

FOSSIL LANTERNFISH OTOLITHS OF CALIFORNIA, WITH NOTES ON FOSSIL MYCTOPHIDAE OF NORTH AMERICA

By JOHN E. FITCH¹

ABSTRACT: Otoliths (sagittae) from 30 species of lanternfishes (Myctophidae) are known from the North American Cenozoic: 15 from Plio-Pleistocene (California), 13 from Miocene (7 California; 5 Veracruz, Mexico; 1 Jamaica), and 2 from Eocene (California). The high incidence of species from California deposits appears to be a reflection of the proximity of the shoreline to preferred myctophid habitat (deep water), rather than a more abundant fauna, but both factors could be involved.

In addition to the 30 species known from their otoliths, skeletal remains (imprints) of seven kinds of lanternfishes have been found in Miocene diatomites of southern California. Otoliths in some of these imprints make it possible to compare them with fossil myctophid sagittae that are unaccompanied by skeletal remains.

Among the fish families inhabiting the ocean off California, only Cottidae and Scorpaenidae contain more members than Myctophidae. A recent listing by Fitch and Lavenberg (1968) shows 33 species of myctophids in 21 genera, while Berry and Perkins (1966) note an additional eight species and two genera from just outside the boundaries of the area covered by the California list. In view of this great variety of species and the density of several nearshore populations (*e.g.*, Paxton [1967] reports 16,500 specimens captured in 48 tows of a midwater trawl in the San Pedro Basin off southern California), it is not surprising that lanternfishes are well represented in California's fossil record.

Fitch (1966, 1967, 1968) and Fitch and Reimer (1967) have noted myctophid otoliths in Pleistocene and Pliocene deposits of southern California, and David (1943) described *Lampanyctus bolini* and *L. petrolifer* from skeletal imprints in Miocene diatomites excavated in the Santa Monica Mountains of southern California. Bagg (1912) illustrated an otolith (sagitta) from *Tarletonbeania crenularis* (Pl. 28, fig. a) in his report on Plio-Pleistocene Foraminifera of San Pedro, but he failed to identify it except as an otolith.

Since 1963, I have investigated fossil exposures whenever possible in an effort to shed light upon the fish faunas that lived here during various periods of the earth's history. To accomplish this, I have developed a routine for washing, screening, and sorting fossiliferous matrix that is very effective for finding otoliths, teeth, vertebrae, and other fish remains (Fitch, 1969). To date, 12 Pleistocene and Pliocene deposits have yielded more than 60,000 otoliths (sagittae) representing over 150 species, and more than 4,500 of these otoliths have been from 15 kinds of myctophids (Table 1). In fact, lanternfish ear

¹Research Associate, Los Angeles County Museum of Natural History; Marine Biologist, California Dept. of Fish and Game, Terminal Island 90731.

stones have been present in every fossil deposit I have examined in southern California that is Miocene or younger in age, and from which I have gleaned more than 1,000 otoliths (Table 2 and unpublished data).

PLEISTOCENE AND PLIOCENE

SITES INVESTIGATED

Since marine fishes from these two epochs, representing possibly 11 million years of time (Downs, 1968), are still living today (Fitch, 1969), I have combined the two in this report for convenience of discussion.

California's youngest marine Pleistocene, Palos Verdes Sand, was deposited between 95,000 and 130,000 years ago (Fanale and Schaeffer, 1965), during a period when ocean temperatures were higher than today at the latitude of San Pedro (Fitch, 1964, 1966). Three southern California sites that I have investigated rather thoroughly ("So. Calif. sites" in Table 1) have yielded over 3,500 otoliths from at least 61 species, but only four otoliths (three species) were from myctophids. The sandy matrix containing these fossils appears to have been laid down at relatively shallow depths, possibly not exceeding 60 feet. A deposit exposed during highway construction north of Arcata (listed as Crannell Road in this report) appears to be a northern California equivalent of the Palos Verdes Sand. Two otoliths, of more than 800 found in material from this site, were from two species of lanternfish (Table 1).

Two widely separated deposits of San Pedro Sand (Miraflores Street and Ventura Freeway) have yielded fish remains indicating that cold oceanic temperatures prevailed when they were being laid down (Fitch, 1967, 1969). No age estimate is available for these early Pleistocene beds, but they too appear to have been formed at depths shallower than 60 feet. Only nine of nearly 4,000 otoliths from these two deposits were from myctophids (four species).

I have investigated Timms Point Silt and its equivalent at Newport Beach (Back Bay), and San Pedro, and near Carpinteria (Bates Road), and otoliths are abundant at all three localities. No age estimate is available for Timms Point Silt, but it is the oldest marine Pleistocene of southern California (Fitch, 1968, 1969), and appears to have been laid down at depths of 400 to 600 feet when ocean temperatures were colder than at the same latitudes today. The 109 myctophid otoliths found in these three deposits were from nine species.

The youngest marine Pliocene of southern California, Lomita Marl, has been estimated as being 3.04 million years old (Obradovich, 1965). Possibly a ton of matrix from a single site yielded over 24 thousand otoliths when it was washed, screened, and sorted. Among the more than 80 kinds of teleosts identified from these remains were many mesopelagics, a few bathypelagics, and a half-dozen kinds of locally extinct northern fishes. The 14 species of myctophids (over 3,100 otoliths) make this the richest assemblage of fossil lan-

TABLE 1
Lanternfish Otoliths Found in Pleistocene and Pliocene of California

SPECIES	PLEISTOCENE						PLIOCENE			
	P.V. Sand		S.P. Sand		Timms Pt. Silt		Lom. Marl		Pico Fm.	
	So. Calif. Sites	Cranl. Rd.	Mrfirs. St.	Vent. Fwy.	Timms Pt.	Nwpt. Bk.By.	Bates Rd.	Mrlst. Cny.	Nwpt. Mesa	Dntn. L.A.
<i>Benthosema</i> sp.							1	926	11	2
<i>Ceratoscopus townsendi</i>					1	1		21	296	12
<i>Diaphus theta</i>		1		5	10	18		537	247	54
<i>Electrona rissoi</i>	1				8				7	
<i>Lampadena urophaos</i>					1			5		2
<i>Lampanyctus regalis</i>								27	2	
<i>Lampanyctus ritteri</i>								8	4	
<i>Myctophum nitidulum</i>								1		
<i>Notoscopus resplendens</i>								5		
<i>Parvilux ingens</i>								8		2
<i>Protomyctophum crockeri</i>				1	8			177		2
<i>Stenobrachius leucopsarus</i>	1		1	1	35	6	1	1120	606	44
<i>Symbolophorus californiensis</i>	2	1						9		1
<i>Tarletonbeania crenularis</i>				1	10	4	3	289	11	7
<i>Triphoturus mexicanus</i>						2		7	2	
Total myctophid otoliths	4	2	1	8	73	31	5	3140	1186	122
No. myctophid species	3	2	1	4	7	5	3	14	9	7
Total otoliths	3535	>800	2746	1200	2601	53	1243	24,299	5103	4285
Total species	>61	>28	>30	>40	>53	14	>37	>83	>55	>48

*otoliths gleaned without aid of microscope

ternfishes known in the world. The material appears to have been laid down at depths exceeding 600 feet.

Two exposures of Pliocene that appear to be referable (or equivalent) to the Pico Formation were sampled extensively during recent years. One of these, on the mesa south of upper Newport Bay, yielded over 5,000 otoliths (1,186 from lanternfishes) representing at least 55 species. Material from the other deposit, in downtown Los Angeles, contained over 4,000 otoliths (122 from myctophids) from 48 species. Sagittae from other mesopelagics and from several bathypelagics were present in both deposits, as were earstones from a few locally extinct northern fishes. Based upon the fish remains, these beds were laid down in depths of at least 600 feet at a time when ocean temperatures were much colder than they are at the same latitudes today.

Myctophid otoliths have turned up in two other Pliocene deposits (Signal Hill and San Diego Fm.), but these were gleaned by student volunteers who were searching for mollusks and did not use a microscope. Thus, neither the species nor the numbers offer reliable indices as to the lanternfish components of these deposits. Five of the six species that were found at these two sites have relatively large otoliths that are difficult to miss when searching through fossiliferous matrix, even without the aid of a microscope. The San Diego Formation yielded nearly 11,600 sagittae from about 50 species, all but one of which (an extinct sciaenid) can be found living at the same latitude today. Most are inhabitants of shallow water, but otoliths of mesopelagics and bathypelagics are also present, although these do not show signs of abrasion by currents and wave action as do the earstones of the shallow water forms. The sagittae of the offshore species apparently arrived in this bed later than those of the inshore fishes, but all appear to have been deposited in relatively shallow water, possibly no deeper than about 60 feet.

SPECIES ACCOUNTS

Benthoosema sp. (Fig. 1b).

Benthoosema sagittae were found in all three deep water Pliocene deposits, and one of the three Pleistocene beds that were laid down in depths greater than 400 feet. Until I have comparative material from *B. glaciale* and *B. suborbitale*, the two most suspect species, they will need to remain unidentified. *B. glaciale* is common in the western north Atlantic and has been reported from the Bering Sea, whereas *B. suborbitale* is an inhabitant of oceanic waters well offshore from California. The fossil otoliths are not from *B. panamense*, a tropical species which is extremely abundant south of Magdalena Bay and in much of the Gulf of California. In the Lomita Marl, *Benthoosema* sagittae comprised nearly four per cent of the 24,300 otoliths I found, so the species was certainly common enough off California some 3 million years ago. Most of these otoliths were from large adults and ranged in length to 2.5 mm, although earstones of juveniles were also plentiful.

Ceratoscopelus townsendi (Eigenmann and Eigenmann, 1889) (Fig. 1o).

Otoliths of *C. townsendi* were found in all but one of the six Plio-Pleistocene deposits that were laid down in depths greater than 400 feet, but they were present in only one of the six shallow water deposits (Table 1). They comprised about six per cent of the 5,100 otoliths from the Newport Mesa locality, and among the nine species of myctophids in this deposits, only *Stenobranchius* was more numerous. Paxton (1967) reported that *C. townsendi* has a center of diurnal distribution above 650 m and that it migrates into the upper 10 m of water at night. It has been considered cosmopolitan in distribution, but recent investigations show that *C. townsendi* inhabits only the eastern north Pacific (Basil Nafpaktitis, pers. comm.). The sagittae of a large adult *C. townsendi* will be about 2.5 mm long; those I have found in fossil deposits are mostly from large adults, and range in length to 2.7 mm.

Diaphus theta Eigenmann and Eigenmann, 1890 (Fig. 1n).

Otoliths of *D. theta* were present in eight of my 12 Pleistocene and Pliocene deposits, being absent in the southern California Palos Verdes Sand (shallow deposition and warm water), in the Miraflores Street deposit (shallow deposition and cold water), in the Bates Road exposure (moderate depth and cold water), and at Signal Hill (material sorted without microscope). They were most abundant at the three Pliocene sites representing deep deposition and cold temperatures, comprising more than two per cent of the total otolith yield from the Lomita Marl, and over five per cent of the total from the Newport Mesa deposit. *D. theta* is restricted to the Pacific Subarctic water mass and the transition area off western North America (Paxton, 1967), so its north-south distribution extends from the Gulf of Alaska to about Cedros Island. It appears to have a vertical distribution similar to that of *C. townsendi*. The largest individuals inhabit more northerly waters and sagittae from these large adults will average about 3.0 mm. All sizes of otoliths were found in the various fossil deposits but most were from adult fish.

Electrona rissoi (Cocco, 1829) (Fig. 1l).

Otoliths of *E. rissoi* were most abundant in the Timms Point Silt, but even there they were not common. They were present in only four deposits, two Pleistocene and two Pliocene, but there is no pattern in their occurrence. One otolith was found in Palos Verdes Sand representing shallow deposition and warm water, and two were in the Signal Hill material which also represented shallow deposition but at normal temperature for the latitude. The remaining *E. rissoi* otoliths (15) were from deep water deposits that were laid down when the ocean was colder than today.

Its present day distribution in the eastern north Pacific does not indicate that it has a preference for cold water. Almost all records of this rarely caught fish have been made offshore from the area between Point Conception and

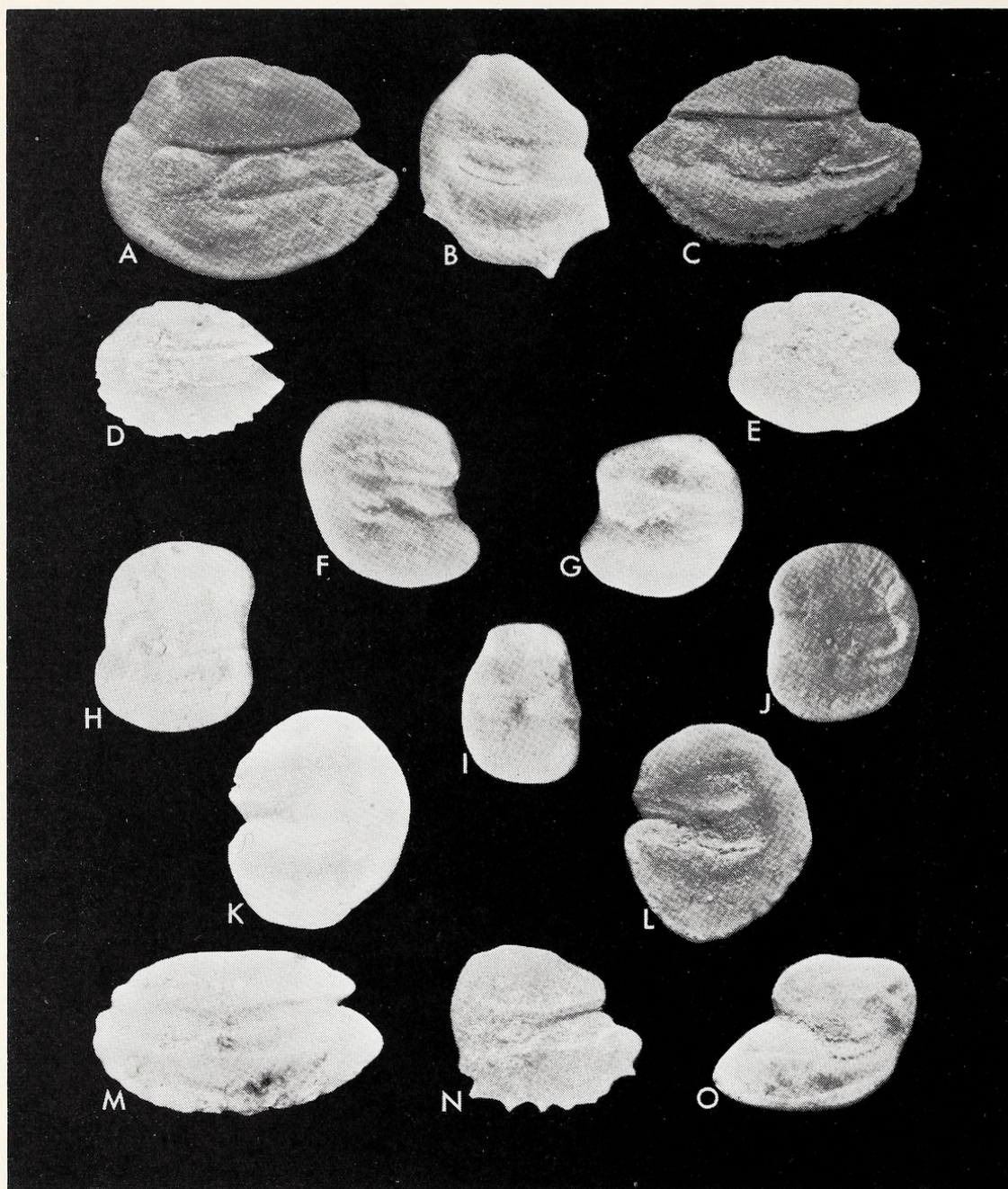


Figure 1. Myctophid sagittae found in Pleistocene and Pliocene of California. Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); and ages and localities of fossil deposits are indicated. a. *Symbolophorus californiensis*, 4.3, l, Lomita Marl, late Pliocene, San Pedro; b. *Benthoosema* sp., 2.3, l, Lomita Marl; c. *Lampadena urophaos*, 6.5, r, Lomita Marl; d. *Myctophum nitidulum*, 3.1, l, Lomita Marl; e. *Tarletonbeania crenularis*, 2.0, l, Lomita Marl; f. *Stenobranchius leucopsarus*, 2.1, l, Lomita Marl; g. *Triphoturus mexicanus*, 1.2, r, Lomita Marl; h. *Lampanyctus regalis*, 2.0, l, Lomita Marl; i. *Parviluxingens*, 0.8, l, Lomita Marl; j. *Lampanyctus ritteri*, 1.3, r, Lomita Marl; k. *Protomyctophum crockeri*, 1.7, r, Timms Point Silt, early Pleistocene, San Pedro; l. *Electrona rissoi*, 3.4, r, Timms Point Silt; m. *Notoscopelus resplendens*, 3.9, l, San Diego Fm., Pliocene, San Diego; n. *Diaphus theta*, 2.5, l, Lomita Marl; o. *Ceratoscopelus townsendi* 2.5, r, Pico Fm., Pliocene, Newport Beach. Photographs by Jack W. Schott.

Magdalena Bay. Sagittae from a large adult will average about 3.8 mm in length. The 18 otoliths noted here ranged from about 2.1 to 4.2 mm long.

Lampadena urophaos Paxton, 1963 (Fig. 1c).

Otoliths of *L. urophaos* have been found in only two deposits, both representing deposition at depths of at least 600 feet and during periods when ocean temperatures were colder than usual. According to Paxton (1967), *L. urophaos* has a diurnal center of distribution below 650 m, but migrates at night to within 50 m of the surface. Nafpaktitis and Paxton (1968) list its geographical range as between 25° N and 42° N in the central and eastern Pacific, and between 21° N and 38° N in the western Atlantic. They illustrate the sagittae of the known species of *Lampadena*, and present characters for differentiating them. *L. urophaos* has the largest otoliths of any lanternfish in the eastern Pacific; those from a full grown fish will exceed 7.5 mm in length. Only one of the six sagittae reported upon in this paper was entire, but the broken fragments were unmistakable because of their size and the 90° notch at the posterodorsal angle.

Lampanyctus regalis (Gilbert, 1891) (Fig. 1h).

Otoliths of *L. regalis* were found only in the Lomita Marl and Newport Mesa (Pico Fm.) deposits, both representing cold water and depths of at least 600 feet. Paxton (1967) states that the diurnal center of distribution for *L. regalis* is below 650 m, but at night it migrates to within 50 m of the surface. He lists it as an inhabitant of the "Subarctic-Central Pacific" water mass, ranging from the Gulf of Alaska to off Cape San Lucas on our coast.

The sagittae of *S. regalis* most closely resemble those of *S. ritteri*, but are somewhat thicker at comparable sizes, and attain a larger maximum size. There is a fair amount of variation in the ratio of length into height, but otoliths from a typical large adult were 1.7 mm long by 2.3 mm high. The fossil otoliths were mostly from adults, and range to about 1.9 mm long.

Lampanyctus ritteri Gilbert, 1915 (Fig. 1j).

Otoliths of *L. ritteri* were present in the same two deposits that contained *L. regalis*, but there were fewer than half as many. Paxton (1967) states that during daylight hours *L. ritteri* has a center of distribution above 650 m, and it migrates to within 50 m of the surface at night, but no shallower. Thus, it inhabits shallower depths during the day than *L. regalis*, but both move into identical depths at night. Paxton classifies *L. regalis* as a "Subarctic-Transitional" species based upon the water masses it inhabits. It is restricted to the eastern north Pacific, having been recorded from the vicinity of Vancouver Island south to about Magdalena Bay. Otoliths from large adults will average about 1.5 mm long by 1.8 mm high, but the ratio of length into height is not constant. The fossil sagittae were primarily from young adults.

Myctophum nitidulum Garman, 1899 (Fig. 1d).

Only a single otolith of *M. nitidulum* has been identified from the Plio-Pleistocene of California. This otolith, from the Lomita Marl, is unmistakable. A *Myctophum* in the western Atlantic is reported to be conspecific with *M. nitidulum* (described from off the west coast of Mexico at lat. 27° 50' N), but differences in the sagittae of the two are so distinctive that they are readily separable on the basis of otolith shape alone. Paxton (1967) did not note *M. nitidulum* from the San Pedro Basin, and Berry and Perkins (1966) captured very few during offshore fishing with a midwater trawl. At times, however, large numbers of *M. nitidulum* can be attracted to a light suspended above the ocean's surface at night, especially in areas well offshore. Their range in the eastern Pacific is from north of San Francisco to south of Cedros Island. Sagittae of large adults will average about 2.5 mm long.

Notoscopelus resplendens Richardson, 1844 (Fig. 1m).

Five otoliths of *N. resplendens* were found in the Lomita Marl, and two were among the sagittae gleaned from the San Diego Formation by student volunteers. Paxton (1967) did not take *N. resplendens* in the San Pedro Basin, but Berry and Perkins (1966) captured them at about 20 offshore stations between San Francisco and Cape San Lucas. Only three of these stations yielded more than three individuals, however, so they appear to be rare even today. The elongate sagittae are impossible to confuse with any other species that occurs off our coast. Those from a large adult will be 3.7 mm long or longer. The fossil material was mostly from somewhat smaller individuals.

Parvilux ingens Hubbs and Wisner, 1964 (Fig. 1i).

Sagittae of *P. ingens* were present only in the Lomita Marl deposit, where sagittae of 13 other myctophid species were found. Paxton (1967) states that *P. ingens* has a diurnal center of distribution below 650 m, and that it migrates to within 50 m of the surface at night, but was never taken shallower. He includes it with *Symbolophorus californiensis* and *Lampadena urophaos* as a "Transitional species," with a coastwise range extending from about the latitude of Cedros Island to just north of San Francisco. The sagittae of *P. ingens* could be confused with those from *Lampanyctus ritteri* and *L. regalis*, but they differ in having a rounded dorsal profile and a deeply arched (concave) inner face. Otoliths from a large adult measured 1.4 mm long by 2.0 mm high. Seven of the eight from Miraleste Canyon were from large adults.

Protomyctophum crockeri (Bolin, 1939) (Fig. 1k).

Sagittae of *P. crockeri* were found at two Pleistocene and two Pliocene sites, all representing deposition during cold periods, and three of the four having been laid down in depths of about 600 feet. They ranked fifth numeric-

ally among the 14 kinds of myctophid otoliths found in the Lomita Marl. All of the deposits containing *Protomyctophum* otoliths also contained earstones of *Diaphus*, *Stenobranchius*, and *Tarletonbeania*, and all but one contained *Ceratoscopelus*. According to Paxton (1967), *P. crockeri* inhabits depths of 400 to 600 m during daytime hours, and has been captured within 50 to 150 m of the surface at night, but never shallower than 50. He classifies it as a "Subarctic-Central Pacific species" according to the water masses it inhabits. It has been captured from south of Cape San Lucas to off Vancouver Island. In more northerly waters its range overlaps that of *P. thompsoni*, and since the otoliths of these two species cannot be separated, some of those from the cold water deposits (*i.e.*, Miraleste Canyon, Timms Point, and downtown L.A.) could be from *P. thompsoni*. Sagittae from large adults will average about 2.4 mm in length. Those in the four fossil deposits were mostly from adult fish, and range to 2.6 mm in length.

Stenobranchius leucopsarus (Eigenmann and Eigenmann, 1890) (Fig. 1f).

S. leucopsarus sagittae turned up in every Plio-Pleistocene deposit I have investigated except Crannell Road (northern California equivalent of Palos Verdes Sand representing warm ocean temperatures and shallow deposition), and Signal Hill, where they could have been overlooked because of their small size. In the Miraflores Street deposit, a single *S. leucopsarus* otolith was the only myctophid represented, while at three localities they were the most abundant of the lanternfish otoliths (*i.e.*, Timms Point, Miraleste Canyon, and Newport Mesa). The 606 otoliths in the Newport Mesa deposit comprised more than ten per cent of the total otolith yield at that site, while the 1,120 found in Miraleste Canyon amounted to only about five per cent of the sagittae from there. Paxton (1967) found their center of distribution during daylight hours at 650 m; at night they migrate from there to within 50 m of the surface, but seldom shallower. He categorizes them as a "Subarctic-Transitional species" ranging from about Cedros Island to the Aleutian Islands. The range of a close relative, *S. nannochir*, overlaps that of *S. leucopsarus* in northern California during some years but is north of there during most years. Sagittae of these two species are indistinguishable, so some of those from the cold water deposits, particularly Timms Point, Miraleste Canyon, and Newport Mesa, could be from *S. nannochir*. The otoliths of a large adult will average about 1.8 mm long. Those in the fossil deposits were mostly from adults, but sagittae from juveniles were also plentiful.

Symbolophorus californiensis (Eigenmann and Eigenmann, 1899) (Fig. 1a).

Otoliths of *S. californiensis* were present in five deposits, but only in the Lomita Marl and San Diego Formation were more than two sagittae found. *S. californiensis* ranges from about off Cedros Island to the vicinity of the Oregon-California border, except during years when the ocean is quite warm,

when it may reach waters off British Columbia. Its presence in the Crannell Road deposit north of Arcata was useful in associating that exposure with the Palos Verdes Sand. During daylight hours its center of distribution is above 650 m, and from there it migrates into the upper 10 m of water at night (Paxton, 1967). It is readily attracted to a light hung above the surface at night. Paxton categorizes *S. californiensis* as an inhabitant of "Transitional" water, along with *Lampadena urophaos* and *Parvilux ingens*. Other species of *Symbolophorus* occur in the central Pacific and south of Cape San Lucas, but their ranges never overlap that of *S. californiensis*. The only larger sagittae among Californian lanternfishes are those of *Lampadena*. Otoliths of large adult *S. californiensis* will average about 4.0 mm long; most of those in the five fossil deposits were from adult fish.

Tarletonbeania crenularis (Jordan and Gilbert, 1880) (Fig. 1e).

Otoliths of *T. crenularis* were present in seven of the 12 Plio-Pleistocene deposits investigated, but they were abundant only in the Lomita Marl, where they comprised more than one per cent of the total otoliths. Only one of the six shallow water exposures contained an earstone from this species, and it (Ventura Freeway) was one of the three deposits laid down when ocean temperatures were colder than usual. Paxton (1967) categorizes *T. crenularis* as a "Subarctic-Transitional species" along with *Diaphus theta*, *Stenobranchius leucopsarus*, and *Lampanyctus ritteri*. Its coastwise range is from about off San Diego to the Aleutian Islands. Its center of distribution during daylight hours is above 650 m, and it migrates from there into the upper 50 m at night. As with *Myctophum nitidulum* and *Symbolophorus californiensis*, *Tarletonbeania* is readily attracted to a light suspended above the water's surface at night. The sagittae of large adult *T. crenularis* will average about 1.8 mm in length. Most of those from the various Plio-Pleistocene deposits were from adult fish, and some were longer than 2.0 mm. Bagg (1912) illustrated an otolith of *T. crenularis* from the Timms Point Silt at San Pedro, but he identified it only as an otolith.

Triphoturus mexicanus (Gilbert, 1890) (Fig. 1g).

Otoliths of *T. mexicanus* were found at only three sites, all representing deposition at depth and during periods of cold ocean temperatures. *T. mexicanus* has a diurnal center of distribution above 650 m, and migrates to 50 m at night, but seldom shallower, according to Paxton (1967). It ranges along the outer coast of Baja California to about the latitude of San Francisco, and is categorized as having an "Eastern Equatorial" distribution by Paxton (1967). The extent of its southern distribution is clouded by the contention of some myctophid specialists (as yet unpublished) that the *Triphoturus* in the Gulf of California and south of Cape San Lucas (to Panama and Peru) represent species that are distinct from *T. mexicanus*. Sagittae of *T. mexicanus* are

never higher than long; those from large individuals will average about 1.5 mm long by 1.4 mm high, but this ratio of length into height may vary somewhat. Most of the 11 fossil otoliths were from young adults.

MIOCENE MYCTOPHIDS

Since teleost otoliths and shells of marine mollusks usually are comprised of the same type of calcium carbonate (*i.e.*, aragonite), one can assume that a fossil deposit containing an assortment of sea shells likely will contain fish earstones also. By using this as a working hypothesis, I have routinely sampled every shelly fossil exposure I have encountered if it is friable or can be broken down without destroying or dissolving the aragonitic constituents. Not all such beds produce otoliths (*e.g.*, oyster reefs and sites where only calcitic sea shells have not leached out generally yield very few sagittae), but deposits occasionally are found that are rich with them. Such is the case with several Miocene outcrops east of Bakersfield where I have conducted extensive investigations. Although these Bakersfield deposits contain an abundance of otoliths, lanternfish sagittae generally are scarce.

No attempt will be made in this report to describe new species based upon

TABLE 2
Lanternfish Otoliths from Miocene of North America

SPECIES	California						
	Hwy. 178	Round Mt. Silt	Barker's Rnch.	Pomona Fwy.	Jamaica Bowden Fm.	Mexico Veracruz	
<i>Diaphus</i> sp.	261						
<i>Diaphus</i> sp.		1					
<i>Diaphus</i> sp.					56		
<i>Diogenichthys</i> sp.?							1
<i>Hygophum intermedius</i>							1
<i>Hygophum</i> sp.		1					
<i>Lampanyctus</i> sp.		353	15				
<i>Lampanyctus</i> sp.				>100			
<i>Myctophum acutus</i>							4
<i>Myctophum pabloensis</i>							2
<i>Myctophum</i> sp.		1					
<i>Notoscopelus</i> sp.	57						
<i>Symbolophorus biatlanticus</i>							2
Total myctophid otoliths	318	356	15	>100	56	10	
No. myctophid species	2	4	1	1	1	5	
Total otoliths	>3,000	>4,000	>25,000	>150	993	21	
Total species	>20	>40	>70	>15	>50	13	

otoliths alone, because in 1968 some diatomite deposits were found that are rich with skeletal imprints of myctophids which still retain their otoliths (Fig. 3). Since the diatomite is the same age (middle to late Miocene) as the friable shelly deposits east of Bakersfield, there is an excellent chance of locating lanternfish imprints to match the otoliths. If "imprints with otoliths" can be matched to "imprints without otoliths" and to "otoliths without imprints," a great deal of cluttering up of the literature through multiplication of specific names can be avoided, and there is hope of obtaining an accurate synoptic picture of the Miocene fish fauna.

A locality beside State Highway 178 (east of Bakersfield) contains otoliths that represent deeper water species than do the faunas in such well known members of the Temblor Formation as Sharktooth Hill, Round Mountain Silt, and "Barker's Ranch." Although many of the mollusk shells in these beds near Highway 178 have leached out so that only their casts remain, sufficient shelly matrix can be found to make sampling worthwhile. Otoliths from two species of myctophids are abundant, and are in a better state of preservation than many Pleistocene sagittae which may be 10 million years younger. The commonest lanternfish is a species of *Diaphus* (Fig. 2b, Table 2). The 261 otoliths from this fish range in length to 2.8 mm, and comprise about 12 per cent of the total otolith yield from these beds. The other lanternfish from the Highway 178 deposit (Fig. 2f) is from a species of *Notoscopelus*. Only 57 otoliths from this species have been found, and most of these are in relatively poor condition. They range in length to 3.1 mm. Morid (family Moridae) sagittae that pass through 20 mesh screen are the most abundant teleost of more than 30 species found at this site.

Narrow lenses of shelly matrix in the Round Mountain Silt south of Stanford University locality 2121 (Keen, 1943) have yielded nearly 4,400 otoliths representing at least 50 species. Four lanternfishes are represented among the 356 myctophid sagittae, but for three of these (*Hygophum* sp., Fig. 2g; *Diaphus* sp., Fig. 2a; and *Myctophum* sp., Fig. 2h) there is but one otolith each, while 353 of the earstones are from a species of *Lampanyctus* (Fig. 2e). Although the *Lampanyctus* sagittae amounted to slightly more than eight per cent of the total otolith yield from the Round Mountain Silt, the number probably would be more than double what it is if I had searched all of the fine residue from my samples. About 99 per cent of the *Lampanyctus* otoliths from Round Mountain Silt have been less than 1 mm long, so they pass through 20 mesh screens with ease. Although they are retained in 30 mesh screen, I have purposely avoided using mesh that fine for processing most of the material I have dug from this site. To sort through residue that passes through 20 mesh, but is retained by 30 mesh, is extremely time consuming; so when initial sub-sampling shows that very few species are escaping the 20 mesh screen, I examine only enough fine residue to assure myself of an adequate quantity of the tiny otoliths.

The oldest beds of the Temblor Formation that I have examined for oto-

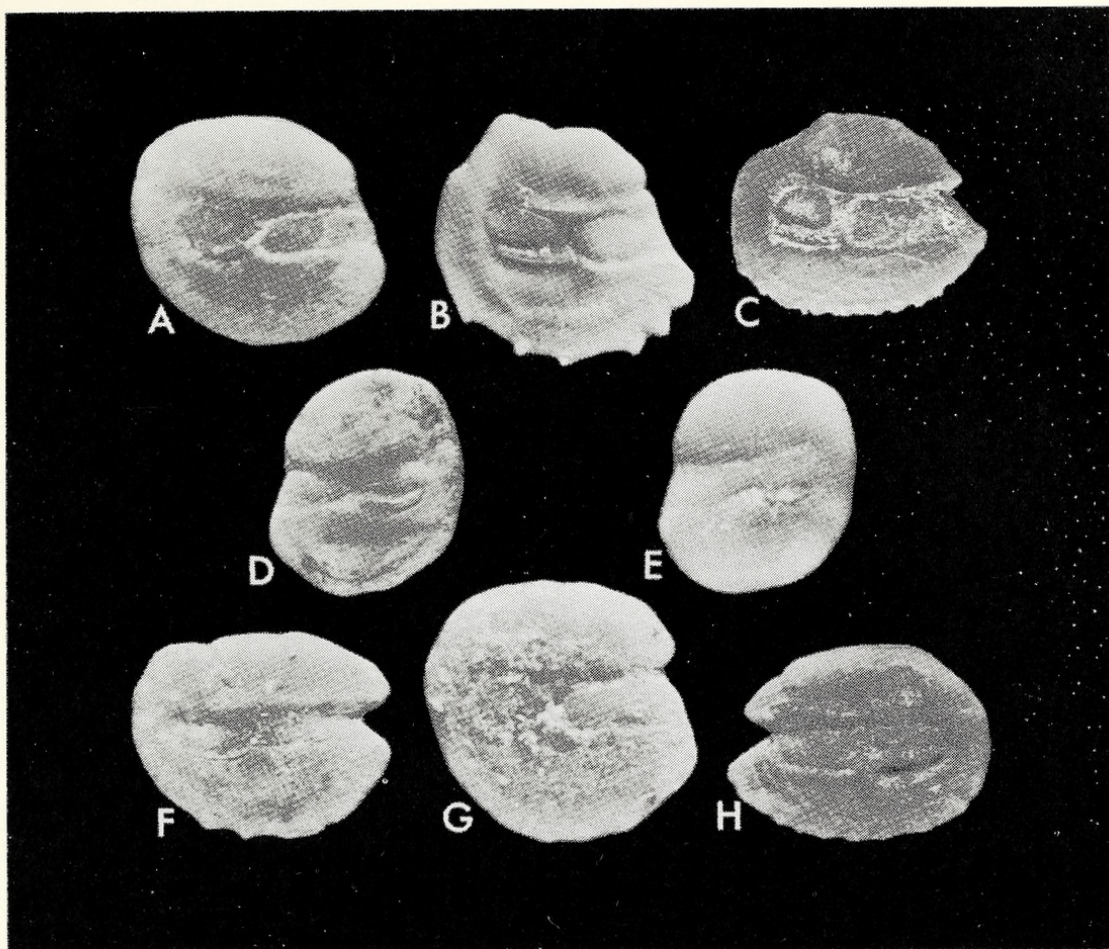


Figure 2. Myctophid sagittae found in Miocene of California and Jamaica. Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); and localities of fossil deposits are indicated. a. badly worn *Diaphus* sp., 1.2, l, Round Mountain Silt, Bakersfield, Calif.; b. *Diaphus* sp., 2.7, l, Hwy. 178, Bakersfield; c. *Diaphus* sp., 4.2, l, Bowden Fm., Jamaica; d. *Lampanyctus* sp., 1.2, r, Barker's Ranch, Bakersfield; e. *Lampanyctus* sp., 1.0, r, Round Mountain Silt; f. *Notoscopelus* sp., 2.6, l, Hwy. 178; g. *Hygophum* sp., 1.3, l, Round Mountain Silt; h. *Myctophum* sp., 2.8, r, Round Mountain Silt. Photographs by Jack W. Schott.

liths are the sandy "Barker's Ranch" exposures. These beds outcrop in dozens of canyons, gullies, and road cuts between the Kern River and Pyramid Hill, and each layer contains a slightly different admixture of otoliths. The fish fauna is predominantly from shallow water (judged by today's standards), but there is a sprinkling of remains from mesopelagics and bathypelagics at most sites. Sagittae from croakers (family Sciaenidae) are dominant in all the beds, from the standpoint of size, numerical abundance, and kinds. Myctophid otoliths, while not quite at the other end of the scale, have generally been small, scarce, and from only one species—a *Lampanyctus* (Fig. 2d) which is identical to the *Lampanyctus* in Round Mountain Silt.

Skeletal imprints of myctophids are abundant in Miocene diatomites and



Figure 3. Left (upper) and right sagittae *in situ* in skeletal imprint of *Lampanyctus* sp. on diatomite slab from west of Pomona, California. Photograph by Jack W. Schott.

shales, and based upon such imprints, David (1943) described *Lampanyctus petrolifer* and *L. bolini* from specimens collected in the Santa Monica Mountains. Examination of her type material (now in the Los Angeles County Museum of Natural History) shows that neither species belongs in the genus *Lampanyctus*. Her *Lampanyctus petrolifer* is a *Lepidophanes*, while her *Lampanyctus bolini* is a *Diaphus* (R. J. Lavenberg, pers. comm.). None of the specimens she selected as "cotypes" (paratypes) of *L. bolini*, including the

imprint on the same slab as her "type," belongs to the same genus (*Diaphus*) as the holotype. To date, seven genera of lanternfishes are represented in the Miocene of southern California as skeletal imprints (R. J. Lavenberg, pers. comm.), but until last year (1968) no imprint found had retained its otoliths. At that time, during freeway construction and other excavating activities west of Pomona, several beds of diatomite were exposed that were rich with fish imprints, especially myctophids, and most have retained identifiable otoliths (Fig. 3). In addition, loose earstones are scattered throughout these deposits and impacted in some of the abundant coprolites.

Although I have examined material from Miocene deposits in Florida, North Carolina, Virginia, Maryland, and Jamaica, none of these except the Bowden Formation (Jamaica) has contained lanternfish otoliths. A 25-pound field sample from the Bowden Fm. contained 993 sagittae from more than 50 species of teleosts, including several kinds of mesopelagics. Fifty-six of the 993 otoliths were from a species of *Diaphus* (Fig. 2c). Nafpaktitis (1968), in his report on taxonomy and distribution of *Diaphus* in the north Atlantic, shows at least 15 species presently inhabiting waters in the vicinity of Jamaica. My comparative collection contains otoliths from 13 of these extant species, but I am lacking in sagittae from *D. garmani* and *D. subtilis*. The fossil otoliths are closest to *D. problematicus* among the species I have compared, but they differ from *D. problematicus* in several significant features, particularly in the texture and amount of spination on the ventral margin. Until sagittae from the other critical species can be examined, it seems both inappropriate and inadvisable to describe these fossil otoliths as new.

The only other fossil myctophids known from the Miocene of North America are five species described (as four) by Weiler (1959) from otoliths found in a core from oil well drilling near Veracruz, Mexico. His holotype of *Hygophus* [= *Hygophum*] *intermedius* appears to be correctly assigned generically, but the otolith he illustrates as figure 19 and calls "*Hygophus intermedius*?" is not *Hygophum*. From its outline and size, it could be *Diogenichthys*, but *Lampanyctus* is also a possibility. In a later publication, Weiler (1968) placed his "Otol. (Nyctophidarum) *acutus*" [sic.] in the genus *Myctophum*, which, from his figured specimens, undoubtedly is correct. His other two species, however, belong to different genera than those he assigned them to. His "*Ceratoscopelus? pabloensis*" very likely is a *Myctophum*, which has a sagitta characterized by a deeply rounded (convex) ventral margin, a slight concavity at the posterodorsal angle, and an antirostrum that is "high up" as in *Hygophum*. *Ceratoscopelus*, on the other hand, has an otolith with a gently rounded ventral margin, an elongate rounded rostrum, and an entirely different shape and placement of the antirostrum (see Fig. 1o, which, although *C. townsendi*, is very similar to *C. maderensis*, the type species of *Ceratoscopelus*). Finally, Weiler's "*Nyctophus* [= *Myctophum*] *biatlanticus*" probably is *Symbolophorus*, but the possibility of it being *Diaphus* should not be overlooked. The evenly curved dorsal and ventral contours, ratio of height into length, and

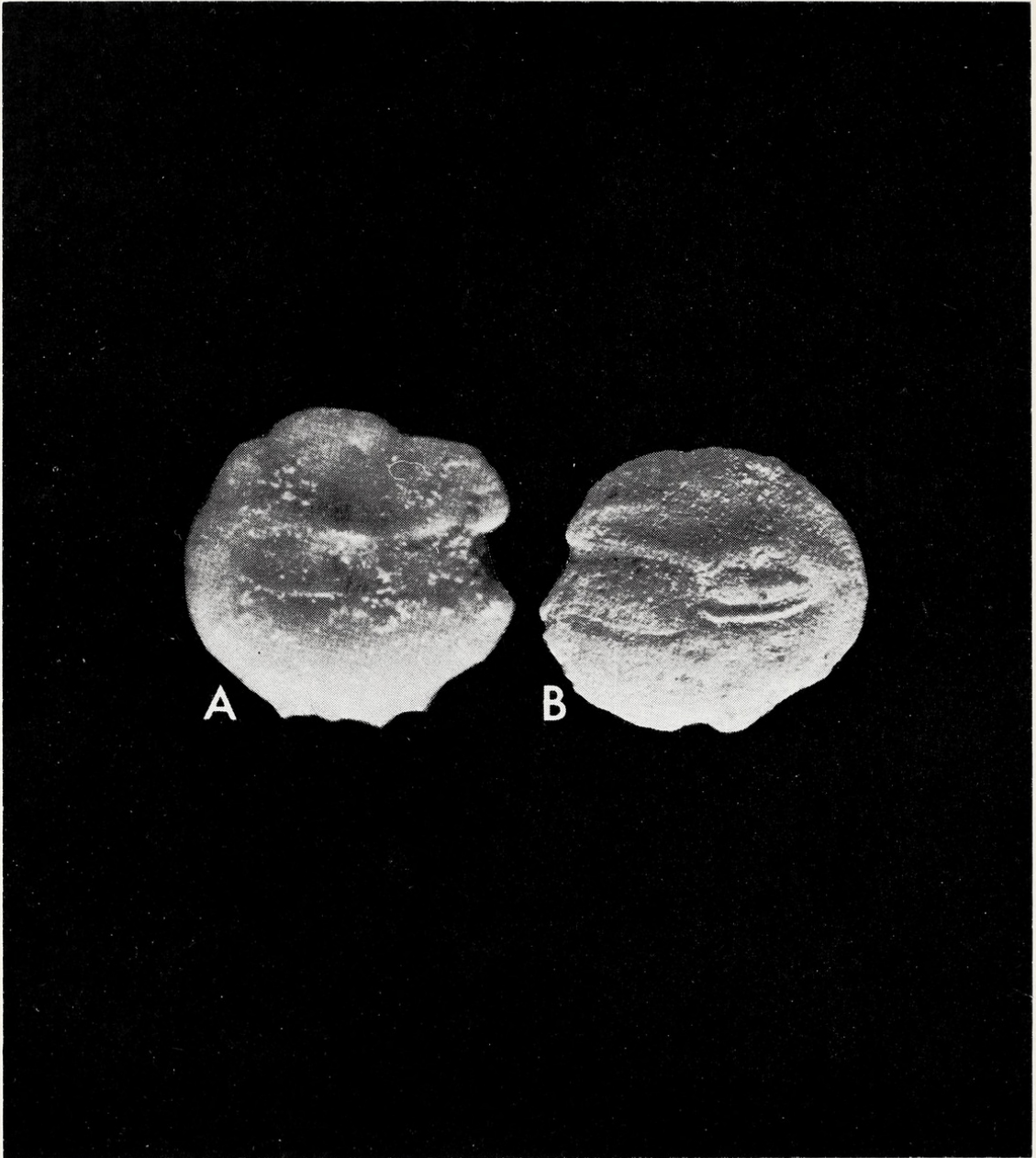


Figure 4. Otoliths from two species of *Diaphus* found in Rose Canyon Fm., Eocene, San Diego County, Calif. a. left sagitta, 1.3 mm long; b. right sagitta, 3.0 mm long. Photographs by Jack W. Schott.

numerous rounded crenations on the dorsal and ventral margins are typical of *Symbolophorus*. The ventral margin of *Diaphus* would be spinose instead of scalloped as in Weiler's illustration of "*N. biatlanticus*," but spines and other frills often are worn down prior to or during fossilization.

EOCENE MYCTOPHIDS

Numerous Eocene beds are exposed in canyons, cliffs, gullies, road cuts, and excavations in San Diego County between Mission Bay and Oceanside

and inland as far as Poway, and some of these contain well preserved otoliths, teeth, and other fish fragmentia. Although I have barely explored two or three of these outcrops, I have found sagittae of several deep sea teleosts, including two species of myctophids (genus *Diaphus*). Although solitary fish scales found in Cretaceous cherts in Alabama are thought to be from lanternfishes (S. P. Applegate, pers. comm.), there is no record of a myctophid skeletal imprint or otolith prior to the Eocene. Danil'chenko (1960) reports lanternfish skeletal imprints from Middle Eocene beds in Russia, and Weiler (1968) lists four species identified from otoliths found in European Eocene. Thus, the *Diaphus* sagittae from the Rose Canyon Fm. north of San Diego match the oldest positive records for the family elsewhere in the world.

Two of the three otoliths I have found to date are from a *Diaphus* with a deeper ostium (the anterior portion of the sulcus or groove that shows on the inner face) than cauda (the posterior portion of the sulcus). The ventral margin of this otolith (Fig. 4b) appears to be roughened, but it is spinose in better preserved material. The other species, represented by a single small otolith with an indentation in the anterodorsal margin (Fig. 4a), has a series of spines along the ventral margin, and there is no visible difference in the depth of the ostium and cauda. Since I have barely begun investigating these beds, and have only three sagittae on hand, it would be premature to give them specific names at this time. In view of the small quantity of matrix I have processed to date, there should be no problem obtaining sufficient otoliths of both species to render satisfactory descriptions, and to place "type" or "referred" material where it will be available to other researchers.

DISCUSSION

Lanternfishes extend as far back into the fossil record of California as they do anywhere in the world, and the presence of *Diaphus* otoliths in Eocene deposits north of San Diego shows that a generic character which evolved in this family upwards of 60 million years ago (at least) has remained stable ever since. *Diaphus* is considered by many ichthyologists to be the most highly specialized of the lanternfish genera, and its lengthy fossil record would certainly bear this out.

Although myctophid remains have not been found in the Oligocene of North America, this probably reflects a shortage of accessible fossiliferous strata that were laid down in deep water, rather than a lack of lanternfishes in the seas bordering our continent during that epoch. Fish remains are abundant at Pyramid Hill (Oligocene) east of Bakersfield, but these represent a shallow water fauna, as do the teleost sagittae in the otolith rich marls and sands of the Gulf Coast Oligocene.

The lanternfishes of our Miocene seas left a better record than their predecessors, and as a result, otoliths from 13 species in 7 genera have been found in deposits in California (7 species in 5 genera), Mexico (5 species in

4 genera), and Jamaica (1 species). In addition, skeletal imprints are abundant in Miocene diatomites and shales of southern California, and although these are known to comprise at least seven kinds of lanternfishes, only two species (in two genera) have been described so far. Thus, myctophid genera which appear to have been well established throughout the Miocene are: *Diaphus* (present since Eocene), *Diogenichthys*, *Hygophum*, *Lampanyctus*, *Lepidophanes*, *Myctophum*, *Notoscopelus*, and *Symbolophorus*.

During the Pliocene and Pleistocene, otoliths from extant species were left in many deposits throughout California, but not elsewhere on the continent. Sagittae from all but *Diogenichthys* and *Lepidophanes*, among the eight genera present during Miocene, were recovered from Pliocene and Pleistocene deposits and nine additional genera were noted: *Benthosema*, *Ceratoscopelus*, *Electrona*, *Lampadena*, *Parvilux*, *Protomyctophum*, *Stenobranchius*, *Tarletonbeania*, and *Triphoturus*. Six of the 12 Pliocene and Pleistocene deposits that yielded myctophid otoliths were laid down at relatively shallow depths, possibly 60 feet or less, yet lanternfishes are not known to inhabit such shallow water. In spite of their mesopelagic existence, their otoliths can arrive in shallow, nearshore deposits in any of several ways: (i) fishes can be eaten by a predator in deeper waters and their otoliths transported to a shallow area in the predator's digestive tract, which they can pass through in a relatively unaltered condition; (ii) mass mortalities can occur and the dead fishes can be transported into shallow areas by currents or wind action, or in the stomachs of scavengers; (iii) in undertaking diurnal migrations near the heads of submarine canyons or where the bottom gradient rises abruptly near shore, straying, predation, and natural mortality can result in otolith deposition at shallow depths; (iv) spawning migrations take some species (and their otoliths) into shallower areas than they inhabit the rest of the year; and (v) deep areas which contain otoliths of offshore species can be, and are, folded and faulted upward so that subsequent deposition will be from shallow species, and vice versa. Each of these factors was responsible at one time or another for sagittae of deep water species being in shallow water deposits.

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