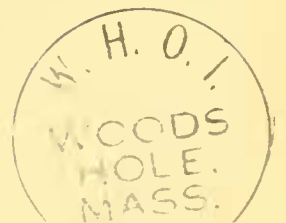


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# STUDIES OF ALEPISAUROID FISHES

By

N. B. MARSHALL



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# STUDIES OF ALEPISAUROID FISHES

By N. B. Marshall

(Plate XIX and Text-figs 1-9)

## INTRODUCTION

THE Alepisauroidea are voracious, bathypelagic fishes which together with the Myctophyoidea form the order Iniomii.

Fishes of the order Iniomii are soft-rayed teleosts, which have evolved beyond the level of the Isospondyli in that the premaxillaries exclude the maxillaries from the gape. The pelvic fins are usually abdominal in position, but when they are set close to the pectorals, as in the Aulopidae, there is no association between the pelvic bones and the pectoral girdle. The swim-bladder when present is closed (physoclistous) and the blood supply to the retina mirabilia enters at the anterior end. There are usually 19 principal rays in the caudal fin and 6-11 rays in each pelvic fin. The dorsal fin and anal fin are never opposed and an adipose dorsal fin is usually present. There is no mesocoracoid, nor is a Weberian mechanism present.

The Alepisauroidea can be defined as bathypelagic Iniomii with no swim-bladder or luminescent organs, with a single row of numerous (more than 20) small teeth on each premaxillary, one or two rows of teeth on each palatine, one to three rows of teeth on each dentary and with gill-rakers in the form of spines or teeth. The anal fin has from 12-50 rays and is usually set close to the caudal. Lastly, there are 3-4+4-5 branchiostegal rays.<sup>1</sup>

Compared with most other oceanic, mid-water teleosts, the Alepisauroidea are large, even very large, fishes.<sup>2</sup> Owing to their size and swiftness, our knowledge of this suborder of the Iniomii—at least from catches of mid-water nets—is very incomplete. Almost without exception, the larger known individuals of the larger species have come either from the stomachs of whales or of oceanic fishes, such as tunny, or have been taken on long lines. *Alepisaurus* itself, which is caught on the tunny hooks of Madeiran fishermen, has contained some relatively large paralepidids.

This report is based mainly on specimens from the Discovery Collections. The material contains some new species and is sufficiently extensive to allow of a revision of the Scopelarchidae and a review of the relationships of the alepisauroid fishes.

## ACKNOWLEDGEMENTS

My thanks are due to Dr N. A. Mackintosh for putting the material at my disposal and to Dr W. A. Gosline, who has read the manuscript and made some useful critical comments.

<sup>1</sup> The plus sign separates the rays on the epiphyal and ceratohyal bones.

<sup>2</sup> *Alepisaurus* reaches a standard length of at least 1500 mm.; the largest known *Anopterus* is 855 mm. in length, while three paralepidids, *Magnisudis barysoma*, *Notolepis coatsi* and *Sudis hyalina*, fall within the standard length range of 400-500 mm. Certain other paralepidids, *Omosudis lowei*, *Eccermannella balbo* and *Neoscopelarchoides elongatus*, grow to within the range 150-300 mm.

## PART I. CLASSIFICATION OF THE INIOMI

In order to give systematic perspective to these studies, an outline classification of the order Iniomi is given. Those workers mainly responsible for this arrangement will become apparent during the course of this paper.

## I. Suborder ALEPISAUROIDEA

## Family SCOPELARCHIDAE

Genera *Scopelarchus* Alcock, *Neoscopelarchoides* Chapman

## Family EVERMANNELLIDAE

Genus *Evermannella* Fowler

## Family PARALEPIDIDAE

## Subfamily SUDINAE

Genus *Sudis* Rafinesque Schmaltz

## Subfamily PARALEPIDINAE

Genera *Magnisudis* Harry, *Paralepis* Cuvier, *Notolepis* Dollo, *Lestidium* Gilbert, *Macroparalepis* Ege

## Family ANOPTERIDAE

GENUS *Anopterus* Zugmayer

## Family ALEPISAUROIDAE

Genus *Alepisaurus* Lowe

## Family OMOSUDIDAE

Genus *Omosudis* Günther

## II. Suborder MYCTOPHOIDEA

## Family AULOPIDAE

Genera *Aulopus* Cuvier, *Hime* Starks and *Latropiscus* Whitley

## Family CHLOROPHTHALMIDAE

Genera *Chlorophthalmus* Bonaparte, *Bathysauropsis* Regan

Family NOTOSUDIDAE<sup>1</sup>

Genera *Notosudis* Waite, *Luciosudis* Fraser-Brunner

## Family BATHYPTEROIDAE

Genera *Bathypterois* Günther, *Benthosaurus* Goode and Bean

## Family IPNOPIDAE

Genera *Ipnops* Günther, *Bathymicrops* Koefoed

## Family NEOSCOPELIDAE

Genera *Neoscopelus* Johnson, *Solivomer* Miller, *Scopelengys* Alcock

## Family MYCTOPHIDAE

Genera *Electrona* Goode and Bean, *Hygophum* (Tåning) Bolin, *Benthoosema* Goode and Bean, *Diogenichthys* Bolin, *Myctophum* Rafinesque, *Ctenoscopelus* Fraser-Brunner, *Loweina* Fowler, *Gonichthys* Gistel, *Ctenobranchus* Fowler, *Tarltonbeania* Eigenmann and Eigenmann, *Diaphus* Eigenmann and Eigenmann, *Notolychnus* Fraser-Brunner, *Lampadena* Goode and Bean, *Lampanyctodes* Fraser-Brunner, *Lampanyctus* Bonaparte, *Ceratoscopelus* Günther, *Gymnoscopelus* Günther, *Lampichthys* Fraser-Brunner, *Notoscopelus* Günther, *Hintonia* Fraser-Brunner, *Scopelopsis* Brauer

<sup>1</sup> It would appear that *Scopelosaurus* Bleeker (Act. Soc. Sc. Indo-Neerl, VIII, 1860, Elfde Bijdr. Amboina, p. 13) should be included in this family.

## Family HARPADONTIDAE

Genera *Harpadon* Le Sueur, *Bathysaurus* Günther

## Family SYNODONTIDAE

Genera *Synodus* (Gronovius) Scopoli, *Trachinocephalus* Gill, *Saurida* Cuvier and Valenciennes, *Xystodus* Ogilby.

## The Family SCOPELARCHIDAE

The first known fish of this family was described by Alcock (1896, 1899) under the name *Scopelarchus guentheri*.<sup>1</sup> It was taken by H.M. Indian Marine Survey Steamer 'Investigator' while trawling between depths of 180 and 217 fathoms off Colombo, Ceylon. Observing that the fish '...is a remarkable generalized form of Scopeloid, showing affinities with *Saurus*, *Chlorophthalmus*, *Scopelus*, *Odontostomus* and *Paralepis*', Alcock (1896) placed it in the family Scopelidae, group Scopelarchina.

'Valdivia' took twelve specimens of scopelarchids at various stations in the Atlantic, Indian and Southern Oceans. These were described by Brauer (1902, 1906) as *Dissomma anale* and placed in the family Scopelidae. Roule (1916, 1919), having examined seven scopelarchids taken off the Azores during the cruises of 'Princesse Alice', described them as a new species, *Odontostomus perarmatus*, of the family Odontostomidae. However, *Odontostomus* Cocco (amended to *Evermannella* by Fowler (1901), on account of *Odontostomus* Cocco, 1838, being a homonym of *Odontostomus* Beck, 1837, a molluscan genus) is quite distinct from *Scopelarchus* (see below).

Regan (1911), in setting out the classification of the Iniomi, defined the family Scopelarchidae and placed it in the suborder Alepisauroidea. Then Parr (1928) pointed out that Regan had included both *Evermannella* and *Scopelarchus* (= *Dissomma*) in the Scopelarchidae, and that the diagnosis of the family was based on a study of *Evermannella hyalina*. Parr showed clearly that *Scopelarchus* and *Evermannella* are so distinct as to warrant separation into different families: he was thus able to give the first critical diagnosis of the Scopelarchidae. In a later paper (Parr, 1929), this diagnosis was extended to include findings from osteological studies. Furthermore, in the 1929 paper a new genus and species, *Scopelarchoides nicholsi*, was described, the type and a paratype being taken by 'Pawnee' off the west coast of Mexico. Additions to this description are to be found in a later paper (Parr, 1931a) in which three more specimens are recorded, one from the Gulf of California, one off the west coast of Central America and one from a locality in the Pacific Ocean.

A further new species, *Scopelarchus elongatus*, was described by Norman (1937) from an individual taken north-east of Kerguelen Island by the B.A.N.Z. Antarctic Research Expedition. This was followed by Chapman's (1939) proposal of a new genus and species, *Neoscopelarchoides dentatus*, the holotype coming from the central part of the Gulf of Alaska. Lastly Mead and Böhlke (1953) have described *Scopelarchus linguoides* from three juvenile individuals taken off northern Japan.

The Discovery material contains two new species and a large larval scopelarchid, descriptions of which, together with a fuller account of Norman's species *elongatus*, now follow. But to anticipate a later section, it must be added, that the study of these individuals has led me to conclude that the scopelarchids can be divided into two well-marked genera, *Scopelarchus* Alcock and *Neoscopelarchoides* Chapman. Synonymies will be discussed on p. 312-14.

*Scopelarchus cavei* sp.n.

(Fig. 1 and Pl. XIX, figs, 5, 6.)

*Holotype*. A specimen 70 mm. in standard length taken by R.R.S. 'Discovery II' in a young fish trawl, hauled obliquely between 500 m. and the surface, at station 1585: 00° 06' S, 49° 45' 4" E., Indian Ocean: about 400 miles north-west of the Seychelles.

<sup>1</sup> In the 1899 publication Alcock gave the specific name as *güntheri*.

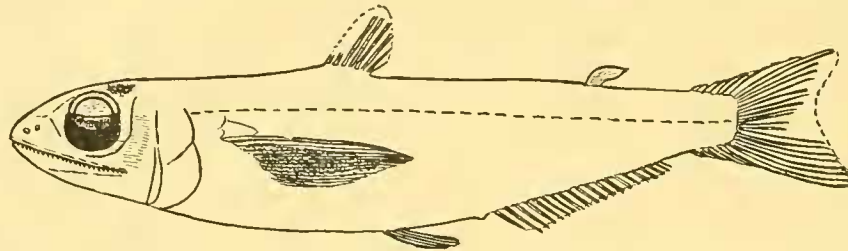
*Body proportions in hundredths of the standard length (70 mm.).* Greatest depth of body 24.3; length of head 25.7; horizontal diameter of eye 8.6; length of snout 7.1; width of bony interorbital 2.6; length of lower jaw 21.4; maxilla 17.8; length from tip of snout to origin of dorsal fin 40; snout to adipose dorsal fin 75.7; snout to pectoral fin 28.6; snout to pelvic fin 47.1; snout to anal fin 61.4; length of pectoral fin 25.7; length of pelvic fin 12.1; length of caudal peduncle 14.3; depth of caudal peduncle 9.3. Body compressed; greatest breadth (at pectoral girdle) 14.3.

*Fin-rays.* D. 9, A. 21, Pect. 21, Pv. 9.

*Scaling.* Large cycloid scales on opercula; probably also present on cheeks. Scales over the trunk and tail well ossified, with a shiny, armoured appearance: cycloid. Scale rows between lateral line and origin of dorsal fin 4; between lateral line and origin of anal fin 7. Number of scales along lateral line (to caudal flexure) 43. Lateral line scales only slightly enlarged, about 1.2 times as deep as those immediately adjacent.

*Vertebrae.* 41.<sup>1</sup>

*Dentition.* About fifty-five small, pointed retrorse teeth on premaxilla. Dentary with about thirty outer, smallish, pointed teeth and 9-10 inner, larger, and depressible teeth of which the second and third are the largest. The first six of these teeth are barbed. Palatine teeth arranged in two closely adjacent rows, each consisting of 5-6 teeth. Lingual teeth ten, the first longest, the rest gradually decreasing in size.



Text-fig. 1. *Scopelarchus cavei*. Holotype ( $\times 1.3$ ).

*Colour* (in spirit). General body colour yellowish brown, the dorsal surface darker, with a fairly dense peppering of small melanophores covering the upper half of the flank-area above the lateral line. Immediately behind each eye is a black lunate area. Dorsal, anal, pelvic and caudal fins transparent or whitish. The pectoral fin is black, except for the two uppermost and five of the lowermost fin rays, which are whitish.

Underlying the scales over the lower half of the abdomen is a layer of silvery pigment, which extends from the isthmus to the anus. (Is it possible that luminescent tissue may be associated with such a light-reflecting layer?) Above this silvery area, the black peritoneum of the body cavity shows through the body wall.

This species is most closely related to *Scopelarchus guentheri* Alcock, but has fewer anal rays (21, cf. 26), fewer lateral-line scales (43, cf. *c.* 50) and these scales are not enlarged as in *S. guentheri*. Perhaps there is also a difference in the interorbital width, which in *S. cavei* is relatively broad, whereas in *S. guentheri* Alcock (1899) described the eyes as being separated by a 'mere linear space'.

I have much pleasure in naming this species after A. J. E. Cave, Professor of Anatomy at St Bartholomew's Hospital Medical College.

<sup>1</sup> In all counts of vertebral numbers the last, upturned, caudal element has been included.

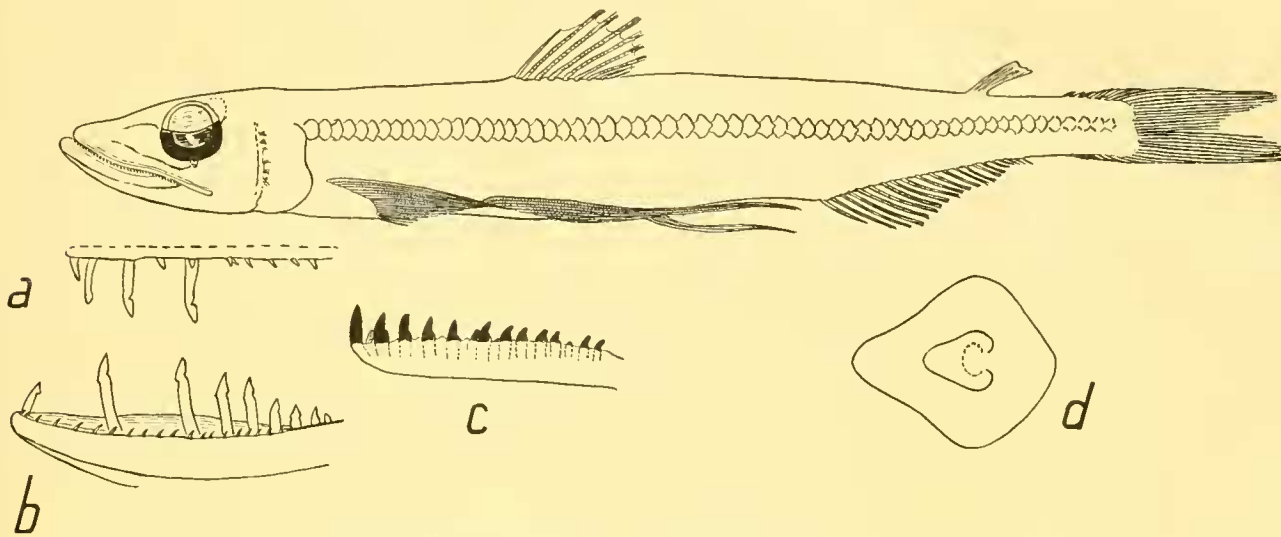
*Neoscopelarchoides dubius* sp.n.

(Text-fig. 2 and Pl. XIX, figs. 3, 4.)

*Holotype.* A female, 138 mm. in standard length, taken in a 450 cm. closing net hauled obliquely between 1800 and 1150 m., at station 1759: 31° 54' 5" S, 51° 27' 9" E., Indian Ocean: about 500 miles south-east of Madagascar.

*Body proportions in hundredths of the standard length (138 mm.).* Greatest depth of body 17.5; length of head 22.8; horizontal diameter of eye 5.8; length of snout 8.7; width of bony interorbital 0.7; length of lower jaw 20.3; length of maxilla 15.2; length from tip of snout to origin of dorsal fin 38.4; snout to adipose dorsal fin 81.2; snout to pectoral fin 25.5; snout to pelvic fin 40.9; snout to anal fin 61.5; length of pectoral fin 21.0; length of pelvic fin 29.0; length of caudal peduncle 11.2; depth of caudal peduncle 6.2. Anus situated a little in front of the origin of the anal fin. Trunk not much deeper than wide at mid-point of body.

*Fin-rays.* D. 9, A. 21, Pect. 27, Pv. 9.



Text-fig. 2. *Neoscopelarchoides dubius*. Holotype ( $\times 1$ ): a, palatine teeth ( $\times 2.5$ ); b, mandibular teeth ( $\times 2.5$ ); c, lingual teeth ( $\times 2.5$ ); d, lateral line scale ( $\times 6$ ).

*Scaling.* Rather small, thin cycloid scales on cheeks and gill covers and over the body, extending a short way in a B-shaped area over the bases of the principal caudal rays. Scales of lateral line much enlarged. Scales along lateral line 59. Transverse rows of scales between origin of dorsal fin and lateral line 8; between origin of anal fin and lateral line 10-11.

*Vertebrae.* 57.

*Dentition.* Premaxilla with about 80 small, pointed, retrorse teeth. Dentary with about thirty outer, smaller pointed teeth and nine inner, long, barbed, depressible teeth, the second and third being the largest. Left palatine with three large, barbed, depressible teeth, these being set somewhat inward from a row of eight small, pointed teeth. Lingual teeth fourteen, moderately compressed, the first the largest, the remainder gradually decreasing in size.

*Gill-teeth.* The first gill arch bears a series of closely set, small, pointed gill-teeth.

*Colour (in spirit).* Dark brown above the lateral line, medium brown below, except where the black peritoneum of the body cavity shows through the abdominal walls. The fins are more or less hyaline, except for the caudal, which has a fairly dense covering of small melanophores.

There is a kidney-shaped iridescent area on the outer walls of the optic cup of the eye, close to the lens. This has been regarded as a luminescent organ, but it must be the elliptical mass of fibrous tissue

which Brauer (1908) called a 'linsen polster' and which is shown on his pl. 40, figs. 2 and 5, of *Dissomma anale*.

Table 1 shows the number of fin-rays in *Neoscopelarchoides dubius* compared with the other known species of this genus.

*N. dubius* is also readily distinguishable from the other species by the highly developed pelvic fins. The proportions of the latter expressed in hundredths of the standard length are: *N. dubius*, 29.0; *N. elongatus*, 13.3-14.4; *N. linguoidens*, 5.3-5.6; *N. dentatus*, c. 17.0 (measured from Chapman's (1939) figure).

NOTE. I have called this species *dubius*, because it is possible that future work may reveal it to be the adult of the larval form, *Benthalbella infans* Zugmayer (see p. 312).

Table 1

Number of fin-rays	Dorsal	Anal	Pectoral	Pelvic
<i>N. dubius</i> sp.n.	9	21	27	9
<i>N. elongatus</i> (Norman)	8-9	26-27	21-22	9
<i>N. dentatus</i> Chapman	6-7	17-21	22-25	9
<i>N. linguoidens</i> (Mead and Böhlke)	9-10	28	25-27	9

### *Neoscopelarchoides elongatus* (Norman)

(Text-fig. 3*b*, *b'* and Pl. XIX, figs. 1, 2.)

*Scopelarchus elongatus* Norman 1937. Rep. B.A.N.Z. Antarct. Res. Exped. 1929-1931 (B), 1 (2), p. 86.

As the original description by Norman (1937) is rather brief, an expanded one is given here. It is based on the type specimen (standard length 198 mm.) which was taken east of Kerguelen Island (45° 53' S, 84° 33' E) and on two individuals taken by R.R.S. 'Discovery II'. The first (s.L. 104 mm.) is from station 391 (55° 48½' S, 52° 35' W), about 300 miles south-east of the Falkland Islands, in a 450 cm. net hauled between 1200 m. and 1300 m.; date, 18. iv. 30 (Text-fig. 3). The second (s.L. 120 mm.) is from station 725 (53° 23.6' S, 74° 57.8' W), about 50 miles south of the western end of the Magellan Strait, in a 100 cm. net hauled obliquely between 250 m. and 196 m.; date 17. xi. 31 (Pl. XIX, figs. 1, 2).

In the following description the data for the type<sup>1</sup> are given first, followed (in parenthesis) by the data for the Discovery specimens, in the above-mentioned order.

*Body proportions in hundredths of the standard length 198 mm. (104 and 120 mm.).* Greatest depth of body 14.1 (11.1, 10.8); length of head 19.8 (22.1, 22.5); horizontal diameter of eye 5.6 (5.3, 5.8); length of snout 6.1 (7.2, 7.9); width of bony interorbital 1.6 (1.6, 1.5); length of lower jaw (20.2, 20.0); maxilla (17.3, 16.6); length from tip of snout to origin of dorsal fin 39.1 (42.8, 41.7); snout to adipose dorsal fin 79.9 (74.0, 75.0); snout to pectoral fin 21.7 (24.0, 23.3); snout to pelvic fin 37.9 (40.4, 38.3); snout to anal fin 64.6 (65.4, 64.2); length of pectoral fin (14.4, 13.3); length of pelvic fin (14.4, 13.3); depth of caudal peduncle 7.1 (6.2, 6.0); length of caudal peduncle 12.6 (12.5, 12.8).

*Fin-rays.* D. 9 (9, 8), A. 26 (27, 27) Pect. 22 (21, 21), Pv. 9 (9, 9).

*Scaling.* (Based on the Discovery specimen from station 725.) Small, thin cycloid scales on cheeks and gill covers and over the rest of the body. Scales of lateral line much enlarged.

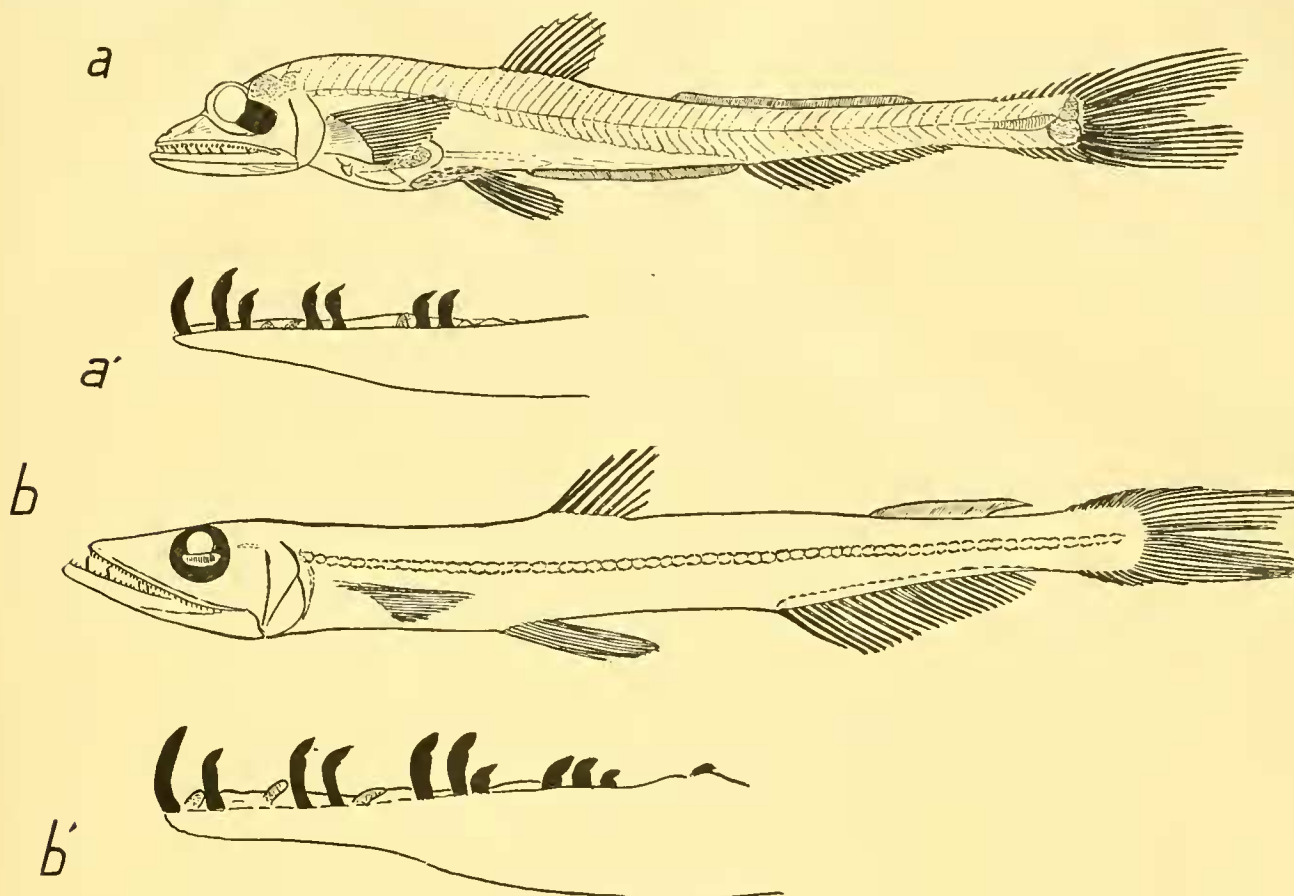
Scales along lateral line 64. Transverse rows of scales between origin of dorsal fin and lateral line 8; between origin of anal fin and lateral line 10-11 (the type specimen has sixty-two scale pockets along the lateral line).

*Vertebrae.* In the type specimen: 61.

<sup>1</sup> Owing to damage, certain measurements for the type specimen had to be omitted.



*Dentition* (based on Discovery specimens). Premaxillary teeth *c.* 70, pointed, retrorse, small. Dentary with *c.* thirty outer, pointed, retrorse teeth; eleven long, depressible, barbed, inner teeth, the 3rd-5th being the largest. Palatine teeth in two closely adjacent rows, 8-10 smaller, pointed teeth in outer row, 5-6 longer, barbed teeth in inner row. Lingual teeth eleven, barbed, decreasing in size from before backward (see Text-fig. 3*b'*).



Text-fig. 3. *a*, *Neoscopelarchoides* sp. late larval stage (= *Benthabella infans*) ( $\times 2$ ); *a'*, lingual teeth ( $\times 9.3$ ); *b*, *Neoscopelarchoides elongatus* (Norman). Specimen from station 391 ( $\times 1.3$ ); *b'*, lingual teeth ( $\times 9.3$ ).

*Neoscopelarchoides* sp.

(Text-fig. 3*a*, *a'*.)

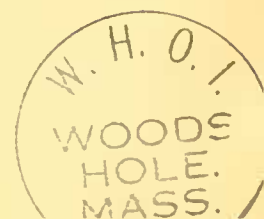
This specimen of a late larval stage was taken by R.R.S. 'Discovery II' off the Azores. Station 3051 (lat. 39° 29' N, long. 9° 50' W), 26. viii. 52. Net TYF (young fish trawl), hauled obliquely between 700 m. and the surface.

*Body proportions in hundredths of the standard length (60.5 mm.).* Greatest depth of body 13.2; length of head 15.4; diameter of forward lens-containing part of eye 4.1; length of snout 6.6; width of bony interorbital 1.0; length of lower jaw 15.3; length from tip of snout to origin of dorsal fin 38.8; snout to origin of adipose dorsal fin 57.8; snout to anterior ray of pectoral fin 18.2; snout to anterior ray of pelvic fin 33.5; snout to origin of anal fin 64.4; depth of caudal peduncle 4.5; length of caudal peduncle 12.4.

*Fin-rays.* D. 9, A. 22, Pect. 24, Pv. 9.

As shown in Text-fig. 3*a* the eyes are tubular and are directed forward and upward.

*Dentition.* About thirty small, pointed, retrorse teeth on premaxilla. Mandible with about twenty outer, small, upright pointed teeth; seven inner, long and slender teeth, all but the first with a tiny



barb and all but the first, which is more or less upright, antrorse. Palatine with about twelve smallish, pointed teeth. The lingual teeth (see text-fig. 3 *a'*) more than any other feature, show that this must be a young scopelarchid.

When caught the fish was almost transparent, the only colour being the black pigment of the eye tube. The body-wall is quite transparent, the internal organs, gut, liver and mesenteries, showing clearly. The muscles associated with the base of the pelvic fins are moderately dense, but over the rest of the body wall there is but a thin muscle-layer, which becomes less and less easy to distinguish as one works upwards from the pelvics. Along the mid-ventral line from the head to the pelvic fins, there is a sharp hyaline division between the musculature of each side of the body wall.

*Relationships.* Following on this section, reasons will be given for recognizing two genera of scopelarchids, *Scopelarchus* Alcock and *Neoscopelarchoides* Chapman. One of the features distinguishing them is the relative position of the dorsal and pelvic fins. In the larval specimen from station 3051, the origin of the dorsal fin lies behind that of the pelvic fins, a characteristic of the genus *Neoscopelarchoides*; hence the larva may be presumed to belong to this genus. It also has the full complement of principal caudal and pelvic rays (and presumably of dorsal, anal and pectoral rays), and at this stage there is unlikely to be much shift in the relative positions of the dorsal and pelvic fins. But it cannot be fitted with certainty into any of the four known species. In numbers of fin-rays it is closest to *N. dubius* and it also agrees with this species in the number of body segments before the origin of the anal fin (the remaining myotomes cannot be counted with certainty). The larva has thirty-five pre-anal fin myotomes, and *N. dubius* has thirty-five pre-anal fin lateral line scales and vertebrae. *N. elongatus* has 33–35 pre-anal fin segments but the anal rays (26–27) are more numerous than those of *Benthalbella*.

I have already drawn attention to the fact that *N. dubius* sp.n. may prove to be the adult of a larval form, *Benthalbella infans* described by Zugmayer in 1911. Zugmayer's young fish and the Discovery larva are very similar, the only difference being in the number of anal rays (17 compared with 22). A number of other specimens, previously recorded, also nearly resemble them:

(1) The fish figured in Murray and Hjort (1912) on p. 746 and labelled 'New fish resembling *Dysomma*' (*sic*). The drawing shows nine dorsal and twenty or twenty-one anal rays.

(2) Two *Benthalbella* larvae from the Bay of Cadiz (Schmidt, 1918). Fin-ray formula: D. 9–10, A. 21–22, Pect. 26, Pv. 8–9.

(3) Two *Benthalbella* larvae from Madeira and one from the Azores (Roule and Angel, 1930) which were regarded as young stages of *Omosudis lowei*. Their Plate III, figs. 75 and 76 show a fin-ray complement of D. 8–9, A. 20.

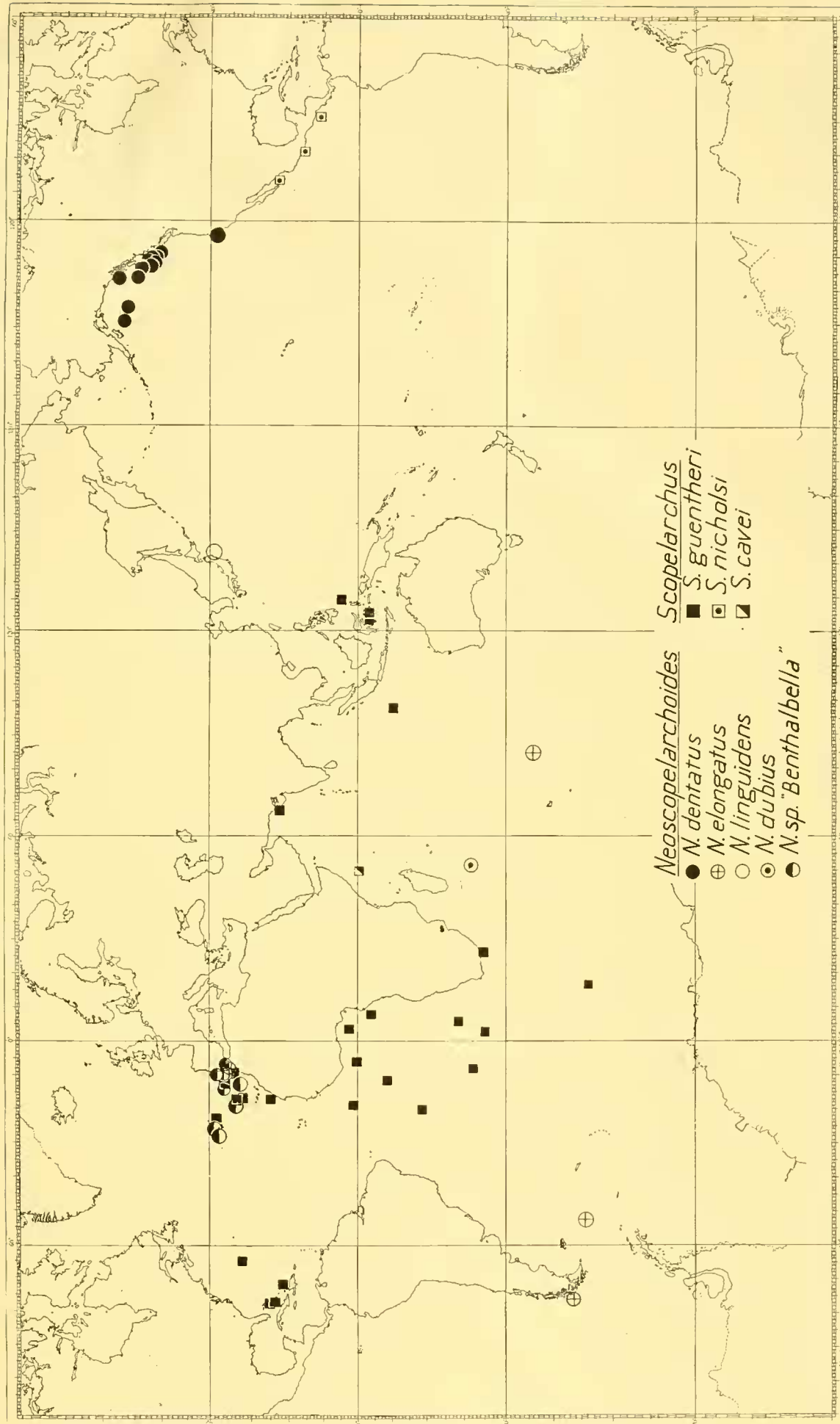
(4) Three post-larval *Benthalbella* from the Strait of Gibraltar (Nybelin, 1948). Fin-ray formula: D. 9–10, A. 20–22, Pect. 27, Pv. 9.

The distribution of these larvae may be seen in the chart, fig. 4.

It would thus seem probable that the Discovery larva and all those listed above belong to one species of *Neoscopelarchoides*. If this is so, the species has a fin-ray complement of D. 9–10, A. 17–22, Pect. 22–27, Pv. 8–9. *N. dubius* comes very close to this; and it may be concluded that either these remarkably large larvae are the young of *N. dubius* or of an unknown, closely-related species.

#### RELATIONSHIPS AND SYNONYMIES OF THE GENERA

Considering in chronological order the genera that have been included in the Scopelarchidae, *Dissomma* Brauer (1902) is clearly synonymous with *Scopelarchus* Alcock (1896), for *S. guentheri* Alcock and *Dissomma anale* Brauer are either very closely related or belong to the same species.



Text-fig. 4. Distribution of the Scopelarchidae: *Scopelarchus* spp. as square symbols; *Neoscopelarchoides* spp. as round symbols (For elucidation see key at bottom of chart). Data on the distributions have come from the authorities mentioned in the text and from Pappenheim (1914) and Koumans (1953).

Regan (1911) thought that *Neosudis* Castelnau (1873) might be a scopelarchid; but *Neosudis* has a dorsal fin of sixteen rays placed two thirds of the way back along the body, whereas the dorsal fin in the Scopelarchidae has 6–10 rays and is placed about half-way down the body. As Parr (1928) has pointed out, the genus is evidently not related either to the Scopelarchidae or Evermannellidae.

*Benthalbella* Zugmayer (1911) has already been considered: its status will be discussed below. Turning to *Promacheon* Weber (1913), which was provisionally included by Parr (1928) in the Scopelarchidae, this genus cannot be fitted into this family. The peculiar triangular tooth on each premaxilla, the number, form and arrangement of the other teeth, the absence of teeth on the palatines, the fin-ray formula (D. 14, A. 17–18, Pect. 15, Pv. 10) and the small number of lateral line scales (*c.* 32), show that *Promacheon* has a character complex quite unlike that of the scopelarchids.

*Scopelarchoides* Parr (1929) is defined as having two areas of abdominal muscles, one surrounding the base of the pelvic fin, the other being an upper lateral musculature with a limited ventral extension. Between these two areas the body-wall is transparent, for the peritoneum is only separated by connective tissue from the outer skin. The division of these muscles is very like that of *Benthalbella* larvae. Chapman (1939) noted that small specimens of *Neoscopelarchoides dentatus* have a translucent abdominal cavity and that the abdominal musculature is fully developed only in the larger individuals. This suggests that the fishes described as *Scopelarchoides nicholsi* were not completely developed. If this is admitted, the differences between *Scopelarchus* and *Scopelarchoides* are clearly no more than differences between different phases of development. The other characters which Parr (1929) has used to define these two genera are nearly all osteological, involving the lesser development of various bones (prootics, opisthotics, preorbitals and subopercula) in *Scopelarchoides*. Evidence from these characters also indicates that *Scopelarchoides* Parr (1929) cannot be retained as a separate genus, and that it is synonymous with *Scopelarchus* Alcock (1896).

It is clear from this study that the scopelarchids can be divided into two genera only: (1) *Scopelarchus* Alcock (1896) comprising the short-bodied species, in which the origin of the dorsal fin is in front of the insertion of the pelvic fins (*S. guentheri* Alcock, *S. nicholsi* (Parr), and *S. cavei* sp.n.). (2) *Neoscopelarchoides*, comprising the long-bodied species having the origin of the dorsal fin behind the insertion of the pelvics (*Scopelarchus elongatus* Norman, *Neoscopelarchoides dentatus* Chapman, *N. dubius* sp.n. *Benthalbella infans* Zugmayer, and *Scopelarchus linguoides* Mead and Böhlke).

Two names are available for the second genus, *Benthalbella* Zugmayer and *Neoscopelarchoides* Chapman. Zugmayer (1911) described *Benthalbella infans* in an Appendix to his report, since he was unable to determine its systematic position, yet he did point out that there were certain resemblances between his fish and Brauer's *Dissomma anale*. Remarking that, 'Ce poisson est très jeune ou plutôt larvaire', he none the less gave it a name because it was then unknown.

Article 30 of the International Rules of Zoological Nomenclature, Section IIe,  $\beta$ , states that: 'Species which were *species inquirendae* from the standpoint of the author of the generic name at the time of its publication', '... are excluded from consideration in determining the types of genera'. In view of Zugmayer's uncertainty as to its systematic position and his admission of its larval character, *Benthalbella infans* cannot be considered as a genotype. *Neoscopelarchoides* Chapman must thus be the name for the second genus, genotype *N. dentatus*.

The characters of the two genera and the main characters of the species are given in the following key. The distribution of the better known species is also given. See also the chart on p. 313.

There is a full description of the family characters in Parr's papers (1928 and 1929).

## KEY TO THE SCOPELARCHIDAE

- I. Origin of dorsal fin in front of insertions of pelvic fins. Scopelarchus Alcock  
 Other generic characters: Short bodied, greatest height of body from 17 to 25 per cent of standard length; number of vertebrae from 41 to 48 (41 in *S. cavei*; 46 in *S. guentheri* and 48 in *S. nicholsi*); number of scales in lateral line 43–50.<sup>1</sup> Pectoral rays 19–23.
- A. Pelvic fins longer than pectorals and extending beyond origin of anal fin. Fin-rays: D. 6–7, A. 21–23, Pect. 20–22. Pv. 9 S. nicholsi (Parr)  
*Distribution.* Gulf of California, off west coasts of Mexico and Central America.
- B. Pelvic fins shorter than pectorals and not reaching origin of anal fin
- b 1. Number of scales along lateral line 43. Fin-rays: D. 9, A. 21, Pect. 21, Pv. 9 S. cavei sp.n.
- b 2. Number of scales along lateral line 48–50. Fin-rays: D. 7–9, A. 23–26, Pect. 19–21, Pv. 9 S. guentheri Alcock
- Synonyms: *Dissomma anale* Brauer (1902 and 1908), *Odontostomus perarmatus* Roule, (1916)  
*Distribution.* Atlantic Ocean, east of Bouvet Island, Indian Ocean, East Indian Archipelago.
- II. Origin of dorsal fin behind insertions of pelvic fins. Neoscopelarchoides Chapman  
 Other generic characters: long-bodied, greatest height of body from 10 to 17.5 per cent of standard length (number of vertebrae 57 in *N. dubius*, 61 in *N. elongatus*). Number of scales in lateral line 56–64 (scales not formed in the holotype and two paratypes of *N. linguoides*). Pectoral rays 21–27.
- A. Pectoral fins less than half-length of pelvic fins; caudal peduncle from 20 to 25 per cent of standard length. Fin-rays: D. 6–7, A. 17–21, Pect. 22–25, Pv. 9 N. dentatus Chapman  
*Distribution:* Gulf of Alaska; off Central California.
- B. Pectoral fins equal to, or considerably more than, half the length of pelvic fins (these fins about equal in length in *N. elongatus*, while in *linguoides* and *dubius* the pectorals are about three-quarters the length of the pelvics). Caudal peduncle from 11 to 15 per cent of standard length.
- b 1. Length of pelvic fin more than one-quarter of standard length. Fin-rays: D. 9, A. 21, Pect. 27, Pv. 9 N. dubius sp.n.
- b 2. Length of pelvic fins considerably less than one-quarter of standard length.
- (i) Pectoral fins with 21–22 rays. Fin-rays: D. 8–9, A. 26–27, Pect. 21–22, Pv. 9  
*Distribution.* Off Kerguelen Island; Falklands-Magellan Strait region. N. elongatus (Norman)
- (ii) Pectoral fins with 25–27 rays. Fin-rays: D. 9–10, A. 28, Pect. 25–27, Pv. 9–10 N. linguoides (Mead and Böhlke)

## The Family PARALEPIDIDAE

*Macroparalepis molestus* sp.n.

(Text-fig. 5.)

*Holotype.* An individual 146 mm. in standard length, taken in a 2 m. net during an experimental haul near station 2209 (53° 07.7' S, 168° 56.4' E), near Campbell Island, south of New Zealand. 27. i. 38. 2000 m. wire.

*Proportions in hundredths of the standard length (146 mm.).* Greatest depth of body 4.1; length of head 16.1; length of snout 8.2; horizontal diameter of eye 2.7; width of bony interorbital 1.8; length of lower jaw 9.5; length from tip of snout to origin of dorsal fin 63.0; snout to pelvic fin 49.7; snout to anal fin 78.7; length of pectoral fins 7.5; length of pelvic fin 4.8; depth of caudal peduncle 2.0; length of caudal peduncle 5.1.

*Fin-rays.* D. 12 (last ray bifid), A. 30, Pect. 12, Pv. 9.

<sup>1</sup> Counted from upper angle of operculum to caudal flexure.

*Scales.* Absent, but there are ossifications along the lateral line, which may be modified scales (Harry, 1953*a*) see Text-fig. 5*c* and *d* and below.

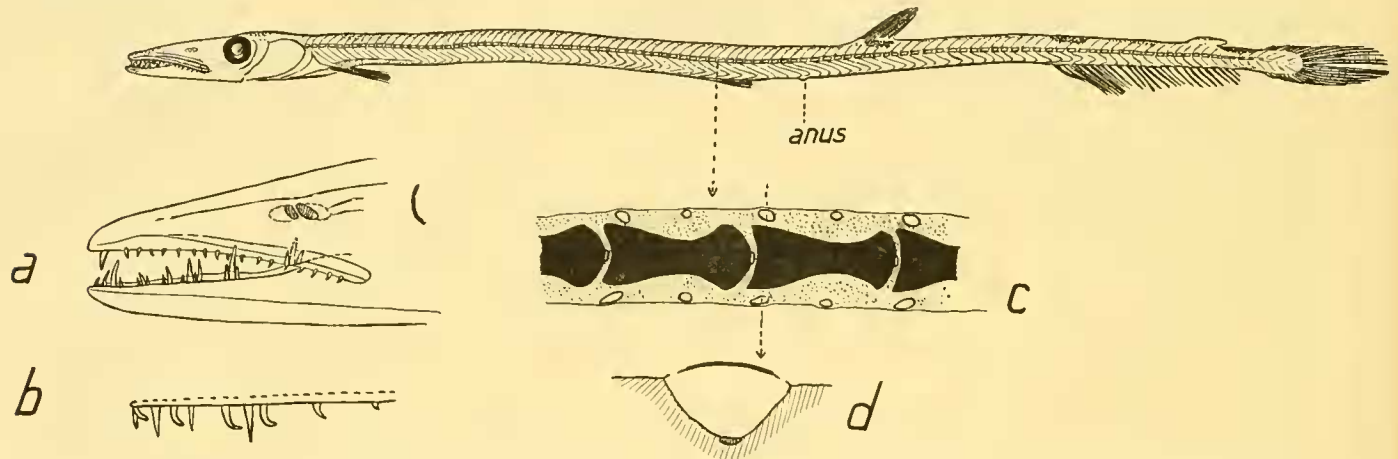
*Lateral line.* Roofing the gutter-like lateral line along the trunk is a fragile skin in which is set a series of dumb-bell shaped ossifications, one per segment. Above and below each ossification are two pores, the anterior larger than the posterior. Immediately at the end of the ossification comes a small median pore (see Text-fig. 5*c*).

About ninety ossifications occur along the lateral line, the series on the right flank ending opposite the origin of the adipose dorsal fin. The last few, posterior ossifications are not fully developed (presumably the complete series is developed at a later stage).

*Number of vertebrae.* 101.

*Ventral carina.* Distinctly developed between the pectoral and pelvic fins.

*Dentition.* About twenty teeth on the premaxillae, the first being the longest, then come about fourteen retrorse, thorn-like teeth followed by eight or so, small antrorse teeth. Dentary with six long pointed teeth, each of which is flanked by smaller pointed teeth, usually one on each side. Palatines with about 10–12 teeth, these being six hooked outer teeth, and four to six larger, depressible, pointed inner teeth (see Text-fig. 5*b*).



Text-fig. 5. *Macroparalepis molestus* sp.n. Holotype ( $\times 1$ ): *a*, maxillary and mandibular teeth ( $\times 3$ ); *b*, palatine teeth ( $\times 3$ ); *c*, part of lateral line to show pores and bony segments ( $\times 25$ ); *d*, transverse section through lateral line.

*Gill-teeth.* Rather widely spaced, in a single row, on the upper part of the lower limb of the first gill arch.

*Colour* (in spirit). Light brown with a peppering of small melanophores along the dorsal surface. Three dorsal 'saddles' of more concentrated pigmentation; the first along the base of the dorsal fin; the second just above the origin of the anal fin, and the third just behind the adipose dorsal fin (see Text-fig. 5).

The study of the above fish has thrown some light on the status of *Macroparalepis* Ege. As a result of his investigations, Harry (1951, 1953*a*) quite reasonably decided to divide *Macroparalepis* Ege into two genera, these corresponding to divisions I and II of Ege's (1933) synopsis of the species. *Macroparalepis* was restricted to division I of the key, while division II was placed under another genus, *Stemonosudis*.

*Macroparalepis molestus* described above is awkwardly intermediate between these two genera. Like *Macroparalepis*, as defined by Harry (1953), the nostrils of *M. molestus* come before the tip of the maxillary; like *Stemonosudis* the body is slightly compressed and very elongate, the tip of the lower jaw is not elevated and the end of the upper jaw is about 1 orbital diameter from the anterior margin of the eye.

In fin-ray counts *Macroparalepis molestus* is intermediate between the two genera.

	Dorsal	Pectoral	Anal
<i>Macroparalepis</i>	11-14	10-11	24-28
<i>M. molestus</i>	12	12	30
<i>Stemonosudis</i>	9	10-13	37-50

Lastly, in colour pattern *Macroparalepis molestus* partly resembles *Stemonosudis* in having saddles of pigment along the back, but there are no alternating blotches on the base of the anal fin. Furthermore, it is interesting that a pigmentation very similar to that described for *Stemonosudis* has been found by Harry (1953b) in a fish that he identifies as a post-larval *Macroparalepis*.

In the present state of our knowledge, it would thus appear advisable to retain *Macroparalepis* as defined by Ege (1933).

### The Family ANOPTERIDAE

#### *Anotopterus pharao* Zugmayer.

*Anotopterus pharao* Zugmayer, 1911. Result. Camp. sci. Monaco, p. 138, pl. 4, fig. 4 (for a full synonymy see Hubbs, Mead and Wilimovsky (1953)).

During the 1949-50 Antarctic whaling season, the captain of one of the whale-catchers attached to F/F 'Balaena' of United Whalers Limited, obtained a large fish belonging to the genus *Anotopterus*: it was swimming at the surface, the position being approximately lat. 69° S, long. 170° E (Ross Sea area).

Our knowledge of this genus is limited and a search was made through the unnamed Discovery Collections in the hope of finding other specimens. Eventually a small individual of standard length 100 mm. was found: it was taken in the South Atlantic (23° 16' S, 01° 51.7' W) in a 450 cm. net hauled obliquely between 600 m. and the surface. The study of these two individuals, as well as of the type of *Eugnathosaurus vorax* Regan and of a specimen of *Anotopterus pharao* from Madeira, forms the basis of this section.

Zugmayer (1911), after examining a fish of total length 165 mm. taken by 'Princesse-Alice' at the North Atlantic station 3028 (36° 54' 30" N, 11° 49' W), described a new genus and species *A. pharao* and furthermore proposed that it should be assigned to a new family, the Anotopteridae. A second fish of 291 mm. taken off Madeira was described by Roule (1927) and compared with the type specimen. Legendre (1934) found five individuals of this species (from 127 mm. to 144 mm.) in the stomachs of *Thunnus alalunga*, caught by fishermen in the Bay of Biscay. These specimens were examined by Roule (1935).

More recently Maul (1946) and Nybelin (1946) have written on *Anotopterus*. Maul obtained specimens of *A. pharao* from the stomachs of *Alepisaurus ferox*, caught off Madeira by local fishermen. Nybelin studied a head (length 150-160 mm.) obtained from the stomach of a halibut (caught by M/S 'Arctica' at 64° 25' N, 53° 30' W), and proposed the species *Anotopterus arcticus*. He also examined a complete specimen, of standard length 650 mm., found in the stomach of a fin whale (harpooned in the Weddell Sea at 62° 02' S, 38° 25' W) which he regarded as another new species, *A. antarcticus*. Nybelin (1946) also reviewed *Eugnathosaurus vorax*, which was described by Regan (1913) from a head trawled off Coats Land by the Scottish National Antarctic Expedition (station 417 at 71° 22' S, 16° 34' W), and he rightly saw that this was a species of *Anotopterus*, but concluded that owing to certain differences in the dentition it was distinct from *A. antarcticus*.

Young *A. pharao* have been recorded from the eastern North Atlantic by Nybelin (1948) and Maul (1952). Nybelin's fish is about 14 mm. long and has 4 palatine teeth: Maul found 14 palatine teeth in a specimen of standard length 47.5 mm.

The foregoing papers were based on fishes from the Atlantic and Antarctic areas, but quite recently Abe (1952) and Hubbs, Mead and Wilimovsky (1953) described specimens from the north-east and north-west Pacific. The latter workers also made a close study of the literature and concluded that there is no good evidence for recognizing more than one species, *pharao*, of the genus *Anotopterus*.

The study of the type of *Eugnathosaurus vorax* and of the two specimens mentioned earlier, together with a specimen from Madeira and published papers, has led me, independently of these ichthyologists, to much the same conclusion. But there is some indication that this one species may be differentiated into a northern and southern form; further material may even show that these 'forms' might better be regarded as separate species. However this may be, my present intention is to bring forward new data on *Anotopterus* and then to point out the differences between fishes from the northern and southern seas. Much of the ground I had intended to cover regarding the status of the species of *Anotopterus* has already been thoroughly dealt with by Hubbs *et al.* (1953).

Comparison of the type specimen of *Eugnathosaurus vorax* Regan (borrowed from the Royal Scottish Museum) with the large Antarctic specimen taken by the whale-catcher has shown them to be closely similar. The measurements in millimetres are given below, those for the type coming first, followed in parentheses by those of the complete fish.

Length of head 150 (147); length of snout 89 (89); horizontal diameter of bony orbit 15.5 (14.5); width of bony interorbital 8.0 (8.0); postorbital length of head 46 (46); length of mandible 111 (108); length of premaxillae 90 (89); length of largest palatine tooth 9.5 (10.5).

*Dentition.* The type specimen has no teeth on the first fifth of the length of the left mandible, then come twelve small, pointed and more or less upright teeth, then seven larger teeth inclined backwards and then two squat teeth, shaped rather like a rose thorn. Between the second to fifth mandibular teeth three smaller ones are inserted. In the complete Antarctic specimen, the arrangement of teeth on the left mandible is very similar: there is a short, foremost toothless part, followed by seventeen small, pointed teeth (the first seven of which are inclined forward), then by seven large retrorse teeth and finally by two small thorn-like teeth.

The palatine dentition of the type is well-illustrated in fig. 1 (p. 234) of Regan's (1913) paper. In addition to the teeth shown in this figure, I have found indications of others. There are certainly the remains of a tooth base between the second and third teeth of the right palatine and there are indications of another base in front of the first tooth. On the left palatine there is a tooth base between the second and third teeth; this base is a clear-cut oval with a brownish centre, perhaps an indication of a resorbed tooth. Thus the type had thirteen functional teeth, two of these having been detached at some time.

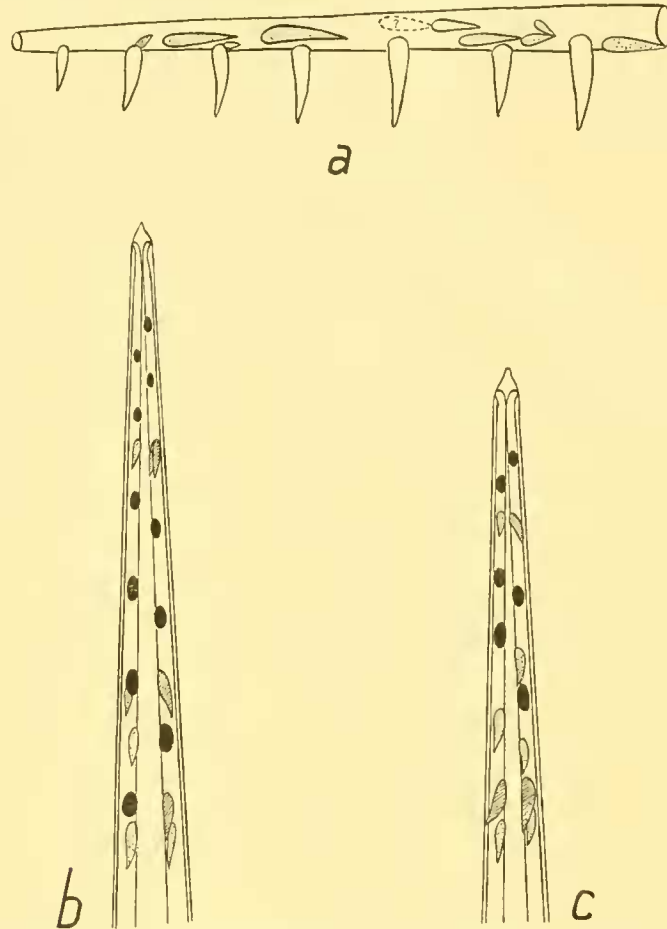
The palatine dentition of the complete individual is shown in Text-fig. 6*b*. As well as the eleven upright, functional teeth, there are a number of recumbent teeth lying in the dental integument and one obliquely set tooth. The latter is quite hard and is evidently moving upwards into position. The recumbent teeth can be divided into two types: (1) moderately ossified teeth (shown in the figure by cross hatching), and (2) soft teeth (shown dotted). On the right palatine it will be seen that the last two teeth have soft replacement teeth, while on the left palatine two of the moderately ossified recumbent teeth, soon to become functional, are closely associated with what must also be replacement teeth. The tooth pattern suggests that at any time there may be from 11 to 14 palatine teeth in use.

Presumably tooth succession goes on all the time as in *Alepisaurus*. It was of such fishes that Owen (1840-5) wrote: '... the succession of teeth is uninterrupted, the pulps of the new teeth are developed in most of the species in the soft gum or integument covering the dentigerous margins of the bones, and the calcification of the pulp is completed as it lies recumbent and buried loosely in the substance



of the gum. The point of the new tooth, which, in this state, is directed backwards, is then exposed by a gradual rotatory movement of the tooth from the horizontal to the vertical position. . . .'

The small individual of standard length 100 mm. taken by R.R.S. 'Discovery II' in the South Atlantic (station 2048, lat.  $23^{\circ} 16' S$ , long.  $01^{\circ} 51.7' W.$ ; 25. iv. 37, N. 450B: 600-0 m.) has six functional teeth on the left palatine and seven on the right. The dentition of the right palatine is shown in Text-fig. 6*a*. On the right mandible there are seventeen teeth: one retrorse tooth near the symphysis + 5 antrorse teeth + 11 upright teeth.



Text-fig. 6. Palatine teeth of *Anotopterus pharao*: *a*, right palatine of a specimen 100 mm. in standard length ( $\times 6.5$ ); *b* and *c* diagrammatic representations of the palatine dentitions of specimens 732 mm. and 278 mm. in standard length (*b*,  $\times 1$ ; *c*,  $\times 1.5$ ). In *b* and *c* the functional teeth are shown in black: the moderately developed replacement teeth are cross hatched; the soft, relatively undeveloped replacement teeth are dotted.

Compared with the type specimen of *Eugnathosaurus vorax*, the proportions of the different parts of the head of the whole fish are as follows. (These figures are in hundredths of the head length, those for the type coming first, followed in brackets by those of the Discovery specimen):

Length of head 150 (24) mm. Proportions per cent: length of snout 59.3 (58.3), width of bony interorbital 5.3 (6.7), horizontal diameter of bony orbit 10.3 (13.3); postorbital length 30.7 (27.1); length of mandible 74.0 (70.8).

The palatine dentition of an individual from Madeira of standard length 278 mm. is shown in Text-fig. 6*c*. There are six completely erect, functional teeth, together with two moderately ossified, obliquely set teeth, one on the left palatine between the first and second upright teeth, the other situated towards the posterior end of the right palatine. Opposite the latter tooth is a fairly well-ossified recumbent tooth, together with a soft replacement tooth. The tooth pattern suggests that, as the fish grows, the complement of these stabbing palatine teeth increases, probably to between eight and ten.

The body proportions and meristic characters of the three complete specimens dealt with above may be seen in Table 2. For other data the reader is referred to Nybelin (1945) and Abe (1952) and the comprehensive tables given by Hubbs, Mead and Wilimovsky (1953).

There are no marked differences in body proportions between all the known individuals of *Anotopterus pharao*. Hubbs *et al.* have remarked that the differences in proportions between *A. pharao* and *A. antarcticus* considered by Nybelin (the pelvic-anal distance, the diameter of the eye, and the depth of the caudal peduncle) are likely to be an expression of age rather than of specific distinctness. Comparison of the 100 mm. and 732 mm. individuals in Table 2 shows them to be closely similar, apart from the relative size of the characters mentioned above. There can be little doubt that these characters are correlated with age. But there seems to be some differentiation within the species in respect of the number of functional palatine teeth and perhaps in the number of vertebrae. (See Table 3.)

Table 2. *Body proportions (expressed in hundredths of the standard length) and meristic features of three individuals of Anotopterus pharao*

Region	Madeira	South Atlantic (23° 16' S, 01° 51.7' W)	Antarctic (69° S, 170° E)
Standard length in mm.	278	100	732
<i>Body proportions:</i>			
Head length	20.0	24.0	23.0
Diameter of orbit	2.2	2.8	1.9
Interorbital width	1.25	1.8	1.2
Length of snout	12.2	14.5	12.0
Greatest depth of body	5.3	5.5	3.3
Depth of caudal peduncle	1.6	1.6	1.0
Length of pectoral fin	Damaged	Damaged	7.4
Length of pelvic fin	Damaged	Damaged	3.3
<i>Length between:</i>			
Snout tip—adipose dorsal	91.7	90.0	91.2
Snout—origin of pectoral fin	23.0	23.0	20.2
Origins of pectoral—pelvic fins	38.8	36.0	36.2
Pelvic—anal fins	27.7	25.0	33.1
Pelvic fin—base of caudal fin	38.5	36.0	43.8
<i>Meristic characters:</i>			
Number of palatine teeth	6	13	11
Number of vertebrae	80	—	83
Number of lateral line 'scales'	—	—	83
Number of fin rays:			
Pectoral fin	12	14	14
Pelvic fin	9	9	9
Anal fin	15	15	14

In general the table indicates that fishes from the North Atlantic and North Pacific tend to have fewer (4–10) palatine teeth than those (11–14) in South Atlantic and Antarctic waters, and although there are certain anomalies, the data also suggest that in fishes from northern waters there is a tendency for the number of palatine teeth to increase with age.

The number of vertebrae [(79 ± 1/2 to 81) in three northern fishes and 83 in two southern fishes] perhaps lends some support to the suggestion that within this wide-ranging species there is a northern and a southern form. However, Maul's (1952) record from Madeira of a 47.5 mm. fish with 14 palatine teeth has to be considered. All that can be done at present is to draw attention to the possibility considered by Hubbs *et al.* (1953) that *Anotopterus*, like certain ceratoid angler fishes, '...occurs chiefly

as young to small adults in the warmer waters and as large adults only in colder waters towards the poles'. Perhaps there is some overlap between the spawning areas of northern and southern forms; perhaps the idea of these two forms is an over-simplification. But these questions must obviously await further data.

Table 3. *Numbers of palatine teeth and vertebrae in Anotopterus pharao*

Authority	Locality	Size of fish (S.L. mm.)	Number of palatine teeth	Number of vertebrae
NORTH PACIFIC				
Hubbs <i>et al.</i> (1953)	Kamchatka	861	10	79 ± 1 or 2 centra
Abe 1952	Kamchatka or Hokkaido	855	10	—
Hubbs <i>et al.</i> (1953)	British Columbia	87.3 (head)	5	—
Hubbs <i>et al.</i> (1953)	Hokkaido	640.0	10	—
Hubbs <i>et al.</i> (1953)	35° 35' N, 122° 25' W	299.0	4	—
Hubbs <i>et al.</i> (1953)	31° 54.3' N, 152° 21.6' W	112.5	8	—
NORTH ATLANTIC				
Nybelin (1946)	Davis Strait, 64° 25' N, 53° 30' W	c 150 (head)	10	—
Collett (1896)	Off Cape Finisterre	253 (head)	7	—
Roule (1935)	Bay of Biscay	126-144 (5)	6?	81
Nybelin (1948)	38° 25' N, 10° 23' W	14	4	—
Roule (1927)	Madeira	276	6	—
Maul (1946)	Madeira	265-342	6	—
Maul (1952)	Madeira	47.5	14	—
Hubbs <i>et al.</i> (1953)	Madeira	247	8	—
Hubbs <i>et al.</i> (1953)	Madeira	260	8	—
Marshall	Madeira	278	6	80
SOUTH ATLANTIC AND ANTARCTIC				
Marshall	23° 16' S, 01° 51.7' W	100	13	—
Nyebelin (1946)	Weddell Sea, 62° 02' S, 38° 25' W	650	14	83
Marshall	Ross Sea area, 69° S, 170° E.	732	11	83
Regan (1913) and Marshall	Coats Land, 71° 22' S, 16° 34' W	150 (head)	11 + 2	—

Lastly, it should be mentioned that the large Antarctic fish bears, on either side of the tail, two basicaudal dermal keels very similar to those described by Hubbs *et al.* (1953) for their large Pacific fishes.

*Distribution.* It will be apparent from the quotation above, that Hubbs *et al.* (1953) concluded that adult *Anotopterus* probably have an antitropical (bipolar) distribution. The facts presented here—the presence of a young fish in the South Atlantic at latitude 23° S and of a 732 mm. individual in Antarctic waters—does not conflict with this conception.

Concerning the vertical distribution there is definite support for the contention of the foregoing workers that *Anotopterus*, at least when adult, is a surface-dwelling fish.

The fish caught at the surface in the Ross Sea area by the whale-catcher had a very distended abdomen. Soon after capture, this individual vomited up two moderately large *Notolepis coatsi* Dollo of standard lengths 180 mm. and 270 mm. The stomach of each of these fishes was bloated with krill (*Euphausia superba*).

*N. coatsi* are often to be found in the stomachs of whale-bone whales: in fact nearly all the sizeable specimens in the museum collections have been obtained from whales (see also Clarke, 1950). Examination of the stomach contents of twelve *Notolepis* has invariably shown them to have been eating adult krill. As *Notolepis* feeds on the krill of the surface waters, it is evidently preyed on by *Anotopterus* and in turn both may be fortuitously swallowed by the krill-engulfing whales. It may be

concluded that in Antarctic waters *Anotopterus* lives, at least for part of the time, in the upper 100 m. But little is known of the vertical limits of distribution and the possibility of tropical submergence needs to be borne in mind.

## PART II. COMPARISON OF ALEPISAUROID AND MYCTOPHOID FISHES

Although the Iniomi have been divided into the suborders Myctophoidea and Alepisauroidea, it is by no means easy to assign clear-cut diagnostic features to these groups. Regan's (1911) definition of the Alepisauroidea was mainly based on the osteology of *Alepisaurus* and *Evermannella*, and he placed the paralepidid fishes and *Sudis* among the Myctophoidea and considered that *Ateleopus* should be put into a third and separate suborder.

Regan's use of the forward attachments of the palatines as a character for separating the alepisauroids and myctophoids cannot be sustained, as a study of Parr's (1929) paper soon shows. The degree of development of the interoperculum (the smallness of this bone in the alepisauroids contrasting with its more normal development in the myctophoids), is a trenchant distinguishing feature, as long as Regan's inclusions within the Alepisauroidea of *Scopelarchus*, *Evermannella*, *Omosudis*, *Alepisaurus* are accepted. But Harry (1951, 1953) has cogently argued that the Paralepididae show a closer relationship to the alepisauroids than to the myctophoids; and in this family the interoperculum is well developed (Parr, 1929). Furthermore, *Anotopterus*, which has many features in common with *Alepisaurus*, differs from the latter in possessing a relatively large interoperculum. Similarly, the preoperculum, which is narrow and almost vertically placed in the Scopelarchidae, Evermannellidae, Omusodidae and Alepisauridae, is broad and boomerang-shaped in the Paralepididae and fairly wide in the Anotopteridae. In both these latter families the preoperculum is obliquely inclined, following the line of the forwardly directed suspensorium.

Regan also based his classification on the design of the pectoral girdle, remarking that in the Myctophoidea the cleithrum is attached to the lower end of the supracleithrum, while in the Alepisauroidea the attachment comes at the upper end of the latter bone. As far as I have been able to extend this observation, it seems true for the myctophoids in which a more 'solid' pectoral girdle is developed, there being a firm join between the supracleithrum and cleithrum. In the myctophoids (*Neoscopelus* and *Lampanyctus crocodilus* were examined) there is a wide area of overlap between these two bones, the cleithrum extending rather beyond the midpoint of the supracleithrum. In the alepisauroids, *Omosudis*, *Evermannella* and *Alepisaurus* the cleithrum is attached to the upper part of the supracleithrum (Regan, 1911; Parr, 1929), but in the paralepidids, although the above attachment is found in *Paralepis speciosa*, Parr (1929) remarks that in *Lestidium intermedium* on the other hand the cleithrum only extends somewhat above the middle of the supracleithrum. Again, in the figure of the pectoral girdle of *Scopelarchus anale* (Parr, 1929), the cleithrum is shown to be attached to the lower end of the supracleithrum. Clearly the type of linkage between these two bones cannot be used as a subordinal diagnostic.

The position of the pectoral fins was also listed as a distinguishing character by Regan, who pointed out that these fins were laterally placed in the myctophoids but were low in position in the alepisauroids. There are a number of exceptions to this generalization and the whole question of the position of the pectoral fins will be more fully discussed in a separate section (pp. 325-28).

Lastly, Regan (1911) said that the Alepisauroidea had '... strong pointed canines in the lower jaw and on the palatines'. This is true for his inclusions, *Scopelarchus*, *Evermannella*, *Omosudis* and *Alepisaurus* and for *Anotopterus*, but this description does not cover certain of the paralepidids, such as *Paralepis* and *Magnisudis* (Harry, 1953). However, there are certain features of dentition possessed

by all alepisauroids, namely, the premaxillae each carry a single row of teeth and there are one or two rows of teeth on each palatine and 1-3 rows on each dentary.

Turning now to more recent studies, Harry (1953*a*) stated that the symphysis of the lower jaw is more or less elevated in the Paralepididae, fitting into a corresponding, arched toothless emargination on the upper jaw. As Harry has pointed out elsewhere, the symphysis of the upper jaw is usually toothless in the Alepisauroidea and may be arched. (A specimen of *Evermannella balbo* which I examined had an arched symphysis provided with teeth.) It is also of interest that certain of the Myctophoidea have a bony boss at the symphysis of the lower jaw, which fits into a toothless emargination of the upper jaw (Chlorophthalmidae, Bathyptheroidea, *Ipnops*, *Bathymicrops*, *Notosudis*, *Luciosudis* and *Neoscopelus*). In many of the Myctophidae there is certainly a small bony boss at the symphysis of the lower jaw, but this fits against a toothless, slightly depressed area between the two premaxillae, but such close-fitting structures are absent in the jaws of the Aulopidae, Harpadontidae and Synodontidae.

Harry (1953*a*) has also drawn attention to the form of the gill-rakers in the Alepisauroidea. In *Magnisudis* each gill-raker consists of a basal part bearing four long, stiff, depressible, filamentous parts. The rakers of *Alepisaurus ferox* are somewhat similar, each consisting of a basal part supporting a number of spines, of which one to four are longer than the others. Needle-like or spinous gill-rakers are also found in *Paralepis*, *Omosudis* and *Evermannella*.<sup>1</sup> In *Scopelarchus*, *Notolepis*, *Lestidium*, *Macroparalepis* and *Sudis* the rakers are tooth-like. All the gill-arches in *Anotopterus* are without rakers.

More normal lath-like gill-rakers are characteristic of all families of the Myctophoidea, except the Harpadontidae and Synodontidae, these having tooth-like or spinous rakers.

There is therefore much justification for the opening remarks concerning the difficulty of defining the suborders Myctophoidea and Alepisauroidea, but before summarizing this discussion in a section on alepisauroid relationships, there are certain interesting morphological trends within this group which will now be considered. Points of contrast with the myctophoids will then be seen.

*The swim-bladder.* A survey of the literature and a number of dissections (*Alepisaurus ferox*, *Anotopterus pharao*, *Omosudis lowei*, *Evermannella atrata*, *Scopelarchus guentheri* and *Notolepis coatsi*) show that a swim-bladder is absent in the Alepisauroidea. In the Myctophoidea this organ is only found in the Myctophidae, Marshall (1951 and unpublished) finding a closed swimbladder in twenty-three of the twenty-six species studied. The absence of the swim-bladder in the Aulopidae, Chlorophthalmidae, Synodontidae, Harpadontidae, Ipnopidae and Bathyptheroidea was recorded by Günther (1864, 1887).

Correlations between environment and the degree of development of the swim-bladder (including its loss) in teleosts have already been considered by Marshall (1950, 1951) and Jones and Marshall (1953), but in these papers little reference was made to the alepisauroids.

The Alepisauroidea are active, voracious, mid-water fishes, while the Myctophoidea, other than the Myctophidae and Notosudidae seem to be predominantly bottom-dwellers. Many benthic fishes lack a swim-bladder, but the absence of this organ in a mid-water group, such as the Alepisauroidea, is of interest and will be further considered. Marshall (1951 and unpublished) has found a well-developed swim-bladder in many of the bathypelagic fishes, which have centres of abundance in the uppermost 1000 m. of the ocean. But notable exceptions to this rule are found in the Melanostomiidae, as well as in the Alepisauroidea. (A consideration of the reports by Ege, 1930, Legendre, 1934, and Maul, 1945, supports the view that many paralepidids occur in the uppermost 500 m. and the same would

<sup>1</sup> In the specimen of *Evermannella balbo* examined, there are no rakers on the first gill arch but some are present on the second arch.



also appear to be true for *Alepisaurus* and *Anotopterus*. Our knowledge of the vertical distribution of the Scopelarchidae, *Evermannella* and *Omosudis* is less complete.)

Fishes without a swim-bladder are heavier than their environment (Jones and Marshall (1953) have reviewed the data on densities). The only pelagic fish that has been well studied is the mackerel, *Scomber scombrus* with a density of 1.071 and a sinking-factor of 1043.<sup>1</sup>

Very probably other pelagic fishes without a swim-bladder are also heavier than the surrounding water, and, like the mackerel keep their level by unceasing activity. A study of their appearance and food suggests that the Alepisauroidea are active swimmers and their lightly ossified skeletons may point to their having lower sinking-factors than the mackerel. Moreover, Taylor's (1921) work on the density of fish tissues would indicate that the sinking-factor of any alepisauroid is likely to be more than 1000. While there are no observations of swimming in alepisauroids which bear on this problem, it is interesting that Skowron (1928), who studied the luminescence of *Chauliodus sloani*, saw that these fishes at first swam vigorously, but on ceasing active movements sank to the bottom of the container. This, as I have seen in the Red Sea, is also true of *Stomias affinis*. Evidently both fishes are heavier than the surrounding water, and it is significant that, like the alepisauroids, both are without a swim-bladder.

*Ossification of the skeleton.* Hubbs, Mead and Wilimovsky (1953) found no reason to accept Roule's chimerical hypothesis that *Anotopterus* is a 'monstre normalisé' or 'teratobionte'. Nor is there evidence that this fish or any other alepisauroid is rachitic. Their skeletons are rather delicately but not abnormally built.

A five foot *Alepisaurus ferox* weighs about 4 lb. (Lowe, 1835), a striking indication of its lightly ossified skeleton as well as of its compressed and rather lean-looking body. Harry (1953a) has drawn attention to the peculiar cartilaginous development of the jaws in the Paralepididae and Anotopteridae. Certainly, the long time of exposure required to get tolerably clear hard-tube X-ray photographs of these fishes provides further evidence of the lack of calcification in the skeleton; and this is also true of *Omosudis lowei* (s.L. 60 mm.) *Evermannella hyalinus* (s.L. 153 mm.), *Neoscopelarchoides elongatus* (s.L. 198 mm.) and *N. dubius* (s.L. 138 mm.). Only in *Scopelarchus cavei* sp.n. (s.L. 70 mm.) does the degree of ossification of scales and skeleton compare with that, say, in a myctophid.

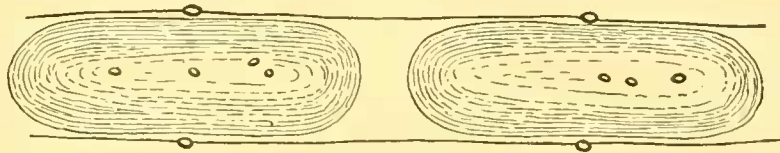
Moreover, in some of the alepisauroids the calcification of the skeleton seems to be a slow, irregular and protracted process. Beebe (1932) remarks that a post-larval *Omosudis lowei* of total length 11.45 mm. did not have '... a particle of bone in the entire body, fins, fin-rays or appendicular skeleton except for a faint trace in the centre of the supracleithrum'. The head bones, particularly the premaxillae and dentary were well ossified. Similarly, in the large 'Benthalbella' larvae of the scopelarchids, the skeleton, except for the skull, has a soft, cartilaginous texture. In *Anotopterus* the thin, scale-like segments along the lateral line canal (see Text-fig. 7) are only plainly visible in larger individuals. Maul (1946), who studied specimens from 265 mm. to 342 mm. in standard length, remarks that, along the anterior half of one individual, they only became visible after alizarin staining. Lastly, in certain paralepidids (Ege, 1930; Parr, 1931; Harry, 1953a), the scaling is not completed until very late in development. I have also found this feature in *Notolepis coatsi*.

Parr (1937) has suggested that the amount of available vitamin D falls off with increasing depth, and that fishes living at deep levels in the ocean have developed lower requirements for this vitamin, this resulting in less extensive ossification of the skeleton. But assuming vitamin D to be necessary for the normal formation of bone in fishes, *Anotopterus*, *Alepisaurus* and the paralepidids live at levels not very far removed from the phytoplankton-bearing, vitamin D-producing, upper layer of the ocean.

<sup>1</sup> Sinking-factor =  $\frac{\text{density of fish}}{\text{density of environment}} \times 1000.$

On the other hand, abyssal benthic fishes might be expected to have poorly ossified skeletons, yet in the Bathypteroidae, and Ipnopidae (to consider only the Iniomi), the skeleton is well formed and much denser than in the alepisauroid fishes. (This is well shown in X-ray photographs.) A more solid skeleton is no handicap to a fish which lives on the deep-sea floor, whereas reduced ossification would appear to be an advantage to the bathypelagic Alepisauroidea. This fact compensates these active predacious fishes for the absence of a swim-bladder, for it must result in the lowering of the sinking-factor, and hence less energy is required to maintain the fish at a particular feeding-level in the ocean.

The correlation between the lack of a swim-bladder and the laying-down of less skeletal material in bathypelagic fishes will be considered more fully in a later paper, but one comparison may be made now. *Gonostoma denudatum* has a large, well-developed swim-bladder, while in *G. bathyphilum* there is no trace of this organ. A specimen of *denudatum* (131 mm.) was placed alongside one of *bathyphilum* (122 mm.) and an X-ray photograph obtained. This strikingly confirmed the impression formed by handling these fishes, that *denudatum* had a better ossified skeleton than *bathyphilum*.<sup>1</sup> If this interpretation comes near the truth, more striking corroboration would be hard to find than these structural differences between the two species.



Text-fig. 7. Part of the lateral line (near the origin of the adipose dorsal fin) of *Anotopterus pharao*, showing two of the scale-like ossifications and the lateral line pores ( $\times 6.6$ ).

*The setting of the pectoral fins.* In defining the two suborders of the Iniomi, Regan (1911) stated that the pectoral fins were lateral in the Myctophoidea, but low in position in the Alepisauroidea. Certainly, the pectorals of *Alepisaurus*, *Anotopterus*, *Omosudis* and *Evermannella* are placed very low on the shoulders, while those of the Aulopidae, Chlorophthalmidae, Synodontidae, Harpadontidae, Ipnopidae and Bathypteroidae are laterally placed. But a number of exceptions to these generalizations are to be found in the Myctophidae, Scopelarchidae and Paralepididae.

Measurements of the angle between the horizontal axis of the body and the axis of the pectoral fin have indicated that such an index comes close to being a diagnostic feature of each suborder. In most alepisauroids this angle is below  $45^\circ$ : in most myctophoids it is above  $45^\circ$ . Data, showing what may be called the pectoral angle, are listed in Table 4.

It is interesting to consider these data in the light of the ideas of Harris (1952) on the function and the evolution of the fins in fishes. Harris contended that, with the evolution of a swim-bladder, there was no longer any tendency for the body to sink or even tilt, because the centres of gravity of the body and the swim-bladder are usually either close together, or else coincident. Pectoral fins set as hydroplanes and an asymmetrical tail, both giving a lift-force (as in sharks) were thus no longer necessary. So the pectorals were freed to become limbs in the Choanichthyes, and brakes (or oars) in the Teleostii, while the caudal fin attained a symmetrical neutral shape, but with a different structural basis, in the Dipnoi, Crossopterygii and Actinopterygii. With increasing specialization of the pectoral fins as brakes, there appears to have been an upward movement of the fins along the sides of the fish and a rotation of the axis of each fin so as to bring the axis near to a vertical position.

Since the Alepisauroidea have no swim-bladder they might be expected to have a specific gravity somewhat greater than their environment (see p. 324). In order to remain at one level, an alepisauroid

<sup>1</sup> Fishes of this size may contain well-developed ova, showing that they are nearing, or have attained, the adult phase. Thus the differences in ossification are unlikely to be due to differences in the phase of life.

must presumably make continual compensating movements. Now the setting of the pectoral fins in alepisauroids gives the strong impression that one of their functions is to produce an upward lift during forward motion. Moreover, during the swinging of the tail, the combined caudal and anal fins, which are set close together, may act rather like a heterocercal caudal fin also giving an upward lift. If this is so, the alepisauroids have certain dynamic parallels with the sharks.

Table 4. *Pectoral fin 'angles' in some iniomous fishes.*

ALEPISAUROIDEA			
<i>Scopelarchus guentheri</i>	20°	<i>Paralepis brevis</i>	35-40°
<i>S. cavei</i> sp.n.	30°	<i>P. coregonoides</i>	25-30°
<i>Neoscopelarchoides elongatus</i>	20°	<i>P. sphyraenoides</i>	30°
<i>N. dubius</i> sp.n.	25°	<i>Anotopterus pharao</i>	10°
<i>Evermannella balbo</i>	15-20°	<i>Alepisaurus ferox</i>	5-10°
<i>Sudis hyalina</i>	45°	<i>Omosudis lowei</i>	20-25°
MYCTOPHOIDEA			
<i>Aulopus filamentosus</i>	50°	<i>Gonichthys cocco</i>	70°
<i>Chlorophthalmus agassizii</i>	45°	<i>Ctenobranchus nigro-ocellatus</i>	75°
<i>Bathysauropsis gracilis</i>	70°	<i>Diaphus coeruleus</i>	60°
<i>Bathypterois filifer</i>	70-80°	<i>D. lutkeni</i>	55°
<i>Ipnops murrayi</i>	70°	<i>D. ostentfeldi</i>	45°
<i>Bathymicrops regis</i>	65°	<i>D. lucidus</i>	40°
<i>Harpadon nehereus</i>	40-45°	<i>D. garmani</i>	60°
<i>H. squamosus</i>	45°	<i>Notolychnus valdiviae</i>	75°
<i>Synodus similis</i>	45°	<i>Ctenoscopelus phengodes</i>	45°
<i>Saurida elongata</i>	40°	<i>Lampadena nitida</i>	70°
<i>Electrona antarctica</i>	40-45°	<i>L. chavesi</i>	60-65°
<i>E. rissoi</i>	60°	<i>Ceratospelus townsendi</i>	55°
<i>Myctophum affine</i>	55°	<i>Notoscopelus elongatus</i>	75°
<i>M. humboldti</i>	50°		

Yet this is to regard the pectorals merely as relatively passive hydroplanes. A study of their structure soon shows that the pectorals of any alepisauroid must have greater mobility than those of a shark. No observations on alepisauroids are available, but Breder and Krumholz (1943) have analysed the functions of the pectoral fins in *Anchoa mitchilli*, which like most clupeids and alepisauroids has low set pectorals, each with an axis making less than 45° with the horizontal axis. (In *A. mitchilli* this angle is about 30°). In spite of a well-developed swim-bladder, an adult *A. mitchilli* is evidently a little heavier than the surrounding water. During swimming there is apparently a slight tendency for the fish to roll, this being counteracted by the constant, irregular beating-down movement of the pectorals. Between these movements, the pectorals also move together in simultaneous down-beats so as to raise the head for swimming. Perhaps the pectorals of the Alepisauroidea have rather similar functions. At all events it is clear that pectorals, with the axis nearer to the horizontal than to the vertical, may act not only as hydroplanes but also as roll-compensating and elevating devices.

But there is another aspect to these considerations. While the evolution of a swim-bladder made possible the evolution of pectoral fins as brakes, the inference that all teleosts with well-developed swim-bladders should have pectorals with this function is only partly true. The remarks above on *A. mitchilli* show this very clearly. When discussing locomotion in the Isospondyli, Breder (1926) remarked that their pectoral fins '...while capable of being folded back do not have the flexibility to be seen in many of the higher teleosts and are not often capable of being used effectively to back water. Their use is more nearly like that of the shark's pectorals...'



It is significant that the little available evidence suggests that certain isospondylous fishes are somewhat heavier than the environment. This is borne out by the observations of Breder and Krumholz (1943) on *Harengula pensacolatae* and *Anchoa mitchilli*, and by measurements of the specific gravity of *Clupea harengus* (Magnan, 1929). Moreover, the studies of the first two authors on *Megalops atlanticus* suggest that the simple, unspecialized type of open swim-bladder, characteristic of most Isospondyli, has a limited function in regulating the specific gravity. After remarking that the pectoral movements of tarpon are not unlike those of *Anchoa mitchilli*, Breder and Krumholz (1943) continue thus: 'Observations in an aquarium of tarpon ranging from 6 cm. to 100 cm. indicate that they seem to become heavier as the time for them to rise for breath approaches. Their pectorals typically work harder and finally with a burst of tail effort they rush to the surface and gulp. . . . After the ingestion of air they are usually lighter than water and frequently have difficulty descending, until they emit small bubbles by way of the gill clefts, after which they reach a state of approximate balance and from then on become heavier again.'

It would appear therefore, that as far as present knowledge goes, the development of a capacious swim-bladder in the Isospondyli has not always led to a close correspondence between the specific gravity of the body and that of the environment. Correlated with a slight tendency of the fish—at least for part of the time—to sink, the pectorals are set in such a way that they can act as hydroplanes and beat downwards to raise the head. The angle between the axis of the pectoral fin and the horizontal axis of the body in a number of isospondylous fishes is given below.

<i>Elops saurus</i> (40°)	<i>Megalops atlanticus</i> (45°)
<i>Chanos chanos</i> (15–20°)	<i>Clupea harengus</i> (25°)
<i>Sardinops sagax</i> (30°)	<i>Harengula pensacolatae</i> (20°)
<i>Ilisha filigera</i> (45°)	<i>Pristigaster cayanus</i> (30–35°)
<i>Odontognathus compressus</i> (45–50°)	<i>Salmo salar</i> (40°)
<i>Coregonus</i> sp. (45°)	<i>Salvelinus alpinus</i> (45°)
<i>Osmerus eperlanus</i> (40–45°)	<i>Retropinna oameroides</i> (40°)
<i>Plecoglossus altivelis</i> (25°)	<i>Galaxias fasciatus</i> (55°)

But not all Isospondyli have an open swim-bladder (see Jones and Marshall (1953)). A closed swim-bladder is commonly found in the Gonostomatidae and Sternoptychidae (Marshall, 1951) and it is of interest to measure the pectoral angle in representatives of these families.

<i>Maurollicus muelleri</i> (60°)	<i>Vinciguerria attenuata</i> (40°)
<i>Gonostoma denudatum</i> (45–50°)	<i>Ichthyococcus ovatus</i> (45°)
<i>Argyropelecus aculeatus</i> (65°)	<i>Sternoptyx diaphana</i> (60°)
<i>Polyipnus nuttingi</i> (50°)	

A comparison of the pectoral angle in *Gonostoma denudatum* with that in *G. elongatum* and *G. bathyphilum* (20–25°) is revealing, when considered in the light of the foregoing discussion. *G. denudatum* has a well-developed gas-filled swim-bladder with a powerful gas-secreting complex; *G. elongatum* has a fat-filled swim-bladder with a degenerate complex; *G. bathyphilum* has no swim-bladder. Since the two latter species are probably heavier than their environment, the presence of pectoral fins with a hydroplane-like setting is not surprising. And as *G. denudatum* can presumably bring its weight in water to vanishing point, the possession of pectorals which are beginning to look more like brakes than hydroplanes is more comprehensible.

From these considerations we may return to the Myctophidae, most of which have a swim-bladder. In all investigated species (Marshall, 1951), this swim-bladder is closed and is usually provided with a highly developed gas-secreting complex. Reference to the list of pectoral angles of myctophids (see p. 326) shows that most species have pectorals with a setting more efficient for braking (or paddling) than for hydroplaning.

It would appear therefore that in the Isospondyli and the Iniomi there is some correlation between the possession of a closed swim-bladder and pectorals having angles greater than  $45^{\circ}$ .<sup>1</sup> But the specialization of pectoral fins as brakes is best seen in the higher groups such as the Percomorphi. It must also be remembered that many of the isospondylous and iniomous fishes with closed swim-bladders undertake considerable diurnal vertical migrations. At the end of a descent, compression of the swim-bladder may leave the fish somewhat heavier than the sea-water, and, until the volume can be restored by gas secretion, the fish will need to make compensating movements. Perhaps this is why the pectorals are not so highly specialized as in the Percomorphi and are set so as to allow some lift-force.

While a closed swim-bladder means that the fish is independent of the surface for replenishing the gases and is able to achieve a finer control of specific gravity, there are certain limitations. Moreover, this discussion does not imply that all fishes with open swim-bladders have only a rough control of their specific gravity. Measurements of their specific gravity (Jones and Marshall, 1953) and observations of their behaviour indicate that cyprinid and esocid fishes are perfectly able to reduce their weight in water to vanishing point. Such fishes are able to manoeuvre more easily than, say, clupeids.

Lastly, the pectorals tend to be lateral and 'brake-set' not only in the Myctophidae but also in other myctophoid fishes, the Aulopidae, Chlorophthalmidae, Synodontidae, Harpadontidae, Ipnopidae and Bathypteroidae. As already mentioned these are predominantly bottom-dwelling fishes and have no swim-bladders, and it is hardly surprising that the pectoral fins should have this setting, for it is a common feature in benthic fishes. Considering only those without a swim-bladder, pectorals with an upright or nearly upright axis are found in the scorpaenids, cottids, nototheniids, gobiids and gobiocids. Certainly the pectorals in these fishes are used in locomotion and, being so placed, may allow of better control of body movements as the fish grubs for food. The similarity in the setting of these fins in the pelagic Myctophidae on the one hand and the remaining benthic myctophoids on the other is therefore probably an instance of an unusual type of convergence (the independent acquisition of like characters).

*The dorsal fin.* Except for *Alepisaurus*, the dorsal fin of alepisauroids has 6–15 rays and is set about half-way down the body length. In *Anopterus* there is no trace of a dorsal fin, while *Alepisaurus* has a long sail-like dorsal, very like that of the sail-fishes (*Istiophorus*). This convergence is, indeed, so striking that it led Dollo (1909) to conclude—on very slender evidence—that *Alepisaurus* uses its dorsal fin as a sail, much in the manner sometimes seen in *Istiophorus*.

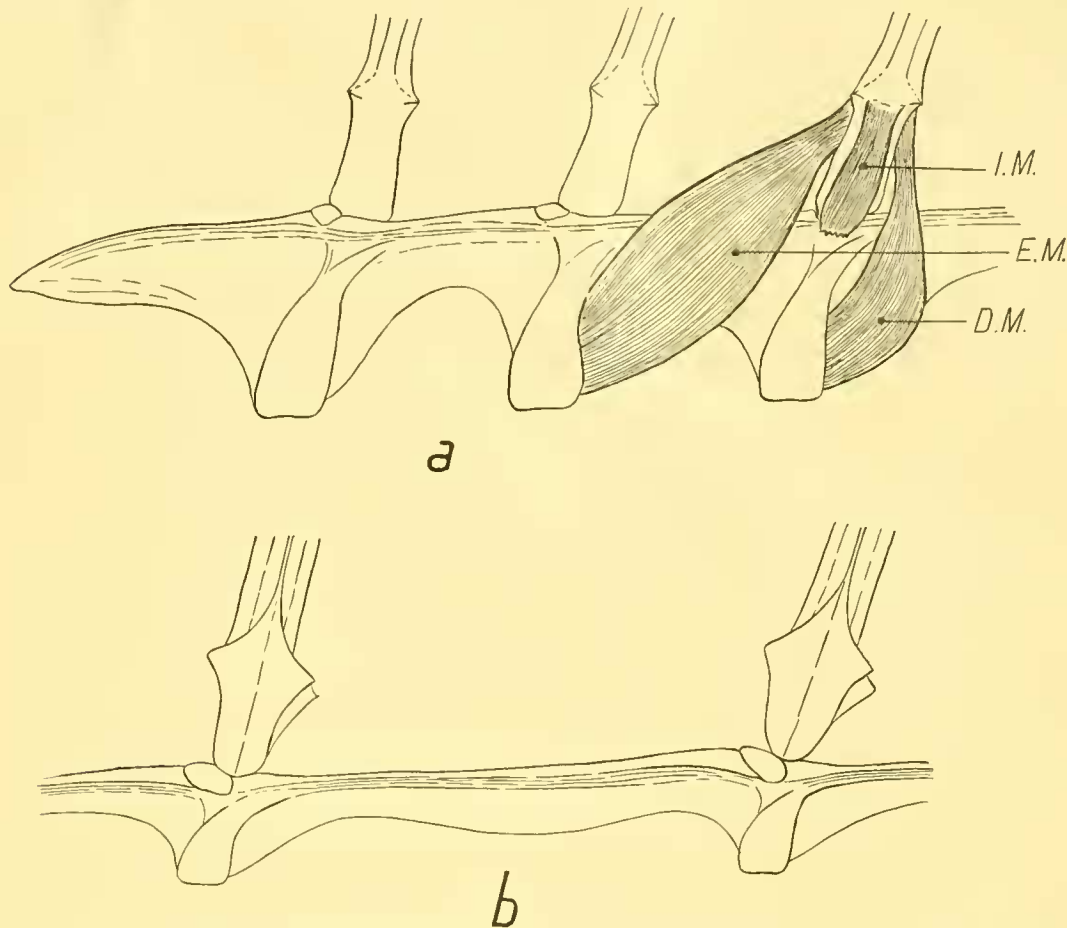
In *Alepisaurus ferox* the dorsal fin, which has about 40 rays, originates just behind the head and ends above the origin of the anal fin, i.e. the base of the dorsal extends over more than two-thirds of the standard length. The longest of the anterior rays may measure at least twice the greatest depth of the body.

The muscles which move the dorsal fin rays are shown in Text-fig. 8a, the upper figure being of the first three rays, the lower of the 14th and 15th rays. It will be seen that the erector muscles are powerfully developed, while the depressors and particularly the inclinators are a good deal smaller.

The basal supports for the dorsal fin are also of interest. At the base of each ray is a distal radial, but it would appear that the intermediate and proximal elements have fused to form a long continuous rod, running the entire length of the dorsal fin, an unusual feature in fishes (Text-fig. 8a, b). But such a development is hardly surprising in view of the strains imposed on the high dorsal as it is hauled up

<sup>1</sup> Two myctophids listed on p. 326, *Gonichthys cocco* and *Ctenobranchus nigro-ocellatus* have no swim-bladder yet have pectoral angles of  $70$ – $75^{\circ}$ . But both species have a more stream-lined, slender body than other myctophids and both may well keep to a particular level by vigorous swimming movements (rather like *Scomber*). Beebe and Vander Pyl (1944) have remarked on the vigorous unceasing swimming movements of *Gonichthys cocco* as compared with other lantern-fishes.

during active movements. Perhaps the sudden raising of the dorsal gives stability during turns and enables turning to be more rapidly effected, a capacity that may well be important in a fish which preys on such large active fishes as the paralepidids.



Text-fig. 8. Dorsal fin of *Alepisaurus ferox*: *a*, the basal elements supporting the first three dorsal rays. *DM*, *EM*, *IM*, depressor, erector and inclinator muscles of fin-ray ( $\times 4.5$ ); *b*, the basal elements supporting the 14th and 15th dorsal rays ( $\times 7.5$ ).

#### Intermuscular bones

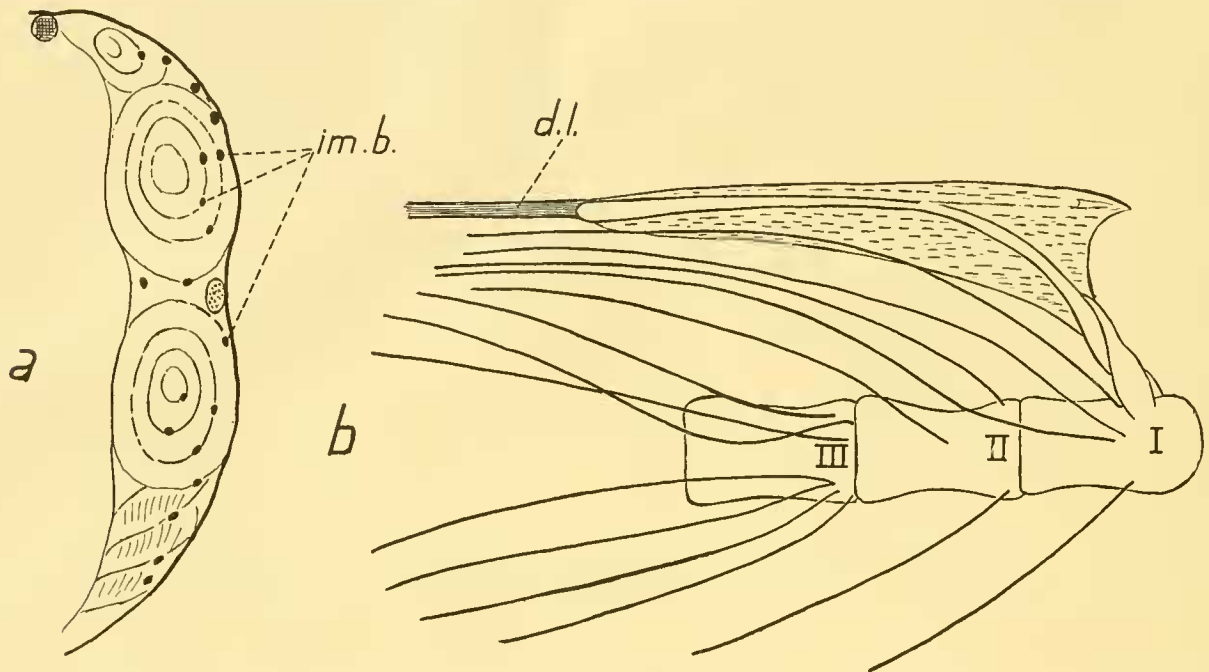
In his *Classification of Fishes*, Berg (1947) remarks that in the lower teleosts true intermuscular bones (epineurals, sometimes also epicentrals) are usually present. In defining the larger groups, Berg states that intermuscular bones are present in the Isospondyli, Haplomi, Ostariophysii (Cyprinoidae) and Apodes. (Definite absence is recorded for the gadoids, Solenichthyes, Microcyprini and Percomorphi.)

Intermuscular bones are also present in certain of the alepisauroid fishes. Hubbs, Mead and Wilimovsky (1953) observed the prominent development of these bones in *Anotopterus* and *Alepisaurus* and described the complex as consisting of a series of thick dorsal elements running horizontally, together with more slender median bones stretching backward and slightly downward. The positions of the intermuscular bones in a transverse section across a medium-sized individual of *Anotopterus pharao* may be seen in Text-fig. 9*a*. The pattern of intermuscular bones in *Alepisaurus* is remarkably similar to that found in *Anotopterus*.

Certain of the Paralepididae and *Omosudis lowei* also have intermuscular bones, which are developed in both the epaxial and hypaxial parts of the myotomes. A drawing of the more conspicuous elements associated with the first three vertebrae of *Omosudis* may be seen in Text-fig. 9*b*. The extraordinary

interneural, median, ossified body connected with the first vertebra is also shown. Parr (1929) has already described and figured this ossification, but it may be added that the median dorsal ligament, which runs down the trunk, is attached to its posterior end. In the Paralepididae, I have found intermuscular bones in *Paralepis speciosa*, *P. brevis*, *P. brevirostris* and *P. coregonoides*, but none were found in *Notolepis coatsi*, *N. rissoi kroyeri*, *Lestidium sphyraenoides* and *Sudis hyalina*.

Lastly, X-ray photographs of *Scopelarchus cavei* sp.n., *S. guentheri*, *Neoscopelarchoides dubius* sp.n., *N. elongatus* and *Evermannella balbo* have not revealed the presence of intermuscular bones. (These show up quite clearly in X-ray photographs of paralepidids, *Anotopterus* and *Alepisaurus*.)



Text-fig. 9. *a*, transverse section through the trunk muscles of *Anotopterus pharao*, showing the intermuscular bones (*imb.*) ( $\times 9.3$ ); *b*, some of the larger intermuscular bones associated with the first three vertebrae of *Omosudis lowei* ( $\times 10.6$ )  
*d.l.* = dorsal ligament.

#### *Distensibility of stomach and body-wall*

*Evermannella*, *Omosudis*, *Anotopterus* and *Alepisaurus* are among the alepisauroids capable of swallowing very large prey. Alcock (1899) has a drawing of *Evermannella atrata* very much distended with a large squid, while in the Discovery Collections there is a specimen of *E. indica* with a gonostomatid fish folded up in its stomach, the length of the prey being appreciably longer than the length of the predator's abdomen. The capacity of *Omosudis* for swallowing large prey is well known since Günther's (1887) account of a *Sternoptyx* in the stomach of one individual, victim and predator being equal in bulk. *Anotopterus* also has a highly distensible stomach and body-wall, as the presence of two large *Notolepis coatsi* in the specimen described earlier (p. 321) must indicate. *Alepisaurus* is a highly voracious fish with a comparable capacity for dealing with large prey: in the collections of the Natural History Museum there is an *A. ferox* considerably distended, having swallowed one of its own kind.

There is no record of a scopelarchid or a paralepidid containing large prey (although I have seen many *Notolepis coatsi*, each somewhat distended by a stomach crammed with *Euphausia superba*) and it is interesting that of all the families of alepisauroid fishes, the scopelarchids and paralepidids are the only ones containing species which are fully scaled. Most probably all the scopelarchids are fully scaled, while among the paralepidids this condition obtains in *Magnisudis*, *Paralepis* and *Notolepis* only (Harry, 1953 *a, b*).

Considering all fishes known to swallow relatively large prey, the striking fact emerges that all are scaleless or have a very reduced squamation. *Omosudis*, *Alepisaurus* and *Evermannella* are completely naked, while *Anotopterus* has scale-like segments only along the lateral line. Other fishes with distensible stomachs and body-walls (the Melanostomiidae, Idiakanthidae, Astronesthidae, Malacosteidae, Lyomeri, Giganturoidea, *Chiasmopus niger* and *Melanocetus* have no scales). The only known scaled fishes which can engulf large prey are *Stomias* and *Chauliodus*. In *Chauliodus*—and probably in *Stomias*—the scales, which are very thin and do not overlap, lie between the epidermis and the pigmented layer of the corium (Brauer, 1908). Moreover, the scales are not held in pockets, which suggests that fishes cannot have both a normal overlapping scale system and a highly distensible body-wall. Presumably the connective tissue pattern associated with an imbricating squamation sets a limit to the degree of tissue distensibility. However this may be, there is no record of a fish with well-developed, overlapping scales being able to cope with large prey. It is interesting that the scaleless (or virtually scaleless) paralepidids, *Lestidium*, *Macroparalepis* and *Sudis* have relatively larger teeth on the palatines and mandibles than the fully scaled *Magnisudis*, *Paralepis* and *Notolepis*. Is it possible that the larger toothed genera are able to capture (and retain) larger prey and that the loss of scales is an adaptation towards distensibility of the stomach and body wall? On the other hand the scopelarchids with a formidable dentition of stabbing, barbed teeth are completely scaled. A study of the food of these fishes would be of particular interest. (In the stomach of *Scopelarchus guentheri* of standard length 65 mm. I found the remains of copepods and ostracods and a mass of nematocysts, probably of Siphonophora.)

The alepisauroids, which are all pelagic, may be compared and contrasted with the pelagic members of the Myctophoidea, the Myctophidae, *Luciosudis* and *Notosudis*. These latter fishes are fully scaled, the myctophids feeding particularly on copepods and smallish members of the zooplankton (Beebe and Vander Pyl, 1944). There is no evidence that any myctophid fish is able to tackle large prey. *Harpadon*, which of all myctophoid fishes has a dentition most like an alepisauroid, feeds on small fishes and shrimps (Hora, 1934).

To summarize: among the pelagic families of the Inioi the predominant evolutionary trend in the alepisauroids has been towards adaptations for dealing with nektonic prey, extraordinary elasticity of the tissues of the stomach and body wall being associated with a loss or marked reduction in the scaling. By contrast, the Myctophidae, which feed on planktonic animals, have a complete scaling.

## INTERRELATIONSHIPS OF THE ALEPISAUROIDEA

Considerations of the interrelationships within the Alepisauroidea are inseparable from the question whether the suborder represents a natural group, but before attempting to deal with this problem the similarities and differences between the families must be elaborated.

Parr (1929) considered that the Scopelarchidae and Evermannellidae were fairly closely related. Moreover, the other four families, the Alepisauridae, Anotopteridae, Omosudidae and Paralepididae have certain common features.

The characters of these two groups can be listed as follows:

### Group 1. *Scopelarchidae* and *Evermannellidae*

Intermuscular bones absent: parietals fused with the frontals; anus near to origin of anal fin or midway between pelvic and anal fins;<sup>1</sup> body short to moderately elongate; definite trend towards development of tubular eyes.

<sup>1</sup> In larval or juvenile scopelarchids, the anus is closer to the pelvis than to the origin of the anal fin, e.g. in *Neoscopelarchoides linguidens* (Mead and Böhlke, 1953) and in *Benthalbella* larvae.

Group 2. *Alepisauridae*, *Anotopteridae*, *Omosudidae* and *Paralepididae*

Intermuscular bones present; parietals not fused with frontals (no information on *Anotopterus*); anus much nearer to insertion of pelvic fins than to origin of anal fin; eyes normally formed; definite trend towards development of elongate to very elongate body forms.

It will be noticed that there are certain morphological trends within these two groups. In addition to those listed under the group headings, mention has been made already (pp. 322-31) to others, which can be briefly summarized here. There are tendencies to the development of a lightly ossified skeleton, to the loss of scales, and to the acquisition of means for dealing with very large prey (certain of the mandibular and palatine teeth have become large stabbing canines, and the tissues of the stomach and body wall are distensible). As in the more generalized Isospondyli, the pectoral fins are also set low down on the shoulders and make an angle of less than  $45^\circ$  with the horizontal axis of the body.

These trends lead to more specialized forms, but within each of the two groups there is one family with a more generalized character complex. For example, in Group 1 the Scopelarchidae are fully scaled and have lingual teeth, whereas both these features are absent in the Evermannellidae. In Group 2, some of the Paralepididae are also fully scaled, in contrast to the other three families, the Alepisauridae, Anotopteridae and Omosudidae. In discussing the relationships of the Paralepididae, Harry (1953*a*) pointed out that *Magnisudis* has many generalized features in common with the Aulopidae and with another myctophoid family, the Chlorophthalmidae. He also considered that the 'Paralepididae are most closely related to the Anotopteridae. They both have the same general proportions, essentially similar osteology, the same peculiar cartilaginous development of the jaws, which is found in these two families alone in the order, and a good number of other similarities.' These two families also show striking resemblances in the development of scale-like ossifications along the lateral line (Text-figs. 5*c* and 7) and in certain skull features already mentioned on p. 322.

The remaining two families in Group 2, the Alepisauridae and Omosudidae, are perhaps the most nearly related of all. Regan (1911) observed that *Omosudis* has a head, mouth and teeth very much like *Alepisaurus*, and both genera have completely lost the scaling, even along the lateral line.

The alepisauroid fishes are difficult to define, lacking diagnostic characters and it might be argued that they are not a monophyletic group. But Simpson (1953), after expressing his belief that the fissipede carnivores are monophyletic, remarked that he was unable to find a single character that occurred in all fissipedes and in no other mammals. Again, Berg (1940), after defining the Clupeiformes (= Isospondyli), concluded by remarking that 'this order, from which a series of higher orders has arisen, represents an artificial assemblage, its separate members, as may be seen from the diagnosis, greatly differing from one another. In time, the Clupeiformes will doubtless be divided in many orders.'

If the Isospondyli are considered to be merely a convenient grouping of fishes of a 'certain level of organization', then the same may be true of the Iniomii. It has been pointed out on p. 305, that the Iniomii have evolved beyond the 'isospondylous level' mainly in that the premaxillaries exclude the maxillaries from the gape, and it is possible that more than one group of isospondylous—or more likely pre-isospondylous—fishes may 'have tried this experiment' with these jaw-bones. There may well be some parallel with the early evolutionary history of mammals. 'Palaeontologists use an arbitrary criterion that a reptile became a mammal when the dentary-squamosal joint developed and the functional jaw-movement ceased to be on the articular-quadrate joint. This line was probably crossed separately by at least five different lineages...' (Simpson, 1953).

It has also been stressed by Simpson that the development of a higher group of animals seems always to be bound up with definitive adaptive features correlated with a spread into some major living

space. 'The adaptive characters involved may be quite broad and varied, as in carnivores and ungulates, or may be quite specific, virtually "single characters" in a taxonomic sense, as in rodents and bats.' As already stated, the alepisauroids are bathypelagic fishes and consideration of the group involves features such as the dentition, type of gill-raker, loss of scales, acquisition of distensible tissues etc., all of which would seem to be correlated with a predacious, large-prey-seizing habit. Such characters remind one more of the broad and varied features of the mammalian carnivores than of those of the bats. (Perhaps in the type of character-complex, the ceratioid angler fishes are the nearest oceanic equivalents to the bats.)

Bearing these theorizings in mind, these studies have done little to dispose of the (partly intuitive) idea that the Iniomi may be no more than an assemblage of lineages, each having attained certain morphological features. When the great differences between, say, a myctophid and *Anotopterus* are considered, the value of keeping the order Iniomi seems questionable. Yet if this is not a compact 'monophyletic' order, it is at the very least a convenient gathering of those 'isospondyloid' fishes with more specialized jaws. Furthermore, there is little reason for discarding the two suborders.

A consideration of the position of the Notosudidae (*Notosudis* Waite, 1916, and *Luciosudis* Fraser-Brunner, 1931), provides something of a test of the usefulness of the classification used in this report (p. 306). The dentition of both genera is somewhat similar to that described for the alepisauroids (p. 305), while the general body-form is reminiscent of certain paralepidids. (Fraser-Brunner, 1931, regarded *Luciosudis* as a paralepidid, while Mead and Taylor, 1953, have listed their new species *Luciosudis harryi* under the Paralepididae.) But the combination of certain features (lath-shaped gill-rakers, anal fins with relatively few rays, lateral pectoral fins with 'axial angles' of more than 45°, pelvic fins set well forward of the mid-standard length and a well-developed scaling) indicates clearly that the Notosudidae have closer affinities with the Myctophoidea.

Similarly there are certain iniomous fishes (not yet described) in the Discovery Collections with no scales and a single row of teeth on the premaxillae, dentaries and palatines—all alepisauroid features—but with an underlying myctophoid character-complex quite like that described for the Notosudidae. But unlike the Notosudidae, one of these new species appears to have a peculiar system of light organs over the flanks. These new fishes must undoubtedly be placed in a new family and if closer examination confirms the presence of light-organs, then the contrast between the Myctophoidea, having three families in which photophores of peculiar structure have arisen, and the Alepisauroidea, in which photophores have not been evolved, will be further emphasized.<sup>1</sup>

But it is also of interest that in number and arrangement of branchiostegal rays (3-4+4-5) the alepisauroids are a more homogeneous suborder than the myctophoids, in which there are three main groups: (1) The Chlorophthalmidae, Ipnopidae, Bathypteroidae, Neoscopelidae and *Luciosudis* most nearly resemble the alepisauroids in having 3-5+4-8 branchiostegal rays. (2) The Myctophidae have 2+5-6+0-2 rays (numbers on the epihyal, ceratohyal and hypohyal). (3) The third group, which consists of the Aulopidae, Synodontidae and Harpadontidae, has more numerous branchiostegal rays. (*Aulopus filamentosus* 8+7, *Hime japonica* 7+7, Synodontidae 12-16; *Synodus lucioceps* 8+10, *Saurida undosquamis* 6+10; Harpadontidae 17-25; *Harpadon uehereus* 9+14. One specimen of each species examined.) Furthermore, the orbitosphenoid bone seems to be consistently absent in the alepisauroids, but may be present or absent in the myctophoids (Regan, 1911; Parr, 1929). However, these aspects of the character-complex of the Myctophoidea will be considered in a later paper.

It is reasonable to conclude that the Myctophoidea and the Alepisauroidea are, at least, useful taxonomic groupings. Each can be adequately defined by a rather loose assemblage of characters and by certain morphological trends. But further discussion of the classification in terms of evolution had

<sup>1</sup> Apart from the deep-sea Isospondyli, no predacious, bathypelagic fish has an elaborate system of light-organs.

best be postponed until we know more of the functional morphology and ecology of these fishes. Perhaps study of the Notosudidae and the new fishes mentioned on p. 333 will throw some light on these interesting but somewhat intractable problems.

### SUMMARY

This report deals with certain aspects of the classification and functional morphology of the alepisauroid fishes. These are voracious, bathypelagic forms, which, together with the sub-order Myctophidea form the order Iniomi.

Part I contains a revision of the Scopelarchidae, which are shown to fall into two well-marked genera, *Scopelarchus* Alcock and *Neoscopelarchoides* Chapman. Two new species, *Scopelarchus cavei* and *Neoscopelarchoides dubius* are described and *N. elongatus* (Norman) is redescribed. The remarkably large larval form, *Benthalbella infans* Zugmayer is shown to be a young stage of a species of *Neoscopelarchoides*.

The remainder of the first part is taken up with a description of *Macroparalepis molestus* sp.n. and a review of the family Anotopteridae. While there is no good evidence for regarding *Anotopterus* as consisting of more than one species, *A. pharao* Zugmayer, there is some indication that this species may be differentiated into northern and southern forms.

Some discussion of the classification of the Iniomi, leading to certain considerations of functional morphology, forms the second part of the report. Alepisauroids are compared and contrasted with myctophoids and possible correlations between the presence and absence of a swim-bladder, the degree of ossification of the skeleton and the setting of the pectoral fins are traced. Adaptations for dealing with large prey and the development of intermuscular bones are also reviewed.

In the concluding section, relationships within the Alepisauroidea are considered; and finally there is some discussion on the status of the order Iniomi.

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