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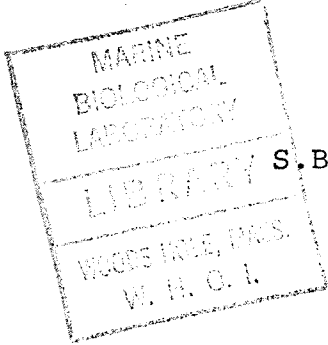
FUNCTIONAL ANATOMY OF  
THE MACROURIDAE  
(TELEOSTEI, GADIFORMES)

by

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## ABSTRACT

## FUNCTIONAL ANATOMY OF THE MACROURIDAE (TELEOSTEI, GADIFORMES)

Tracy McLellan

Submitted to the Department of Biology on May 28, 1976 in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Osteology and myology of the head of 21 species of macrourids and two closely related species are described. A general model of the mechanics of the macrourid head during feeding has been developed based on the anatomical findings. The structure of the head and integration of morphological units are used to explain specializations in the utilization of different food resources. Pelagic prey are the source of food for the most primitive species and for a few of the more specialized ones. A highly protrusible mouth and long rostrum are adaptations for benthic feeding and have appeared in three independent evolutionary lines within the group. Macrourids that are predators on benthos tend to be small and live at depths shallower than 2000 meters.

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## BIOGRAPHICAL NOTE

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## INTRODUCTION

Fishes of the family Macrouridae are the dominant component of the benthopelagic fauna of the deep sea. They show a number of unique morphological characteristics which have been used to unite them into a fairly well-defined group and which are presumably adaptations to the benthopelagic environment. There are several possible sources of food for animals that swim over the bottom, including benthic invertebrates, epibenthic animals and large pieces of detritus that have fallen to the bottom and midwater animals. This study is an attempt to understand the role of the benthopelagic fauna in benthic food chains through the examination of functional anatomy of the heads of the Macrouridae, which show adaptations to many of the possible sources of food on the bottom of the deep sea.

The head of a fish serves several functions. It is the bow of a streamlined body that moves through water and holds the organs of smell, sight, hearing, taste and most of the lateral sense organs. The gills are ventilated by movements of the gill covers and the mouth. The most striking differences between the heads of different kinds of fishes are related directly to feeding habits (Gregory, 1933).

The heads of teleosts are complex structures with

numerous joints and possibilities for movement. The function of several of the bones and muscles are the same throughout teleosts, while there is great variation in the morphology and in the function of some of the other components of the head. Functional analysis of morphological characters has been used in explaining the interdependency of the evolution of morphological characters in some groups of fishes (Liem, 1967, 1970, 1973).

The movements of the fish head have been investigated in a number of groups of fishes by examination of preserved or freshly killed specimens (Tchernavin, 1953; Alexander, 1966, 1967a, 1967b), by filming live fish (Nyberg, 197 ; Liem, 1967; Lauder, 1976), by surgically impairing ligaments (Liem, 1970; Lauder, 1976) and by measurement of muscle contraction by electromyography (Osse, 1969; Ballintijn, van den Burg and Egberink, 1972; Liem and Osse, 1975). Methods used depend in part on the ability to keep the fish in captivity. Deep sea fishes rarely show any signs of life after they have been trawled out of the ocean, so that a study of the mechanical workings of the head of fishes from great depth is limited to the examination of dead specimens. The work that has been done on live fishes serves as a basis on which to interpret the functions of the morphological characters found in other fishes that are not so convenient to work on. The morphology of the macrourids is so extreme in some ways that the functions show up more clearly than in more generalized fishes.

It is possible to study the functional morphology of the Macrouridae by examining the anatomy of the bones, muscles, connective tissue and joints of the head of several species of the family. A general model of the possible movements of the head is presented here that is based on those morphological characters which were found in all macrourids. Comparison of the differences between species will illuminate the morphological characters which are important in adaptations to the utilization of different types of food resources.

#### I. Distribution of the Macrouridae

The Macrouridae are the dominant fishes of the benthopelagic fauna - those animals that hover just off the bottom of the deep sea. There are more than 300 species in the family, more species than in any other family common in that environment (Okamura, 1970b; Marshall and Iwamoto, 1973). They have been found in all oceans of the world except the Arctic (Marshall and Iwamoto, 1973), and frequently comprise more than half of the fishes in trawls taken below a depth of 1000 meters.

Macrourids are most abundant on continental slopes between 500 and 2000 meters depth. The greatest number of species occur in the western Pacific (Gilbert and Hubbs, 1920). There are many extremes within the group with respect to distribution. Sampling of the deep ocean has not been complete in many areas of the world, so that some of the



anomalies of distribution may be artifacts of limited sampling rather than actual distribution. One species is known only from depths greater than 5000 meters in the eastern North Atlantic (Echnomacrurus mollis: Nybelin, 1957). Another was first described from a specimen that had washed up on a beach during a storm (Lepidorhynchus denticulatus: Richardson, 1846). Some have been caught over a great range of depths (Coryphaenoides armatus: 1600 to 4700 meters; Marshall and Iwamoto, 1973; Iwamoto and Stein, 1974), while others are limited in their depth range (Macrourus berglax: 200 to 600 meters; Marshall and Iwamoto, 1973).

The geographic range varies between species as well, with some of the deeper living species found in the Pacific, Atlantic, and Indian Oceans (Coryphaenoides armatus and Coryphaenoides leptolepis: Marshall and Iwamoto, 1973; Iwamoto and Stein, 1974). Sixteen species are known only from the Sulu Sea (Gilbert and Hubbs, 1920; Hubbs, 1930, 1954). One species has been caught only near Hawaii and in the North Atlantic (Nezumia bubonis: Iwamoto, 1974). Another is known only from Japan, the Gulf of Mexico, and the equatorial Atlantic (Squalogadus modificatus: Marshall and Iwamoto, 1973). These disjunct distributions may represent a lack of adequate sampling at the appropriate depths and bottom types, or a lack of suitable habitat in areas between the widely separated points where these two species have been found.

The abundance of macrourids and their dominance in the benthopelagic community has been demonstrated by the use of cameras set on the bottom to photograph animals attracted to bait (Isaacs, 1969; Isaacs and Schwartzlose, 1975; Dayton and Hessler, 1972). Large numbers of fish came to bait and showed great activity over several days in depths as great as 6000 meters. The distance travelled by the fish to bait is not known, so that density cannot be estimated from these photographs.

Photographic surveys and observations from submersibles have been used to study the distribution of macrourids over small areas (Barham, Ayer and Boyce, 1964; Marshall and Bourne, 1967; Grassle, Sanders, Hessler, Rowe and McLellan, 1975). The typical head-down pose of macrourids over the sediment surface was first described from photographs (Marshall and Bourne, 1964). The analysis of one series of photographs taken from a remote underwater manipulator revealed that the macrourid (Coryphaenoides acrolepis) common in the area appeared in photographs only in a few frames following the disturbance of sediment by the vehicle (Hessler, in preparation). It is apparently attracted to the sediment cloud or to the animals exposed when the sediment is disturbed.

## II. Trophic Ecology of the Macrouridae

It has been suggested that macrourids derive their nourishment from small animals inhabiting the sediments of the

deep ocean (Joubin, 1933; Marshall and Bourne, 1964). These suggestions were made on the basis of the specialized nature of macrourids and knowledge of the limits of their distribution at the bottom of the deep sea.

Recent studies of the stomach contents of several large macrourid species have shown that pelagic organisms are an important component of the diet of macrourids (Pearcy and Ambler, 1974; Haedrich and Henderson, 1974; Geistdorfer, 1973). Further comparison of the stomach contents of different species shows differences in the type of food ingested. In a study of the macrourids of Japan, Okamura (1970b) found that the proportion of benthic organisms in stomachs increased in an evolutionary sequence leading to the most specialized genus of the family, Coelorinchus. There are differences in the stomach contents of the five species of Coryphaenoides studied by Pearcy and Ambler (1974) with respect to benthic or pelagic origin of prey and size of prey.

The appearance of large numbers of macrourids and other animals at bait placed on the sea floor has led to the hypothesis that large pieces of detritus may serve as food for mobile scavengers that live near the sediment surface and can swim long distances to food (Dayton and Hessler, 1972; Isaacs and Schwartzlose, 1975). There has been little direct evidence from the stomach contents of macrourids, with the exception of one species, Coryphaenoides armatus, that large carcasses are an important food source. Remains of large

animals have been found in the stomachs of other fishes, notably sharks, caught near the bottom in fairly great depths (Clarke and Merritt, 1972).

There are some limitations in the study of stomach contents of macrourids to elucidate the role they play in benthic food chains. Macrourids have large swimbladders with no direct opening to the digestive tract or mouth. As fish are brought to the surface from depth, gas in the swimbladder expands and causes the stomach to evert through the mouth and thereby lose its contents. Stomach eversion occurs at different frequencies depending on the species and size of the specimens as well as on the depth and means of capture. It is difficult to tell the relation between prey organisms found inside stomachs and available prey without detailed information about all organisms of the same environment. This type of information is known in detail for only a few areas of the ocean (for example, Grassle et al., 1975). Generalizations about the influence of fish predation on their prey community must be made cautiously until there is detailed knowledge of the dynamics of the entire community.

### III. Systematics of the Macrouridae

The Macrouridae is allied with the Eretmophoridae, Gadidae, Melanonidae, Merlucciidae, Muraenolepidadae, and Steindachneriidae in the order Gadiformes, or Anacanthini (Marshall and Cohen, 1973). The Gadiformes has been included

with the Percopsiformes, Batrachoidiformes, Lophiiformes and Gobiesociformes in the superorder Paracanthopterygii (Greenwood, Rosen, Weitzman and Myers, 1966; Rosen and Patterson, 1969). The macrourids form a fairly distinct group within the Gadiformes. There are a few forms intermediate between the Merlucciidae and the Macrouridae (Marshall, 1966; Marshall and Cohen, 1973). The Macrouridae are a highly specialized group limited in distribution which have not given rise to any other groups of fishes.

The Macrouridae have been divided into four subfamilies, the Bathygadinae, Macruoroidinae, Tracyrincinae and Macrourinae (Marshall and Iwamoto, 1973). The first three of these subfamilies are quite distinct from each other and contain few species. The fourth subfamily includes most of the species of the family and can be divided into several groups of genera (Iwamoto, 1972). The evolutionary relationships between these generic groups are confusing because of the seeming convergence of two evolutionary lines (Okamura, 1970b).

The species level taxonomy of the macrourids has been thoroughly studied in the western North Atlantic (Marshall and Iwamoto, 1973), tropical Atlantic (Iwamoto, 1970), northern East Pacific (Iwamoto and Stein, 1974), central eastern Pacific (Iwamoto, in preparation) and Japanese waters (Okamura, 1970a) and Sulu Sea (Gilbert and Hubbs, 1916, 1920).

#### IV. Functional Anatomical Approach to Trophic Ecology

Many of the anatomical specializations of fishes are adaptations for the utilization of one type of food source or another. The comparative anatomy of the digestive system of teleosts has been studied with an interest in understanding feeding habits (Tyler, 1973; Geistdorfer, 1972). Gill raker structure, mouth size, and tooth morphology are often used to explain the type of food a fish is adapted to feed on.

The mechanical workings of the jaws of teleosts have been studied for the most part on relatively unspecialized fishes that can be easily kept alive in tanks of freshwater (Anker, 1974; Osse, 1969; Lauder, 1976). Analysis of highly specialized fishes can illustrate more clearly the functioning of anatomical features that are not so obvious in intermediate forms, and thus make the more generalized forms easier to understand (Liem, 1967).

Deep sea teleosts possess some of the most bizarre anatomical adaptations of any fishes. In addition, their feeding habits are often difficult to study because they cannot be kept in captivity and stomach content analysis is difficult when stomachs are frequently empty and few specimens have been caught. The feeding adaptations of some very specialized deep sea fishes have been examined through the study of the mechanics of their heads. Tchernavin (1953) described the functional anatomy of the viperfish, Chauliodus sloani, and was able to explain how C. sloani is capable

of capturing both very large and very small prey organisms. Differences in mouth size and gill raker structure of several melamphoids have been studied with regard to their importance in differences in predator strategy between species of different depths (Ebeling and Cailliet, 1974). The mechanics of the head of the chimaera, Callorhynchus capensis, and the contents of stomachs have been studied together to understand its evolutionary biology and ecology (Ribbink, 1971).

The Macrouridae are suited to a comparative study of jaw mechanics for several reasons. There are a great number of species within the family, nearly all of them live at the bottom of the deep sea, and there is a large variety in the morphology of the head, including several generalized forms and a number of specialized ones that show different specializations. There are only a few possibilities of available food in the environment of the macrourids, and they have been recorded to feed on most of the types of potential food. The extremes in the morphology of the head of the macrourids are likely to be specializations related directly to the ability to utilize the different food resources on the bottom of the ocean. The extreme specializations can also be used to explain the functional significance of characters of the more generalized species.

## METHODS

Preserved museum specimens were dissected, examined, photographed and drawn. For species where small specimens were available, trypsin-cleared and alizarin-stained preparations of the skeleton were made according to the method of Taylor (1967). Ligamentary-articulated dried skeletons were made from frozen and fresh specimens according to the method of Konnerth (1965).

The possible movements of the head were investigated by manipulating freshly caught specimens of Nezumia bairdii, Malacocephalus occidentalis, Coryphaenoides rupestris, Coryphaenoides armatus, Coryphaenoides leptolepis, Macrourus berglax and Coelorinchus coelorinchus carminatus during a cruise of the R.V. Gilliss during September 1975.

The contents of the stomachs of the study material were examined and identified.



## MATERIALS

The following list of specimens examined in this study is in the order in which they are considered here, which follows the phylogeny proposed by Okamura (1970b). \* denotes cleared and stained material and + denotes ligamentary articulated dried skeletons.

## MERLUCCIIDAE

Macruronus novaezelandiae

MCZ 48944, 4 specimens, 33-59 mm HL

MCZ 51164, 2 specimens, 37,41 mm HL

\*MCZ 51165, 1 specimen, 31 mm HL

## STEINDACHNERIIDAE

Steindachneria argentea

USNM 188852, 3 specimens, 37-43 mm HL

## MACROURIDAE

## Bathygadinae

Bathygadus macrops

UMML 15193, 3 specimens, 68-69 mm HL

+MCZ 51168, 1 specimen, 79 mm HL

## Macrourinae

Lepidorhynchus denticulatus

MCZ 51515, 4 specimens, 53-63 mm HL

Malacocephalus occidentalis

UMML 25600, 3 specimens, 47-51 mm HL

\*MCZ 51471, 3 specimens, 21-26 mm HL

+MCZ 51167, 1 specimen, 68 mm HL

Nezumia bairdii

MCZ 51167, 7 specimens, 46-65 mm HL

\*MCZ 51174, 2 specimens, 21, 32 mm HL

+MCZ 51466, 1 specimen, 61 mm HL

Mataeocephalus acipenserinus

USNM 55249, 3 specimens, 40-43 mm HL

USNM 126542, 2 specimens, 42, 50 mm HL

Coryphaenoides rupestris

VIMS 00899, 3 specimens, 40-43 mm HL

MCZ 51172, 3 specimens, 114-133 mm HL

+MCZ 51462, 1 specimen, 142 mm HL

Coryphaenoides carapinus

MCZ 51178, 15 specimens, 23-52 mm HL

MCZ 51864, 1 specimen, 54 mm HL

\*MCZ 51177, 1 specimen, 37 mm HL

Coryphaenoides armatus

MCZ 51868, 1 specimen, 78 mm HL

\*MCZ 51470, 1 specimen, 31 mm HL

+MCZ 51154, 1 specimen, 118 mm HL

+MCZ 51464, 1 specimen, 99 mm HL

Coryphaenoides acrolepis

MCZ 51931, 1 specimen, 156 mm HL

MCZ 51932, 3 specimens, 57-77 mm HL

\*MCZ 51933, 1 specimen, 35 mm HL

Coryphaenoides leptolepis

MCZ 51155, 2 specimens, 66,78 mm HL

+MCZ 51465, 1 specimen, 98 mm HL

Coryphaenoides pectoralis

MCZ 51930, 2 specimens, 98,110 mm HL

Macrourus berglax

MCZ 37779, 1 specimen, 90 mm HL

VIMS 03536, 1 specimen, 130 mm HL

+MCZ 51463, 1 specimen, 145 mm HL

Abyssicola macrochir

USNM 77248, 3 specimens, 68-75 mm HL

Coelorinchus coelorinchus carminatus

UMML 13169, 1 specimen, 66 mm HL

+MCZ 51169, 1 specimen, 59 mm HL

Coelorinchus chilensis

LACM Eltanin 1989, 3 specimens, 42-51 mm HL

Coelorinchus longissimus

MCZ 47740, 1 specimen, 57 mm HL

Coelorinchus occa

UMML 26794, 1 specimen, 133 mm HL

+MCZ 51166, 1 specimen, 117 mm HL

Coelorinchus jordani

USNM 77197, 2 specimens, 49,51 mm HL

Coelorinchus innotabilis

LACM Eltanin 1718, 3 specimens, 52-55 mm HL

Coelorinchus japonicus

SU 7939, 2 specimens, 97,121 mm HL

## Trachyrincinae

Trachyrincus helolepis

SOSC Reg. No. 309, 3 specimens, 96-98 mm HL

## ABBREVIATIONS

mm millimeter

HL head length

## Institutional Abbreviations

LACM Los Angeles County Museum

MCZ Museum of Comparative Zoology

SOSC Smithsonian Oceanographic Sorting Center

SU Stanford University collections, housed at the California  
Academy of Sciences

UMML University of Miami, Rosenstiel School of Marine and  
Atmospheric Sciences

USNM United States National Museum

## ANATOMICAL ABBREVIATIONS

AAP	Adductor arcus palatini
AM1 $\alpha$	Adductor mandibulae 1 $\alpha$
AM1 $\beta$	Adductor mandibulae 1 $\beta$
AM1 $\beta'$	Adductor mandibulae 1 $\beta'$
AM $\omega$	Adductor mandibulae $\omega$
AM2	Adductor mandibulae 2
ALV	Alveolar process of the premaxilla
ART	Articular process of the premaxilla
ASC	Ascending process of the premaxilla
CL	Cleithrum
DO	Dilatator operculi
ECT	Ectopterygoid
ENT	Entopterygoid
EPO	Epiotic
EPX	Epaxial muscles
FR	Frontal
GH	Geniohyoideus muscle
HPX	Hypaxial muscle
HAB	Hyohyoidei abductores muscle
HAD	Hyohyoidei adductores muscle
HMX	Head of the maxilla
HY	Hyoid
HYM	Hyomandibular
IB	Infraorbital bones

