

Studies on the Bathypelagic Fishes of the Family Paralepididae.

1. Survey of the Genera

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INTRODUCTION

THE PARALEPIDIDAE are large-eyed, elongate fishes lacking light organs and are members of the suborder Alepisaurioidea (Alepisaurina, using the recently proposed endings of Stenzel, 1950: 94) of the order Iniomi (also called Scopeliformes by Berg, 1940: 256; Iniomida by Schultz, 1948: 233; Iniomida or Myctophida, using Stenzel's endings). These abundant pelagic and deep-sea teleosts of worldwide distribution have been termed barracudinas by Fowler (1936). The family appears to be most closely related to the Anotopteridae and Alepisauridae.

While I was endeavoring to determine the relationships of a new species of the genus *Lestidium* from off the coast of central California, it became evident that the classification of the Pacific paralepidids was in deplorable confusion, especially in regard to generic grouping. Comparison of the form and development of various parts of the body in the different genera has shown, unexpectedly, that certain structures not heretofore used are of phylogenetic or taxonomic importance. Among the most useful are the structure of the maxillaries, the form and distribution of the dentition and gillrakers, modifications of squamation, and variation of the lateral-line tube. These new observations form the basis for this revision of the Paralepididae.

In addition, these fish form an important food of tunas and other large oceanic fishes. A more complete knowledge of them, particularly in regard to speciation and limits of

distribution, would furnish a valuable tool for obtaining information on the migration of these larger food fishes by means of stomach analyses.

In the course of the present study I have been able to examine material totaling several hundred specimens, representing all the known genera (*Sudis*, *Notolepis*, *Paralepis*, *Lestidium*, *Macroparalepis*, *Arctozenus*, *Bathysudis*, and *Lestidiops*), and all the generic types. One genus and one species are described as new. The revision is divided into parts comprising (1) a survey of the genera, (2) a review of the North Pacific species, and (3) a synopsis of the South Pacific species. The illustrations are by the author.

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The work was done in the Natural History Museum of Stanford University and in the Research Laboratory of the George Vanderbilt Collections of the California Academy of Sciences.

HISTORY OF GENERIC CLASSIFICATION

The family Paralepididae has been variously expanded and restricted. It has, in the past, encompassed a wide assortment of remarkably divergent groups (*vide* Regan 1911, Parr 1928, Fowler 1944), but it is generally accepted by recent authors that the family includes only the genera *Paralepis*, *Lestidium*, *Macroparalepis*, and *Sudis*. The genus *Luciosudis* Fraser-Brunner belongs in the suborder Myctophoidea, probably in the family Chlorophthalmidae. The genus *Notosudis* Waite may belong in the suborder Alepisauroidea, but, if it does, it definitely does not belong in the Paralepididae. It is perhaps near the family Anotopteridae. The genus *Neosudis* Castelnau (1873) has not been rediscovered since the original account, and its systematic position is not known. Many characters are attributed to this genus which do not agree with the suborder Alepisauroidea as presently understood, and it is not included in the present study.

The recent workers who have contributed most toward a better understanding of the classification of the Paralepididae are Regan, Parr, Ege, and Maul.

Regan's arrangement of the order Iniomi (1911) has been generally accepted as the first reasonably natural system proposed for these forms. He relegated Paralepididae (using the name Sudidae, which he later sometimes abandoned in favor of Paralepididae) to the suborder Myctophoidea together with Synodontidae, Aulopidae, and Myctophidae. Unfortunately, he placed Sudidae in the wrong suborder because he based his family description on *Chlorophthalmus* instead of on *Sudis*, *Paralepis*, or a genus closely related to them. While *Chlorophthalmus* is obviously close to the three families Regan placed in the suborder Myctophoidea, its relationships to the paralepidids are distant. This unfortunate linkage of *Chlorophthalmus* with the Paralepididae has contributed to the subsequent confusion of the subordinal relationships of the Myctophoidea and Alepisauroidea — confusion which has extended to the present. Actually it is clear that *Sudis* and its allies are more closely related to the Alepisauroidea than to the Myctophoidea and, therefore, should have been placed in the former suborder. Furthermore, Regan used Sudidae as a catch-all for forms that did not fit into his system, and he divided it into three groups containing nine genera which previous authors had apportioned to several families. Recent authors regard his third section, exclusive of *Parasudis*, as the only one of his three divisions that really belongs in the Paralepididae.

The most important extensive studies of the Iniomi have been those of Parr. In his survey of the Paralepididae (1928), he accepted and named Regan's three groups as subfamilies and added the problematical *Notosudis*, which was described subsequent to Regan's paper, as a fourth subfamily.

Parr's discussion of his "Paralepidini" includes a review of all genera and species (mostly prepared from the literature, as he had little material) but his entire classification was greatly revised, immediately after it appeared, in a series of papers by Ege and himself. Parr (1928) recognized only two genera

as valid, on the basis of the presence of scales in one genus and their absence in the other. Parr and Ege attempted by subsequent investigation to demonstrate that this type of division was not justified. The two reasons why Parr's classification of 1928 was not accepted by subsequent authors (including himself) are: (1) he did not recognize that *Sudis hyalina* was so distinct from all other paralepidids that it deserved monotypic generic status; (2) he based his generic characters for *Sudis* and *Lestidium* solely on the presence or absence of scales. It was not known at that time that the species of the family could be arranged in a uniformly graded series from (a) those completely scaled on head and body, through (b) those scaled only on body or head, through (c) those scaled only late in development, to (d) those lacking scales at all stages of development. Furthermore, he used the generic name *Sudis* for the scaled species, but the generic type (*hyalina*) is almost completely naked at all stages. In addition, each of his genera included both naked and scaled species.

Parr (1929: 4, 7) in a paper on the osteology and classification of the Iniomi, pursued further the relationships of the families. His investigations of the Paralepididae are based on the partial osteology of two representatives of "*Lestidium*" (*Paralepis brevisrostris* and a species of *Lestidium*). It represents the first research of this kind on the family. Parr proposed a phylogenetic line on the basis of osteological characters, from *Chlorophthalmus* through *Bathysudis* to *Omosudis*, "thereby indirectly establishing a relationship between the Sudidae and Alepisauridae."

The generic relationships of the Paralepididae adopted by Parr (1928, 1929) and others were subsequently greatly modified on the basis of an extensive distributional and systematic research on the genus "*Paralepis*" of the North Atlantic by Ege (1930). His rich material was composed almost exclusively of larval to juvenile specimens. The identifications he made of these early stages with pre-

viously known adult forms are particularly valuable for the elucidation of the taxonomic and nomenclatural problems which had developed in the earlier literature. His generic classification is essentially the same as that used by most previous European authors. He retained the genus *Sudis* as monotypic and expanded the limits of *Paralepis*. Although the relationship of the genus *Lestidium* to *Paralepis* was considered by Ege to be a matter beyond the scope of his investigation, he maintained that the recognition of *Lestidium* on the premise of its being devoid of scales was completely untenable. The Mediterranean and North Atlantic material available to him was represented by young material completely devoid of scales; but he did not consider the lack of scales in the younger individuals necessarily to indicate their absence in the fully adult stage. For example, he found an individual of "*Paralepis rissoi*" (which is scaled when adult) 188 millimeters in length which completely lacked any trace of scales.

Unfortunately, Ege did not investigate the generic classification of the Paralepididae as carefully as he did the specific. He never defined the limits of the genus "*Paralepis*" as he accepted it, but apparently used it in the broad sense of early European authors. Actually he did not realize the bearing of *Lestidium* to his work. He claimed that the genus *Lestidium* was beyond the scope of his investigation, but included all species of this genus of which he had material in "*Paralepis*" and excluded almost all the others which he had not seen.

While he claimed that *Lestidium* is untenable on the basis of the lack of scales, Ege proved on morphometric grounds that the naked species can be recognized (*vide* the differentiation of groups I and II in his key). Apparently he never realized that his first division included all the scaly forms, and the second division all the forms naked even as adults. The mention of such discrepancies is not meant to detract from the value of his work. He was not concerned particularly with

the major classification of the family, but was primarily interested in development and speciation. In fact, he has made the Paralepididae the best-known group of the order Iniomi in this respect.

Ege's results were interpreted by Parr (1931*b*), who assumed that *Lestidium* was untenable and that the limits of the genus *Paralepis* had to be considerably extended to encompass a highly variable group—at least as long as practicable generic distinctions had not become re-established on a different morphological basis. Thus, if Parr's classification of 1928 were altered to fit this idea, all the species of "Paralepidini," except *Sudis hyalina*, would be placed in the genus *Paralepis*.

Ege (1933) preliminarily diagnosed 15 new species and a new genus, *Macroparalepis*, from a part of the paralepidid material collected—usually at great depths—by the 1928–30 "Dana" Expedition around the world. Unfortunately, the specimens are all postlarvae or juveniles, the descriptions are brief, and the relationships are not indicated for the species of *Macroparalepis*. *Lestidium* and *Paralepis* were compared with *Macroparalepis*. Dr. Ege is still studying this material and plans to publish more complete accounts.

Gregory and Conrad (1936: 28) also attempted to give a natural phylogeny of the order Iniomi. Their classification, which appears to have been done primarily by a comparison of illustrations of the species and superficial examination of the literature, adds little to our knowledge of the family Paralepididae. They apparently misinterpreted some of Parr's findings of 1929 and did not include the papers of Ege (1930, 1933) and Parr (1931).

Jensen (1942), in his critical review of the paralepidids of Greenland, gives important discussions of the genus *Paralepis*. One of the most important parts of his results is a detailed account of the structure of the lateral-line and scales. It is important to note that Jensen confuses the ossified sections of the

lateral-line tube and the overlying lateral-line scales.

In a monograph of the paralepidid fishes in the collection of the Municipal Museum of Funchal, Madeira, Maul (1945) included material of *Sudis*, *Paralepis*, and *Macroparalepis* and confined the limits of the family to these genera. He presented definitions of the genera for the first time since Parr (1928). Maul described more adult material than any other recent worker and described larger specimens of *Macroparalepis* for the first time.

These classifications of Parr, Ege, and Maul differ essentially from my results, presented in the next section, in that I place *Sudis* in a distinct subfamily (Sudinae) and divide the Paralepidinae into two basic groups of genera that can be easily distinguished by osteological characters, by gillraker structure, by extent of squamation in the adults, and by morphometry. These two basic divisions of the Paralepidinae correspond to groups I and II of Ege's key (1930: 7). An outline of this classification is presented with the description of the paralepidids collected by the Bermuda Oceanographic Expeditions of the New York Zoological Society (Harry, 1951).

DISCUSSION

Family PARALEPIDIDAE

Paralepidini Bonaparte, 1832–41 (no pagination), 1846; Bellotti, 1878; Parr, 1928: 17, 32; Parr, 1929: 28.

Paralepidina Günther, 1864: 418.

Paralepididae Gill, 1874: 16; Gill, 1893: 131; Goode and Bean, 1895: 118.

Paralepidinae Jordan and Evermann, 1896: 599.

Paralepidae Dollo, 1908: 59; Jordan, 1923: 154.

Sudidae (in part) Regan, 1911: 125; Parr, 1928: 15; Parr, 1929: 27; Ege, 1933: 223; Fowler, 1944: 438.

Sudini Berg, 1940: 257, 437.

Sudidae Jensen, 1942: 3; Maul, 1945: 3.

DIAGNOSIS: Body compressed, elongate. Belly usually constricted, forming a pro-



FIG. 1. Front of snout of a paralepidid (illustrated from the holotype of *Lestidium prolixum*, n. sp.). The teeth in the emargination of the upper jaw are those of the palatines. The premaxillary lacks teeth in this emargination.

nounced mid-ventral carina. Anus moves posteriorly during early ontogeny; finally situated in region of pelvic fins. Eyes moderately large, with adipose lids. Mouth with extensive buccal valves. Rictus well before eye; tip of maxillary not reaching past a vertical from anterior border of eye except in early postlarvae. Symphysis of lower jaw more or less elevated. Corresponding arched, toothless emargination of upper jaw below end of snout (see Fig. 1). Lower jaw included when mouth is closed. Mandibles with 1 to 3 rows of teeth (sometimes atrophied in adults of scaled genera); if present, inner series is composed of depressible canines which recline

backward, the outermost series of short fixed teeth of similar shape. Premaxillary closely bound to maxillary and not protractile. Premaxillaries anteriorly with a single row of depressible canines, situated on the inner face of this bone, followed by single series of short fixed teeth on edge of bone. Dorsal process of premaxillary with wide circular foramen in all genera except *Sudis*. Supramaxillary slender, approximately 0.5 length of maxillary. Vomer toothless, or with 1 or 2 tiny teeth. Palatine long and slender, anteriorly attached to sides of mesethmoid and vomer. Teeth on palatines in 1 or 2 rows. Teeth on tongue absent or minute.

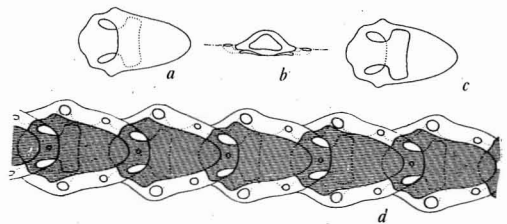


FIG. 2. Lateral-line segments of a paralepidid (illustrated from the holotype of *Lestidium thunnorum*, n. sp.). *a*, Top of an ossified segment; *b*, posterior view of an ossified segment with adjoining pores stippled; *c*, bottom of an ossified segment; *d*, a series of ossified segments in normal position along the lateral-line. The lateral-line scales of the genera *Megalosudis*, *Paralepsis*, and *Notolepis* overlie these ossified segments.

Scales when present cycloid, generally caducous. Lateral-line tube large, imbedded in the skin, enclosed in characteristic partly ossified segments (see Fig. 2), which perhaps are highly modified scales. In the naked genera, the outer shield-like section of each partly ossified segment forms an imbedded scale-like structure. In scaled genera, these structures overlain by lateral-line scales. Tube variously pierced by pores medially, above, and below.

Dorsal fin small, with 9–15 rays, situated near middle of body length. Adipose dorsal fin present over posterior end of anal fin. Anal fin far posterior, with long base and numerous rays (21–50). Caudal fin small, very short and forked, free from adipose and anal

fins, with 18–20 principal rays. Pectoral fins moderately low, below midaxis of body, with 9–17 rays. Pelvic fins small, close together, behind middle of standard length, with 8–12 rays; their position varies from far before dorsal fin to behind dorsal base. Vertebrae 65–102, as far as known. No light organs present.

Secondary sexual dimorphism not known. Specimens have been taken up to approximately 20 inches in length.

Sudis Rafinesque (1810) was the first genus of the barracudinas to be described, but it was indicated as being related to *Sphyaena* and placed in "Esocidi." Cuvier described *Paralepis* in 1817 for two species mentioned by Risso (1810) and also related it to *Sphyaena*. Apparently Bonaparte (1832–46) first elevated one of the genera to familial status when he placed "Paralepidini" as a subfamily of Sphyaenidae (1832–41) and of Scopelidae (1846), using, *ipso facto*, *Paralepis* as the family type. He recognized both *Sudis* and *Paralepis* in this group. As far as I can find, all authors up to the time of Regan (1911) used *Paralepis* as the type genus, with Gill (1874) the first author to raise the group to the status of a full family (Paralepididae). Dollo (1908) and many subsequent authors shortened the name to Paralepidae, but this is not proper form. Regan (1911) based the family name on *Sudis* because it is the oldest generic name. According to the Rules of the International Commission of Zoological Nomenclature as clarified by Opinions 133 and 141, however, this is not acceptable, because Paralepididae was proposed before Sudidae. Unless I have missed a reference earlier than Bonaparte, in which a family name was based on *Sudis*, Paralepididae is the proper name. It seems unlikely that there is an earlier reference, since Bonaparte was apparently the first ichthyologist to use family endings.

Relationships within the Family

Most authors, except Ege, have examined only a few of the genera and usually only very immature material. As a result, few workers have attempted to analyze the major parale-

pid relationships. Most current authors have accepted Ege's classification of the family which is based primarily on differences of postlarval development and recognizes only a few generic units. My investigations have primarily stressed the morphological aspects of as mature material as possible although I have utilized several complete ontogenetic series. As there is some important variation between stages of development, it is believed that a clearer picture of paralepidid classification can be obtained by utilizing more than one growth stage.

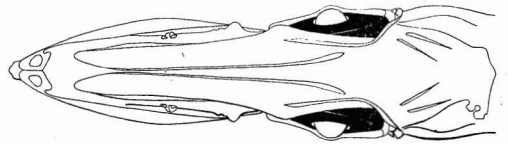


FIG. 3. Top of head of a paralepidid (illustrated from a paratype of *Lestidium Thunnorum* n. sp.), showing the cranial ridges and the foramina in the premaxillaries.

Although our present knowledge of these fishes is so inadequate as to make very extensive splitting seem premature, certain aggregates of species appear to be so widely separated from their nearest relatives on the evidence of prominent characters in stages older than postlarvae that their inclusion in *Paralepis* seems much too conservative. The retention of only three genera does not allow us to depict several important and easily recognized lines of evolution. In my own investigations, conclusions have been reached which involve a splitting of the genus *Paralepis*, a resurrection of the previously suppressed genera *Les-*

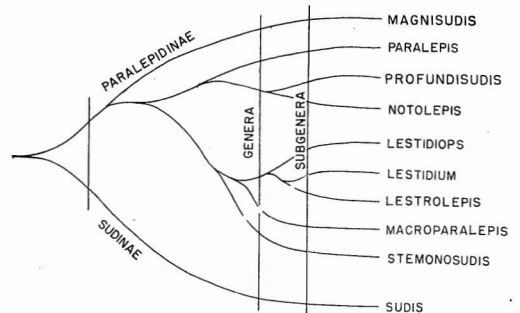


FIG. 4. Diagram of the extent of relationships between the genera of the family Paralepididae.

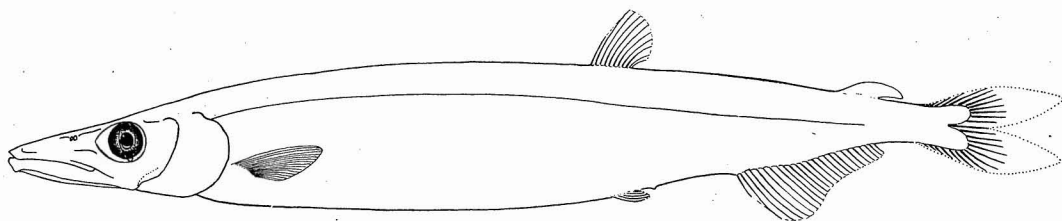


FIG. 5. Genotype of *Magnisudis* (*M. barysoma*, n. sp., paratype, 510 mm. in standard length, from off Lower California).

tidium and *Notolepis*, and the drawing of relationships along lines somewhat different than those given by Ege.

There is no doubt that *Sudis* is unique and remote from the other barracudinas, and there may be some question whether this genus even belongs in the same family with them. *Sudis* is distinguished from all other paralepidids primarily by lack of a foramen in the premaxillary and by other osteological peculiarities, by the unique mandibular dentition, by the reduction of the anterior nostril to a minute pore in adults, by the presence of scales only on the preopercles, and by the different larval development, particularly of the pectoral fins (Ege, 1930: 6). Despite these differences, it is believed that family relationships within the suborder Alepisaurioidea can best be shown by retaining *Sudis* in the Paralepididae. The family would then be divided into the subfamilies Paralepidinae and the monotypic Sudinae. The Sudinae most closely resemble the genus *Lestidium* in gillraker structure, lack of body squamation, lateral-line form, and other characters.

The subfamily Paralepidinae falls into two basic generic subdivisions, which are separated in part by the characters given in Ege's key (1930: 7) to separate "Groups I and II" of *Paralepis*. The most obvious differences between the main groupings are that all species in division I are scaled as adults and have numerous teeth in two or more rows on each gillraker and that those of division II are scaleless as adults and have a few teeth in one row on each gillraker. This classification cuts across Ege's system. His groups I and II of *Paralepis* are apparently only remotely related,

representing groups of genera that might be designated as tribes (e.g., Paralepidini and Lestidiini).

In determining the relationships within the family, the following characters are probably primitive and apparently trace back into the stock now represented by the Chlorophthalmidae and Aulopidae, the two most generalized families in the order Iniomi: short and massive head; completely scaled body; lack of nonossified prolongation on the lower jaw or snout; large eye far forward; tiny fixed teeth on the jaws, vomer, and palatines; lack of or slight development of an anterior foramen in the premaxillary; hyoid apparatus extending far forward, with gillrakers strongly developed on all five arches; simple lateral-line tube and unmodified lateral-line scales; low number of dorsal and anal rays.

Such characteristics are approached to a remarkable degree by a new species in a new genus, *Magnisudis barysoma*. The conservative *Magnisudis* has a short, broad, massive head and snout, a moderately short, heavy body. The eye is large. The teeth on the jaws are minute; this species is the only paralepidid with teeth on the vomer in the adult. The supramaxillary is free at its posterior end. The gillrakers are reduced to flat bases armed with 4 long filaments (it is of interest that this type of gillraker is unique to *Magnisudis* within the Paralepididae and is known in only one other family of the Iniomi, the Alepisauridae). The gillrakers on the first arches extend far forward on each side of the tongue into the anterior part of the mouth. The tip of the tongue is far forward, near the symphysis of the lower jaw. The lateral-line structure is the

simplest in the family. A single row of large, round, tenaciously adherent scales is present over the lateral-line tube; each scale is pierced by a median pore only. The scales over the remainder of the body are very small, round, and deciduous. The anal fin has comparatively few rays.

Paralepis, which is restricted to a few species, is undoubtedly a derivative of the *Magnisudis* line of evolution. These fishes resemble *Magnisudis* and differ from all the remaining paralepidids in the short, heavy head and body, anteriorly free supramaxillary, long anterior teeth on the gillrakers, and low number of anal rays. The relationship is, however, not really close, since *Paralepis* differs from *Magnisudis* in several important characters. The gillrakers are shorter and more spine-like than in *Magnisudis*, and there are numerous teeth on each raker. Only a few anterior teeth on each gillraker are long, and all the posterior teeth are very short and needle-like. The tongue is long, farther back in the mouth than in *Magnisudis*, and the gillrakers do not extend as far forward on each side of the tongue. The lateral-line structure is more complex. There are one and one-half or two rows of caducous scales over the lateral-line tube. Instead of having but a single median pore, each lateral-line segment is often pierced above and below by another pore. In most species the upper scale row over the lateral line is penetrated near the lower margin by the upper pore, and the lower scale row receives the middle and lower pores, although there is extreme variability in pore structure and a tendency for the reduction in number of pores piercing the lateral-line scales. The body scales are longer than broad, the same size as the lateral-line scales, and extremely caducous. There is little variation within the genus *Paralepis*; except in the case of the inadequately known *P. elongata* Brauer, the species are very closely related and somewhat difficult to tell apart.

The most specialized of the scaled genera is *Notolepis*, which approaches *Lestidium* more

closely than any other scaled form. The snout is prolonged and pointed, and the body is more elongate and less deep than in *Paralepis*. The teeth in the adults are not lacking or reduced as in the other scaled genera but are fairly long and well developed. They are distinctly arranged in two or three rows, the outer row of short, fixed teeth, and the inner series of long, hastate, depressible canines. The lateral line is essentially similar in structure to that of *Paralepis* but has more pores; the upper scale row is sometimes peculiarly modified, being notched to receive the large upper pore instead of being pierced by this pore series. The body scales are round, overlapped for most of their length, and are the same size as the lateral-line scales. The teeth on the gillrakers are reduced in length and consist of numerous tiny teeth in oblique rows on each raker. The pharyngeal teeth are reduced in number. It is known from Ege's investigations that the scales tend to form late in life in at least one of the species (*N. rissoi*), and it is very probable that there is a tendency for the suppression of scales in this group. The three species of *Notolepis* are widely separated in distribution: *N. rissoi* from the North Atlantic, *N. coruscans* from the North Pacific, and *N. coatsi* from the Antarctic. The two northern species are much more conservative in form than is *N. coatsi*, which has an extreme development in dentition, gillrakers, and lateral line, and these two species are separated in the new subgenus, *Profundisudis*.

The next evolutionary step appears to involve a greater development of the elongate form and dentition, an important reduction in the number of gillraker teeth, loss of all scales, further specialization of the partly ossified lateral-line segments into characteristic scale-like structures, a wide variability in the position of the pelvic fins in relation to the dorsal fin, and a wide range in the number of anal rays. The most generalized genus of this group is *Lestidium* which corresponds to group II of Ege (1930: 7).

Lestidium can be distinguished from the

genera *Magnisudis*, *Paralepis*, and *Notolepis* by the complete absence of scales, by the greater length of the mandibular teeth, by the arrangement of the teeth on each gillraker into a single row of short needle-like structures, and by the reduction of the pharyngobranchial teeth to a single patch.

The ancestral stock evidently split rather early into three developmental lines. One of these, which can be designated as the subgenus *Lestidiops*, is the most conservative. It is characterized by a somewhat massive head and blunt snout, a deep and heavy mandibular symphysis, the absence of nonossified prolongations on the jaws, a low number of anal rays (26–28), and the position of the dorsal fin in the middle third of the space between pelvic and anal fins.

The second evolutionary line, the subgenus *Lestidium*, comprises the majority of the species from both the Atlantic and the South Pacific. It has retained a relatively low number of anal rays (27–33) but has developed a slightly less massive head and snout and, in the most specialized species, a prominent, nonossified prolongation on the lower jaw (*neles*, *pacificum*, *nudum*). In all members of the subgenus *Lestidium* the position of the dorsal fin is over the pelvic fins. The third evolutionary line of the genus *Lestidium*, which is similar to the subgenus *Lestidiops* in the position of the dorsal fin in the middle third of the distance between the pelvic and anal fins, constitutes a new subgenus, *Lestrolepis*. This clearly delimited group of the genus *Lestidium* is distinguished by a high number of anal rays (33–49), a slender and elongate lower jaw, a distinctive preorbital pigmentation, a well-developed, nonossified prolongation of the lower jaw, and the position of the dorsal fin.

The remaining Paralepididae have been placed by Ege in the genus *Macroparalepis*. He differentiated this group on the basis of four characters, presumed to be unique: (1) the nonossified prolongation on the tip of the lower jaw; (2) the shape of the lateral-line

segments, which have the greatest height at or very near the anterior margin; (3) the presence of two pores above and below on each



FIG. 6. Postlarva of *Lestidium sphyraenoides* (Risso), approximately 8 mm. in length, showing the position of the intestine behind the eye (after Ege, 1930).

lateral-line segment; and (4) the position of the intestine under the eye in postlarvae (see Figs. 6 and 7). My investigations show that at least three of these characters are shared by other paralepidids, and it may be questionable that the other is unique to *Macroparalepis*. The subgenera *Lestidium* and *Lestrolepis* both have nonossified prolongations of the lower jaw, and many species of the genus *Lestidium* possess characters 2 and 3. The condition stated for (3) has been found to be the basic pore pattern for all naked genera and is not unique to any particular paralepidid group. In regard to point 4, Ege has stated in correspondence that his groups I and II of "*Paralepis*" both have the same postlarval development, with the intestine behind the head, differing markedly from that of *Macroparalepis*. No one, however, has been able to examine the postlarvae of the species in *Lestidium* that most closely approach *Macroparalepis*, and there may be some intergradation in these larval characters.



FIG. 7. Postlarva of *Macroparalepis brevis* Ege, approximately 8 mm. in length, showing the position of the intestine below the eye. (This illustration prepared from a tracing generously supplied by Ege.)

Ege considers that *Macroparalepis* is very distinct and that *Lestidium* [*Paralepis* group II] is much more closely related to *Paralepis* [*Paralepis* group I] than it is to *Macroparalepis*. This opinion is based primarily on the differences in postlarval development. My conclusions are entirely the opposite in regard to Ege's *Macroparalepis* group I. In every adult

character, such as in head and body form, prolongation of the lower jaw, dentition, gill-rakers, maxillary structure, lateral line, and lack of squamation, *Macroparalepis* group I is very close to *Lestidium* and can be differentiated from this genus only with difficulty. While there may be a consistent difference in the position of the intestine in the postlarvae of these two genera, I doubt that it is of great significance.

Ege divided *Macroparalepis* into two remarkably distinct groups. The first division, which was just discussed, contains four species which have the anus situated behind the origin of the dorsal fin, 13-14 dorsal rays, and 24-28 anal rays. Its high number of dorsal rays surpasses that known for any other form in the Paralepidinae. The dorsum pigment pattern is different from that of all other paralepidids. This group most closely resembles the subgenus *Lestidiops* in general form, anal ray count, position of dorsal fin, and lateral-line form and is probably related to the ancestral stock of this subgenus. It approaches the subgenus *Lestidium* in its nonossified prolongation of the upper jaw. The genus *Macroparalepis* is hereby restricted to Ege's group I (since no genotype has been previously designated).

The second group of Ege's *Macroparalepis*, comprising seven species, is very different from the first. The anus is situated in front of the dorsal fin and there are 9-11 dorsal rays and 37-50 anal rays. The species are very elongate and some even eel-like, the angle of the gape extends back almost to the tip of the maxillary, the tongue is unusually small and far back, the dentition is considerably reduced, and the lower jaw is very slender and pointed with only a slight elevation at its tip. Also, the shape of the lateral-line segments is very different from that found in group I and all other paralepidids, as the length of each segment is twice the height. Despite the fact that groups I and II have similar postlarval development, prolongation of the lower jaw, and pore pattern, their similarities end with

these characters. If these similarities to group I are put aside for the moment, group II clearly approaches the subgenus *Lestrolepis* with which it shares the prolongation of the lower jaw, the high number of anal rays, and the same position of the dorsal fin in relation to the pelvic fins. In fact, it may very well be that group II is more closely related to *Lestrolepis* than to group I, and that the similarities to the latter group are due to parallel development or convergence. In any event, group II is far more different from group I than group I is from *Lestidium*, and it is here placed in the genus *Stemonosudis*. A provisional generic tree showing the degree of relationship of the genera as this now appears to me is given in Figure 4.

Comparison of specific paralepidid anatomical structures throughout the family shows some interesting speculative results on the mode of barracudina evolution. In most characters I have examined there is evident a straight-line evolution from the primitive condition in the genus *Magnisudis* to the specialized in *Stemonosudis* through the line of genera as shown in Figure 4. In almost every instance this evolutionary pattern involves a loss or reduction from the form as found in *Magnisudis*. In general, specialization in this family means a loss or reduction in some pre-existing character. Such specialization is exemplified by the gillraker form, which is reduced in the Paralepididae to a flat bony base. This structure is most elaborate in the genus *Magnisudis*, being proportionately large and peculiarly notched. Each raker is armed with 4 long cartilaginous filaments with bony cores arranged in a square. The genus most closely approaching this condition is *Paralepis*. In this group and all remaining genera the rakers are flat and simple in outline. Each raker in *Paralepis* is armed anteriorly with fairly long cartilaginous filaments grading posteriorly into short bony spines. The next step is found in the genus *Notolepis* where all the armature of each gillraker consists of short spines. Thus, we see a trend for the simplification of

the form of the gillraker base, the loss of a cartilaginous sheath from the gillraker spines, and a progressive reduction in the length of these spines. There has been, however, an increase in the number of gillraker teeth. In *Magnisudis* there are 3–4, in *Paralepis* about 5–10, and in *Notolepis* about 15–30 spines on each raker. In all three genera the spines are in two or more rows.

All the rest of the genera in the family (*Lestidium*, *Macroparalepis*, *Stemonosudis*, and *Sudis*) have a singular form of gillraker and gillteeth which is also characteristic of the alepisauroid families Scopelarchidae, Evermannellidae, Omosudidae, and Anotopteridae. It approaches most closely the condition in *Notolepis*. The raker base is considerably reduced in size; the raker spines are very short, similar in form to those of *Notolepis*, but in a single row of 1–7 teeth. There is a tendency for the loss of gillrakers in *Stemonosudis*, as indicated by the fact that they appear to develop later than in other genera.

The degree of similarity of the gillrakers between the various genera is the same as the composite similarity of important characters and very likely expresses the degree of relationship. If this hypothesis is true, we could expect on the basis of gillraker form that *Magnisudis* and *Paralepis* are more closely related than either is to *Notolepis*. This statement is corroborated by many other characters. For instance, the dentition of *Magnisudis* and *Paralepis* is strikingly reduced and tends to be completely absent in adults. The dentition of *Notolepis*, however, is well developed, not atrophied in adults, and approaches more closely the condition of *Lestidium*. This same balance of relationships is found in supra-maxillary form. The supra-maxillary in *Paralepis* and *Magnisudis* is strongly arched and widely separated from the maxillary except at its posterior insertion, but in *Notolepis* and all other paralepidid genera it is attached along its entire border to the maxillary. As a result, the genus *Notolepis* is an important link between the scaled and naked genera; in most

structures it is most closely related to *Paralepis* and *Magnisudis*, but in some revealing characteristics it is the same as, or similar to, the naked genera, particularly *Lestidium*. Nevertheless, the genus *Notolepis* represents an end point, but in the line of scaled genera evolution. It has an extreme development of dentition (particularly in the subgenus *Notolepis*) and a unique form of lateral-line scales and tube not equaled elsewhere in the family. The genus is somewhat intermediate between *Paralepis* and *Lestidium* but the ancestral stock of the latter genus must have split off rather early from the *Magnisudis-Paralepis-Notolepis* stock. The sharpest break along the evolutionary line of the Paralepidinae as shown in Figure 4 is definitely between *Notolepis* and *Lestidium*, and the impressive differences of *Magnisudis*, *Paralepis*, and *Notolepis* (tribe Paralepidini) from the scaleless genera (tribe Lestidiini) within this subfamily have already been discussed. The scaleless genera of the family have very similar gillrakers, and, as would be expected, all of these genera are closely related on the basis of a large number of characters.

Not all characters, however, follow as simple an evolutionary pattern as the gillrakers. As has already been demonstrated, the lateral-line is a structure of considerable phylogenetic importance but has to be studied carefully because it can be highly variable even among individuals of the same species. In the Paralepididae the simplest form of the lateral-line tube and scales is found in *Magnisudis*, where each segment has a single pore. In *Paralepis* there is usually the addition of a pore above and below in the tube, and in *Notolepis* there are numerous pores in each segment. The most complex pore patterns and lateral-line segment shapes are in the genus *Lestidium*, and there is finally the stabilization of pore number in *Macroparalepis* and *Stemonosudis* to two pores above and two below. While comparison of lateral-line structure among the genera will show that the same degree of relationship exists between the various genera

as illustrated by the gillrakers, there is not a progressive reduction in complexity of lateral-line structure from *Magnisudis*. On the contrary, there is a general increase in complexity of form in the scaled genera from *Magnisudis* through *Paralepis* to the extreme condition found in *Notolepis*. Then there is a progressive reduction in complexity of lateral-line form in the naked genera from the most complex in *Lestidium* through *Macroparalepis* and *Stemonosudis*.

Jensen (1942) has presented the most important discussion on the structure of the lateral-line tube and its overlying scales. However, in some species he has confused the imbedded segments of the tube with overlying lateral-line scales. Therefore, for *Paralepis coregonoides* and *Paralepis brevis*, he figures segments of the lateral-line tube as lateral-line scales. As the scales are so caducous in this genus, the overlying scales were probably missing (see Fig. 11). Jensen points out that the lateral-line scales are extremely variable as to number of pores, which is fully corroborated by the present study.

List of Species Currently Recognized

The following list shows all the known living species of Paralepididae currently recognized in the literature. The synonyms are as given by Ege (1930), Parr (1931*b*), and Maul (1945). No attempt is made to put closely related species together as so many are inadequately known.

Sudis squamosa Chapman (1939: 519) from south of the Aleutian Islands and *Lestidium (Bathysudis) parri* Chapman (1939: 519) from the Gulf of Alaska do not belong in the family Paralepididae. Hubbs and Chapman (1951) have conclusively identified *Sudis squamosa* as *Mallotus catervarius* (Steller) and *Lestidium parri* as *Thaleichthys pacificus* (Richardson).

Subfamily PARALEPIDINAE Bonaparte, 1846.

Magnisudis, n. gen.

**barysoma*, n. sp. (generic type). Pacific, off California and Mexico.

Paralepis Cuvier, 1817.

**coregonoides* (Risso, 1810) (generic type). North Atlantic.

**speciosa* Bellotti, 1878. Mediterranean. *elongata* (Brauer, 1906). Indian Ocean.

**brevis* Zugmayer, 1911. North Atlantic.

**brevirostris* (Parr, 1928). North Atlantic. *bronsoni* (Parr, 1928). Bahamas.

danae Ege, 1933. Off Cape Verde, West Africa.

Notolepis Dollo, 1908.

**risoi* (Bonaparte, 1841). North Atlantic.

**coruscans* (Jordan and Gilbert, 1881). North Pacific.

**coatsi* Dollo, 1908 (generic type). Antarctic.

Lestidium Gilbert, 1905.

sphyraenoides (Risso, 1810). North Atlantic.

intermedium (Poey, 1867). West Indies.

**ringens* (Jordan and Gilbert, 1881). California.

jayakari (Boulenger, 1889). Indian Ocean, off Arabia.

**nudum* Gilbert, 1905 (generic type). Hawaiian Islands, New Zealand (?), Japan (?).

japonicum Tanaka, 1908. Japan.

**sphyraenopsis* (Hubbs, 1916). California.

**pseudosphyraenoides* (Ege, 1918). North Atlantic.

atlanticum (Borodin, 1928). North Atlantic.

thori (Ege, 1930). North Atlantic.

danae (Ege, 1930). North Atlantic.

**affine* (Ege, 1930). North Atlantic.

**pacificum* (Parr, 1931). Pacific off Mexico.

proximum (Ege, 1933). Celebes Sea.

simile (Ege, 1933). Off Cape Verde, West Africa.

luetkeni (Ege, 1933). Mozambique Channel.

bellottii (Ege, 1933). New Guinea.

mirabile (Ege, 1933). Celebes Sea.

**philippinum* (Fowler, 1934). Philippine Islands.

**bathyopteryx* (Fowler, 1944). Pacific, off Mexico.

- **vanderbilti* (Fowler, 1944). Caribbean.
- **neles*, n. sp. California.
- **atrox*, n. sp. Hawaiian Islands.
- **thunnorum*, n. sp. Northeastern Pacific.
- **prolixum*, n. sp. Japan.
- **pofi*, n. sp. Hawaiian Islands.
- Macroparalepis* Ege, 1933.
- **affine* Ege, 1933 (generic type). North Atlantic.
- **danae* Ege, 1933. Fiji Islands, Bermuda (?).
- **brevis* Ege, 1933. Off St. Helena, North Atlantic.
- egei* Maul, 1945. Madeira Island, North Atlantic.
- Stemonosudis* Harry, 1951.
- macrura* (Ege, 1933). Sumatra.
- elegans* (Ege, 1933). Lord Howe Island, South Pacific.
- miscella* (Ege, 1933). Sumatra.
- elongata* (Ege, 1933). Ceylon.
- gracile* (Ege, 1933). Straits of Macassar, South Pacific.
- **intermedia* (Ege, 1933) (generic type). Caribbean Sea.

Subfamily SUDINAE Regan, 1911.

- Sudis* Rafinesque, 1810.
- **hyalina* Rafinesque, 1810 (generic type). Mediterranean and Madeira.

Distribution of Genera and Species.

The family Paralepididae is one of the largest in the order Iniomi, consisting of 48 known bathypelagic species. It is world-wide in distribution and apparently occurs in large numbers in deep water to a depth of about 4,000 meters. The species are generally wide-ranging. Adult specimens seldom fall into the hands of ichthyologists, and the majority of the adult material has been taken from the stomachs of *Alepisaurus*, tuna, other larger pelagic fishes, and whales. The general form of paralepidids indicates that these are swift-moving voracious fishes. Larger specimens have very rarely been taken by net and apparently never by hook and line. No sexually mature indi-

viduals have been reported, and Dr. Bruun informs me that the "Dana" expeditions were not able to find or, at least, to determine the eggs of this family. It is possible that some or most of the species grow to large size and that no sexually mature adults have been obtained.

The best-known group, the genus *Lestidium*, apparently is the only genus whose members come to the surface where adults may be taken by light at night. The range and abundance of the various species of barracudinas are best understood in the North Atlantic and Mediterranean, mainly because of the extensive Danish Oceanographical Expeditions, which obtained the large collections reported on by Ege. No examples have been recorded from the South Atlantic (excluding the Antarctic), but 20 species are recognized in the North Atlantic. *Sudis hyalina* is apparently fairly common in the Mediterranean and is also known from Madeira.

About half of the known species of the Paralepididae occur in the Pacific Ocean. The northernmost form is a species of *Notolepis* taken off the coast of Washington. Eleven species of *Lestidium* and *Magnisudis barysoma* are variously recorded in the North Pacific from off Japan, the Philippine Islands, the Hawaiian Islands, Mexico, and California. These species of *Lestidium* (except *L. nudum*, which is apparently known from the Hawaiian Islands, Japan, and New Zealand) are known only from restricted localities. The barracudinas have been collected in the more southerly Pacific in the East Indies and off New Zealand where five species of *Lestidium*, *Macroparalepis danae*, and five species of *Stemonosudis* have been recorded. All the East Indian species are known only from postlarval or juvenile material, except *Lestidium nudum*.

Very little material has been collected from the Indian Ocean, two of the three recorded species being represented by the holotypes only. These forms are *Lestidium luetkeni* from the Mozambique Channel, *L. jayakari* from Muscat, Gulf of Oman and *Paralepis elongata* from the Seychelles Islands, Chagos Archi-

* Species examined in the present study.

pelago, south Ceylon, Bay of Bengal, and Cocos (Cocos Keeling) Islands. The distinction between the Indian and Pacific faunas cannot be sharply defined. *P. elongata*, the only species known from the eastern Indian Ocean, is recorded very near the Pacific. This species apparently has the greatest latitudinal range of all barracudinas, but, considering that Brauer's types are postlarvae ranging from 8–30 mm., there may be more than one species represented. It is expected that more collecting will reveal various species ranging through the Indo-Pacific region.

The distribution of the Paralepididae in the Antarctic is fairly well known. The "Erebus and Terror," "Challenger," "Pourquoi Pas," "Scotia," "Terra Nova," and the B.A.N.Z. (British, Australian, and New Zealand) Antarctic Research Expeditions collected material from this region, but it was composed almost exclusively of larval to juvenile specimens whose relationships and classification were generally not understood by the original describers. Such confusion has resulted in the subsequent identification of these forms, that only one abundant species, *Notolepis coatsi*, of circumpolar distribution, is definitely recognized from the Antarctic.

No species has been recorded from both the Atlantic and Pacific Oceans, although this apparent distinctiveness may be due to a lack of sufficient material and of proper comparison. Dr. Ege is presently examining the relationships and supposed differences between the Atlantic and Pacific species and plans to publish his findings.

Apparently no paralepidids have been recorded from the Arctic Ocean. The distribution of the three species of *Notolepis* in the North Pacific, North Atlantic, and Antarctic gives a good example of bipolar (pantemperate) distribution.

Explanation of Morphological Figures.

Figures 8, 10, 13, 14, 16, 18, 20, and 22 have been prepared in a standard manner to facilitate comparison of some of the more important morphological characters. These

drawings are somewhat diagrammatic but are accurate for the characters involved. These figures present the following information:

A: Anterior part of snout. The teeth that are solid black are depressible; the remainder are fixed. The buccal valves and supra-maxillary membranes are stippled. The nostrils on the snout and larger pores on the lower jaw are indicated.

B: Lateral aspect of an enlarged section of the fixed teeth on the middle of the premaxillary.

C: The anterior lateral-line segments on the left side. The stippled area represents the weak membranous part of the tube. The area with longitudinal parallel lines delimits the partly ossified center shield in the naked genera (*Lestidium*, *Macroparalepis*, and *Stemonosudis*) and the central row of scales in the scaled genera (*Magnisudis*, *Paralepis*, and *Notolepis*). The dotted lines show the outline of the internal limits of the lateral-line tube. The crossed lines indicate the scales above and below the central lateral-line row. The characteristic pigmentation in the lateral-line region is presented for some of the species.

D: A section of the ceratobranchial of the first arch showing the gillrakers and gill-teeth. The parallel lines indicate the gill arch. The light line over the tips of the teeth shows the mucus line.

E: Dorsal surface of tongue (glossohyal) and anterior portion of first basibranchial. The stippled area represents the fleshy tongue. The glossohyal and basibranchial are indicated by longitudinal parallel lines. The small hooked circles indicate the teeth.

KEY TO GENERA AND SUBGENERA

- Teeth on mandible large, triangular, strongly compressed, with serrate edges; always present. Anterior process of premaxillary without a foramen. Outer rays of pelvic fins longer than inner rays. (Subfamily SUDINAE, one genus) . . . *Sudis*
- Teeth on mandible slender, basally round, sometimes hastate, but never

- serrate; sometimes absent. Anterior process of premaxillary with wide circular foramen. Outer rays of pelvic fins distinctly shorter than inner rays (Subfamily PARALEPIDINAE)..... 2
- 2. Teeth on each gillraker in 2 or more rows (Fig. 10D). Two large, separate tooth patches on pharyngobranchials on each side. Teeth on lower jaw comparatively short or (in some adults) missing, their length up to as much as 5 per cent of snout length. Body scaled in adults..... 3
 - Teeth on gillrakers in one row (Fig. 16D). One tooth patch on pharyngobranchials. Teeth on lower jaw long, their length 5–11 per cent (generally above 7) of snout length Fig. 16A). Body naked..... 6
- 3. Each gillraker with 4 long filaments in 2 rows (Fig. 8D). Gillrakers extending far forward into mouth, beyond angle of gape. Each lateral-line scale tenacious, much larger than surrounding scales, bordered above and below by at least 3 scales (Fig. 8C)..... **Magnisudis**
 - Each gillraker with many spine-like teeth in numerous series (Fig. 13D, 14D). Anterior limb of gillarches naked; gillrakers not extending forward to angle of gape. Each lateral-line scale caducous, same size as surrounding scales, bordered above and below by single scale (Fig. 10C)..... 4
- 4. Teeth on each gillraker not uniform in size, arranged in a bunch, anterior ones long, extending over next raker; posterior teeth short, needle-like (Fig. 10D). Supramaxillary free from maxillary except at posterior insertion (Fig. 10A). Upper jaw terminating slightly before to slightly behind a vertical from anterior border of eye. Nostrils placed one-fourth or more of upper jaw length anterior to posterior tip of maxillary..... **Paralepis**
 - Teeth on each gillraker very short, sub-uniform in size, arranged in oblique rows (Fig. 13D). Supramaxillary closely bound to maxillary (Fig. 13A). Upper jaw terminating almost an eye diameter before orbit. Nostrils over posterior tip of maxillary..... **Notolepis** 5
 - 5. Mandible with 3 rows of teeth, each series having approximately 35 canines (Fig. 13A). Palatine with approximately 50 short fixed teeth in single irregular row..... Subgenus **Notolepis**
 - Mandible with 2 rows of teeth, totaling approximately 25 canines (Fig. 14A). Palatine anteriorly with 3 long, widely spaced, depressible canines accompanied by short fixed teeth; posteriorly 30 or fewer fixed canines in single row..... Subgenus **Profundisudis**
 - 6. Lower jaw fairly massive, blunt, tip distinctly elevated. Nostrils distinctly before a vertical from posterior tip of maxillary (except in *Lestidium neles*). Angle of gape far before posterior tip of maxillary. Pattern of dorsum variable, but without saddle-like blotches..... 7
 - Lower jaw very slender, pointed, tip not elevated (Fig. 20A). Nostrils distinctly behind posterior tip of maxillary. Angle of gape near tip of maxillary. Dorsum not evenly pigmented; posteriorly several saddle-like blotches on dorsum, alternating with similar blotches on base of anal fin (Fig. 19)..... **Stemonosudis**
 - 7. Dorsal fin with 9–12 rays. Dorsum lightly and evenly pigmented only part way down to lateral-line (Fig. 15) except in *Lestidium pofi*, which is evenly pigmented all over. Lateral-line segments unpigmented or with a few scattered melanophores. Anterior lateral-line segments usually longer than broad. (Fig. 16C)..... **Lestidium**, 8
 - Dorsal fin with 11–14 rays (usually 13–14). Dorsum heavily pigmented with large melanophores down onto lateral-line scales (particularly posteriorly). Adults with lateral-line segments usually broader than long (Fig. 18C)..... **Macroparalepis**

- 8. No prominent markings before eye. Anal rays 26-33* 9
 Prominent round black spot covering vertical finger-like projection immediately before eye. Anal rays 33-49.....
 Subgenus **Lestrolepis**
- 9. Origin of dorsal fin more than half a head length behind a vertical of pelvic fins. Anal rays 26-28.....
 Subgenus **Lestidiops**
 Dorsal fin over or nearly over pelvic fins, origin less than one third of a head length behind pelvic base. Anal rays 28-33..... Subgenus **Lestidium**

Subfamily PARALEPIDINAE

Head and lower jaw moderately large. Pair of large nostrils on each side of snout. Anterior process of premaxillary with large circular foramen. Teeth on mandibles, if present, slender, basally round, sometimes hastate, but never serriform. Dorsal fin with 9-14 (seldom 14) rays. Pectoral fin moderately developed, not proportionately larger in younger stages. Pelvic fins with inner rays distinctly longer than outer rays. Scales, if present, never just restricted to preoperculum.

MAGNISUDIS new genus

Figs. 5, 8, 11a

Recently, Dr. Carl L. Hubbs obtained two adults of scaled paralepidids a foot long from the stomachs of marlin and the great blue shark off Lower California. In addition, the California Division of Fish and Game obtained two adults approximately 20 inches long and some smaller examples from California. Not only are these specimens the largest paralepidids known, but they represent the most generalized of the scaled barracudinas and are distinct in many important characters from all known genera.

DIAGNOSIS: Body large and massive, mod-

* Matsubara's material of "*Lestidium japonicum*" with 35 anal rays (1941: 8) is not included, as it appears to be a new species and the description is not complete enough to place it in a subgenus. Probably it belongs to the subgenus *Lestrolepis*.

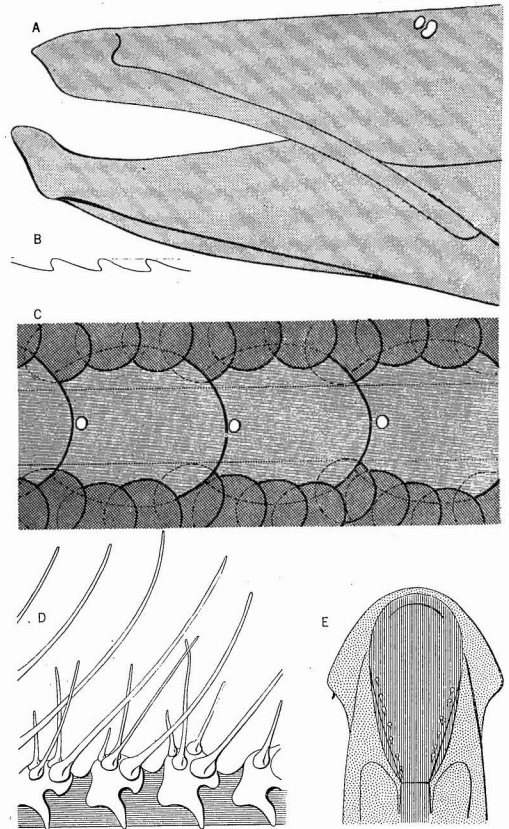


FIG. 8. Genotype of *Magnisudis* (*M. barysoma*, n. sp., paratype, 510 mm. in standard length, from off Lower California). A, Anterior part of snout; B, enlarged section of teeth on middle of premaxillary; C, anterior lateral-line scales; D, gillrakers on first arch; E, dorsal surface of tongue. (See explanation of morphological figures in text.)

erately compressed. No carinae. Head large, conical, moderately compressed. Eye larger. Pupil small, crescent or half-moon shaped. much smaller than lens. Snout massive. Nostrils well before end of maxillary. Tip of lower jaw elevated. Upper jaw terminating well before vertical from anterior border of eye. Supramaxillary long, approximately 0.33-0.5 as long as maxillary, curved and rod-shaped, free from maxillary except at posterior insertion. Teeth on lower jaw sparse or absent; if present very short; all fixed. Teeth on upper jaw very tiny, closely spaced; fixed teeth in saw-like row. Vomer toothless or with single median tooth. Teeth on palatines very short,

in single row, fixed. Tongue (glossohyal and its fleshy expansion) small and short, but projected far forward near tip of lower jaw. Gillrakers and entire branchial apparatus extending far forward into mouth. Gillrakers well developed on all 5 arches. Each gillraker with 4 long, stiff, cartilaginous, depressible filaments, longest filament 1.5 times greatest pupil diameter. Pharyngobranchial teeth developed in 2 tooth patches on each side. Gill membranes free and separate, joined far forward under vertical from nostrils. Left branchial membrane overlaps right.

Sides of head heavily scaled forward onto preorbital. Occiput covered with scales and lacking tubes or ridges. Body completely scaled. Scales small and moderately adherent, slightly pointed posteriorly and often indented anteriorly, appearing heart-shaped. Scales extending on middle of caudal base for approximately 0.25 its length. Circuli of each scale not continuous except for inner 8 ridges or so; remaining circuli run obliquely off scale. Lateral-line tube fairly small with single median pore on each segment. One row of enlarged, strongly adherent, membranous scales over the tube; each lateral-line scale bordered by 3 or more scales above and below. Body scales much smaller than lateral-line scales.

Pectoral fin with 17 rays. Anal rays 22–25. Dorsal fin origin slightly in advance of pelvic fin origin. Anus behind vertical from dorsal base. Pelvic fins very short, approximately 0.33 length of pectoral fins.

Generic TYPE and only known form, *Magnisudis barysoma* n. sp.

The name *Magnisudis* is formed from *magnus*, L.—large + *sudis*, L.—stake, pile, pike.

The above description will serve to distinguish and demonstrate the relationships of both the genus *Magnisudis* and its single species *M. barysoma*, although the full specific description will appear only in Part 2 of the present study. The holotype of *M. barysoma*, from off southern California, and the paratypes are deposited at Stanford University.

Genus PARALEPIS Cuvier

Figs. 9, 10, 11b

Paralepis Cuvier, 1817: xi, 289 (generic type by subsequent designation of Jordan and Evermann, 1917: 104, 120, *Paralepis coregonoides* Risso); Bosc, 1818: 520; Cuvier, 1829: 156; Cuvier and Valenciennes, 1829: 556; Risso, 1826: 472; Günther, 1864: 418; Goode and Bean, 1895: 118; Jordan and Evermann, 1896: 602; Regan, 1911: 127; Jordan and Evermann, 1917: 104; Jordan, 1923: 154; Parr, 1928: 34, 71; Parr, 1929: 29; Ege, 1930: 6; Parr, 1931a: 19; Parr, 1931b: 152; Whitley, 1937: 11; Maul, 1945: 4; Harry, 1951: 18.

Arctozenus Gill, 1865: 188 (generic type by original designation, *Paralepis borealis* Reinhardt); Goode and Bean, 1895: 516; Jordan and Evermann, 1896: 601; Jordan, 1919: 330; Jordan, 1923: 154; Parr, 1928: 33.

Sympropterus Cocco, 1885 (no generic type, see Jordan, 1920: 430).

Sudis (in part) Parr, 1928: 34.

Bathysudis Parr, 1928: 41 (generic type by original designation, *Paralepis speciosa* Bellotti); Ege, 1930: 53; Parr, 1931b: 153; Gregory, 1933: 207, 209; Gregory and Conrad, 1936: 33; Chapman, 1939: 524.

The author of *Paralepis* has been often given as Risso. However, Cuvier was the first to use the name in a generic sense. According to Whitley, the generic name was introduced strictly in vernacular form (*Les Paralepis* Cv.) by Cuvier, 1817, and Bosc was the first to latinize it, thus becoming the author of the genus. However, Cuvier listed *Paralepis* as a generic name (*Paralepis* C.) in the "Table Méthodique," and there appears to be no reason for not accepting Cuvier as the author of the genus (see Opinion 39 of the International Commission of Zoological Nomenclature for a similar case involving Cuvier, 1800).

DIAGNOSIS: Body compressed, moderately short and deep. Ventral carina on belly little developed. Head and eye large. Pupil round, larger than lens. Snout short and broad. Nostrils well before end of maxillary. Tip of lower

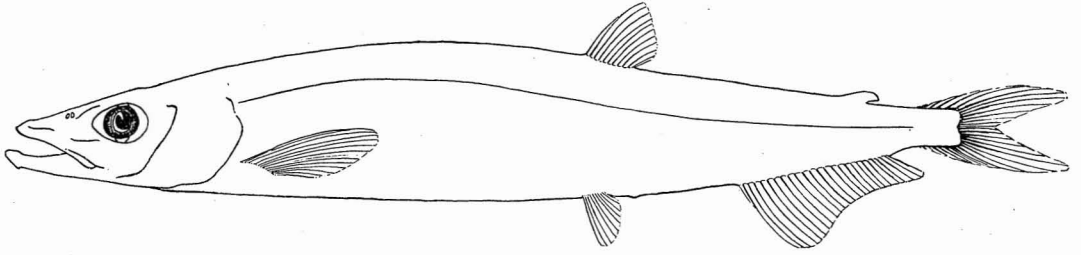


FIG. 9. Representative of *Paralepis* (*P. brevirostris* (Parr), 137 mm. in standard length, from off Madeira).

jaw strongly elevated. Upper jaw reaching to or slightly beyond vertical from anterior border of eye. Supramaxillary long, in adults almost 0.5 as long as maxillary, curved and rod-shaped, free from maxillary except at posterior insertion. Teeth on lower jaw short and weak, tending to be absent in adults. Teeth on palatines short, in 2 irregular rows anteriorly, one row depressible; posteriorly in one row of up to approximately 15 short, fixed teeth. Tongue large, moderately forward in mouth. Gillrakers developed on all 5 arches, not ex-

tending forward beyond angle of gape. Gillrakers spinous, anterior teeth on each raker long; posterior teeth very short, needle-like, in numerous rows. Longest rakers as long as pupil diameter. Pharyngobranchial teeth developed in 2 tooth patches on each side. Branchial membranes do not overlap.

Body fully scaled. Scales very deciduous, moderately pointed posteriorly, lacking any indentation on posterior margin. Circuli on scales not continuous except for inner 5 rings or so; remaining circuli run obliquely off the scales (see Fig. 11*b*, and Jensen, 1942: 23, Fig. 9). Lateral-line tube moderately large; 1.5 or 2 scale rows lying over tube. (In the basic pore pattern for this genus the upper scale row over the lateral-line is pierced by the upper pore, and the scale row over the middle of the tube is penetrated by the median and lower pores. There is often reduction in the number of pores piercing the scales.) Body scales same size as lateral-line scales. Pectoral fin rays 14-17. Anal rays 21-26. Vertebrae 67-74.

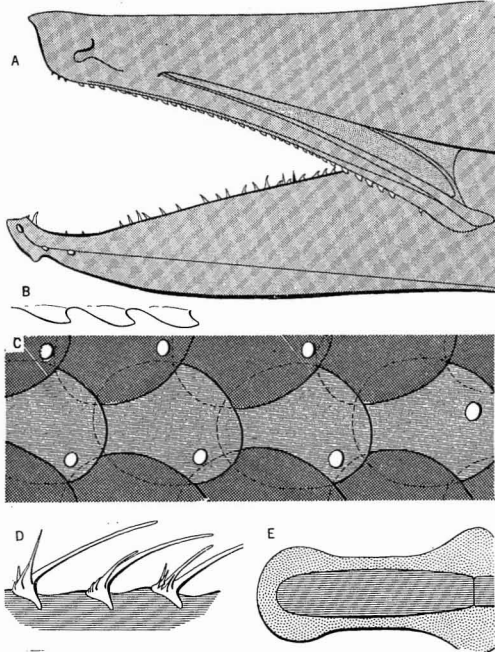


FIG. 10. Genotype of *Paralepis* (*P. coregonoides* Risso, from off Funchal, Madeira, 145 mm. in standard length). A, Anterior part of snout; B, enlarged section of teeth on middle of premaxillary; C, anterior lateral-line scales; D, gillrakers on first arch; E, dorsal surface of tongue. See explanation of morphological figures in text.

Disregarding the inadequately known *Paralepis elongata* (Brauer), the genus *Paralepis* could be divided into two subgenera by segregating the generic type, *P. coregonoides*, in the subgenus *Paralepis* and recognizing the remainder of the species in the subgenus *Bathysudis*. I have not done this because these forms are quite similar and closely related. *Paralepis elongata* is distinct in several basic characters from the remaining species of this genus. If it belongs in *Paralepis* it could be readily placed in a new subgenus.

Species I have examined that are undoubted

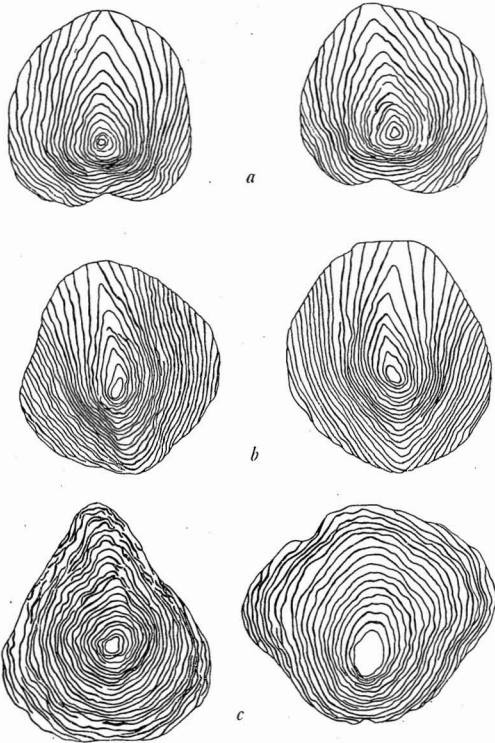


FIG. 11. Scales taken from behind and above the pectoral fins of three genera: a, *Magnisudis* (*M. barysoma*, n. sp.); b, *Paralepis* (*P. coregonoides* Risso); c, *Notolepis* (*N. coatsi* Dollo). (Illustrations prepared from direct projections.)

members of the genus *Paralepis* are: *P. brevis* Zugmayer, *P. brevisrostris* (Parr), *P. coregonoides* (Risso), and *P. speciosa* Bellotti. I believe that *P. danae* Ege (1933) and perhaps *P. elongata* (Brauer) also belong here. *P. bronsoni* (Parr) appears to be a synonym of *P. brevisrostris* (Parr) (Harry, 1951: 19).

Genus NOTOLEPIS Dollo

Figs. 11c, 12, 13, 14

?*Prymnothonus* Richardson, 1845: 51 (generic type by monotypy, *Prymnothonus hookeri* Richardson); Günther, 1870: 175; Günther,

1889: 39; Dollo, 1904: 8; Dollo, 1908: 35; Fage, 1910: 16; Regan, 1911: 127; Regan, 1913: 233; Regan, 1914: 38; Regan, 1916: 125; Jordan, 1920: 527; Jordan, 1923: 154; Parr, 1928: 33; Norman, 1937: 83.
Notolepis Dollo, 1908: 58 (generic type by monotypy, *Notolepis coatsi* Dollo); Regan, 1911: 127; Regan, 1913: 233; Regan, 1914: 38; Regan, 1916: 125; Jordan, 1920: 527; Jordan, 1923: 154; Parr, 1928: 33; Norman, 1937: 83; Harry, 1951: 26.

Paralepis (in part) Ege, 1930; Maul, 1945: 4.
 ?*Prymnothonooides* Whitley and Phillips, 1939: 228 (generic type by original designation, *Prymnothonooides regani* Whitley and Phillips).

Although this genus was very poorly described by Dollo and was based on irrelevant and insignificant characters, it was erected for one of the most distinctive scaled forms of barracudinas. *Notolepis* is resurrected on entirely different characters of both postlarvae and adults.

DIAGNOSIS: Body compressed and elongate. Ventral carina on belly moderately developed. Head and snout long and sharply pointed. Nostrils behind or over posterior tip of maxillary. Eye moderately large. Pupil round or elliptical, larger than lens. Tip of lower jaw moderately elevated. Upper jaw terminating approximately one orbital diameter before eye. Supramaxillary short, splinter-like, closely bound to maxillary. Teeth on lower jaw well developed, in 2 or 3 rows. Teeth on palatines short, in 1 or 2 rows anteriorly; posteriorly in one row of 30–50 teeth. Tongue narrow, well forward in mouth. Gillrakers not extending forward beyond angle of gape; gillrakers spinous, entirely reduced to many rows of short fixed needle-like teeth. Longest rakers much shorter than pupil diameter. Pharyngobran-

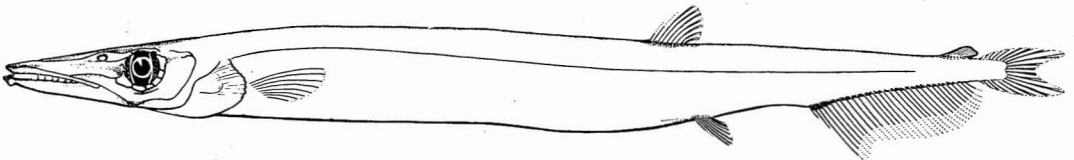


FIG. 12. Representative of *Notolepis* (*N. coruscans* Jordan and Gilbert, from the Pacific off Washington, 159 mm. in standard length).

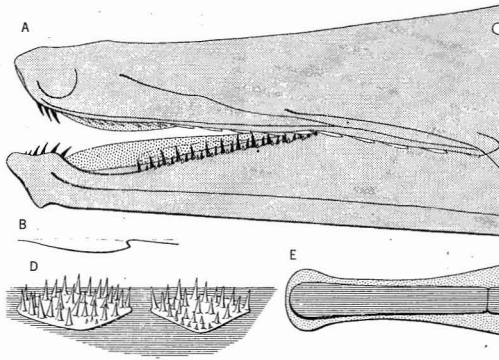


FIG. 13. Genotype of *Notolepis* (*N. coatsi* Dollo, from the Antarctic, 302 mm. in standard length). A, Anterior part of snout; B, enlarged section of teeth on middle of premaxillary; D, gillrakers on first arch; E, dorsal surface of tongue. (See explanation of morphological figures in text.)

chial teeth developed in 2 patches on each side. Branchial membranes do not overlap.

Body fully scaled. Scales very deciduous, rounded or pointed posteriorly, occasionally with indentation on anterior margin. The circuli are continuous for inner 8 rings or more, outermost rings run obliquely off the scales (see Fig. 11c, and Jensen, 1942: 22, Fig. 6). Lateral-line tube large, with at least 1 pore above, medially, and below on each segment; tube covered by $1\frac{1}{2}$ rows of scales. Upper scale row sometimes notched to receive upper pore, as shown in Fig. 14c, or may be pierced by pore series as in *Paralepis*. Lower scale usually penetrated by median and lower pores. Body scales same size as lateral-line scales. Pectoral fin with 11–13 rays. Anal rays 27–34. Vertebrae 78–95.

All three known species of the genus *Notolepis* have been examined. These can be divided into two subgenera as *N. coatsi* Dollo differs markedly from *N. rissoi* (Bonaparte) and *N. coruscans* (Jordan and Gilbert) in several characters.

Subgenus NOTOLEPIS Dollo

Fig. 11c, 13

DIAGNOSIS: Mandible with 3 series of teeth, each row with approximately 35 canines. Palatine with approximately 50 short fixed teeth in single row. Each gillraker on ceratobran-

chial of first arch with approximately 30 short, fixed, needle-like teeth. Apparently, each lateral-line segment with large median-pore at posterior margin and tiny pore above and below near anterior margin. Anal rays 27–29.

This subgenus is monotypic, containing only *Notolepis coatsi* from the Antarctic.

PROFUNDISUDIS new subgenus

Figs. 12, 14

Arctozenus (in part) Jordan and Evermann, 1896: 601.

DIAGNOSIS: Mandible with 2 series of teeth, totaling approximately 25 canines. Palatine anteriorly with long widely spaced depressible canines accompanied by short fixed teeth, posteriorly with 30 or fewer short fixed canines in single row. Each gillraker on ceratobranchial of first arch with approximately 15 short fixed spine-like teeth. Each lateral-line segment with 1 large pore above and another below at posterior margin, with pair of minute

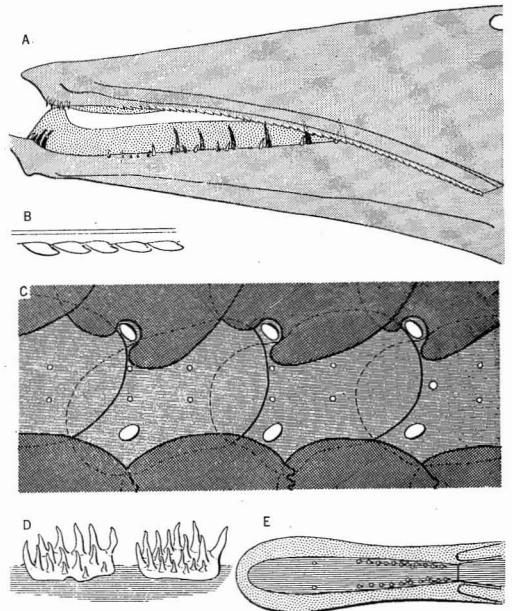


FIG. 14. Representative of the genus *Notolepis* and the new subgenus *Profundisudis* (*N. coruscans* Jordan and Gilbert), from the Pacific off Washington, 159 mm. in standard length). A, Anterior part of snout; B, enlarged section of teeth on middle of premaxillary; C, anterior lateral-line scales; D, gillrakers on first arch; E, dorsal surface of tongue. (See explanation of morphological figures in text.)

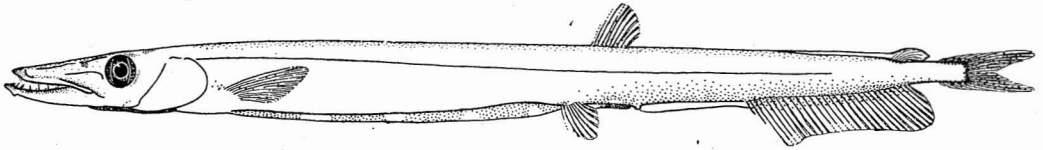


FIG. 15. Representative of the genus *Lestidium* (*L. pacificum* (Parr), holotype, from the Pacific off Mexico, 164 mm. in standard length). This species is closely related to the genotype.

pores between; another pair of minute pores near anterior margin of each section. Anal rays 30–34.

Subgeneric TYPE, *Arctozenus coruscans* Jordan and Gilbert, from the North Pacific. This subgenus also contains *N. rissoi* from the North Atlantic.

The name is formed from *profundus*, L.—of the depths + *sudis*, L.—stake, pile, pike.

Genus LESTIDIUM Gilbert

Figs. 1, 2, 3, 6, 15, 16

Paralepis (in part) Cuvier, 1817: xi, 289; Ege, 1930; Maul, 1945: 4.

Lestidium Gilbert, 1905: 607 (generic type by original designation, *Lestidium nudum* Gilbert); Regan, 1911: 127; Hubbs, 1916: 154; Jordan, 1920: 513; Jordan, 1923: 154; Borodin, 1928: 10; Parr, 1928: 33; Parr, 1929: 29; Parr, 1931a: 19; Parr, 1931b: 153; Gregory, 1933: 209; Gregory and Conrad, 1936: 33; Ege, 1933: 229; Norman, 1937: 83; Chapman, 1939: 524; Harry, 1951: 26.

Lestidiops Hubbs, 1916: 154 (generic type by original designation, *Lestidiops sphyraenopsis* Hubbs); Jordan, 1920: 559; Parr, 1928: 33; Parr, 1931a: 19; Parr, 1931b: 153.

This genus is the largest in the family and also the most abundant. Generally it has been taken wherever the family has been recorded. It is best known in the northern hemisphere where the majority of the species have been found. It will probably be found to be abundant also in the Central Pacific, particularly from the region of the Philippine Islands northward to Japan. *Lestidium* is most closely related to the genera *Macroparalepis* and *Stemonosudis* and appears to be the least specialized of these three groups.

Adults are attracted by light at night and can be most readily taken by this means. In

fact, Dr. Earl S. Herald and Dr. A. W. Herre have informed me that large examples of *Lestidium philippinum* are found in the fish markets of the Philippine Islands and are taken by the native fishermen with lights.

Gilbert (1905) described *Lestidium* as having "a photophore directed downward and backward at lower orbital margin". This was in error; no paralepidid has any light organ.

DIAGNOSIS: Body compressed, elongate. Ventral carina on belly well developed. Head and snout long, pointed. Eye large. Pupil oval or round, larger than lens. Nostrils before or over posterior tip of maxillary. Tip of lower jaw strongly elevated. Upper jaw terminating at or well before vertical from anterior margin of orbit. Angle of gape well before tip of maxillary. Supramaxillary short, splinter-like, closely bound to maxillary. Teeth on lower jaw long and well developed, with antrorse and retrorse canines. Vomer sometimes with few teeth in young. Teeth on palatines long, in 2 rows anteriorly, 1 row depressible; posteriorly with approximately 5–15 fixed teeth in 1 row. Tongue large, moderately forward in mouth. Gillrakers not extending beyond angle of gape; spinous, with 1 row of short fixed teeth on small base. Pharyngobranchial teeth developed in 1 patch only on each side.

Body and head naked, lacking scales. Lateral-line tube large. Membrane over lateral-line modified into scale-like structures which are highly variable between species. Each lateral-line segment variously pierced above and below by 1 to 5 pores but basic pore pattern of 2 pores above and below. Some forms also with median pore. Greatest height of each lateral-line segment variously at front, middle, and hindmost point. Pectoral fin with 11–13 rays. Dorsal rays 9–12. Anal rays 27–49.

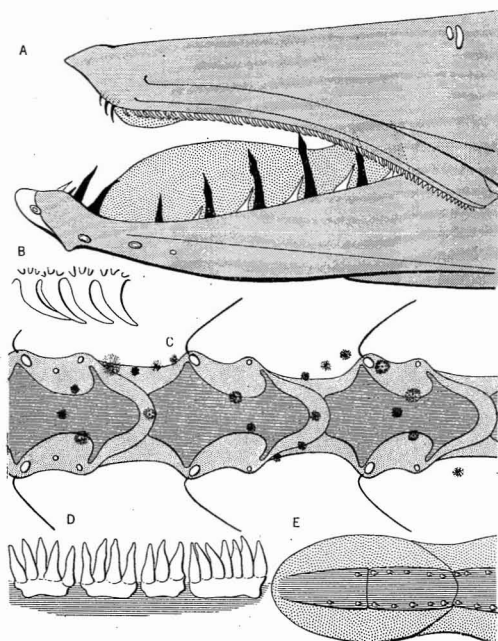


FIG. 16. Representative of the genus *Lestidium* (*L. pacificum* (Parr), holotype, from the Pacific off Mexico, 164 mm. in standard length). A, Anterior part of snout; B, enlarged section of teeth on middle of premaxillary; C, anterior lateral-line segments; D, gillrakers on first arch; E, dorsal surface of tongue. (See explanation of morphological figures in text.)

Vertebrae 77-94, so far as known.

As previously stated, the genus *Lestidium* can be split into three distinct evolutionary lines that may be designated as subgenera.

Subgenus LESTIDIOPS Hubbs

DIAGNOSIS: Head massive. Snout deep and blunt. Tip of lower jaw with 3 vertical non-ossified ridges on symphysis, but lacking any prolongations. Eye large, 4.2-5.7 into head. No distinct markings before eye. Dorsal fin behind pelvic fins; distance between dorsal and pelvic fins more than 0.5 length of head. Anal rays 27-28. Each lateral-line segment with 1 to 5 pores (generally 1 or 2) above and below.

This subgenus contains *L. sphyraenopsis* (Hubbs), *L. thunnorum* n. sp., and *L. affine* Ege. All three species have been examined. Subgeneric TYPE, *Lestidiops sphyraenopsis* Hubbs.

Subgenus LESTIDIUM Gilbert

DIAGNOSIS: Head slender. Snout moderately pointed, not deep. Tip of lower jaw with or without nonossified ridges or prolongations. Eye large. No distinct markings before eye. Dorsal fin near or over pelvic fins; distance between dorsal and pelvic fins less than 0.33 length of head. Anal rays 28-33. Each lateral-line segment with 3-5 pores above and below.

Among the species that belong in this subgenus I have examined *L. nudum* Gilbert, *L. pseudosphyraenoides* (Ege), *L. neles* n. sp., *L. pofi* n. sp., *L. prolixum* n. sp., *L. pacificum* (Parr). Other species that apparently belong here: *L. proximum* (Ege), *L. sphyraenoides* (Risso), *L. simile* (Ege), *L. luetkeni* (Ege), *L. mirabile* (Ege), *L. atlanticum* Borodin, *L. iayakari* (Boulenger).

Subgeneric TYPE, *Lestidium nudum* Gilbert.

LESTROLEPIS new subgenus

DIAGNOSIS: Head slender. Snout pointed, not deep. Tip of lower jaw with prominent nonossified prolongation. Eye relatively small, 6.3-7.5 into head. Prominent round black spot immediately before eye. Each lateral-line segment with 3-5 pores above and below. Dorsal fin behind pelvic fins; distance between dorsal and pelvic fins less than 2.5 times into head. Anal rays 35-49.

Subgeneric TYPE, *Paralepis philippinus* Fowler. This subgenus probably also contains *L. japonicum* Tanaka, *L. intermedium* (Poey), and *L. bellottii* (Ege), but only the subgeneric types, *L. vanderbilti* (Fowler), and *L. atrox* n. sp. have been examined.

The name is formed from *lestro*, Gr.—pirate + *lepis*, Gr.—scale.

Genus MACROPARALEPIS Ege

Figs. 7, 17, 18

Macroparalepis Ege, 1933: 229 (generic type not given or subsequently designated; here designated as *Macroparalepis affine* Ege); Maul, 1945: 26; Harry, 1951: 29; Maul, 1952: 51.

This genus is here restricted to group I of *Macroparalepis* as delimited by Ege. Group

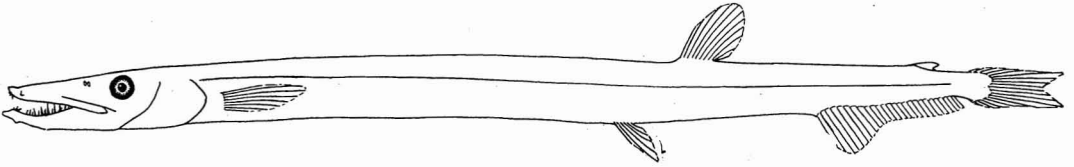


FIG. 17. Genotype of *Macroparalepis* (*M. affine* Ege, from off Madeira, 129 mm. in standard length).

II of Ege's *Macroparalepis* is placed in another genus, *Stemonosudis*.

DIAGNOSIS: Body compressed and elongate. Ventral carina on belly well developed. Head and snout long and pointed. Nostrils before tip of maxillary. Tip of lower jaw strongly elevated. Upper jaw terminating slightly before vertical from anterior margin of orbit. Angle of gape well before tip of maxillary. Supramaxillary short, splinter-like, closely bound to maxillary. Teeth on lower jaw long and well developed, in 2 rows. Teeth on upper jaw well developed antrorse and retrorse canines. Vomer toothless. Teeth on palatines long, in 2 series anteriorly, 1 row depressible;

few short teeth in single row posteriorly. Tongue large, moderately forward in mouth. Gillrakers not extending forward beyond anterior border of eye or angle of gape. Gillrakers spinous, with 1 row of short fixed teeth on small base. Pharyngobranchial teeth developed in 1 patch on each side.

Body and head lacking scales. Lateral-line tube large. Membrane over lateral-line modified into large scale-like structures, pierced above and below by 2 pores on each segment. Lateral-line segments partly ossified in double concave form as in *Lestidium*. Greatest height of each lateral-line segment variously at front or hindmost point. Pectoral fin with 10–11 rays. Dorsal rays 11–14. Anal rays 24–28.

I have examined the following species of *Macroparalepis*: *M. danae* Ege, *M. brevis* Ege, and *M. affine* Ege. The genus also contains *Macroparalepis egei* Maul. Generic type *Macroparalepis affine* Ege.

Genus *STEMONOSUDIS* Harry

Figs. 19, 20

Macroparalepis (in part) Ege, 1933: 229. *Stemonosudis* Harry, 1951: 32 (generic type by original designation *Macroparalepis intermedia* Ege).

DIAGNOSIS: Body slightly compressed and very elongate. Ventral carina on belly moderately developed. Head and snout long and pointed. Nostrils behind posterior tip of maxillary in *Stemonosudis intermedia*. (Dr. Ege examined the types of *Stemonosudis elongata*, *S. gracile*, and *S. intermedia* [his other species of this genus are represented by postlarvae only] and finds them also with the nostrils behind posterior tip of maxillary.) Tip of lower jaw not elevated or only slightly so. Upper jaw terminating approximately 1 orbital diameter

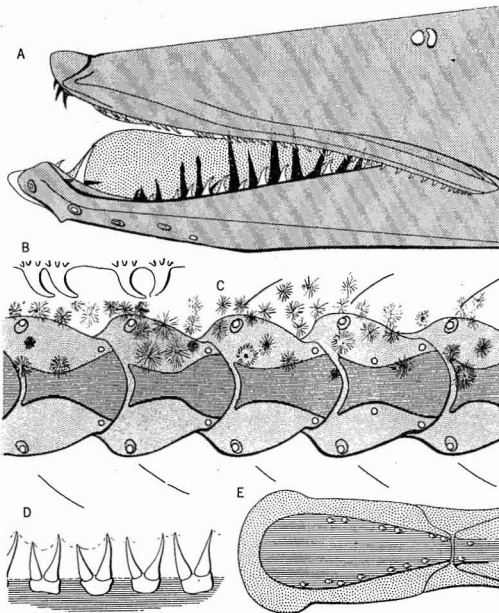


FIG. 18. Genotype of *Macroparalepis* (*M. affine* Ege, from off Madeira, 129 mm. in standard length). A, Anterior part of snout; B, enlarged section of teeth on middle of premaxillary; C, anterior lateral-line segments; D, gillrakers on first arch; E, dorsal surface of tongue. (See explanation of morphological figures in text.)

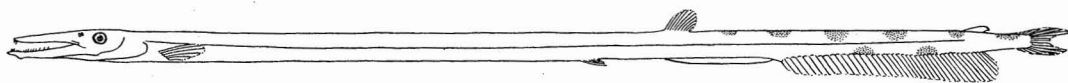


FIG. 19. Genotype of *Stemonosudis* (*S. intermedia* (Ege), from off Bermuda, 125 mm, in standard length).

before anterior margin of eye. Angle of gape near tip of maxillary. Supramaxillary short, thread-like, closely bound to maxillary. Teeth on upper jaw well-developed antrorse and retrorse canines. Vomer toothless. Teeth on palatines short, in 2 rows anteriorly, 1 row depressible; posteriorly few short teeth in single row. Tongue very small, far back in mouth, its anterior tip somewhat near angle of gape. Gillrakers and pharyngobranchial teeth completely undeveloped on material examined. (Dr. Ege informs me that the types of *Stemonosudis elongata*, *S. gracile*, and *S. intermedia* have "gillrakers present on the lower part of the first gill arch, although very small, their length equal to about a fourth of the breadth of the bone of the gill arch.")

Body and head scaleless. Lateral-line tube very large. Membrane over lateral-line tube

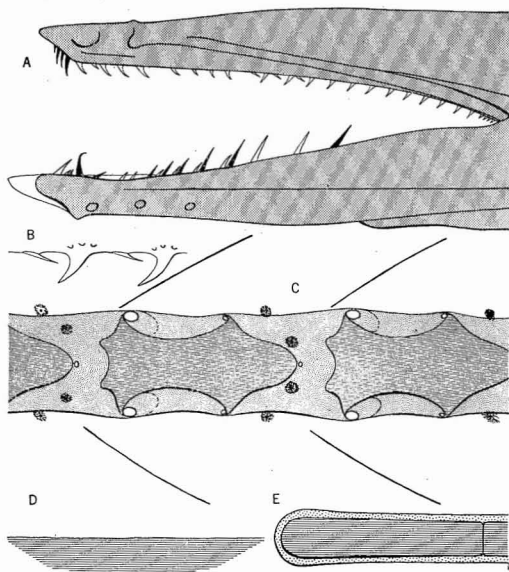


FIG. 20. Genotype of *Stemonosudis* (*S. intermedia* (Ege), from off Bermuda, 125 mm, in standard length). A, Anterior part of snout; B, enlarged section of teeth on middle of premaxillary; C, anterior lateral-line segments; D, toothless first gill arch; E, dorsal surface of tongue. (See explanation of morphological figures in text.)

modified into large scale-like structures pierced above and below by 2 pores on each segment. Greatest height of each lateral-line segment variously at front or hindmost point. Pectoral fin with 10–13 rays. Dorsal rays 9–11. Anal rays 37–50.

Generic TYPE *Stemonosudis intermedia* (Ege). It is presumed that *S. macrura* (Ege), *S. elegans* (Ege), *S. elongata* (Ege), and *S. gracile* (Ege) belong in this genus, although I have been unable to examine any of them. *S. intermedia* is from the West Indies; all other members of the genus are East Indian. Further investigation might show that the East and West Indian forms belong in separate genera or subgenera.

Subfamily SUDINAE

Head and lower jaw very large and massive. Nostrils of equal size in young. Adults with posterior nostril normal, anterior nostril reduced to tiny pore in anterior rim of other nostril. Anterior process of premaxillary without foramen. Teeth on mandible very large, triangular in shape and strongly compressed; edges finely serrate, not accompanied by smaller teeth. Dorsal fin with 14–15 rays. Pelvic fins with outer rays distinctly longer than inner rays. Pectoral fin very long and large, proportionately greatly enlarged in post-larvae and juveniles. Body naked. Head scaled in 2 series on preoperculum.

This group contains a single genus and species, *Sudis hyalina*, known from the Mediterranean and Madeira.

Genus SUDIS Rafinesque Schmaltz

Figs. 21, 22

Sudis Rafinesque Schmaltz, 1810: 60 (generic type by monotypy *Sudis hyalina* Rafinesque Schmaltz); Bonaparte, 1846: 35; Canestrini, 1877: 127; Ege, 1930: 6; Maul, 1945: 33; Harry, 1951: 33.

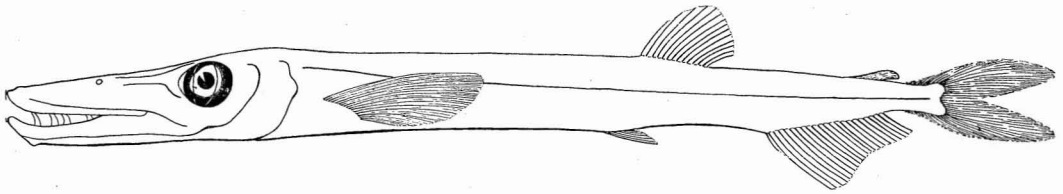


FIG. 21. Genotype of *Sudis* (*S. hyalina* Rafinesque, from off Madeira, 315 mm. in standard length).

Paralepis (in part) Cocco, 1839: 49; Carus, 1893: 566; Sanzo, 1917: 1.

Sudis (in part) Parr, 1928: 34.

DIAGNOSIS: Body compressed and elongate. Ventral carina on belly moderately developed. Head large, strongly compressed. Snout very large and deep. No nonossified prolongations on tip of lower jaw. Nostrils situated almost 0.33 length of maxillary before posterior tip of maxillary. Eye very large. Pupil vertically oval, much larger than lens. Supramaxillary large, more than 0.5 as long as maxillary, splinter-like, closely bound to maxillary. Teeth on lower jaw very large, in 1 or 2 series, of triangular shape and strongly compressed; edges minutely serrate. Few mandibular teeth depressible. Teeth on premaxillary minute, serrate, all fixed. Teeth on palatines moderately reduced, all fixed; anterior teeth in 2 rows with long teeth sometimes accompanied by short ones; anterior double series followed by single series of short or minute teeth. Tongue large, moderately far forward in mouth. Gill-rakers tiny, spinous; each raker composed of 2-4 short teeth in single row; rakers not extending forward beyond angle of gape. Pharyngobranchial teeth well developed in single patch on each side.

True scales developed on preoperculum in 2 series. Otherwise body and head scaleless. The lateral-line tube covered by single row of distinct, overlapping, scale-like segments lacking all trace of circuli or annuli. Each segment pierced by 5-8 pores above and below near upper and lower margins. Dorsal fin with 14-16 rays. Vertebrae 59, as far as known.

FOSSIL HISTORY

The order Iniomi first appeared in the Cretaceous, in which the recent families Aulopo-

dididae, Chlorophthalmidae, Myctophidae, and probably Bathypteroidae are clearly evident. The suborder Alepisauroidae (= Paralepidoidea Gill, 1893) appears to be represented in the Cretaceous by the family Ichthyotringidae (new family name to replace Rhinellidae Jordan, 1905, because the monotypic genus *Rhinellus* Agassiz, 1844, is preoccupied; *Ichthyotringa* Cope, 1878, is the next name available), and perhaps the Dercetidae also belong here. *Ichthyotringa* resembles a *Sudis* with an especially prolonged snout. The exact extent of relationships are obscure, however, because the head bones are inadequately known. The Dercetidae, containing perhaps six genera (see the list by Romer, 1945: 584), look remark-

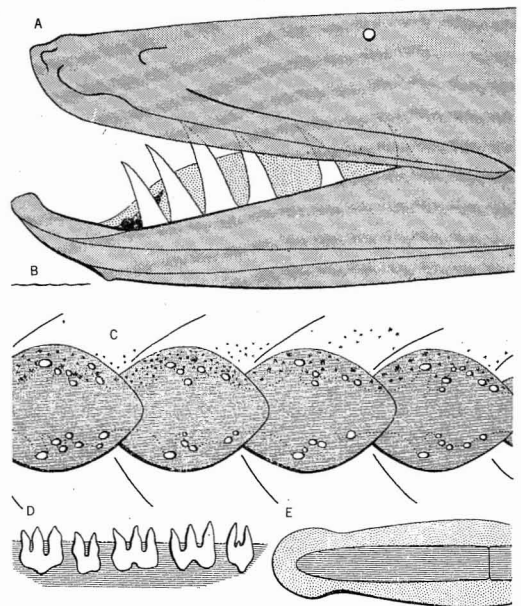


FIG. 22. Genotype of *Sudis* (*S. hyalina* Rafinesque, from off Madeira, 315 mm. in standard length). A, anterior part of snout; B, enlarged section of teeth on middle of premaxillary; C, anterior lateral-line segments; D, gillrakers on first arch; E, dorsal surface of tongue. (See explanation of morphological figures in text.)

ably similar to an elongate paralepidid or anotopterid, but again the head bones are inadequately known, and the resemblance may be only superficial.

The first definite representative of a recent alepisauroid family appears in the Eocene on the basis of the paralepidid genus *Holosteus* Agassiz. *Scopeloides* Wettstein from the Oligocene might be a scopelarchid. A fossil *Alepisaurus* has been discovered in the Miocene of Europe. The genus *Apateodus* Woodward of the Cretaceous family Enchodontidae has a dentition similar to the Alepisauridae, and several authors have suggested a close relationship.

The Paralepididae are the best known iniformous group found in the Tertiary, comprising six fossil genera (*Paralepis* Cuvier, *Trosulus* Jordan, *Lestichthys* Jordan, *Drimys* Jordan, *Holosteus* Agassiz, and *Parascopelus* Sauvage) and approximately 10 species. The references to fossil members of the genus *Sudis* belong with *Paralepis*. The paralepidids from the Miocene diatom beds at Lompoc, California, and *Parascopelus* from the Miocene of Europe appear to provide a complete intergradation between this family and the Chlorophthalmidae. Thus it would appear that the suborder Alepisauroidea had not become fully differentiated until relatively recently. This is corroborated by the degree of relationships of the recent forms. The family Paralepididae is distinctly the most generalized group in the suborder Alepisauroidea, and particularly the genus *Magnisudis* shows a revealing number of similarities to chlorophthalmids. The other alepisauroid families (Alepisauridae, Anotopteridae, Scopelarchidae, Evermannellidae, Omosudidae) are much more specialized and probably were well differentiated by the beginning of the Tertiary. The Dercetidae resemble Anotopteridae in which the size of the dorsal fin is between that of the Paralepididae and the Alepisauridae. If there is a relationship here, it indicates that these groups were highly evolved even by the Upper Cretaceous.

Despite the fact that the Miocene fossils seem to show no distinction between the Chlorophthalmidae and Paralepididae, the Eocene, Pliocene, and certain Miocene forms are so similar to recent paralepidid genera that only minor differences are evident in the osteology.

Among recent groups 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. In turn, the Anotopteridae are very closely related to the highly specialized Alepisauridae. There are secondary modifications of the suspensorium that separate the Anotopteridae from the Alepisauridae, but the cranial osteology and dentition is very similar, the skin has exactly the same pore system in the adults of both families, which is found only in the adults of these two families in the order, and the proportions are closely similar. Therefore, these three families appear to represent one line of evolution arising from a chlorophthalmid-like ancestor, with the Alepisauridae representing the most highly specialized end-point. On the basis of their postlarval development and morphology the Scopelarchidae, Evermannellidae, and Omosudidae appear to have branched off from the alepisaurid line of evolution in various directions and each represents its own unique end-point of evolution. Among these three families the Scopelarchidae are closest to the Chlorophthalmidae, and the Omosudidae are most closely related to the Alepisauridae.

The Alepisauroidea seems to be a valid suborder despite the fact that at least one of its families (Paralepididae) may have become separated from the Chlorophthalmidae of the suborder Myctophoidae (= Aulopodoidea Gill, 1893) as late as the Miocene or Pliocene. In fact, future research may very well reveal intermediate recent forms between the chlorophthalmid line and the Paralepididae. If this

happens, the retention of the Alepisauroida should be still justifiable because the greatest phylogenetic break in this suborder is between the Paralepididae and the other families.

The earliest known paralepidid, *Holosteus esocinus* Agassiz (1844: 85, Pl. 43, Fig. 5) appears to be very close to the recent genus *Lestidium* and may actually belong in it. The dorsal fin seems to have been pushed back out of position during fossilization, and it appears from the illustration that it should be approximately equidistant between verticals from the ventral and anal fins.

The most primitive fossil paralepidid seems to be *Drimys defensor* Jordan (1925: 14, Pl. 4b), the clearest intermediate stage yet found between the Chlorophthalmidae and Paralepididae. Unfortunately the only known Miocene fossil is badly crushed. There are 45 vertebrae, a number considerably lower than known for any recent paralepidid. The presence of large, coarsely striated scales is more like a chlorophthalmid, whereas the description of the dentition of the upper jaw is very much like that of a paralepidid.

Trossulus exoletus Jordan (1921: 250, Pls. 8c, 28a) is another Miocene fossil from the Lompoc diatom beds. In general appearance it seems to be a generalized paralepidid with a foreshortened body. It shows closest similarities to *Magnisudis* but actually may be an intermediate form between a chlorophthalmid and a paralepidid. The eye is small, the last dorsal rays are over the anterior anal rays. Of particular significance is the fact that the maxillary is narrow and the premaxillary forms the margin of the upper jaw. There are 50 vertebrae, a number most closely approaching the genera *Paralepis* and *Magnisudis*.

The fossil *Lestichthys porteousi* Jordan (1921: 250, Pls. 10b and 22b) from the Lompoc Miocene diatom beds appears to be very close to the genus *Lestidium*. The vertebral count of 86, proportions, and osteological notes seem to place it in the tribe Lestidiini of the subfamily Paralepidinae.

One of the best known fossils is *Paralepis albyi* Sauvage (= *Paralepis sphaekodes*) from the Pliocene. This form is very ably reviewed by Arambourg (1927), who cites the scattered literature and gives sketches of the jaw bones and scapula.

The genus *Parascopelus* Sauvage appears to belong in the Paralepididae near the genus *Sudis*, but the position of the ventral fins far forward is unique in the family.

SUMMARY

The family Paralepididae comprises seven genera (*Paralepis*, *Notolepis*, *Magnisudis*, *Lestidium*, *Macroparalepis*, *Stemonosudis*, *Sudis*) and 48 living species. It is differentiated from all other families of the order Iniomi by a characteristic toothless emargination in the upper jaw below the end of the snout, by a large foramen through the premaxillary in all genera except *Sudis*, by the rictus being well before the eye, and by the position of the dorsal fin which is near the middle of the body length far behind the pectoral fins. The Paralepididae are regarded as most closely related to the Anotopteridae and Alepisauridae of the suborder Alepisauroida.

The Paralepididae are divided into two subfamilies—the Paralepidinae and Sudinae. The former is characterized by the presence of a foramen in the anterior process of the premaxillary, by slender smooth teeth, by the inner pelvic rays being longer than the outer, and by the pectoral fins remaining small throughout ontogeny. In the Sudinae the premaxillary lacks a foramen, the mandibular teeth are broad and serrate, the outer pelvic rays are longer than the inner rays, and the pectoral fins are greatly prolonged during early postembryonic stages. The subfamily Sudinae is monotypic, containing the genus *Sudis* which is known from the Mediterranean and Madeira.

Evolution in the family generally appears to have progressed by losses of pre-existing characters. This is particularly evident with such structures as squamation, gillteeth, pig-

mentation, and massiveness of form. In this regard the subfamily Paralepidinae has two basic divisions. The members of one division, comprising the genera *Paralepis*, *Magnisudis* (described herein as new), and *Notolepis*, are scaled as adults and have numerous teeth in two or more rows on each gillraker; the genera of the other division (*Lestidium*, *Macroparalepis*, and *Stemonosudis*) are completely scaleless and have few teeth in one row on each gillraker. This classification cuts across the system currently recognized in the literature.

The new genus *Magnisudis* appears to be the most primitive in the family and shows the closest link back to the Chlorophthalmidae and Aulopidae, the most generalized families in the order Iniomi. The genus *Notolepis* has many unique characteristics and represents the end point in scaled genera evolution, approaching more closely the scaleless genera than do either *Paralepis* or *Magnisudis*. The genus *Lestidium* appears to be the most generalized of the scaleless genera and clearly approaches the scaled genera more closely than either *Macroparalepis* or *Stemonosudis*.

The fishes of the family Paralepididae are world-wide in distribution, except for the Arctic. The genus *Notolepis* is bipolar (pan-temperate) in distribution. One of its subgenera (*Notolepis*) is known from the Antarctic and the other (*Profundisudis*) occurs in the North Pacific and North Atlantic. Most of the other genera are also wide-ranging.

The suborder Alepisauroidea appears to be represented in the Cretaceous by the family Ichthyotringidae (new name to replace Rhinellidae Jordan, 1905) and perhaps by the Dercetidae. Six fossil genera (*Paralepis* Cuvier, *Trossulus* Jordan, *Lesticthys* Jordan, *Drimys* Jordan, *Holosteus* Agassiz, and *Parascopelus* Sauvage) and approximately 10 species of the Paralepididae are known from the Tertiary. Even as recently as the Miocene there seems to be intergradation between the Chlorophthalmidae and Paralepididae, and as a result the Alepisauroidea became fully differentiated

from the suborder Myctophoidea relatively recently.

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