1. INTRODUCTION

The purposes of this catalogue are to provide a convenient means for the identification of ophidiiform genera, and species to the extent possible, which are most likely to be encountered by fishery workers, ecologists and other marine biologists, to summarize fisheries, distributional and other biological information, to guide users to the most relevant literature, and to illustrate the wide diversity of this important group of fishes. Many ophidiiform species are abundant in nature and play a significant role in the ecology of their habitats, but their identification often presents such great difficulty that they are referred to family or genus level only.

This catalogue includes keys to and accounts of all genera of ophidiiform fishes as well as lists of referred species and keys to most of them. Because many ophidiiforms are fishes of the deep sea, are rare in collections and have a relatively small and often imprecise literature, keys to species of all genera are not possible.

Much of the information here included has been selectively compiled from the literature. Taxonomic descriptions have been verified to the extent possible, using both preserved museum and freshly caught specimens. This catalogue also constitutes an updating and enlargement of Cohen and Nielsen (1978). It does not purport to present a definitive phyletic classification of the order.

1.1 General Remarks on the Order Ophidiiformes

A hierarchical classification that differed in several respects from then current usage was presented by Cohen and Nielsen (1978). They wrote that the purpose of their classification was chiefly to distinguish genera from each other and that it was not intended as a phylogeny. Although the relationships of various taxa were suggested, the problem of aligning taxa on the basis of synapomorphies (the possession of shared special characters) received little explicit attention.

Although most of the research on ophidiiform fishes over the past 2 decades has been concerned with distinguishing species and other taxa from each other, several ichthyologists have attempted to discover a classification based on phyletic relationships for all or parts of the order. The order Ophidiiformes was identified by Cohen and Nielsen (1978) using a combination of characters. One or more specialized characters shared by all presumed ophidiiforms have yet to be discovered.

In a search for uniquely ophidiiform characters Rosen (1985) implied that the order is not monophyletic because of marked differences between, and absence of specialized similarities among, the 2 suborders: Ophidioidei and Bythitoidei. Patterson and Rosen (1989) placed the 2 groups as adjacent but separate clades or evolutionary lines. A survey of 36 genera (out of about 93) for a suite of osteological, myological, and cranial nerve characters failed to provide Howes (1992) with data that would establish the order as monophyletic. For present purposes, due to lack of anything better, we use the following definition of the order:

1. Pelvic fins with 1 or 2 soft rays in each or fin completely absent (in some species a basal spine-like splint may be present).
2. Pelvic fins inserted at about the level of the preopercle or farther anteriorly.
3. Pelvic fins bases close together (in all but ***Tauredophidium***).
4. Dorsal and anal fins with long bases, extending to and often joined with the caudal fin.
5. Fin rays soft (except as noted above in no. 1).
6. Dorsal- and anal-fin pterygiophores more numerous than adjacent vertebrae.
7. Nostrils paired on each side of the head.

Our presently used classification of the order Ophidiiformes is shown in Fig. 1.

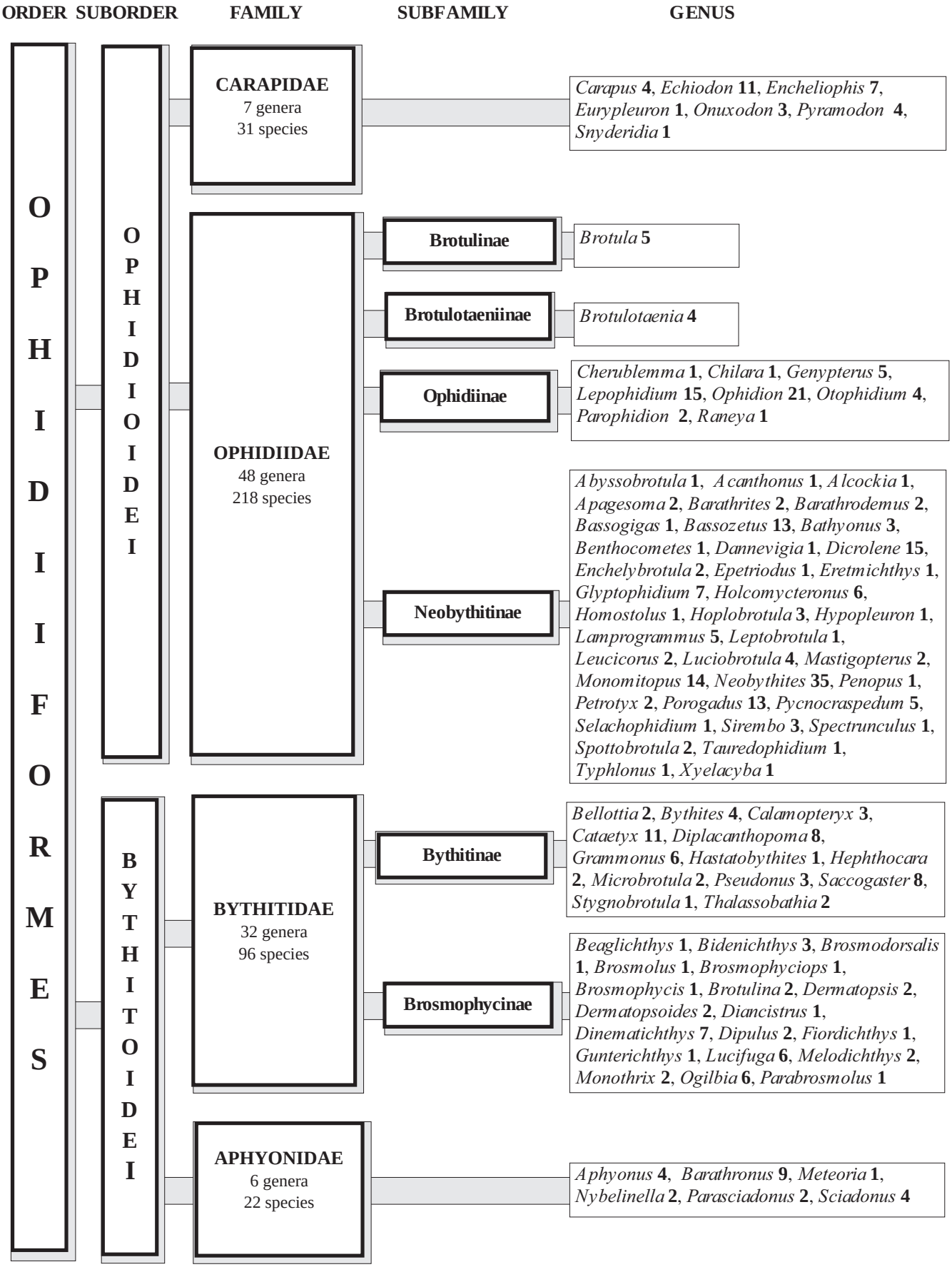

Fig. 1 Arrangement of Ophidiiformes followed in this catalogue. Entries under each taxonomic category are alphabetical. Figures in boldface refer to the number of species

1.2 General Remarks on Suborders and Families

The suborder **Ophidioidei**, as herein treated, was distinguished by Cohen and Nielsen (1978) with a suite of characters that Gordon et al. (1984), Rosen (1985), Patterson and Rosen (1989), and Howes (1992) found to be primitive, negative, or otherwise unsatisfactory for phylogenetic purposes. These authors noted that although some of the constituent taxa or un-named clusters of genera posses specialized characters, there is no presently known encompassing synapomorphy for the entire suborder.

The family **Carapidae** is a monophyletic group of elongate fishes that have pelagic larvae with a specialized first dorsal-fin ray called a vexillum. According to Howes (1992) the Carapidae is the closest relative of all other ophidiiform fishes. Carapids include 7 genera and about 30 species and are found around the world from tropical reefs and warm-temperate shallow water to the continental slope. Many species live as adults inside of sea cucumbers and other large bottom dwelling invertebrate animals.

The family **Ophidiidae** as herein treated has not been shown to be monophyletic. It contains about 50 genera that we here subdivide into 4 subfamilies.

The subfamily **Brotulinae**, the brotulas, consists of a single genus, ***Brotula***, which is most obviously characterized by the possession of barbels on the snout and chin. Similarities of ***Brotula*** to the gadiform genus ***Muraenolepis*** have been described by Markle (1989), and Howes (1992) found similarities between ***Brotula*** and several neobythitine genera (an expanded family Brotulidae once contained many genera now classified in other ophidiiform groups). There are at least 5 species of ***Brotula***, some of which are quite common, living at shallow to mid-depths in tropical and subtropical waters around the world.

The subfamily **Brotulotaeniinae** is most obviously characterized in having its scales modified into small prickles. Its closest relative is not known. There is a single genus, ***Brotulotaenia,*** with 4 uncommonly encountered species found in the meso- to bathypelagic of tropical and subtropical seas.

The subfamily **Ophidiinae**, containing the cusk-eels, is an apparently monophyletic group characterized in having the pelvic fins far forward and supported by an anterior extension of the pectoral girdle. The closest relative of the cusk-eels is not known, although Howes (1992) finds similarities with ***Brotula*** and several neobythitine genera. There are 8 genera and about 50 described and many undescribed species of cusk-eels which are found around the world in tropical, subtropical and temperate seas, mostly on the continental shelf. Some of the common species classified in the southern hemisphere genus ***Genypterus*** grow large enough to support fisheries.

The subfamily **Neobythitinae** contains 38 genera and about 170 described species (many of which were formerly classified in an expanded family **Brotulidae**) and numerous undescribed species. It does not at present meet the requirements for monophyly (Howes, 1992). Further research is required to define several clusters of genera and help decide whether they should remain in this subfamily. Although a single genus of neobythitines, ***Petrotyx***, lives on tropical reefs, most are found in deeper water, from the continental shelf to a depth of 8 370 m where ***Abyssobrotula galatheae***, the deepest known fish, has been caught.

The suborder **Bythitoidei** was distinguished by Cohen and Nielsen (1978) chiefly on the basis of viviparity and associated anatomical features, which Patterson and Rosen (1989) considered as specialized. Thus the mantle of monophyly was bestowed on bythitoids.

The family **Aphyonidae** is a monophyletic group of fragile, scaleless, and mostly rare fishes with a high number of precaudal vertebrae and many neotenous features. The closest relative of Aphyonidae is the **Bythitidae**. Aphyonids include 6 genera and 22 species and are found close to the bottom in all oceans at depths ranging from the continental shelf to the abyss. Nelson (1994) moved the Parabrotulidae from the Zoarciformes to the Ophidiiformes as it might be a derivative of the Aphyonidae. He based the reassignment on M.E. Anderson's remarks in Smith and Heemstra (1986) even though Smith and Heemstra kept the Parabrotulidae in the Zoarciformes. Until more research has shown the proper placement of the Parabrotulidae we exclude them from the Ophidiiformes.

The family **Bythitidae** is considered a monophyletic group which is here divided into 2 subfamilies. The structure of the male intromittent organ has proven useful for defining many of the genera.

The subfamily **Bythitinae** contains 13 genera and at least 50 species which have their dorsal, caudal and anal fins joined. Bythitines live in diverse habitats ranging from temperate to tropical reefs, to the deep sea where most are benthopelagic, although ***Thalassobathia*** and perhaps others are pelagic. One species, ***Bythites fuscus***, is known from as far north as Greenland and ***B. islandicus*** has been taken at Iceland.

The subfamily **Brosmophycinae** has 19 genera and at least 43 and perhaps far more species. Brosmophycines have the caudal fin free from the dorsal and anal fins (this character is variable in some of the species of the genus ***Lucifuga***). Most of the species are secretive, small-eyed, temperate to tropical reef dwellers, and species of ***Lucifuga*** are found in shallow fresh, brackish, and marine waters.

1.3 Developmental Stages

Larvae and juveniles of ophidiiform fishes are known only from relatively few species. Some are found in the epipelagic, others somewhat deeper in the pelagic, while still others remain near the bottom at great depths like adults.

From the oviparous suborder Ophidioidei, larvae of the family Carapidae are easily recognizable by their vexillifer stage (Fig. 2). The vexillum is of taxonomical importance. Carapid larvae are found near the surface in all oceans.

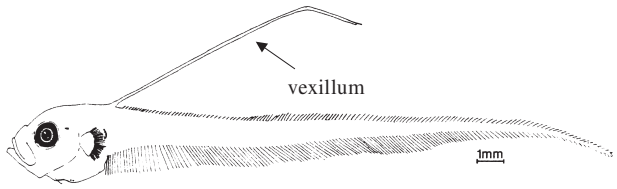

Fig. 2 Family Carapidae, vexillifer stage of *Pyramodon ventralis*
(from Markle and Olney, 1990)

Among the subfamilies of Ophidiidae the meso-and bathypelagic Brotulotaeniinae are known from a single 59 mm long pelagic larva. Small juveniles of the coastal-living Brotulinae are found in surface waters, often far from the shore. Larvae of the Ophidiinae, which occur on the continental shelf and upper slope are numerous in the epipelagic. They are easily recognized as ophidiins because of an elongate body and anteriorly placed pelvic fins (Fig. 3) but are

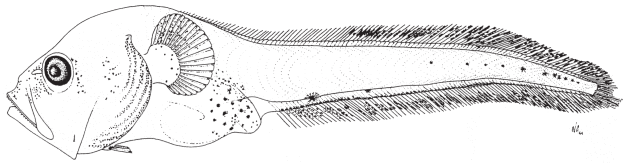

Fig. 3 Family Ophidiidae, subfamily Ophidiinae, larva of *Cherublemma emmelas*
(12.2 mm) (from Ambrose, 1996)

difficult to identify to genus. Most adult Neobythitinae are benthopelagic at great depths. Although larvae of this subfamily are rarely caught they are apparently pelagic at depths of 100 to 300 m and even deeper, judging from larval material in the DANA collections. Some of the larvae have the anterior dorsal-fin rays prolonged, as for instance ***Benthocometes robustus*** (Fig. 4).

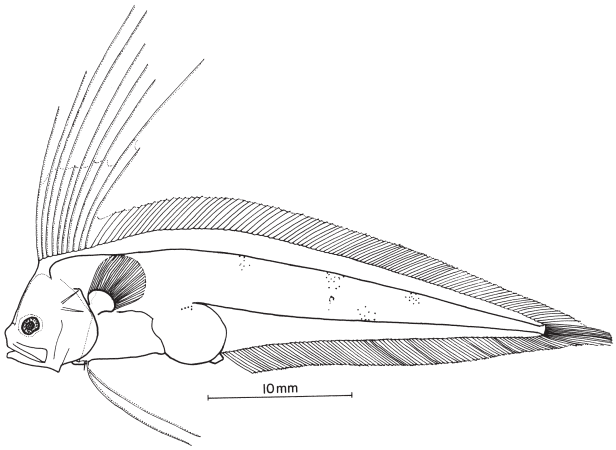

Fig. 4 Family Ophidiidae, subfamily Neobythitinae, larva of *Benthocometes robustus*
(from Nielsen and Evseenko, 1989)

In the viviparous suborder, Bythitoidei, newly born fish of the family Bythitidae are generally small. Most species live at shallow depths and the few identified larvae for example ***Brosmo-***

phycis marginata (Fig. 5) and ***Cataetyx rubrirostris*** are caught in the epipelagic.

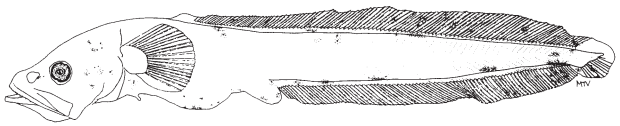

Fig. 5 Family Bythitidae, larva of *Brosmophycis marginata*
(17.2 mm) (from Ambrose, 1996)

The family Aphyonidae, is represented by very deepliving species, except for some species of ***Barathronus***. Of the few larvae known, only 1 (Fig. 6) has been identified, ***Barathronus pacificus***, caught in the epipelagic (Okiyama and Kato, 1997). Judging from the large size of embryos of deepliving species, newly born larvae might be expected to live near the bottom.

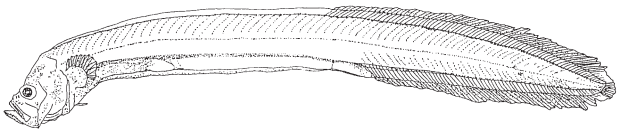

Fig. 6 Family Aphyonidae, larva of *Barathronus pacificus*
(42 mm) (from Okiyama and Kato, 1997)

1.4 Information on Fisheries

Among the ophidiiform fishes, only some species of the genus ***Genypterus*** are important targets of commercial fisheries, namely ***G. blacodes, G. capensis, G. chilensis*** and ***G. maculatus***. The highest landings, approaching 30 000 t per year, are recorded for the former, mostly from the Southwest Atlantic fisheries. Catches of ***Brotula barbata*** by fleets from West African countries also have some commercial importance, probably improving local food security. Information on fisheries is included under the respective accounts of commercial species. Most species of the order have very limited or no fishing interest.

1.5 Plan of the Systematic Catalogue

Four families of ophidiiform fishes are presented; Carapidae, Ophidiidae, Bythitidae and Aphyonidae. For each family a description is given with the diagnostic characters in boldface, notes on habitat, distribution and biology and a key to subfamilies or genera. Within each of the categories the genera are arranged alphabetically. Within each genus, a key to species is given whenever possible, and an annotated list of species including synonyms. A full species account is given only for 10 species of interest to fisheries. Information is presented for each genus on the following subjects:

1. **Scientific name**. Reference is given to the type species, which is the species on which the genus is based.
2. **Synonyms**. Later or more recent names used for the genus in question with indication of the type species.
3. **Number of recognized genera/species**.
4. **Diagnosis and description**. This is a combination of descriptive and diagnostic characters with the latter ones appearing in bold face.
5. **Revision**. References to taxonomic revisions are cited.
6. **Geographical distribution**. A summary statement is presented of geographical distribution.
7. **Habitat and biology**. Although data are scant for most species, a summary is presented whenever possible.
8. **Interest to fisheries**. Data are presented for the few genera that are fished commercially.
9. **Size**. Unless otherwise indicated, standard length (a straight line from tip of snout to base of caudal fin) is given. Since many species are known from very few specimens the “size” will undoubtedly increase when more material is available.
10. **Key to species**. A key to the species is given whenever possible. For most genera the key is based on a revision of the genus.
11. **Remarks**. Various information is here included such as knowledge about undescribed species, need for a generic revision.

12. **List of (nominal) species**. The species are listed alphabetically. When only currently recognized species are listed the paragraph is titled “List of species”. When junior synonyms also are included it is titled “List of nominal species”. When more than 1 species is listed data on distribution and depth are added for each species. When a genus has only a single species, reference is made to distribution and depth for the genus. A species is noted as “rare” when less than 10 specimens are known, “uncommon” when 10-50 are known and “common” when more than 50 are known.

13. **Illustrations** are either original for this publication or have been copied from earlier publications with reference to the source.

1.6 Problems with Identification

Highly technical characters used in the keys or defined in the glossary are illustrated with diagrams. If in doubt refer to the relevant genus illustration.

1.7 Illustrated Glossary of Technical Terms

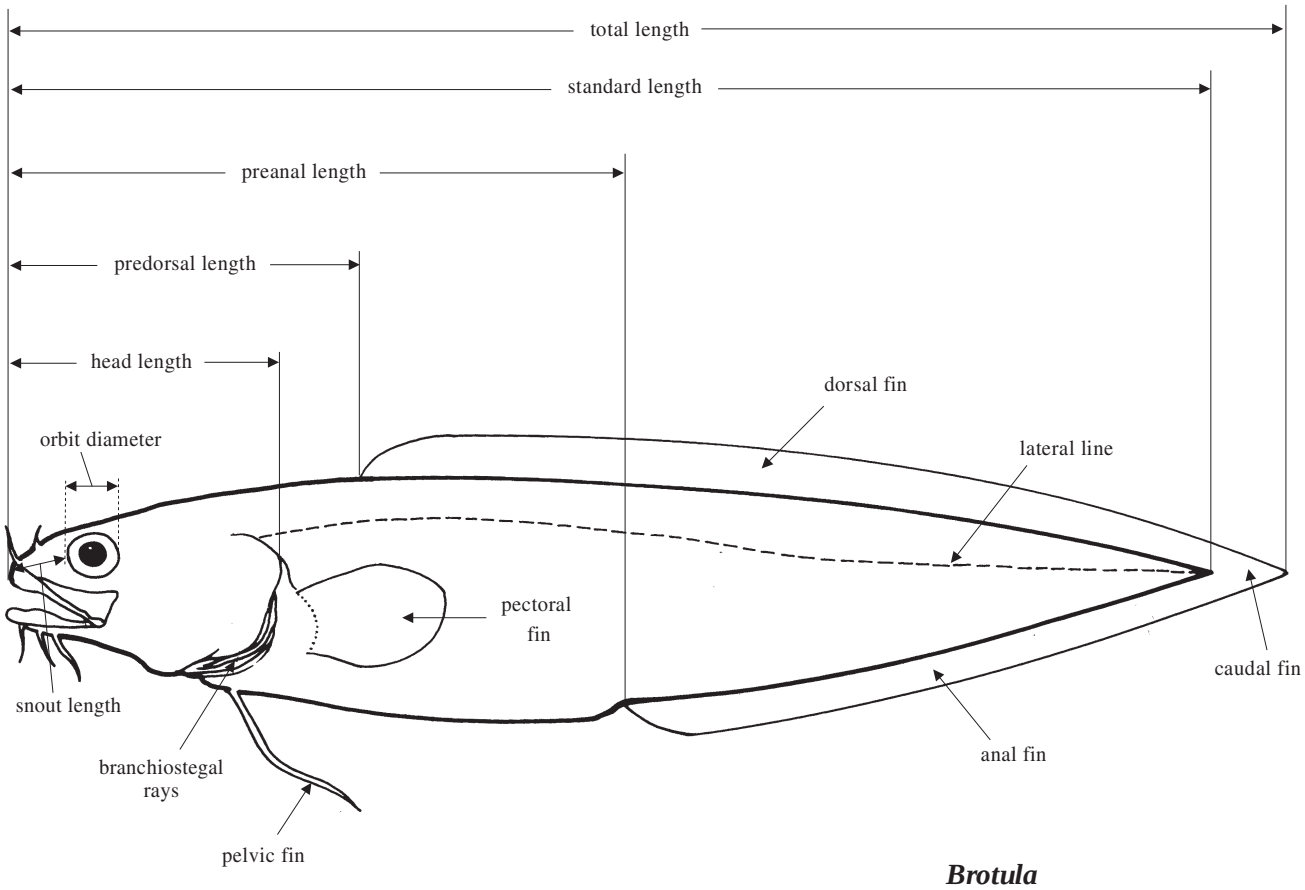

Fig. 7 External morphology and measurements

Adnate - Upper jaw bone (maxillary) attached to rather than free from side of head; like a snake's jaw.

Basibranchial tooth patch - Dentition of floor of mouth in ***Holcomycteronus***. Stippled areas include 2 median and 1 pair of basibranchial tooth patches and the dentaries. The dark areas are the bases of the fifth gill arches (Fig. 8).

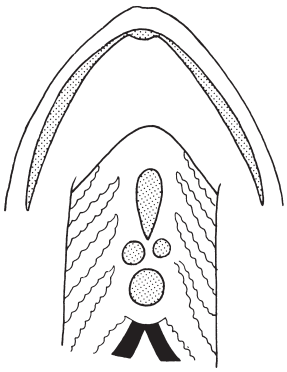

Fig. 8 Floor of mouth
(from Cohen and Nielsen, 1978)

Branchiostegal rays - Bony stays that support the membrane that seals the opening to the gill chamber (see Figs 7, 11).

Diastema - A gap in the dentition sometimes found between fangs and smaller teeth in the jaws.

Exterillium stage - Larval stage with a looped, trailing gut.

Fin rays - The flexible supporting struts of the fins. The pelvic fins of ophidiiform fishes consist each of 0 to 2 rays [see Fig. 9: diagrams of cross-sections through the pelvic fins of 3 kinds of ophidiiform fishes; the dotted line in each separates the 2 halves of a single ray; a) 1 ray in each fin; b) 2 separate rays in each fin; c) 2 joined rays in each fin].

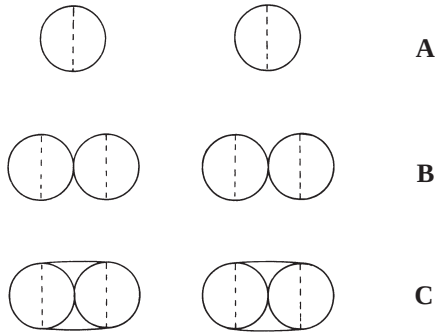

Fig. 9 Cross-section of pelvic fins
(from Cohen and Nielsen, 1978)

Gill rakers - Long bony protuberences along the anterior (inner) edges of the gill arches. [see Fig. 10: anterior gill arches of ophidiiform fishes; a) ***Saccogaster tuberculata***, lateral view of right side showing 3 developed rakers; b) ***Leucicorus atlanticus***, lateral view of left side showing 10 developed rakers].

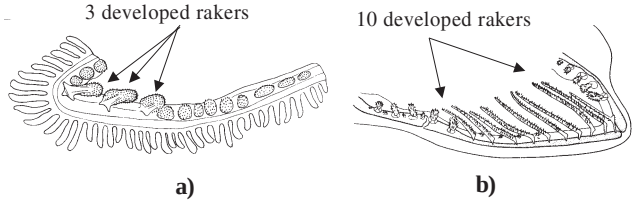

Fig. 10 Gill rakers
(from Cohen and Nielsen, 1978)

Head bones - See Fig. 11 for names of bones used in this work.

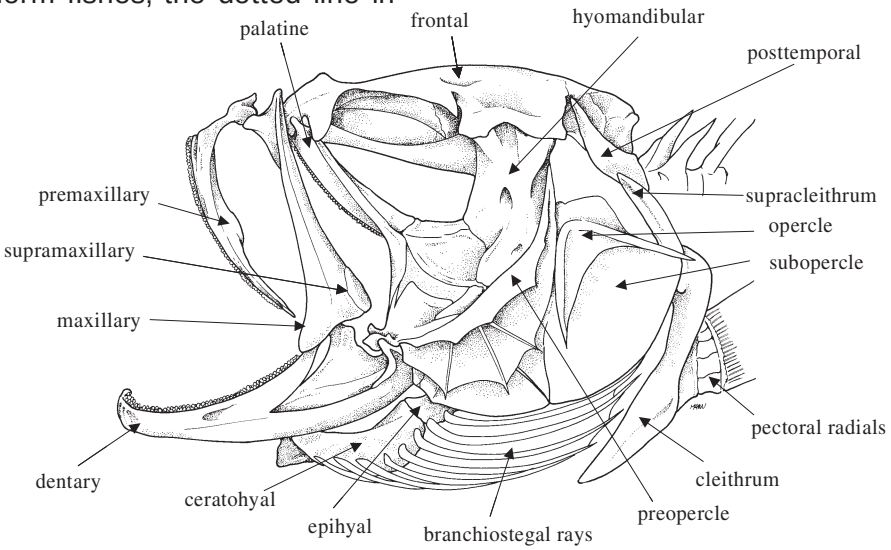

Fig. 11 Skull (after Gregory, 1959)

Intrinsic swimbladder - A constriction separating the swimbladder in 2 subequal parts.

Lateral line - A sensory system that runs in a line along the body (Fig. 7) and is also present on the head.

Male genital appendages - See Fig. 12, intromittent organ in ventral view in ***Ogilbia*** (note the 2 pairs of ossified pseudoclaspers).

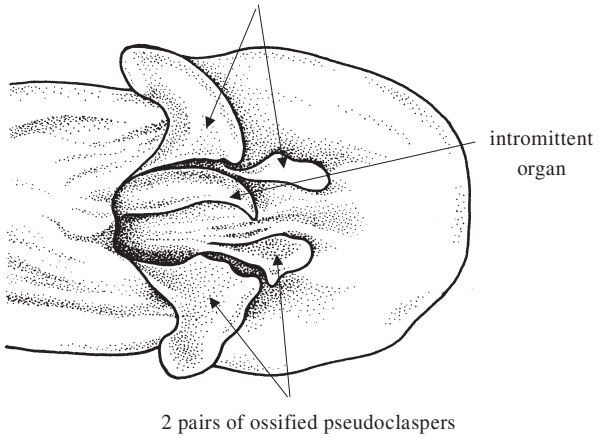

Fig. 12 Male genital appendages

Male intromittent organ - See **male genital appendages**.

Maxillary sheath - Skin fold covering the posterior, upper part of the maxillary bone.

Parapophyses - A pair of lateral processes on the precaudal vertebrae.

Pectoral-fin peduncle - A free, fleshy structure supporting the pectoral fin in some fishes.

Pectoral radials - A series of support bones at the base of the pectoral fin, buried in the pectoral-fin peduncle in some fishes.

Rocker bone - A hardened, modified anterior section of the swimbladder (see Fig. 13).

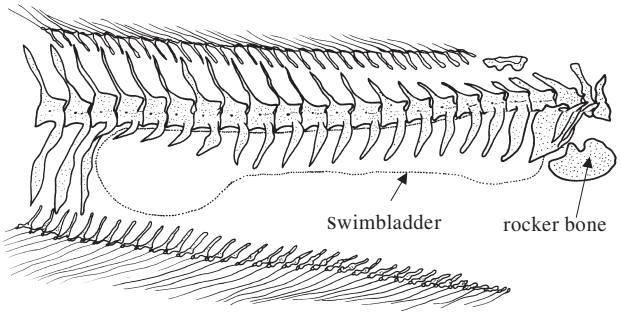

Fig. 13 Anterior axial skeleton of *Onuxodon fowleri*

Symphyseal fangs - Large, pointed teeth located at or close to the anterior junction of the upper or the lower jaws.

Teeth - Cardiform teeth (= heart-shaped teeth), premaxillary teeth (= teeth in upper jaw, see Fig. 11), dentary teeth (= teeth in lower jaw, see Fig. 11), palatine teeth and vomerine teeth (= teeth in roof of mouth, see Fig. 14)

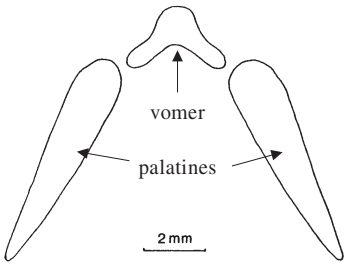

Fig. 14 Tooth patches on roof of mouth

Tenuis stage - Larval stage in Carapidae without enlarged anterior dorsal-fin ray often following vexillum stage.

Tunic ridges - Thickenings in the wall of the swimbladder of some Carapidae.

Vertebrae - Backbones often separated into precaudal (or abdominal) and caudal vertebrae; all caudal vertebrae bear a strong ventral spine. Total number of vertebrae does not include the ural centra.

Vexillum stage - Pelagic larval stage with anterior dorsal-fin ray much prolonged and often highly ornamented (see **vexillum**) found in the family Carapidae (Fig. 2).

Vexillum - Deciduous, elongate, highly vascularized, ornamented first dorsal-fin ray found in carapid larvae (Fig. 2).