this site. The fish fauna is composed of many mesopelagics, a few bathypelagics, two extinct forms, nine locally extinct northern and/or offshore species, and an assortment of species that are typical inhabitants of 37–90 m depths at the latitude of San Pedro today. The 2424 otoliths from an extinct morid represented the greatest yield for a single species, but four other species yielded more than 1000 otoliths each; a flatfish, *Lyopsetta exilis* (2158); a goby *Coryphopterus nicholsii* (1842); a cottid, *Radulinus asprellus* (1373); and a myctophid, *Stenobrachius leucopsarus* (1119). The fourteen species of myctophids from this site (over 3100 otoliths) have been reported upon by Fitch (1969*b*), who speculated that the Lomita Marl was laid down 'at depths exceeding 600 feet'.

The 185 squid statoliths noted by Clarke and Fitch (1975) from the Lomita Marl were from this site (LACMIP 435) and represent four or possibly five species as reported herein.

CEPHALOPODA, TEUTHOIDEA

Family LOLIGINIDAE

Loligo stillmani n. sp.

Plate 54, figs. 6–10

Material. This species is represented by thirteen statoliths in good condition and twenty-five broken or badly chipped statoliths. The holotype (LACMIP 5822) is a right statolith having the characteristics of a mature loliginid (Pl. 54, figs. 6–10). Paratypes LACMIP 5823–5826.

Diagnosis. Distinctive features of this species based on the holotype are as follows (Pl. 54, figs. 6–10): The lateral dome is broadest at the dorsal end which is slightly more pointed than in *Loligo barkeri* n. sp. or *L. opalescens*. There is no indication of an inferior lobe to the lateral dome. There is no posterior dome groove. The lateral dome is thinner than in *L. barkeri* n. sp. The rostral angle is obtuse but distinct. The dorsal dome extends dorsally much more than the lateral dome and is longer than wide. It is separated from the lateral dome on the dorsal edge by a shallow but distinct indentation and forms a rather narrow anteriorly curving 'blade'. The spur is distinct but not so prominent as in *L. opalescens* and is much longer than wide.

Remarks. The larger paratypes agree with the holotype in the above features. Dimensions of the holotype are given in Table 1 and of paratypes in text-figs. 4–6. The most obvious differences between the species and *L. barkeri* n. sp. are the more dorsally directed dorsal dome, the sharper lateral point and flatter ventro-lateral side of the lateral dome, the slimmer rostrum and the longer spur of this species.

From text-figs. 4–6 the dimensions of this species and *L. barkeri* n. sp. would appear to have different but overlapping distributions. Rostral length is generally shorter in *L. stillmani* for statoliths of the same length (text-fig. 4), the maximum width tends to be smaller in statoliths of the same size (above about 1·3 mm length, text-fig. 4), the distance from the dorsal tip to the spur is greater in statoliths of the same size and the spur length tends to be greater (text-fig. 6). However, when the calculated regressions were tested (Table 2) they were not statistically significant at the 95% level.

The species is named after Dr. Stillman S. Berry who has collected extensively in the Lomita Marl and has made a great contribution to the taxonomy of living cephalopods over a period of almost 70 years.

Loligo sp. D

Text-fig. 7M–O

Material. One small statolith having characteristics which suggest immaturity were also present in this sample. It is possibly an immature *Loligo stillmani* n. sp. but may represent a distinct species.

Remarks. Characteristic features of this statolith are as follows: The lateral dome is widest at the dorsal end. The inferior lobe of the lateral dome is relatively large. The lateral dome is long compared with the rostrum (suggesting immaturity). The rostral angle is obtuse and indistinct. The dorsal dome does not extend dorsally much more than the lateral dome from which it is only very indistinctly separated. The medial fissure is shallow. The spur is longer than wide. The surface is rough and in places pitted.

Dimensions of the specimen shown in text-fig. 7M–O are given in Table 1.

Family OMMASTREPHIDAE

Two statoliths, although clearly belonging to different species have some features which relate them to this family. While the one is probably in the genus *Dosidicus* the generic status of the other is not certain but it has close similarities to *Symplectoteuthis*. Characteristics which suggest that these belong to this family are the large size and rough surface of the dorsal dome, the smooth inferior lobe of the lateral dome, the distinct medial fissure, the prominent spur and the rostral angle which is almost a right angle.

Dosidicus lomita n. sp.

Text-fig. 8A–E

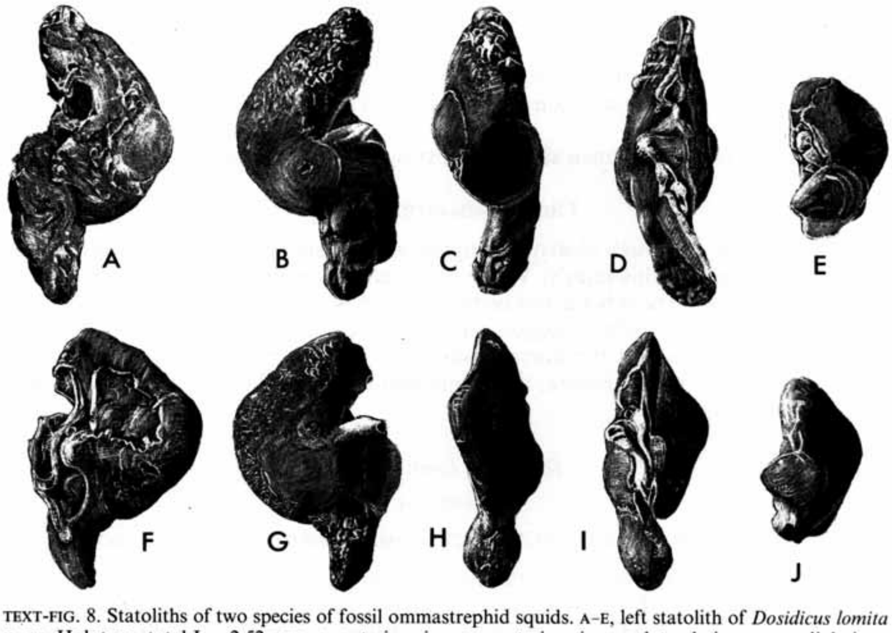
Material. A single specimen, holotype LACMIP 5827, is a right statolith having mature features.

Diagnosis. Distinctive features of this statolith are as follows (text-fig. 8A–E): The lateral dome is divided into a slightly rough superior lobe, a prominent, smooth postero-inferior lobe, and a smooth antero-lateral lobe. The surface is slightly lumpy on the antero-ventral side. There is a distinct posterior dome groove. The rostral angle is close to a right angle. The dorsal dome is very large, rough, and indistinctly separated from the lateral dome. A distinct spur is present but is eroded on the dorsal side. Well-defined indentations are present but the margins are eroded. The medial fissure is deep and forms a well-defined, triangular posterior indentation. A distinct posterior ventral ridge is present. The rostrum has a lumpy surface, is approximately circular in cross section at the base flattening towards the tip, and is fairly thick. The tip is slightly flexed laterally.

Remarks. Dimensions of this statolith are given in Table 1.

This statolith resembles *Dosidicus gigas* caught off the Californian coast by its general shape, particularly the relative proportions of the dorsal dome, lateral dome, and rostrum, by the lumpy surface of the dorsal dome and superior lobe of the lateral dome, by the possession of a distinct superior lobe of the lateral dome, by the very distinct posterior dome groove, by the lumpy surface of the rostrum, and by having a posterior ventral ridge. It differs from *D. gigas* in having a smaller lobe placed anteriorly instead of laterally on the dorsal end of the lateral dome and in having a rather thicker and blunter rostrum. The first difference is certainly sufficient to show the fossil is a distinct species although it seems possible the antero-lateral lobe of the fossil has evolved into the superior lobe of the living species.

The species name is taken from the name of the fossil deposit in which it was first discovered.



TEXT-FIG. 8. Statoliths of two species of fossil ommastrephid squids. A–E, left statolith of *Dosidicus lomita* n. sp. Holotype, total L = 2·52 mm; A, anterior view; B, posterior view; C, lateral view; D, medial view; E, ventral view; F–J, the same views of the left statolith of *Symplectoteuthis pedroensis* n. sp. Holotype, total L = 2·26 mm.

Symplectoteuthis pedroensis n. sp.

Text-fig. 8F–J

Material. Holotype LACMIP 5828.

Diagnosis. Distinctive features of this species are as follows (text-fig. 8F–J): The outline of the lateral dome and dorsal dome together form an approximate semicircle in anterior or posterior aspect. The statolith is wide. The lateral dome has a distinct, shallow groove separating a lobe from a postero-inferior lobe. There is no distinct posterior dome groove. While the rostral angle is obtuse because of the presence of a small dorso-lateral rostral lobe, the ventral side of the lateral dome forms a right angle with the rostrum. The dorsal dome is rough and is not separated from the lateral dome by a distinct groove. The spur is well-defined and is joined by a prominence to the superior lobe of the lateral dome. The medial fissure is deep and forms a pointed posterior indentation with a posterior ventral ridge. There is a dorsal spur, and a distinct anterior dorsal ridge. The rostrum is relatively small, equalling about one quarter of the total length of the statolith and being rather narrow.

Remarks. Dimensions of this statolith are given in Table 1. This species differs from *Symplectoteuthis oualaniensis* caught off California by having a relatively shorter rostrum and a lateral lobe near the base of the rostrum which is closer to the rostral angle than in *S. oualaniensis*. It is quite possible that *S. pedroensis* n. sp. is ancestral to *S. oualaniensis*. The fossil, however, is much larger than statoliths of the *S. oualaniensis* normally collected off California and very large specimens of the latter might differ less from the fossil. *S. oualaniensis* grows much larger in some other localities (e.g. the Indian Ocean).

Family GONATIDAE
Berryteuthis sp.

Plate 55, figs. 1–20; text-fig. 11, figs. 1–5

Material. This species is represented by twenty-six almost intact statoliths and eighty-five large, identifiable fragments. LACMIP 5829–5839.

Diagnosis. This species has the following distinctive features (Pl. 55, figs. 1–20 and text-fig. 11, figs. 1–5): The lateral dome looks almost spherical in posterior and, in some specimens, also in lateral view. In lateral aspect it is usually oval with its longitudinal axis on the same axis as the statolith. The lateral dome has a smooth surface and has no posterior dome groove. The rostral angle is almost a right angle (in some specimens the lateral dome bulges ventral to it and so forms an acute angle). The dorsal dome has a smooth surface and is large; it extends dorsally well beyond the lateral dome from which it is clearly separated by a shallow groove on the dorsolateral surface. The spur is distinct but is much longer than wide. The indentations are indistinct, narrow and shallow. The medial fissure is shallow. There is no dorsal spur or anterior dorsal ridge. The rostrum is long, about the same length as the lateral dome and thick. Its thickest point is not usually at its base. The wing is thick.

Remarks. Dimensions of one specimen are given in Table 1 and of others in text-fig. 9, and variation in form is shown in Plate 55, figs. 1–20.

The shape of the large statoliths is very close to that of the very characteristic statolith of *Berryteuthis magister* and there can be little doubt of their generic affinity. However, statistical comparisons of the measurements show conclusively that the fossil is a different species from *B. magister* (in preparation). A second species of the genus, *B. anonychus* (Pearcy and Voss, 1963) lives off the western coast of North America and, as we have not yet had an opportunity to examine statoliths from this species, we have not given the fossils a specific name in case they should later prove to belong to the latter species.

The form of the statoliths of *Berryteuthis* has some superficial similarities to both the ommastrephid *Todarodes* and the sepioid *Sepia*. All three genera have large statoliths with lateral domes having semicircular outlines in posterior aspect, large dorsal domes, and thick rostra. As all three species live close to the sea bottom on the continental shelf and upper slope at some time in their lives, the similarities in statolith shape could have some relationship to their way of life.

RINCON HILL ROAD

Age. Early Pleistocene.

Location. Rincon Hill Road (Bates Road) Santa Barbara, California. Santa Barbara Formation (this deposit is equivalent to Timm's Point Silt to judge from the type of matrix and fish otoliths sorted by Fitch). The exact spot is on the west bank of Rincon Hill Road about 0·25 km from the intersection of Rincon Hill Road and California State Highway 150.

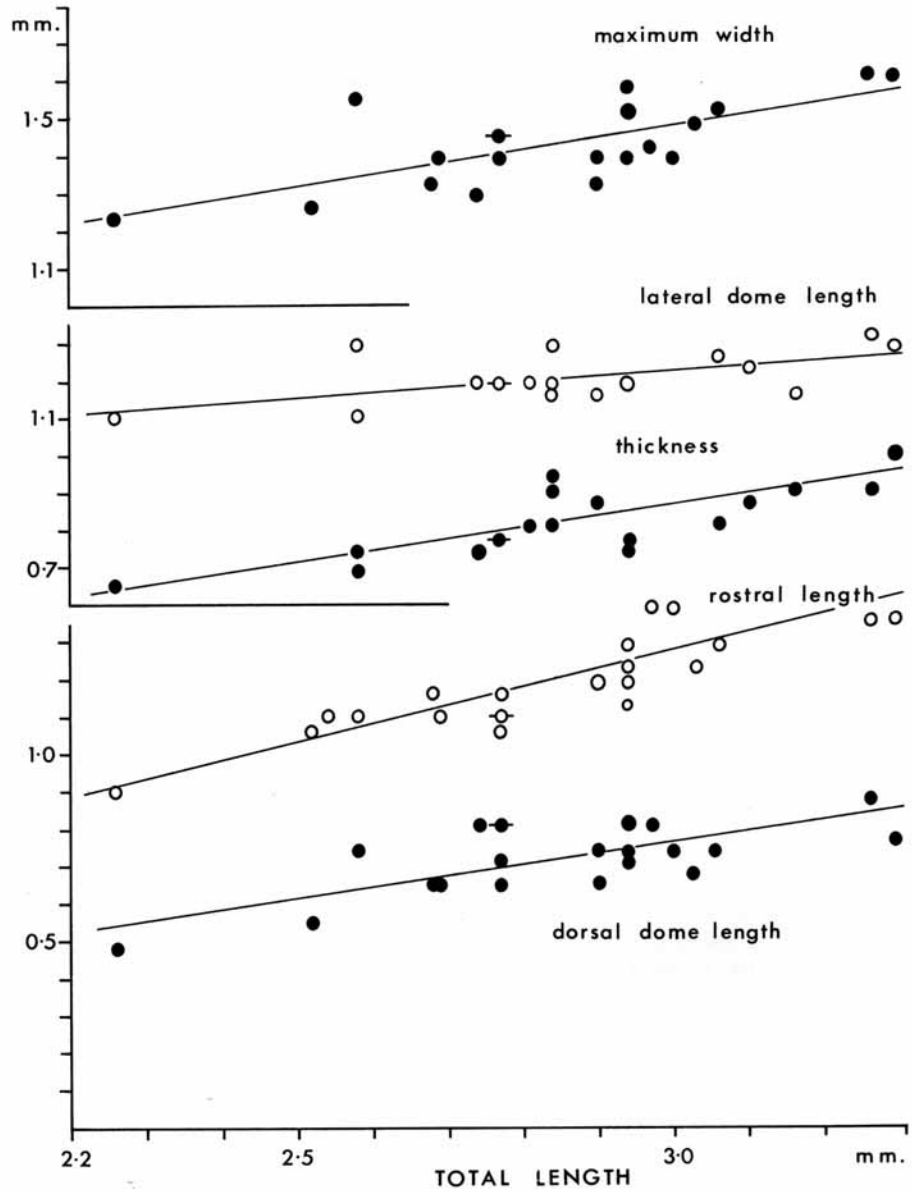
Previous reports and associated fauna. Approximately half a tonne (1000 lbs) of fossiliferous matrix from a Pleistocene exposure on Rincon Hill Road contained slightly more than 2000 fish otoliths, three squid statoliths, and a small assortment of shark, skate, and ray teeth (Fitch and Huddleston MS.). Some of the fish otoliths found at this site were mentioned under the heading of 'Bates Road locality' by Fitch (1969*a*, 1969*b*). In all, more than fifty species of fish from twenty-one families were represented among the 2000 otoliths. Four kinds of otoliths (two kinds of Gobiidae, a morid, and an embiotocid) were from extinct species, one was from a locally extinct northern species (*Lyconectes*), and one was from a locally extinct offshore myctophid (*Benthosema*); the remaining forty-five or more kinds were from fishes that today inhabit depths of 20–180 m at the latitude of this site. Fitch (1969*a*, 1969*b*) speculated that this deposit was laid down at a depth of 120–180 m (400–600 ft) at a time when ocean temperatures were colder at this latitude than they are today.

The most conspicuous molluscs at this site were species of *Turritella* and *Dentalium*. Other large molluscs encountered while digging out field samples were species of *Astraea*, *Bursa*, *Polinices*, *Nassarius*, *Panopea*, and *Saxidomus*. Several large abalone shells, *Haliotis rufescens*, have been unearthed in a lens of material adjacent to this site but unquestionably of the same age.

This site has been registered as vertebrate palaeontology collecting locality LACM 3784.

CEPHALOPODA, TEUTHOIDEA
Family LOLIGINIDAE
Loligo opalescens Berry, 1911

Remarks. One complete right statolith and two damaged statoliths cannot be distinguished from this species which now lives in inshore waters off the western coast of the United States of America. The statolith of this species will be described elsewhere with other living species of the genus (Clarke, in preparation).



TEXT-FIG. 9. Dimensions of statoliths of *Berryteuthis* sp. plotted against their total length. Coefficients and standard errors of the regressions plotted are given in Table 2.

EVOLUTION

While the specimens described are too few to enable general deductions on the evolution of teuthoids, the fact that at least six species of *Loligo* are represented, provides a basis for a discussion of the evolution of this one genus. If we first consider the *Loligo* from the Atlantic, *L. applegatei* n. sp. is distinguished from any other *Loligo* examined, fossil or living, by its very large, pointed lateral dome. It is unlikely to have evolved into the Oligocene *L. mississippiensis* n. sp. The latter might have evolved from the *Loligo* sp. A of the Vacaville which is not likely to be a young stage of *L. applegatei* n. sp.

The early Pliocene *L. valeriae* n. sp., also from the Atlantic side of the continent, differs from *L. mississippiensis* n. sp. in having a rounded ventro-lateral side of the lateral dome, a very long spur, and a relatively smaller and less dorsally directed dorsal dome. These suggest an independent line of development.

On the Pacific side of the continent the Miocene *L. barkeri* n. sp. is much closer to the living *L. opalescens* than either is to the Pliocene *L. stillmani* n. sp. which has a sharper point to the lateral dome, no posterior dome groove, a very long spur, and a narrower, more pointed, rostrum. *L. barkeri* sp. quite possibly evolved into the present-day *L. opalescens* but *L. stillmani* n. sp. is likely to be from a different line of evolution.

The two living ommastrephid genera *Dosidicus* and *Symplectoteuthis* are now known to have lived in the Pliocene although the statoliths are sufficiently different from the living species to consider them different species; their form does not preclude evolution of the Pliocene forms into the living species.

Similarly, the fossil *Berryteuthis* sp. is very close to *B. magister* from the North Pacific and it is clear that squids of this genus lived in the Pliocene seas of the western side of North America.

Moroteuthis addicotti n. sp. is close to, but distinct from the living *M. robusta* (Verrill, 1876) which is frequently caught off California and may be its ancestor.

ECOLOGY

The living species of *Loligo* are neritic species living in midwater or just above the bottom in water less than 200 m for much of their lives. At times, some species extend into deeper waters to 500–600 m near the bottom on the continental slope but otherwise they are not found away from the continental shelf or in oceanic water. Only one species of *Loligo*, *L. opalescens* lives off California and two, *L. pealei* Lesueur,

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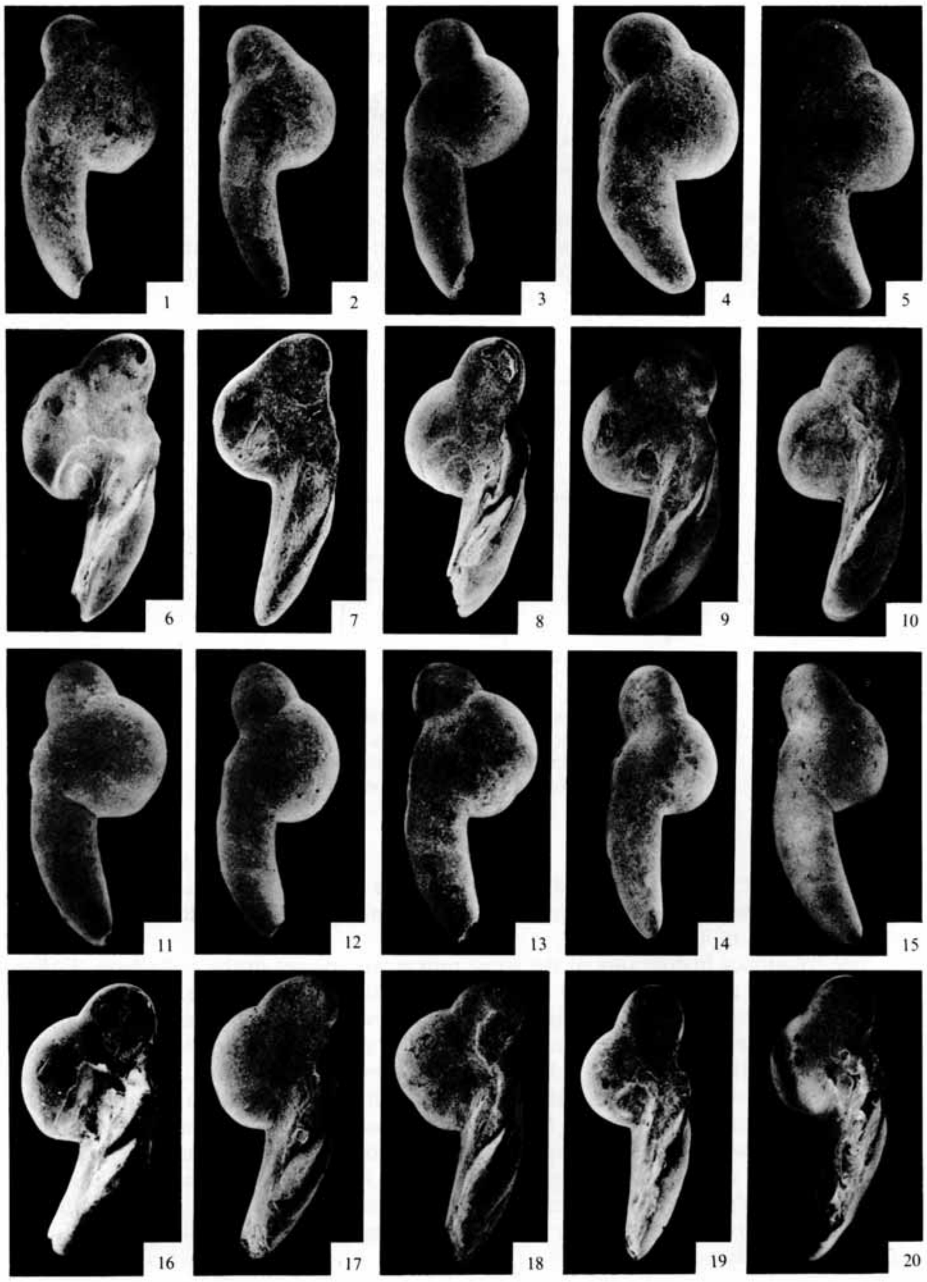
EXPLANATION OF PLATE 55

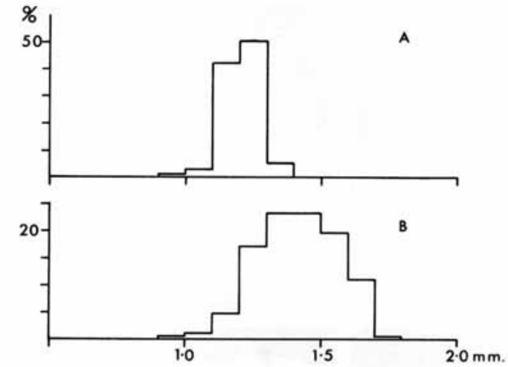
Figs. 1–20. Ten statoliths of *Berryteuthis* sp. to show variation in shape. 1–5, 11–15, posterior views of right statoliths. 6–10, 16–20, anterior views of the same statoliths. Total lengths 1 and 6 = 2·56 mm; 2 and 7 = 2·68 mm; 3 and 8 = 2·76 mm; 4 and 9 = 2·80 mm; 5 and 10 = 2·80 mm; 11 and 16 = 2·92 mm; 12 and 17 = 3·00 mm; 13 and 18 = 3·00 mm; 14 and 19 = 3·20 mm; 15 and 20 = 3·40 mm.



CLARKE and FITCH, *Statoliteuthis enigmaticus* n.sp.

1821 and *L. plei* (Blainville, 1823), live off the Atlantic side of the continent. Other loliginids from the shelf around North America are *Sepioteuthis sepioidea* (Blainville, 1823), and *Lolliguncula brevis* (Blainville, 1823) which only live on the Atlantic side and *L. panamensis* from the Gulf of California. The statoliths of all these except *S. sepioidea* have been examined and compared with the fossil statoliths (Clarke, in preparation).

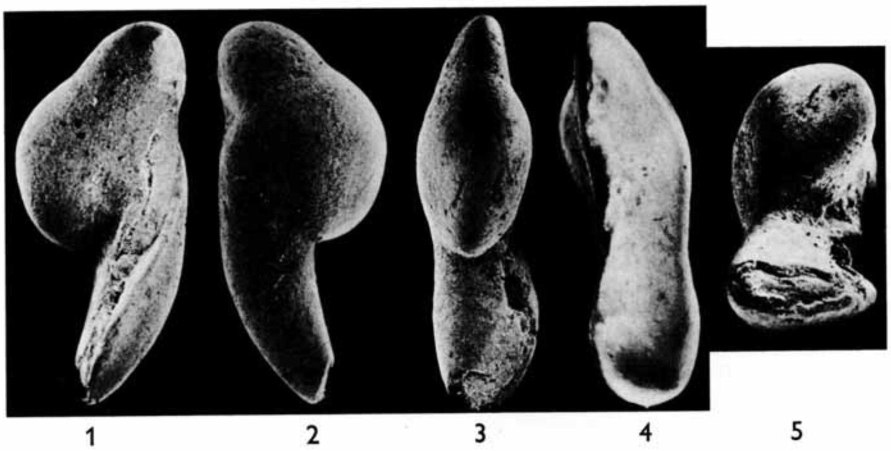
The ommastrephids *Symplectoteuthis oualaniensis* and *D. gigas* and the onychoteuthid *M. robusta* are all caught close to the Californian coast at times. *Berryteuthis magister* lives close to the sea floor on the upper part of the continental slope.



TEXT-FIG. 10. Percentage frequency distributions for the two most numerous fossil statoliths. A, *Statoliteuthis enigmaticus* n. sp. based on 117 measurements of lateral dome length. B, *Loligo barkeri* n. sp. based on 311 measurements of total length.

Thus, all the species described here support the view that all sediments examined in the present work originated from water which was probably shallower than 200 m on the margin of a continent.

Size frequency histograms of the most numerous species in the collection, *Loligo barkeri* n. sp. and *Berryteuthis* sp., are not distinctly skewed (text-fig. 10). This suggests that the mesh size used in their collection was sufficiently small to collect the majority of the statoliths of these species which were present in the 'dirt' sample; otherwise the distributions would be positively skewed. In addition, the lack of such skewness also shows that the statoliths were not from a population including every stage of growing squid. Instead, they were from 'adult' or near 'adult' squid which, from our knowledge of living species, were probably spawning and dying in the locality. When such spawning aggregations occur in living squids they are seasonal. We may therefore be fairly confident that *L. barkeri* n. sp. and *Berryteuthis* sp. aggregated at some season of the year for spawning and death as do living species of *Loligo* and *Todarodes*.



TEXT-FIG. 11. Figs. 1–5. The right statolith of *Berryteuthis* sp., total L = 2·77 mm; 1, anterior view; 2, posterior view; 3, lateral view; 4, medial view; 5, ventral view.

DISCUSSION

The present work forms a basic framework for a study of the evolution of shallow-water teuthoids, particularly *Loligo*, during the Cenozoic of North America. Because living teuthoid species are not very numerous and there are only three living species of *Loligo* known from North America, an evolutionary tree is not likely to be as complicated as in many other animal classes. Because there are so few fossil remains of teuthoids, evolutionary conclusions based upon statoliths are not likely to conflict seriously with conclusions based upon other remains.

The function of the cephalopod statolith is not known precisely at present but it is probably concerned with monitoring motion of the animal. It might be expected, therefore, that the shape relates in some way to the type of motion and hence to the features of the animal concerned with locomotion such as development of mantle musculature, fin size, and presence of a means to attain neutral buoyancy. Such a relationship is not obvious at present but may become more obvious as our knowledge of locomotion and the role of the statolith develops.

Acknowledgements. Many individuals contributed towards this work. Some informed us of fossil exposures or helped excavate and process samples from various sites. Others gave or lent comparative material, and almost everyone we consulted willingly shared their ideas or special talents. We especially appreciate assistance received from Warren O. Addicott, J. A. R. Ally, Shelton P. Applegate, Warren C. Blow, Lloyd, W. Barker, Martin W. Cawthorn, S. Stillman Berry, David K. Caldwell, William L. Craig, Valerie Facey, Richard A. Fitch, Kurt Geitzenauer, Jack and Mary Hopkins, Richard W. Huddleston, George Kanakoff, Tsunemi Kubodera, Robert J. Lavenberg, Heinz Lowenstam, Richard McGinnis, Mamoru Murata, Roger D. Reimer, Mark Roeder, Graham J. B. Ross, Jack W. Schott, Teruo Tobayama, Bruce Welton, and Charles Wenner. If we have failed to acknowledge assistance, and in a project extending over such a lengthy period we are certain to have overlooked someone, it has not been intentional. John Fitch received partial support with a grant from the Penrose Fund of the American Philosophical Society.

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Typescript received 21 July 1978
Revised typescript received 31 October 1978