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Synopsis of the Whalefishes (Family Cetomimidae) with Descriptions of Four New Genera

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ABSTRACT. This study of more than 500 specimens recognises two cetomimid subfamilies (one newly described), nine genera (four newly described) and about 35 species (four newly described). Characters of the gill arches, head laterosensory canals, lateral line scales, cavernous tissue, anal lappets and subpectoral organ (the last three of unknown function) are used to distinguish taxa. A cladistic analysis of 39 characters utilised *Rondeletia* and *Barbourisia* as outgroups to polarise character states within the family and the beryciform families to polarise family characters. Three synapomorphies, the presence of gill rakers in some form other than elongate and flattened and the absence of pelvic fins and pleural ribs, support the monophyly of the family. The monotypic Procetichthyinae, defined by four autapomorphies, is the primitive sister group of all other cetomimids. It retains such pleisiomorphic features as a fully developed nasal organ, a fully developed eye with lens, a pseudobranch and 19 principal caudal rays. *Ditropichthys* is the primitive sister group of the remaining seven genera, with the next line including the related *Cetichthys* and *Notocetichthys*. The relationships of the remaining five genera are equivocal, except that *Cetomimus* and *Gyrinomimus* are sister taxa defined by lateral line scale shape. A working hypothesis of relationships is presented that places *Danacetichthys* and *Cetostoma* as sister groups of the remaining three genera. Multistate characters of gill raker-tooth plate shape and extent of the fourth gill slit support the hypothesis. *Cetostoma* and *Rhamphocetichthys* are highly derivative forms, with each monotypic genus defined by three or four autapomorphies. The genera *Gyrinomimus* and *Cetomimus* each have more than ten species, which will be reviewed in later papers. The other genera each have one or two species that are fully detailed here. All examined specimens with recognisable gonads are females, confirmed by histology of eight specimens representing four genera. Egg sizes of at least 2.0, 1.3 and 0.6 mm diameter are attained by the genera *Procetichthys*, *Gyrinomimus* and *Cetostoma* respectively. The vast majority of examined specimens had eggs 0.1 mm diameter or less. The few specimens with larger eggs had bimodal egg sizes. Males and individuals less than 25 mm are unknown. Maximum size is at least 390 mm in one species of *Gyrinomimus*, while *Ditropichthys* and *Cetostoma* apparently do not exceed 140 mm and 250 mm, respectively. Crustaceans are the primary food of whalefishes. The family is distributed in all oceans, from 52°N to 72°S. At the species level, two distribution patterns are apparent. The two commonest species, *Cetostoma regani* and *Ditropichthys storeri*, have cosmopolitan distributions between 50°N and 40°S. The two most frequently captured species of *Gyrinomimus* are restricted to the north Pacific between 39° and 52°N and circumglobally in the Southern Ocean between 32° and 72°S. There are too few collections of the other species to ascertain distributional limits, but some have been taken in all three oceans and others only in a part of one ocean. The centres of vertical distribution for all species are below 1000 m. Only smaller specimens of *C. regani* and *D. storeri* have been taken above 1000 m, where some nocturnal vertical migration is indicated. Closing net captures confirm large specimens of both species live between 1200 and 1500 m. Four separate closing net captures of *Cetichthys parini* between 2700 and 3200 m demonstrate this to be the deepest living known whalefish. At least some cetomimids are more abundant than previously thought, with 55% of the ISH midwater trawls in the Atlantic fishing to 1800 m or deeper catching whalefishes. Up to 11 specimens and six different species of whalefishes were taken in a single deep trawl. With about 35 species, cetomimids are second only to the anglerfish family Oneirodidae as the most speciose bathypelagic fish family and may be the most abundant below 1800 m. As four of the eight species considered in this paper are represented by less than five specimens, it seems probable that additional species of cetomimids will be captured.

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Contents

Whalefishes of the family Cetomimidae inhabit the meso- and bathypelagic waters of all oceans. Although 18 species have been described since 1895 (Table 1), the cetomimids remain one of the most poorly known fish families, with fewer than 100 specimens recorded in the literature. Parr (1934) and Harry (1952) summarised what was known of the family. Since 1952 nine additional species have been described, but little synthetic work has been done; Maul (1969) included a key to the known species of *Cetomimus*.

All but two species in the family were originally described from a single specimen and few additional specimens have been described in detail. Characters such as the numbers of fin rays, lateral line pores and rows of teeth in the jaws and vomer have been used to diagnose new species, but the range of variation within a single species has not been recorded, due until relatively recently to the paucity of specimens in collections. Most of the described specimens have been less than 100 mm standard length (SL); the largest specimen recorded to date was 174 mm. As many species exceed 200 mm SL and the largest specimen collected is 390 mm SL, it appears that most previous descriptions have been based on juveniles. Little information has been published concerning whalefish biology and no data are available on reproduction or food. With all previously recorded specimens caught in open nets, the vertical distribution of the family has not been detailed. However most were caught with nets fishing at least to 1000 metres, and the family has long been considered bathypelagic.

The systematic placement of the Cetomimidae has been the subject of controversy. Parr (1929), on the basis of osteological features, included the family within the order Iniomi (= Myctophiformes *sensu lato*), while removing the family Rondeletiidae to the order Xenoberyces (= Stephanoberyciformes). Parr (1945, 1946) and Myers (1946) indicated the Cetomimidae and Barbourisiidae were closely related, but disagreed as to whether the latter should be recognised at the familial or subfamilial level. All subsequent authors have considered all three families closely related, differing in their ordinal placements: as a separate suborder of Myctophiformes (Harry, 1952); as a distinct order Cetomimiformes with or without other families included (Greenwood *et al.*, 1966; McAllister, 1968; Gosline, 1971; Ebeling & Weed, 1973); in the order Beryciformes (Rosen & Patterson, 1969) or with other families in a "stephanoberycoid group" (Rosen, 1973).

A complete family monograph is obviously required. Problems to be solved include those at the alpha taxonomic level (determination of the genera and species represented by the more than 500 currently available specimens), determination of evolutionary relationships at both the generic and familial levels and description of the biology of the whalefishes based on examination of gonads and stomach contents. The present paper summarises knowledge of the family at the generic level based on examination of most of the available specimens, describes four new genera and four new species, defines the other five genera in the family and presents an analysis of generic relationships based mostly on external characters. Future papers will revise the species within the genera *Gyrinomimus* (about 12 species) and *Cetomimus* (perhaps 15 species), describe the osteology of the genera and analyse family relationships.

Table 1. Nominal taxa of the family Cetomimidae, including new taxa described herein; synonyms are placed in brackets.

Subfamily Procetichthyinae n.subfam.
  Procetichthys n.gen.
    Procetichthys kreffti n.sp.
Subfamily Cetomiminae Goode & Bean, 1895
    (Subfamily Ditropichthyinae Parr, 1934)
  Ditropichthys Parr, 1934
    Ditropichthys storeri (Goode & Bean, 1895)
  Cetichthys n.gen.
    Cetichthys indagator (Rofen, 1959)
    Cetichthys parini n.sp.
  Notocetichthys Balushkin, Fedorov & Paxton, 1989
    Notocetichthys trunovi Balushkin, Fedorov & Paxton, 1989
  Danacetichthys n.gen.
    Danacetichthys galathenus n.sp.
  Cetostoma Zugmayer, 1914
    Cetostoma regani Zugmayer, 1914
  Gyrinomimus Parr, 1934
    Gyrinomimus myersi Parr, 1934
      (*Gyrinomimus parri* Bigelow, 1961)
    Gyrinomimus simplex Parr, 1945
    Gyrinomimus bruuni Rofen, 1959
    Gyrinomimus grahami Richardson & Garrick, 1964
      (*Gyrinomimus notius* Fedorov & Balushkin, 1983)
    Gyrinomimus andriashevi Fedorov, Balushkin & Trunov, 1987
  Cetomimus Goode & Bean, 1895
    (*Pelecinomimus* Gilchrist, 1922)
    (*Cetomimus* (*Psapharocetus*) Harry, 1952)
    Cetomimus gilli Goode & Bean, 1895
    Cetomimus picklei (Gilchrist, 1922)
    Cetomimus kerdops Parr, 1934
    Cetomimus craneae Harry, 1952
    Cetomimus teevani Harry, 1952
    Cetomimus compunctus Abe, Marumo & Kawaguchi, 1965
    Cetomimus hempeli Maul, 1969
  Rhamphocetichthys n.gen.
    Rhamphocetichthys savagei n.sp.

Vitiazella Rass (1955) and *Cetomimoides* Koefoed (1955), originally described in the family Cetomimidae, have since been placed in the family Megalomycteridae (Myers & Friehofer, 1966).

Materials and Methods

More than 500 specimens from 25 institutions were examined during the course of the study (Table 2). Most specimens of *Cetomimus* were only cursorily examined for identification to genus, while all others were examined in detail. Museum abbreviations follow Leviton *et al.* (1985). Unless otherwise indicated, all lengths are standard lengths (SL).

Descriptions follow the format of Harry (1952). Vertebral counts and confirmation of questionable fin counts were made from x-rays. Methods of counting and measuring follow Hubbs & Lagler (1949), except that the last dorsal and anal fin element was included in the count (the last ray was sometimes single and sometimes double, see next section). Measurements were made with dial calipers to the nearest 0.1 mm; measurements less than 50 mm were usually made under a dissecting microscope.

In the materials examined sections of each species, only one latitude and longitude are given for each collection. For most stations, this is the midpoint of the trawl; however for some collections (like ISH), it is the start of the trawl. Most whalefishes were caught with open nets and the depth given is from the surface to the maximum depth fished. If no depth gauge was available, the approximate deepest fishing depth for the amount of wire out is given (e.g. 0-ca.2000 m). For a few collections, notably those of the *Discovery*, Oregon State University, Tokai Fisheries and recently of Scripps Institution of Oceanography, closing nets were used and these are indicated. When available the time of day has been converted to an indication of hours of daylight (D) or darkness (N); consideration was given to both latitude and time of year in making the conversions.

Drawings of lateral line scales and anal lappet scales were made with the aid of a dissection microscope and camera lucida. A section of lateral line containing at least two lateral line scales was dissected out of at least one specimen of each genus and stained with alizarin.

The following specimens were measured and/or examined for characters in the outgroup analysis:

Barbourisiidae
  Barbourisia rufa
    AMS I.26869-001, 89.5 mm, Zanzibar
    AMS I.27260-001, 91.7 mm, Hawaii
    AMS I.18824-001, 100 mm, Hawaii, cleared and stained (C+S)
    AMS I.22812-002, 110.9 mm, northwest Australia
    AMS I.27261-001, 133 mm, central Pacific (C+S)
    MCZ 49148, 165.8 mm, Hawaii
    CSIRO H1150-01, 305 mm, Tasmania
Rondeletiidae
  Rondeletia bicolor
    AMS I.18415-001, 59.9 mm, north Atlantic

Rondeletia loricata
AMS I.20306-005, 44.7 mm, southeast Australia
AMS I.21368-005, 44.7 mm, southeast Australia
AMS I.20307-011, 60.7 mm, southeast Australia
AMS I.24859-001, 76.1 mm, southeast Australia
LACM 9571-5, 77.5 mm, southern California
LACM 9254-33, 94 mm, southern California (C+S)

Diagnostic Characters

Previous descriptive studies on cetomimids have utilised primarily meristics, morphometrics, dentition, the shape of lateral line pores and the location of cavernous tissue to distinguish taxa. Description of these and other characters of the eye, nasal organ, lateral line system and gill arches are given here.

Meristic characters. Counts useful in distinguishing taxa include dorsal, anal, pectoral and caudal fin rays, vertebrae and lateral line pores and scales. Pelvic fins are absent and branchiostegal rays were counted only in a few cleared and stained specimens.

The first four or five dorsal and anal rays are often much shorter than the remaining rays, and in some genera embedded in tissue with only the tips of the first two or three rays exposed and often associated with cavernous tissue. Dissection or x-rays are sometimes necessary to confirm these counts. The last ray of the dorsal and anal fin is almost always single and much smaller than the penultimate ray. In cleared and stained specimens of *Cetostoma regani*, *Ditropichthys storeri* and *Gyrinomimus grahami*, the last anal ray has its own separate radial while the last dorsal ray shares the radial of the penultimate ray. Not enough specimens have been cleared and stained to determine if the radial/ray relationship is consistently different in the two fins throughout the family. All rays of each fin have been counted in this study and the cetomimid counts represent fin rays, not necessarily radials. However the last two rays are counted as one in the outgroup families considered in the last section, as *Rondeletia* and *Barbourisia* have the last two rays of each fin on a single radial. The tips of the dorsal, anal and caudal fins are usually lost due to abrasion in the net; usually no distinction has been made between simple and branched rays, because this may be artificial, depending on how much of the distal portions of the branched rays has been lost.

Similarly recognition of principal caudal fin rays was often subjective when the ends of the rays were lost; unlike some other fishes such as myctophids (Paxton, 1972), the rays immediately outside the branched rays, the first and last principal rays, are not greatly enlarged relative to the series of procurrent caudal rays, in all genera except *Cetostoma*. The principal rays could only be counted with assurance when some of the branched portions of each ray were present. The number of procurrent caudal rays could only be determined on cleared and stained specimens or on those with badly torn skin; dissections were not made on other specimens.

The pectoral fins in all cetomimids except *Procetichthys* are small and have 17 to 24 rays. In most genera the ventral-most six to eight rays decrease in size and are often difficult to count in small specimens, even with dissection. It was often necessary to dissect the thick skin over the

Table 2. Specimens by genus and collection.

Inst.	*Procetichthys*	*Ditropichthys*	*Cetichthys*	*Notocetichthys*	*Danacetichthys*	*Cetostoma*	*Gyrinomimus*	*Cetomimus*	*Rhamphocetichthys*	Totals
ISH	1	24	1		1	55	39	22	1	144
SIO		13	2		1	14	18	39		87
LACM		12	1			8	19	26	1	67
IOS		4				27	1	12		44
ZIN		5	2	2		5	18	8		40
ZMUC		3	1		2	7	4	16		33
MCZ		7				7	3	12	1	30
AMS		6	1			3	7	11	1	29
USNM		2			1	4	3	9		19
OSUO		1	2			7	9	1		20
TH		3					2	8		13
UMML		2				6		5		13
BOC		1				3	2	1		7
CAS		1				2	1	2		6
ORI								3		3
NSMT			2		1					3
MMF								3		3
ORSTOM							1	1		2
BCPM							1			1
FAKU								1		1
HUMZ						1				1
MOM						1				1
NMNZ							1			1
RUSI								1		1
Totals	1	84	12	2	6	150	129	181	4	569

pectoral base to count the rays.

The distinction between precaudal and caudal vertebrae was not clear on the x-rays and every count involved some degree of subjectivity. In cleared and stained specimens of *Cetostoma regani* and *Ditropichthys storeri* fused neural and haemal spines were only present posterior to the dorsal and anal fins, while in a cleared and stained *Gyrinomimus grahami* the haemal arch under the second anal pterygiophore was closed and the next 11 arches were open. Therefore the vertebral count was divided arbitrarily into preanal and anal vertebrae, with the first anal vertebra defined as that directly over the internal end of the first anal pterygiophore. The caudal complex, including the first preural and ural centra, was counted as the last single anal vertebra. Although the second preural vertebra, immediately before the caudal complex, usually carries double neural and haemal spines indicating fusion (see Rosen, 1973: figs 54, 55), these were counted as a single vertebra if only one centrum was apparent. The first vertebra is incomplete, lacking the broad anterior face typical of other centra where it articulates with the skull; it can usually be distinguished on x-rays by the presence of a neural spine.

In the gill raker or gill tooth plate counts the element in the angle of the arch is included in the count of the ventral arm, and all rudiments, even the smallest tooth plates, are included in the dorsal and ventral arm counts. In the tooth plate counts of the gill arches of *Cetostoma*, the individual tooth plates are recognisable and counted as separate even in the largest specimens where some fusion has begun. In contrast, plates are counted as one when partial fusion has begun in *Gyrinomimus* and *Cetomimus* where fusion eventually obliterates the original margins.

The lateral line pore count begins at the top of the gill slit and includes the last pore on the caudal fin base. More details are discussed in the section on the lateral line system.

Morphometric characters. A total of 20 body proportions was measured for each species and analysed as percentages of standard length. Although all measurements were made to 0.1 mm, and some critical measurements of distorted specimens were made on both sides and averaged, the accuracy of all but the smallest measurements is closer to 1 mm than 0.1 mm, due to the flabby nature and damaged condition of most specimens. For the new species in the four new genera, all specimens were measured. For the monotypic genera *Ditropichthys* and *Cetostoma*, at least 20 specimens of each were measured and analysed for allometric growth. For the genus *Cetomimus* 15 specimens representing at least six species were measured. The ranges of measurements for *Gyrinomimus* include data on 60 specimens representing eight species.

Shrinkage of fishes in preservative is well known and seems to affect cetomimids more than many others. No specimens were measured freshly caught, but numerous specimens were measured twice, at least for standard length, over a number of years and considerable shrinkage noted. A specimen of *Gyrinomimus grahami* was measured within six months of original preservation in 1964 and again 22 years later; the standard lengths were 227.5 mm and 202.8 mm, involving a shrinkage of 10.9%. It is possible that differential shrinkage occurs, with those proportions supported by bone (i.e. standard length) shrinking at a different rate than those not supported by bone (i.e. body depth) (S.H. Weitzman, personal communication, 2 Aug. 1988). In the absence of a detailed study over time, it is here assumed that all parts shrink proportionally and that ratios are not adversely affected provided all measurements are made in the same year.

The methods of measurement follow Hubbs & Lagler (1958), with the following exceptions or elaborations: lower jaw length (LJL) - from the anterior tip of the dentary to the posterior tip of the lateral spine of the lower jaw; posterior premaxilla to opercular margin (Pm-Op) - from the posterior tip of the upper jaw to the opercular margin at the level of the pectoral fin; eye width (EW) - from the centre of each eye; head width (HW) - from the bony projections of the sphenotics anterodorsal to each eye; postpremaxillary width (PmW) - from the posterior tip of each premaxillary; body depth (BD) - at the level of the pectoral base; anus to anal origin (An-AO) - from the centre of the anus to the base of the first anal ray.

Other abbreviations used in the tables are as follows: SL - standard length; HL - head length; SnL - snout length; PmL - premaxillary length; ED - eye diameter; D-A - dorsal origin to anal origin; CPD - caudal peduncle depth; CPL - caudal peduncle length; Sn-P - snout to pectoral base; PL - pectoral length; Sn-D - snout to dorsal origin; DB - dorsal base length; Sn-A - snout to anal origin; AB - anal base length; CopL - copular tooth plate length; CopL/W - copular tooth plate length to width ratio; D - dorsal fin; A -anal fin; P - pectoral fin; C - caudal fin; Vert. - vertebrae; LLSc - lateral line scales; GR - gill rakers or tooth plates.

Eye morphology. A number of authors have remarked on the small size of the eye in cetomimids, but few have studied the morphology in detail. Brauer (1908) described the eye of *Cetomimus gilli* (*C.* sp. *fide* Parr, 1928:176) based on microscopic sections. Harry (1952) stated that *Ditropichthys* had no eyes and only the optic nerve branches were present in the pigmented areas. Munk (1965) summarised the information on cetomimid eyes, described the eyes of *Gyrinomimus* and *Ditropichthys storeri* based on microscopic sections and showed that Harry's interpretation of the eye in *Ditropichthys* was erroneous. All of the three cetomimids studied had small, degenerate eyes. Brauer's (1908) *Cetomimus* had a rudimentary lens which was lacking in the specimens described by Munk (1965). Munk described a number of other degenerate features, including reduced or absent iris and acellular retinal pigment granules associated with the degenerate retina. The eye of *Gyrinomimus* was considered more degenerate than that of *Ditropichthys*, and it was suggested that the eye of this latter genus was probably fully differentiated before degeneration. Munk

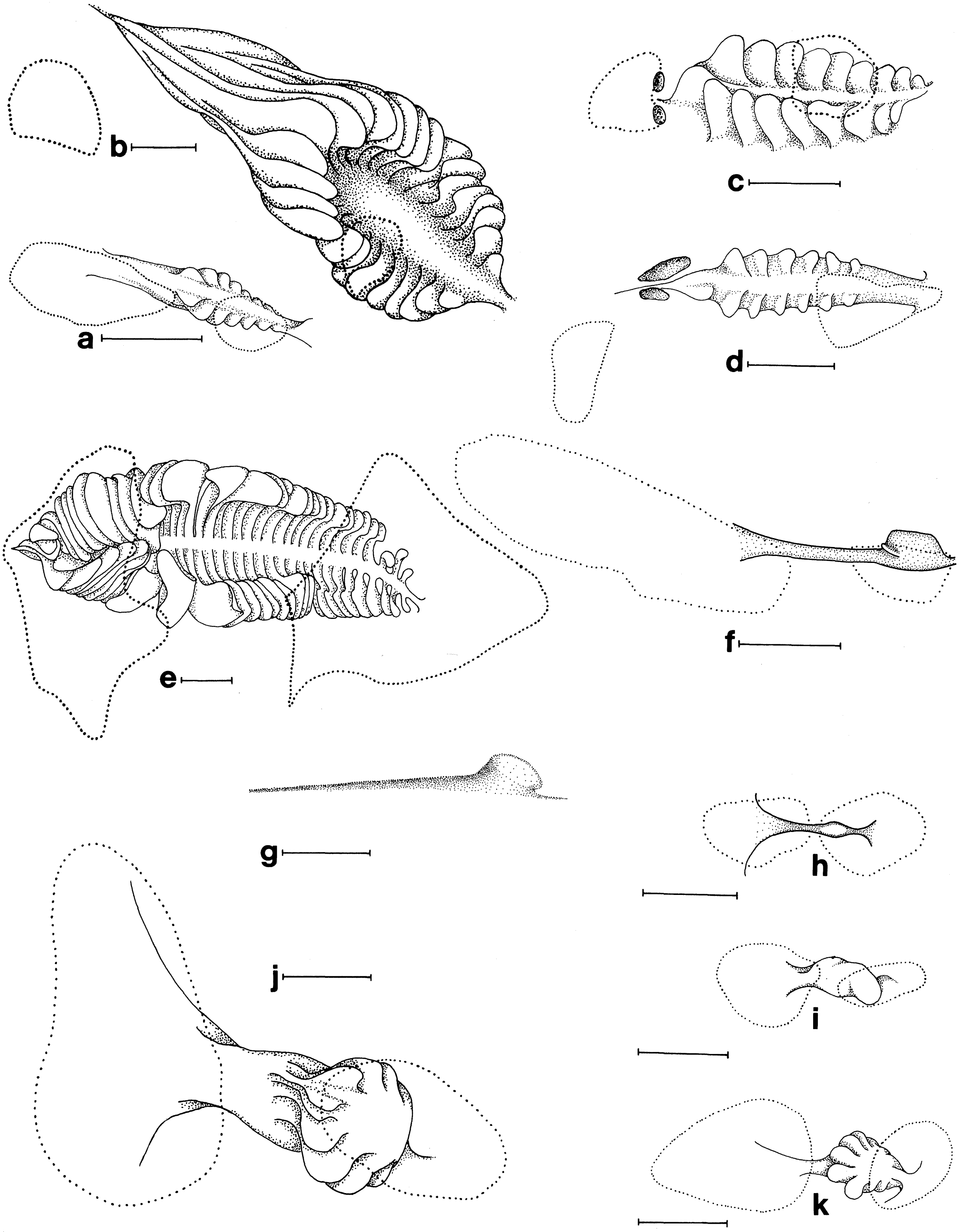

Fig.1. Nasal organs; nostrils shown with dotted lines; right side, anterior to right; scale bars equal 1 mm. a, *Barbourisia rufa*, 91.7 mm, AMS I.27260-001; b, *B. rufa*, 296 mm, ORSTOM New Caledonia; c, *Rondeletia bicolor*, 59.9 mm, AMS I.18415-001; d, *R. loricata*, 82 mm, AMS I.18814-001; e, *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71; f, *Ditropichthys storeri*, 84.4 mm, AMS I.18816-001; g, *Cetichthys parini* paratype, 96.0 mm, AMS I.27258-001; h, *Danacetichthys galathenus* paratype, 53.9 mm, NSMT P60002; i, *Rhamphocetichthys savagei*, 110 mm, ISH 2297/71; j, *Gyrinomimus* sp. D, 151.0 mm, AMS I.20314-010; k, *Cetomimus* sp. A, 79 mm, AMS I.20524-001.

(1965:28) concluded that light detection might be possible in the degenerated retinas.

No comparative microscopic sections were attempted in this study. Although Munk (1965:21) warned that ocular degeneration can only be studied seriously by histological methods, some comparative observations are made here. The relative size of the eye is easily measured with calipers under a dissecting microscope, and the horizontal diameter is given in this study as a percentage of standard length. While very small eyes of fishes can be functional (e.g. female ceratioid anglerfishes, Munk, 1965), none of the degenerated eyes described in previous studies were moderate or large in diameter. A second feature that is discernible without histology is the presence of a lens. The two states reported here (lens present or absent) are based on examination under a dissecting microscope.

Nasal organ. In all cetomimids there are two nostrils on each side of the head, located about halfway between the eye and the tip of the snout. The anterior nostril is usually about half the size of the posterior nostril and the skin bridge between the nostrils about half the size of the anterior nostril. In the only specimen of *Procetichthys* the nostrils are much larger than the head pores of the lateral line system and the olfactory epithelium is developed into a large nasal organ consisting of a central raphe and fully developed lamellae on each side, almost filling the nasal cavity (Fig. 1e). In all other cetomimids both nostrils are smaller, about equal in size to the head pores, and the nasal organ is greatly reduced, usually consisting of a raised area of olfactory epithelium, presumably homologous to the central raphe, but without lamellae (Fig. 1f--i). In some species of *Gyrinomimus* and *Cetomimus* a spherical mass of olfactory epithelium arises from a ventral ridge and low, thin lamellae are found around the sphere (Figs 1j,k). Kleerekoper (1969:50) summarised data on the number of lamellae for a variety of species and pointed out that both the number of lamellae and their size increase with age. Lamellae were absent in a number of cetomimid taxa that were represented only by juveniles, as indicated by their immature gonads.

Dentition. Three different arrangements of teeth are found in cetomimid jaws. In most genera the teeth are very small and closely set in approximately diagonal rows and are either conical or triangular in shape (Fig. 2b,d-f). In *Gyrinomimus* and *Danacetichthys* the teeth are small and closely set, but are in longitudinal rather than diagonal rows (in all but one species) and are distinctly elongate, with the older teeth more than three times longer than wide at the base (Fig. 2c). The teeth of *Procetichthys* are widely spaced in 1-2 longitudinal rows and while elongate, are distinctly more pointed than those of *Gyrinomimus*, almost approaching canines in shape if not in size (Fig. 2a).

In *Gyrinomimus*, new teeth are added both to the outer edge of the jaws, as additional rows, and at the posterior of the jaws, as additional series of rows. The inner row of teeth is always the longest, indicating continual growth of teeth. In some specimens, these new, shorter teeth are not fully calcified and are soft and flexible under a probe. In a very few specimens of *Gyrinomimus* all of the jaw teeth (and palatal teeth as well) are decalcified, soft and flexible, as if some basic chemical reorganisation were taking place; the condition is not correlated with size or preservation history.

In almost all species, teeth are also found on the vomer, palatine, ectopterygoid, copula, and four gill arches. These teeth, particularly those on the gill arches (Fig. 3), are similar to but smaller than the jaw teeth. All of these bones also add teeth with growth. Previously the number of tooth rows in the jaws and vomer has been used as a diagnostic character, particularly for species of *Gyrinomimus*. However the number of tooth rows increases with size; the number of vomerine tooth rows ranges from two to eight in *G. grahami* from 68 to 282 mm SL (Paxton, ms).

All of the teeth are depressible towards the centre of the

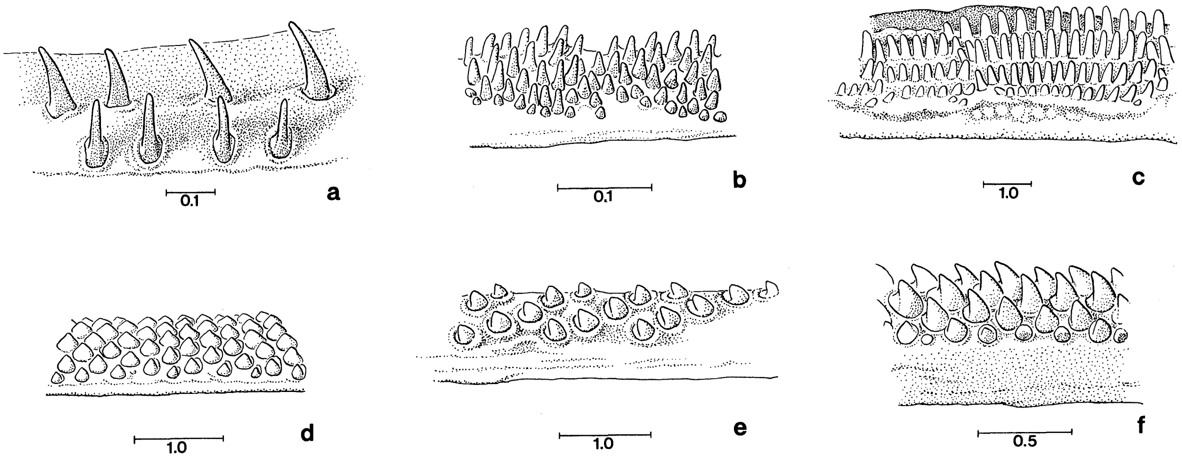

Fig.2. Premaxillary teeth; right side, anterior to right; scale bars in mm; a, *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71; b, *Cetichthys parini* paratype, 96.0 mm, AMS I.27258-001; c, *Gyrinomimus* sp. D, 151.0 mm, AMS I.20314-010; d, *Rhamphocetichthys savagei* paratype, 90.8 mm, LACM 30034-11; e, *R. savagei*, 110 mm, ISH 2297/71; f, *Cetomimus* sp. A, 116.7 mm, LACM 11500-1.

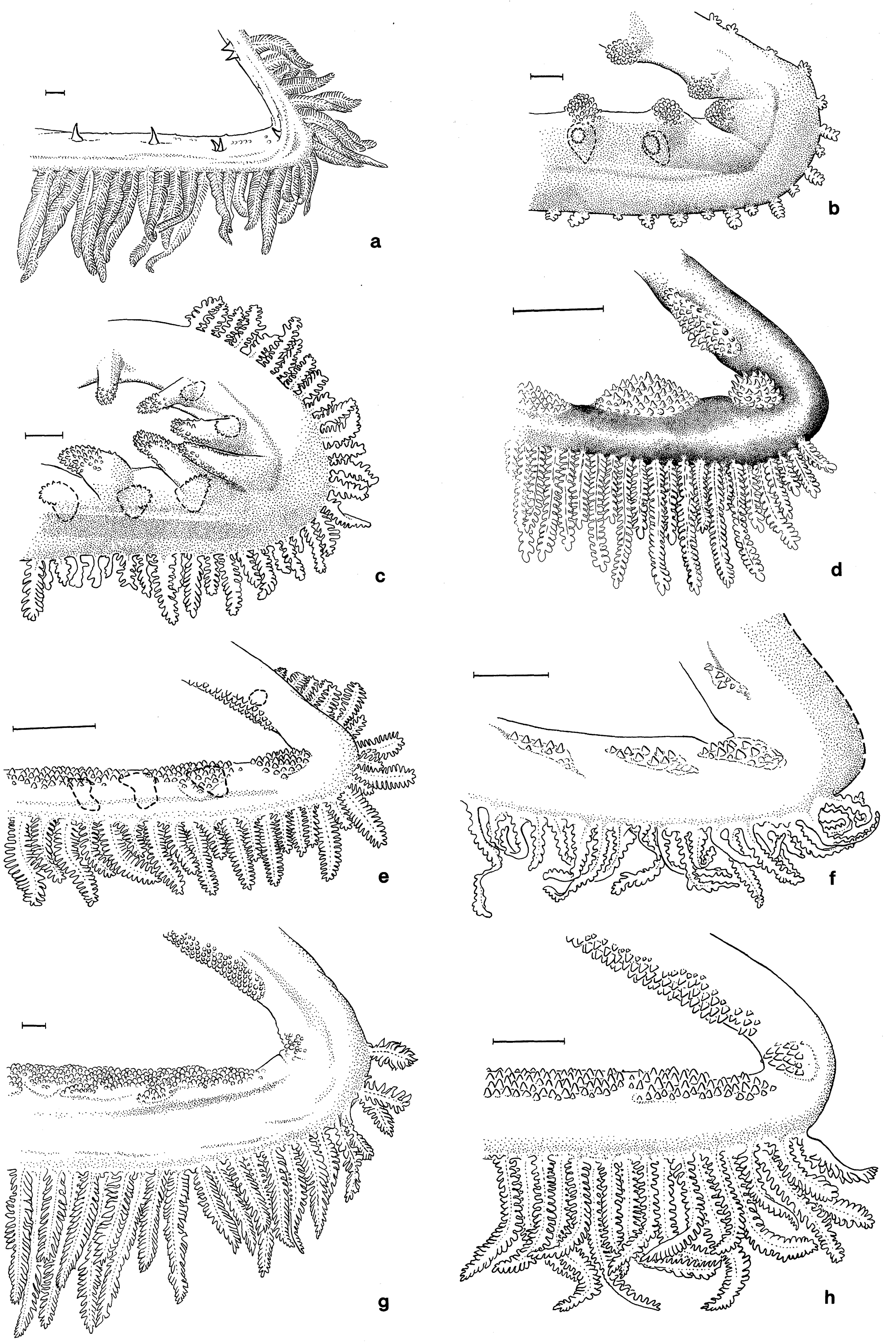

Fig.3. First gill arches; lateral view, left side, anterior to left; medial tooth plates shown with dashed lines; scale bars equal 1 mm; a, *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71; b, *Cetichthys parini* paratype, 96.0 mm, AMS I.27258-001; c, *Ditropichthys storeri*, 84.4 mm, AMS I.18816-001; d, *Danacetichthys galathenus* paratype, 53.9 mm, NSMT P60002; e, *Cetostoma regani*, 83.5 mm, ZIN 47884; f, *Rhamphocetichthys savagei* paratype, 90.8 mm, LACM 30034-11; g, *Gyrinomimus* sp. J, 231.3 mm, ZIN 47889; h, *Cetomimus* sp. A, 79 mm, AMS I.20524-001.

oral cavity, except the non-depressible jaw teeth of *Procetichthys*. Fink (1981) has differentiated four types of tooth attachment, with three types involving depressible teeth. In a 141 mm SL cleared and stained specimen of *Gyrinomimus grahami*, there is a large area of unmineralised tissue (presumably collagen) on the oral (posterior/medial) side of the base of each tooth. On the labial (anterior/lateral) side the base meets the underlying jawbone. It is not clear whether there is a thin layer of unmineralised tissue over the labial side of the base, but the hinge appears to involve primarily the tissue on the oral side, indicating a type 4 tooth attachment. The jaw teeth of *Gyrinomimus* can be depressed to an angle approaching 90°. Of the other cleared and stained specimens, only *Cetomimus* has teeth large enough to determine that tooth attachment is also probably type 4.

Gill arches. Elements of five gill arches are present in all cetomimids, with the fifth only visible in a few genera as ventral pharyngeal tooth plates. In most genera, four free gill arches are apparent, with a small to moderate gill slit behind the ventral arm of the fourth arch. The dorsal arm of the fourth and usually the third arches are bound in the skin of the gill chamber. In three genera there is no slit behind the fourth gill arch and only three free arches are present, while in *Cetostoma* the slit is in the form of a small tubular opening behind the angle of the fourth arch.

A range of gill raker types is displayed by the family, from fully developed club-shaped rakers of *Ditropichthys* (Fig. 3c), to the toothed knobs of *Cetichthys* (Fig. 3b) and *Notocetichthys* (Fig. 19c), the individual gill teeth of *Procetichthys* (Fig. 3a) to the tooth plates, either individual or coalesced, of the other genera (Figs 3d-h). Tooth plates are present on the medial face of the first arch in some genera. Gill rakers or tooth plates are present on arch two and three in all genera except *Rhamphocetichthys*.

The shape and extent of the holobranchs are also variable. The two species of *Cetichthys* are extraordinary in having greatly reduced holobranchs (Fig. 3b). The extent of the dorsal arm of the various arches that bears holobranchs is variable. While the holobranchs on the first three arches are fully developed, except in *Cetichthys*, those on the fourth arch are large in some taxa and tiny in others.

There are two pairs of upper pharyngeal tooth plates, associated with the pharyngobranchials of arches three and four. As with the jaw and vomerine teeth, the individual numbers of teeth on the upper pharyngeals, and copula, have been considered important in previous descriptions. However as with the jaws and palate, tooth numbers increase with growth, and individual counts have not been included here. Although the copular tooth plate adds teeth with growth, allometry is uncommon and the relative length differs significantly amongst genera. The size and shape of the copular tooth plate are shown in the individual species drawings (Figs 10, 13, 18, 19, 20, 21, 26, 27, 28). The shape of this tooth plate, expressed as a length/width ratio, differs between species, particularly within *Gyrinomimus*. Functionally the pharyngeals and copular tooth plate do not act as a grinding or crushing organ as they are not directly opposed. Rather food items are apparently moved posteriorly as the copular tooth plate presses against the edentate roof of the mouth behind the vomer and the upper pharyngeals press against the edentate floor of the mouth behind the copula. The lower pharyngeals, when present, are located behind the level of the upper pharyngeals. In contrast to all other genera, *Notocetichthys* has the dorsal pharangeals oriented medially rather than ventrally, so the tooth plates of either side move against each other. Perhaps this is related to the edentate condition of the rest of the palate in this genus.

Lateral line system. The lateral line system is well developed and in all genera, except *Rhamphocetichthys*, consists of a series of wide head canals pierced by large pores in the skin forming the roof of the canals, with receptor organs, the neuromasts, in the floor of the canal between the pores; a large trunk canal is present in all but two genera. The various head canals lie on top of dermal head bones, but the sides and top of the wide canals are formed by skin. The various dermal bones are flat, without raised edges, and do not form the bony troughs typical of many beryciform and stephanoberyciform fishes (see Ebeling & Weed, 1973). The basic pattern of head canals is that typical of teleost fishes, with a continuous canal (supraorbital plus main) extending from the tip of the snout to the top of the gill slit where it becomes the main trunk canal in all genera except *Procetichthys* and *Rhamphocetichthys*, one branch behind and under the eye (infraorbital) and another down the preopercle (preopercular) and along the lower jaw (mandibular). The nomenclature of the various canals follows Coombs *et al.* (1988). The number and arrangement of pores, as well as the connections and cross connections between the main branches, differ between species and genera (Fig. 4). In some species the head is damaged so that connections between canals could not be determined. In *Rhamphocetichthys* no canals or pores are evident; rather, a series of large papillate neuromasts are present and what appear to be nerves, just under the surface of the skin, follow the typical canal pattern (Fig. 4g).

Coombs *et al.* (1988) have summarised the diversity of canal variation in fishes. Their nomenclature for the canals is used here, with some modification. The supraorbital, infraorbital, mandibular and preopercular canals are easily identifiable in cetomimids. However the three portions of the main canal between the juncture of the supraorbital and infraorbital branches and the beginning of the main trunk canal just dorsal to the top of the gill opening are not clear in whalefishes. The three portions, the otic, postotic and temporal canals, are distinguished by their innervation and defined by the junctures of the preopercular and supratemporal canals with the main canal (Coombs *et al.*, 1988, fig. 22.11). In cetomimids, the preopercular canal does not join the main canal, and the distinction between otic and postotic canals cannot be determined externally, while the temporal canal posterior to the supratemporal branch is absent in at least *Cetichthys* (Fig. 4c). Therefore in the following discussion these three portions of the main canal

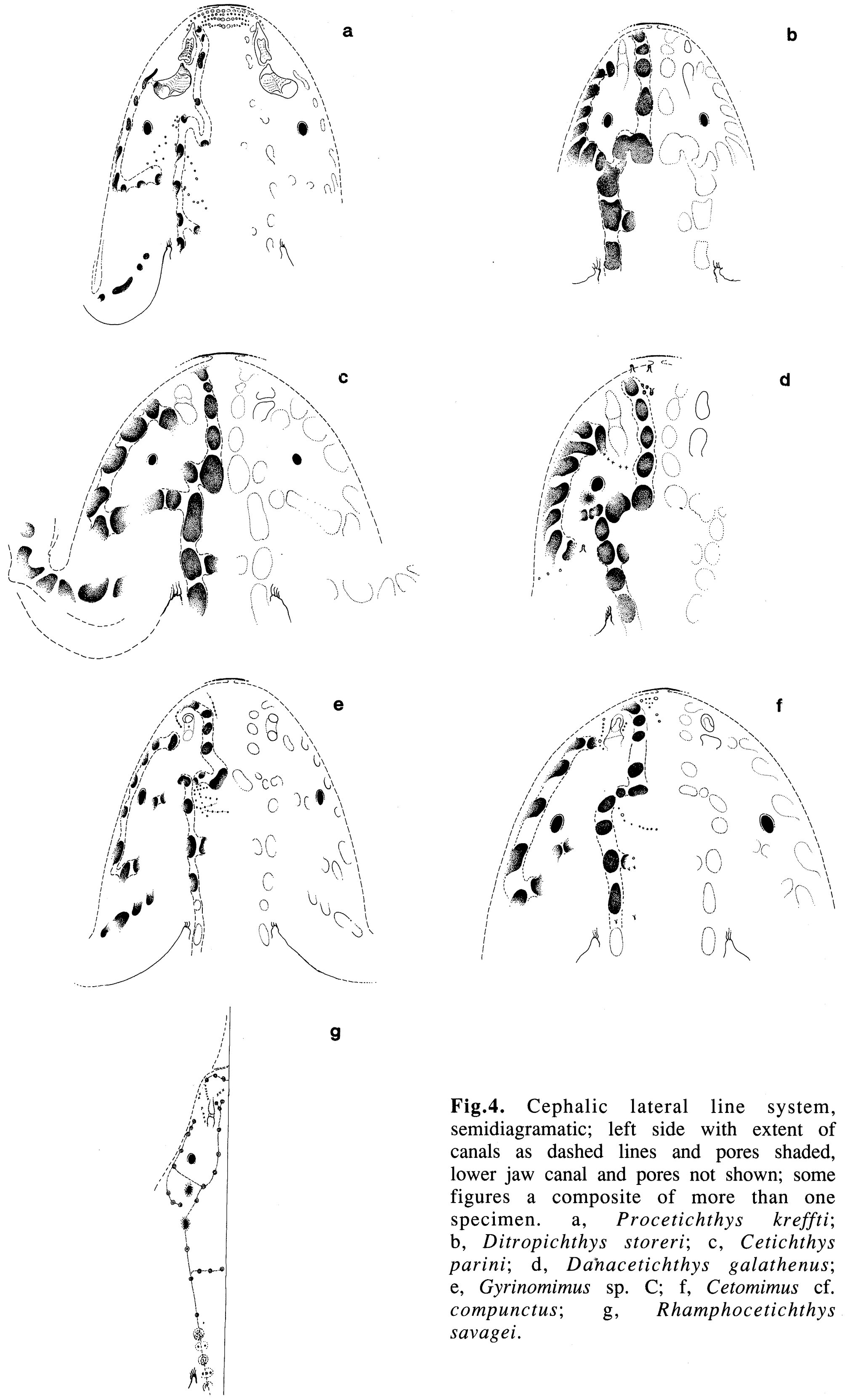

Fig.4. Cephalic lateral line system, semidiagramatic; left side with extent of canals as dashed lines and pores shaded, lower jaw canal and pores not shown; some figures a composite of more than one specimen. a, *Procetichthys kreffti*; b, *Ditropichthys storeri*; c, *Cetichthys parini*; d, *Danacetichthys galathenus*; e, *Gyrinomimus* sp. C; f, *Cetomimus* cf. *compunctus*; g, *Rhamphocetichthys savagei*.

are not distinguished. Because the infraorbital canal does not join the supraorbital canal in all cetomimid genera, the division between supraorbital and main canals is occasionally subjective. In *Cetostoma*, *Gyrinomimus* and *Cetomimus* the supraorbital canal (with six to seven pores) is not joined to the main head canal (Fig. 4e,f).

The supraorbital canal runs from the tip of the snout, anteromedial to the anterior nostril, along the dorsal midline to the fifth pore (the coronal pore of Fedorov & Balushkin, 1983:741), then curves laterally about the level of the eye for one or two pores. The first two supraorbital pores are usually smaller than average and the fifth pore is the largest of the series. The fifth pore is separated from that on the other side of the dorsal midline by a narrow or wide strip of skin. In those genera with the largest head canal pores (*Ditropichthys*, *Cetichthys*, *Danacetichthys* and presumably *Notocetichthys*), the infraorbital canal joins the supraorbital canal at or just behind the lateral curve of that canal, thus restricting the supraorbital to six pores (Fig. 4b-d). In *Procetichthys*, the infraorbital approaches the supraorbital further posterior (Fig. 4a).

The main canal includes two to five pores, with a single pore, representing the supratemporal branch, lying medial to the second or third pore of the main canal. The short supratemporal branch does not reach the dorsal midline in any cetomimid. The total number of pores in the combined supraorbital and main canals ranges from eight to 12.

The infraorbital canal has seven to ten pores, with the first posterolateral to the nostrils. The next four to five pores are under the eye just above the upper jaw, before the canal turns dorsal and somewhat anterior behind the eye. Only in *Cetichthys* is the infraorbital canal continuous with the main canal; these are joined at main canal pore 1 with a small but distinct skin bridge over infraorbital neuromast 8. In *Ditropichthys* there is no remnant of a skin bridge in any specimen, although there is a neuromast between infraorbital pore 8 and main canal pore 1. In all other genera the canals are separate or the condition is unknown. In *Gyrinomimus* and *Cetomimus* the last infraorbital neuromast is usually displaced dorsally and/or anteriorly so the last segment of the canal is separate and either the seventh or eighth pore has two parts that appear as separate, half moon-shaped pores; however these are counted as a single pore so there is always one more pore than neuromast in the infraorbital series (except for *Cetichthys* and *Ditropichthys* where a neuromast follows the last pore, and *Procetichthys* where a neuromast precedes the first pore). Even in the genera with infraorbital canals joining or approaching the main canal, there is a considerable distance between the last two infraorbital neuromasts and the third before the end, but not in *Cetostoma* where the last organ is close to and directly above the penultimate neuromast of the infraorbital series.

The mandibular canal runs along the ventral sheet of the dentary and articular and has five to eleven pores (more than eight only in some species of *Gyrinomimus* and *Cetomimus*) and four to ten neuromasts. The last pore is located just anterior to the ventral spine at the posterior end of the lower jaw. In all but three genera the mandibular canal is separate from the preopercular canal. In *Notocetichthys*, *Gyrinomimus* and *Cetomimus* the two canals are joined, with a neuromast between the two adjacent pores. The first, ventralmost preopercular pore is defined as the one immediately posterior to a line joining the lateral and ventral spines of the lower jaw. The preopercular canal begins just behind the posterior edge of the lower jaw and runs dorsally behind the posterior tip of the premaxilla, usually to the level of the eye; the preopercular canal does not join the main canal in any species of cetomimid. The preopercular canal has four to five pores and three to four neuromasts in all cetomimids except some species of *Gyrinomimus*; in one undescribed species there are three neuromasts but two or all three of the overlying skin bridges are undeveloped.

The lateral line system on the trunk in all genera except *Procetichthys* and *Rhamphocetichthys* consists of a wide canal sloping gradually from the top of the gill opening to the base of the caudal fin posterior to the hypural bones. This type of main trunk canal is the complete (straight) pattern, considered primitive for teleost fishes (Webb, 1989). The canal is pierced by a series of large pores (that are often smaller on the posterior third of the canal), which differ in number and shape among taxa. The largest pores are as wide as the lateral line canal and can be so extensive that the canal is reduced to a series of small bridges of skin over the lateral line neuromasts and scales; in a few species the posterior pores are less than one quarter the width of the canal. The last pore, however, is usually as wide as the tube itself. Various keels and flaps project from the lateral wall of the canal between pores in some species of the genera *Cetomimus*, *Gyrinomimus* and *Cetostoma*, and can be quite extensive. The pores, flaps and superficial neuromasts are best observed with the specimen submerged in liquid.

A series of small to large, thin scales lies in the floor of the lateral line canal. The number of scales and overlying neuromasts is one less than the number of lateral line pores, as one scale is present in the area between two pores. The pore counts were determined by counting scales and adding one when the lateral wall of the canal was lost. The shape of the scales differs among taxa, with the most elaborate scales in *Cetomimus* and *Gyrinomimus* having dorsal and ventral projections that support the sides of the lateral line canal (Fig. 5c). The entire series of scales were examined in each of the cleared and stained specimens and a section of lateral line canal containing three or four posterior scales was removed from at least one specimen of most genera and cleared and stained. The scales begin just behind the supracleithrum and extend the length of the canal to just anterior to the terminal pore. All of the scales are thin and weakly ossified, although the posterior scales are somewhat more ossified than the anterior scales in some species. None of the cephalic canals have scales (although most of the circumorbital bones underlying the infraorbital canal are similar to the lateral line scales, with a median foramen). Each lateral line scale is pierced by a median foramen, through which runs a branch of the underlying lateral line nerve. The neuromasts sit on top of the scales in

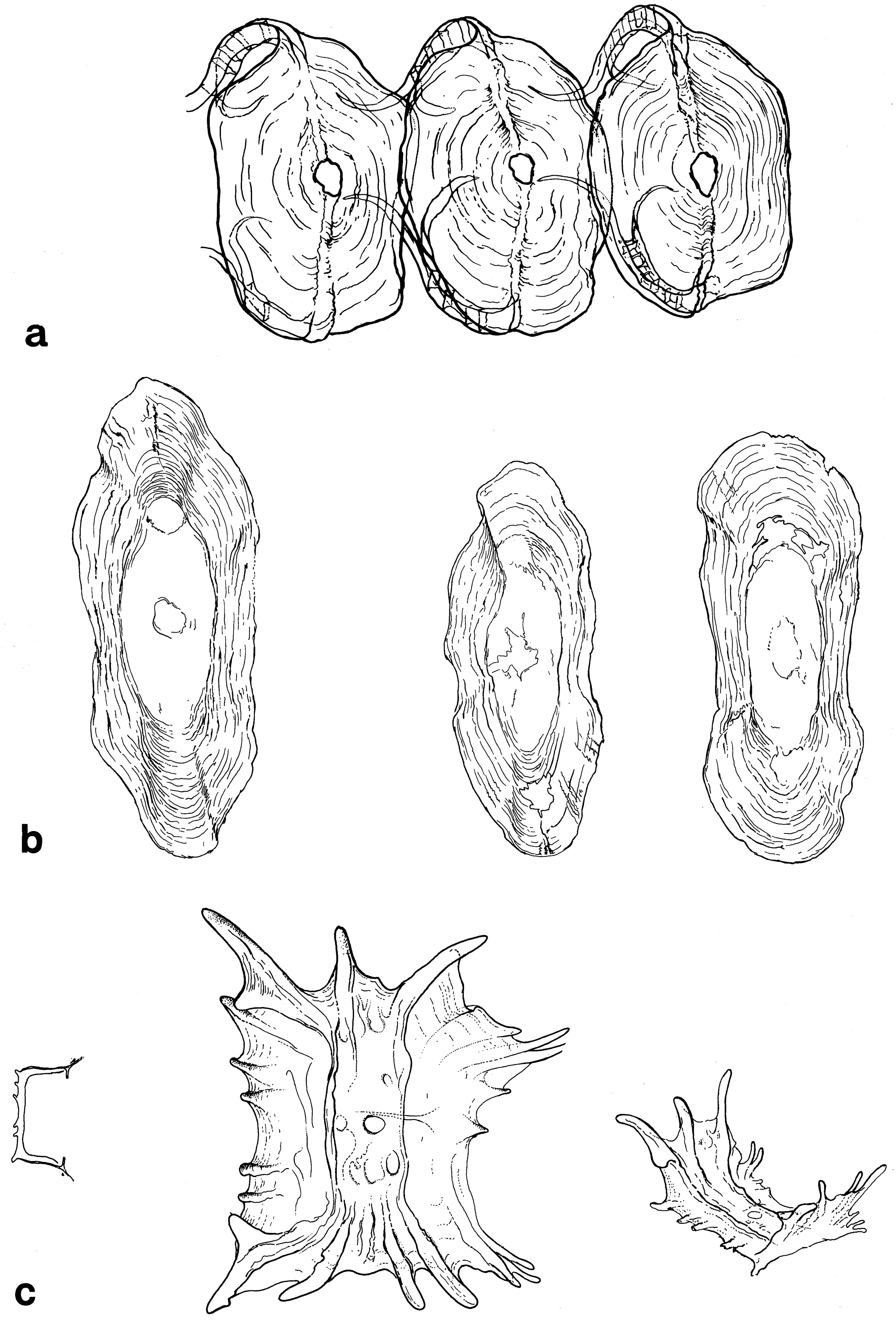

Fig.5. Lateral line scales; a, *Barbourisia rufa*, 133 mm, AMS I.27261-001, medial view of left scales 29-31, anterior to left; b, *Ditropichthys storeri*, 83 mm, AMS I.18821-001, lateral view of left scales 10-12, anterior to left; c, *Gyrinomimus* sp. B, 358 mm, ISH 1115/79, posterior, lateral and three-quarter views of right scale 19.

the floor (median wall) of the lateral line canal. These internal lateral line scales are not similar to the external lateral line scales found in most bony fishes, as the lateral line canal runs over the entire scale, not through a pore in the scale.

In *Procetichthys* and *Rhamphocetichthys* no lateral line canal is present on the body. The lateral line consists of vertical rows of papillate superficial neuromasts, from one to many in the former genus (Fig. 6b) and usually three in the latter. In both genera a series of buried scales underlie the papillae.

Numerous large and small papillae are found in various regions of the head, trunk and caudal fins. These appear to be papillate superficial neuromasts, of which the distribution and nomenclature have been summarised by Coombs *et al.* (1988); their nomenclature is based on innervation and position and is adopted here. It has not been possible to compare the cephalic superficial neuromasts in all cetomimid genera, because of their fragile nature; they seem to be one of the first features lost when whalefishes are abraded in the net. Some generalities are possible, based on those genera with undamaged specimens. One to four rows of papillae cross the snout, representing either or both the supraorbital rostral replacement line and/or the rostral fork replacement of the infraorbital canal line (Coombs *et al.*, 1988: fig. 22.11, tables 22.3-4). A row of papillae from the posterior nostril to above the eye represents the supraorbital accessory line. A vertical row of widely spaced superficial neuromasts anterior to the preopercular canal may represent the dorsal and/or median mandibular lines, while papillae on the posterior lower jaw dorsal to the mandibular canal presumably represent the ventral mandibular line. Opercular papillae appear to represent the dorsal and ventral opercular lines. A small row of papillae anterior to or in the first pore of the mandibular canal is the rostral mandibular replacement line. Scattered groups of superficial neuromasts are typically present medial to the main canal and posterior to the fifth supraorbital canal pore; a study of innervation will be required to establish which of the four possible lines are represented.

The papillate superficial neuromasts on the body are in fewer groups and display less variation than those on the head. A dorsal trunk line appears to be present in all taxa, extending from the back of the head just below the dorsal midline to near the dorsal fin origin. In some species the line of neuromasts is so close to the dorsal midline, with neuromasts from the other side alternating in position, that they appear to form one wavy line posteriorly. The total number of neuromasts ranges from less than ten to more than 30. Papillate superficial neuromasts are also associated with the main trunk canal in all taxa where the latter occurs. Papillae are present on the dorsal and/or ventral margins of the lateral line pores, usually two or less per pore, and on the skin bridges between pores where these are large and well developed. The distribution patterns of superficial neuromasts on the lateral line canal differ among taxa. Finally there is a curved row of papillae on the basal quarter of the caudal fin behind the posterior opening of the lateral line canal. This caudal line of neuromasts, varying from less than one to about one organ per fin ray, usually extends from the top quarter to the bottom quarter of the fin and is present in all taxa.

Cavernous tissue. Harry (1952:57, 58, 70, fig. 2) first described the cavernous tissue in cetomimids. The tissue was considered luminous because of its similar appearance to the luminous caudal organ of *Saccopharynx harrisoni* (Beebe, 1932). Harry (1952) suggested that the cetomimid cavernous tissue secretes a mucous layer which covers most of the head and body with red luminescence. Unfortunately no cetomimid has been captured alive to confirm this hypothesis. Nielsen & Bertelsen (1985) described and figured the caudal organs of all nine species of *Saccopharynx* and figured a microscopic section of the caudal luminous organ of *S. ampullaceus*. Based on the single observation of luminescence in a living specimen of *S. harrisoni* by Beebe (1932), dorsal and ventral photogenic

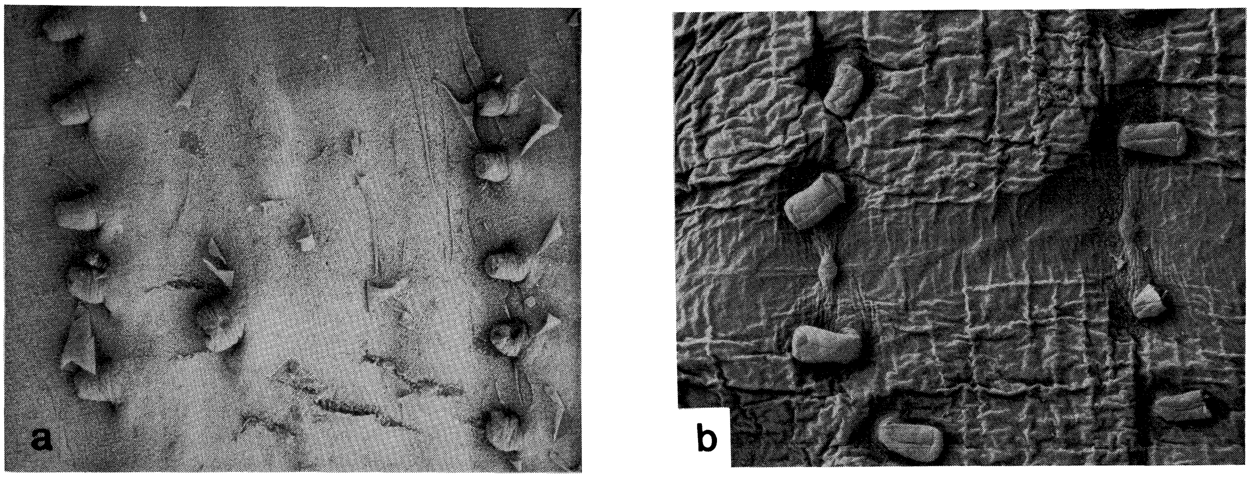

Fig.6. Lateral line neuromasts, right side, anterior to right; a, *Rondeletia loricata*, 83 mm, AMS I.21141-001 (flaps of skin = artefacts of preparation); b, *Procetichthys kreffti*, 236 mm, ISH 1188/71, magnifications approximately 25x; SEM photos D. Hughes, University of Sydney.

tubules with photocytes were identified by Nielsen & Bertelsen (1985), but no reflective tissue nor pigment in the walls of the tubules were found.

Cavernous tissue was dissected from around the anus of *Cetomimus* sp. J and *Gyrinomimus bruuni* and stained and sectioned by Ole Munk of ZMUC; his conclusion was "epidermal tissue of unknown function." The tissue is glandular, with tubules or lobules, but is not microscopically similar to that of *Saccopharynx* (Fig. 7; Nielsen & Bertelsen, 1985: fig. 9). With no evidence that the tissue is luminescent, it is here termed simply cavernous tissue.

Cavernous tissue is developed at least anterolateral to the anus (or the urogenital papilla in *Cetichthys* and *Notocetichthys*) in all cetomimids except *Procetichthys* and *Rhamphocetichthys*. The tissue is most extensive in some species of *Gyrinomimus*, where it may extend over the anal (Fig. 26) and/or under the dorsal fin bases and posteroventral to the pectoral fin base, and *Cetomimus*, where it may occur on the caudal peduncle (Fig. 27), the isthmus, and in one undescribed species as a patch posteriorly on the upper jaw. In *Ditropichthys* an additional small area is present just anterior to the upper portion of the caudal fin.

The cavernous tissue appears more sharply defined and more clearly organised in smaller specimens of all taxa. Within the area around the anus, the cavernous tissue is organised in a series of diagonal rows that are best seen in small specimens of *Danacetichthys*; within each row appear a series of small bundles or tubules (Fig. 20b). In *Gyrinomimus* sp. B, the four known specimens range from 63 to 356 mm SL. While the cavernous tissue covers a larger area in the largest specimen, it is also more superficial and seems to lack the deeply set bundles of white tissue found in the smaller specimens.

Anal lappets, ridges, folds and curtains. A continuous fold of skin hangs over the base of most of the anal fin of *Ditropichthys storeri*. Rofen (1959: 258) mentioned four small lappets over the anterior portion of the anal fin base of *Gyrinomimus bruuni*. These two structures are homologous, being either separate or joined flaps of skin with internal supporting scales originating over the anal fin base, and are here termed the anal lappets. In *Ditropichthys* the anal lappets are continuous, with the outer edge scalloped (Fig. 13). However the internal supporting scales are widely spaced and approximate one per anal ray (Fig. 9). In *Cetostoma* the anal lappets are continuous basally but deeply scalloped distally for about half their width, where they approximate the width of the internal scales (Fig. 21b). In the three other genera where anal lappets occur at least in some species, *Cetichthys*, *Rhamphocetichthys* and *Gyrinomimus*, the lappets are either widely spaced or joined only at the bases (Figs 18b, 26b, 28c). The scales themselves are elongate and very weakly ossified, being thinner and holding less stain than the lateral line scales. In *Cetostoma* the lappets are highly

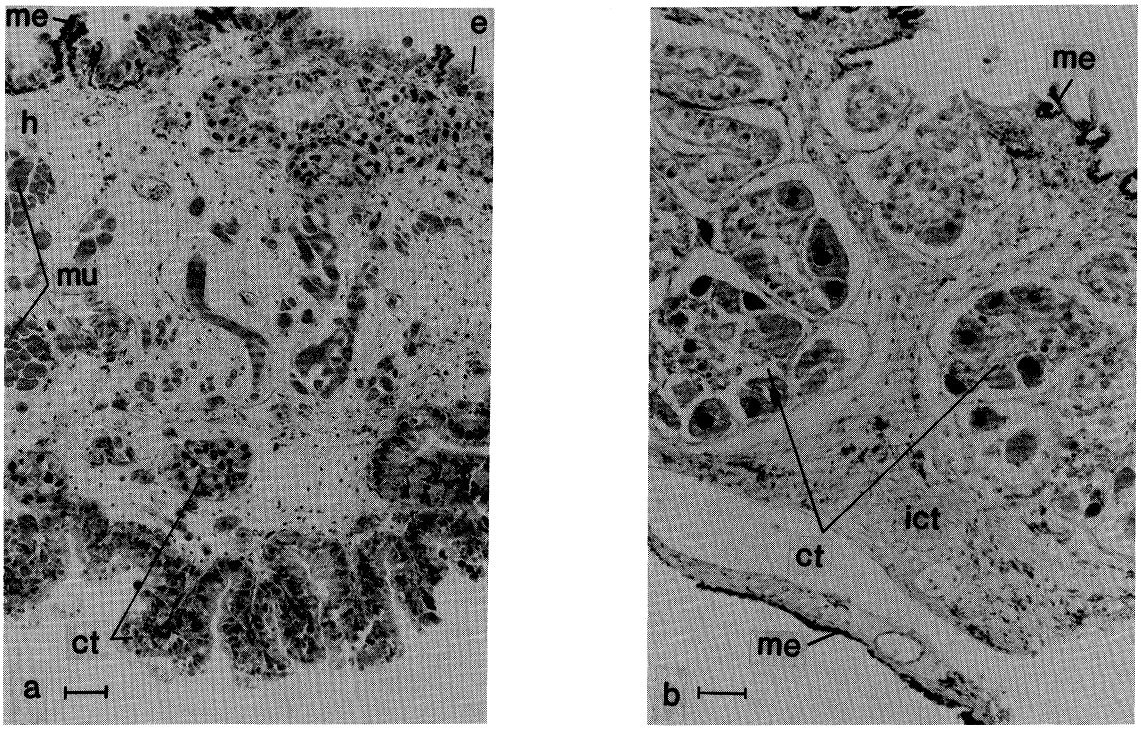

Fig.7. Section of cavernous tissue near anus, stained with haematoxylin and eosin; a, *Cetomimus* sp. J, 90 mm, ZIN 47895; b, *Gyrinomimus bruuni*, 118 mm, AMS I.26870-001; scale bar = 0.1 mm; ct - cavernous tissue, e - epidermis, h - hypodermis or connective tissue, ict - interstitial connective tissue, me - melanophores, mu - muscle; photos R.J. Oldfield, Macquarie University.

vascularised, with numerous presumed blood vessels lateral to the scale (Fig. 21c). In some species of *Gyrinomimus* the cavernous tissue is associated with the anal lappets, extending posteriorly above the anal fin at the base of the anal lappets (Fig. 26b).

The range of number of anal lappets is relatively constant for species, at least in the genus *Gyrinomimus*. In three species the numbers range from ten to 14 (4 specimens), three to six (9 specimens) and four to nine (12 specimens); the number of anal lappets does not increase with size. Unfortunately the lappets are very fragile and easily torn off in capture. None of the 150 specimens of *Cetostoma* had a complete set, and the internal scales of *Ditropichthys* are so thin they can only be counted with assurance if they are cleared and stained with alizarin. In those species with separate anal lappets, small tears in the skin at the anal base are thought to represent the scars of lost lappets. These structures, like the details of the lateral line canal, are best viewed with the specimen submerged in fluid.

In some specimens the anal lappets appear to originate on a low thin ridge of skin. In some instances the ridge may be an artefact of preservation, as the flabby skin is easily moved over the side of the body. In other cases the low ridge is the ventral margin of the cavernous tissue. In a number of specimens of *Cetomimus*, a low, thin skin ridge is present over the anal base, but no anal lappets have been found in any species. In many specimens of this genus tiny ridges run bilaterally down the anterior anal rays. In a few specimens a series of low ridges are present on the membrane between each anterior ray, perpendicular to the rays. These will be described in more detail in the revision of *Cetomimus*.

The skin ridges on the belly of *Cetostoma* do not extend to the anal fin and appear to be associated with the cavernous tissue (Fig. 21c). The diagonal skin ridges of *Notocetichthys* are associated with the middle portion of the lateral line. The two belly keels of *Ditropichthys* are not superficial organs of the skin, but internally based structures.

The posterior portion of the anal fin of *Cetostoma* is voluminous, with extra membrane between the rays creating curtain-like folds. Some vessel-like internal structure within the curtain is apparent.

The function(s) of these unique features remain(s) unknown. The vascularisation of the anal lappets in *Cetostoma* suggests respiration. However vessels are not apparent in other taxa, where in some cases an association with cavernous tissue is indicated. Experimentation with live specimens would help solve the puzzle of these enigmatic structures.

Subpectoral organ. Anteroventral to the pectoral base in *Rhamphocetichthys* is a darkly pigmented structure lying beneath the surface of the skin. In the holotype a pore through the skin appears to be present. This organ is only visible when the overlying skin has faded to a lighter brown, with the organ remaining a darker brown. The subpectoral organ was present in the best preserved

Fig.8. Section of ovary, stained with haematoxylin and eosin; a, Right bladder and ovary, posterior end near junction, *Gyrinomimus grahami*, 310 mm, ISH 398/76(1); b, Posterior ovary, *Ditropichthys storeri*, 112 mm, ISH 607/74; scale bar = 0.1 mm; e - developing eggs, lb - lumen of bladder, lo - lumen of ovary, me - melanophores; photos R.J. Oldfield, Macquarie University.

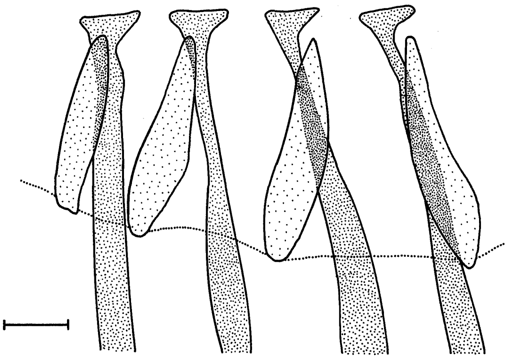

Fig.9. Anal lappet scales over anal rays 3-6, left side, anterior to left, scale equals 1 mm, *Ditropichthys storeri*, 112 mm, AMS I.27260-001.

specimens of *Danacetichthys* and only in some small specimens of *Cetostoma* and some species of *Gyrinomimus* and *Cetomimus*. It appears best developed in the smaller specimens and does not proportionally increase in size with growth. No indication of an open pore is present in larger specimens. Sectioning of the subpectoral organ from specimens specially fixed upon capture will be required to determine details of its structure and function.

Internal anatomy. Most specimens were dissected to examine gonads. The length of the gonad was measured *in situ* with dial calipers under a dissecting microscope, and the widest point, usually near the anterior end, was occassionally measured; both measurements are accurate only to 0.5 mm. The size of eggs was noted, usually measured with an ocular micrometer, as well as any distinctive features. Routine examination of numerous specimens failed to reveal any obvious males.

Gonads and associated tissues of eight specimens representing four genera and species were embedded, sectioned and stained with haemotoxylin and eosin. All but one of the specimens were at least half of the maximum size recorded for the species, ranging from a 59 mm *Ditropichthys storeri* to a 310 mm *Gyrinomimus grahami*. In every case the gonads were ovaries, with eggs in various stages of development (Fig. 8). Sections were made through all areas of the gonads and no testicular tissue was found. Microscopic examination up to 50 times magnification of numerous dissected specimens, including almost the full size ranges in *Ditropichthys* and *Cetostoma*, failed to reveal any obvious male gonads. Future study will section the gonads of specimens in the smaller half of the size range before hypothesising on where the male cetomimids may be hiding.

One structure that resembled a testis was found to be a thick-walled urinary bladder. In some specimens, ducts (ureters?) appeared to lead to the posterior kidneys. The histology of these organs was that typical of bladders (Fig. 8a). The bladders took a variety of forms in different taxa: usually but not always paired, usually thick walled but occasionally very thin walled, and often coiled and covered with pigment. The bladders, when paired, arise from the lateral surface of the posterior ovary, extend anteriorly into the abdominal cavity and posteriorly exit behind the anus.

Where stomachs were obviously distended, or contents showed up on x-rays, stomach contents were removed for identification. Dissection of all stomachs was not attempted and fewer than 10% of the specimens were analysed in order to determine general feeding preferences for each genus.

No detailed comparative studies of the digestive tracts were attempted. Limited dissection revealed that all members of the family apparently lack pyloric caeca, the intestine arises from the anterior end of the stomach and increases in relative length and number of folds with age. The length of the oesophagus anterior to the stomach appears longer in *Cetostoma* than in other genera. Some comparisons were systematically noted. The amount of melanin pigment covering the stomach and peritoneum varies considerably, from none to complete heavy covering. Also the shape and size of urinary bladder(s) dorsoposterior to the gonads were noted. The position of the anus relative to the anal fin origin varies considerably in different genera, but was measured externally.

Colour. Herring (1975) described the pigmentation of the Cetomimidae, Barbourisiidae and Rondeletiidae. The orange-red pigments found beneath the skin along the myotomes and lateral line in the cetomimid genera *Cetostoma* and *Gyrinomimus* were identified as the carotenoid pigment astaxanthin and its esters. The same pigments were found in all three families. However, in the cetomimids and rondeletiids the skin is also heavily pigmented with melanophores that combine with the underlying carotenoid pigments to give an overall brownish hue, while *Barbourisia* is orange-red in colour because it lacks melanophores. Herring (1975) made his observations on fresh and frozen specimens.

The carotenoid pigments are completely bleached in alcohol and preserved specimens retain no orange colour. The melanin in the epidermis also fades with time; light speeds the fading and weaker rather that stronger concentrations of alcohol also appear to increase fading. While some specimens appear black when freshly caught, all preserved specimens are some shade of brown. Although there appear to be differences in the colour of freshly caught cetomimids, the subjective nature of these observations is compounded by the fullness of the stomach (stretched skin is lighter than loose skin), the often battered condition of the specimens and the time in alcohol. While colour may be of value if quantified for fresh or frozen specimens, only the preserved colour is mentioned in the descriptions and is not considered in the phylogenetic analyses.

Artificial Key to the Genera of Cetomimid Fishes

1. Nasal rosette long, filling both nostrils, with more than 30 large lamellae (Fig. 1e); lateral line without canal and pores, consisting of vertical rows of papillae with at least 8 papillae per row posteriorly; jaw teeth small, widely spaced and sharply pointed in 1-2 uneven rows (Fig. 2a); pseudobranch present; pectoral rays 15; principal caudal rays 19...*Procetichthys*

------ Nasal organ small and short, mostly in anterior nostril, with no or less than 10 small lamellae (Fig. 1f-k); lateral line consisting of a canal with pores or vertical rows of papillae with less than 5 papillae per row; jaw teeth tiny and triangular or elongate, closely spaced in 3-10 rows (Fig. 2b-f); pseudobranch absent; pectoral rays 17-24; principal caudal rays 12-16, rarely 17...2

2. Dorsal rays 29-37; anal rays 26-34; dorsal and to a lesser extent anal fins abruptly elevated on bases higher than body; slit behind angle of fourth gill arch tiny and tubular; 3 separate copular tooth plates; fin membrane between last 10 anal rays voluminous and curtain like; snout-dorsal origin 1.7-2.0 in SL............................*Cetostoma*

------ Dorsal and anal rays 12-21; dorsal and anal fin bases not abruptly elevated above body; slit behind ventral arm of fourth gill arch either elongate or absent; 1 copular tooth plate; fin membrane between posterior anal rays not voluminous and curtain like; snout-dorsal origin 1.3-1.6 in SL...3

3. Snout elongate and beak-like, 5.1-6.2 in SL; no lateral line canal with pores, but vertical rows of 1-3 papillae; no lateral line system of canals on head, only sensory papillae; no cavernous tissue around anus; gill arches 2 and 3 without tooth knobs or plates; underlying lateral line scales 31-40.................................*Rhamphocetichthys*

------ Snout not elongate and beak-like, rounded, 6.9-12.7 in SL; lateral line a canal with 9-25 pores, no vertical rows of papillae; lateral line system on head with canals and pores; cavernous tissue anterior to or around anus, often elsewhere; gill arches 2 and 3 with tooth plates or knobs; underlying lateral line scales 8-24.............................4

4. Free gill arches 4, with gill slit behind ventral arm of fourth gill arch; gill tooth plates separate and raised, club shaped to domed (Fig. 3b-d); lateral line scales round to rectangular and flat, without dorsal and ventral projections; vertebrae 38-46...5

------ Free gill arches 3, with no gill slit behind ventral arm of fourth gill arch; gill tooth plates contiguous, fusing with age, flat (Fig. 3e-h); lateral line scales elongate and curved with dorsal and ventral projections supporting lateral line canal; vertebrae 44-59...8

5. All jaw teeth in distinct longitudinal rows, elongate with length more than 3 times basal width; gill arch tooth plates elliptical and slightly raised; premaxillary length 3.2-3.4 in SL; ventral pharyngeal tooth plates present; lateral line scales (=pores - 1) 17-18; vertebrae 43-46...*Danacetichthys*

------ Jaw teeth in indistinct diagonal or longitudinal rows, with only inner row elongate or all tiny and triangular with length less than 2 times basal width; gill arch tooth plates on club-shaped gill rakers or raised rounded knobs; premaxillary length 3.5-5.2 in SL; no ventral pharyngeal tooth plates; lateral line scales 10-16; vertebrae 38-43...6

6. Dorsal rays 19-23, dorsal base 3.8-4.8 in SL; anal rays 15-18, anal base 5.1-6.6 in SL; lateral line scales rectangular; flap of skin with internal anal lappet scales over base of anal fin; cross section of belly posteriorly truncate with 2 ventral ridges; anus very close to anal fin origin, distance 23-100 in SL; palatine teeth present; ectopterygoid tooth plate long, extending to or slightly before rictus; gill rakers fully developed, club shaped .... *Ditropichthys*

------ Dorsal rays 13-16, dorsal base 5.8-8.5 in SL; anal rays 11-14, anal base 7.0-14.1 in SL; lateral line scales round; no flaps of skin with internal anal lappet scales over anal fin; cross section of belly posteriorly rounded with no ventral ridges; anus far anterior to anal fin origin, distance 10-20 in SL; palatine teeth absent; ectopterygoid teeth absent or patch very short, ending far before rictus; gill rakers as very short knobs 7

7. Lateral line scales 15-16; cavernous tissue between anus and anal fin with free posterior margin and long, free posterior extension; 5-7 diagonal skin ridges on midbody, each ridge passing over lateral line scale; vomerine and ectopterygoid teeth absent; copular tooth patch very short, 90-110 in SL, beginning behind level of eye; gill rakers on first arch 2+8; holobranchs on gill arches 1-4 long and closely spaced .... *Notocetichthys*

------ Lateral line scales 8-14; cavernous tissue anterior to anal fin origin, without free posterior margin or extension; no diagonal ridges of skin on midbody; vomerine and ectopterygoid teeth present; copular tooth patch long, 8.5-25 in SL and beginning before level of eye; gill rakers on first arch 3+7-10; holobranchs on gill arches 1-4 very short and widely spaced .... *Cetichthys*

8. Jaw teeth in distinct longitudinal rows (indistinct diagonal rows in smallest specimens of 2 species), all but newest teeth elongate with length more than 3 times basal width; vomerine tooth plate flat and rectangular or oval .... *Gyrinomimus*

------ Jaw teeth in indistinct diagonal rows, all teeth short with length less than 2 times basal width; vomerine tooth plate domed and round or rarely oval .... *Cetomimus*

Diagnoses and Descriptions

Family Cetomimidae Goode & Bean, 1895

Diagnosis. Body soft and flabby, whale shaped with dorsal and anal fins far posterior and opposite; no body scales; head large to very large, less than 5, usually less than 4 or 3, in SL; mouth enormous, extending far behind eye, less than 2 in head length, end of premaxilla usually closer to posterior margin of operculum than eye; eye tiny, usually degenerate without lens in specimens over 100 mm SL, less than 10 in HL in small specimens, less than 20 in HL in larger specimens. No supramaxillae, orbitosphenoid or subocular shelf; palate usually toothed; 3 or 4 free gill arches; ventral pharyngeal tooth plates of fifth ceratobranchial present or absent; copular tooth plate present, very short, or broad and shield shaped or very long and narrow, single or as three separate plates; pseudobranchiae usually absent; gill rakers club shaped, or as toothed knobs, tooth plates or individual teeth. No pelvic girdle or fins. No fin spines; almost all rays segmented, most dorsal, anal and caudal rays usually branched; dorsal and anal fins with 11-37 rays; caudal fin with 10-19 principal rays; pectoral fin with 15-24 rays; pectoral girdle reduced, with unforked post-temporal (not confirmed in all taxa). Vertebrae 38-59; second preural centrum usually with double neural and haemal spines. Lateral line a broad tube pierced by large pores, or series of vertical rows of papillate superficial neuromasts; 2 parallel rows of superficial neuromasts anterior to dorsal fin; scales present beneath lateral line organs; lateral line system of head a series of cavernous canals with moderate to large pores in all taxa except one. Stomach highly distensible; no pyloric caeca; no pleural ribs; no predorsal bones. Colour brownish-black mixed with reddish orange, resulting from carotenoid pigment astaxanthin and its esthers and melanin; cavernous tissue usually present around anus, sometimes at fin bases and other areas.

Subfamily Procetichthyinae n.subfam.

Diagnosis. This monotypic subfamily differs from all other known cetomimids in having large nasal organ with well-developed olfactory lamellae; connection between infraorbital canal of lateral line system and posterior nostril; eye with well-developed lens in specimens over 100 mm; 1-2 uneven rows of small, widely-spaced jaw teeth; small pseudobranch; only 15 pectoral rays; lateral line system on body incorporating vertical rows of papillate superficial neuromasts with at least 8 papillae in each row posteriorly without overlying tube or pores; caudal fin with 19 principal rays; peritoneum unpigmented.

Content. A single genus and species.

Procetichthys n.gen.

Type species. *Procetichthys kreffti* n.sp.

Diagnosis. As for the subfamily.

Description. D. 14; A. 13; P. 15; principal C. 19; vertebrae 48; trunk canal lateral line organs 86. Size large, attaining at least 236 mm; head large, 3.3 in SL, and wide, width at eye 2.5 in HL; mouth very large, jaws ending much closer to opercular margin then level of eye; snout rounded and moderate, 2.7 in HL; dorsal and anal bases short, 1.9-2.4 in HL; caudal peduncle long, 1.5 in HL and moderately deep, 2.7 in CPL; anus moderately anterior to anal fin origin, distance 1.1 in CPD.

Nasal organ large with well-developed olfactory lamellae. Eye small, 29 in HL, but with well-developed lens. Lateral line system of head a series of large canals with wide pores; supraorbital canal with 7 pores joined to main canal with 3 pores; infraorbital canal with 8 pores, not joined to main canal, last neuromast not displaced; mandibular canal with 7-8 pores, not joined to preopercular canal; preopercular canal with 4-5 pores and 3 neuromasts; neuromasts of head large, flat, diamond shaped. Lower jaw without lateral or ventral spines posteriorly. Jaw teeth small, widely spaced and sharply pointed in 1-2 uneven rows; 2 vomerine teeth; palatine and ectopterygoid teeth confluent, extending almost to rictus; copular tooth patch on 1 plate, moderately long, length 3.2 in HL, and narrow width, 13.9 in length.

Free gill arches 4, with small slit behind ventral arm of fourth arch; holobranchs well developed on all 4 arches, present on all of dorsal arm of first arch; small pseudobranch present. Gill rakers as small canine teeth on first 3 arches, none on medial face of gill arches; ventral pharyngeal tooth plates present.

Lateral line a series of vertical rows of papillae, 1-3 per row anteriorly and 8-18 per row posteriorly; no lateral line tube with pores; lateral line scales flat and narrow. No cavernous tissue. No subpectoral organ. No abdominal ridges or diagonal midbody ridges. No lappets, ridges, folds or membranous curtain associated with anal fin. Stomach unpigmented.

Etymology. From the Greek *pro* - first, *cetus* (*ketos*) - whale, *ichthys* - fish, in reference to its primitive sister group relation to other whalefishes. The gender is masculine.

Remarks. Only one specimen of the genus has been collected, in bathypelagic waters of the south-eastern Atlantic.

Procetichthys kreffti n.sp.

Figs 1e, 2a, 3a, 4a, 6b, 10-12

Type material. HOLOTYPE: ISH 1188/71, 236.5 mm female, *Walther Herwig* 412-II/71, south-east Atlantic, 37°08'S, 5°23'E, 0-2200 m, 192-2400 hrs, 21 Mar. 1971.

Diagnosis. As for the subfamily.

Description. The only known specimen is in moderate condition with the body wall torn open anterior to the anal fin and behind the pectoral girdle on one side. Most of the skin and fin ray tips are present. The anterior third of the left premaxilla is lost and the head is distorted.

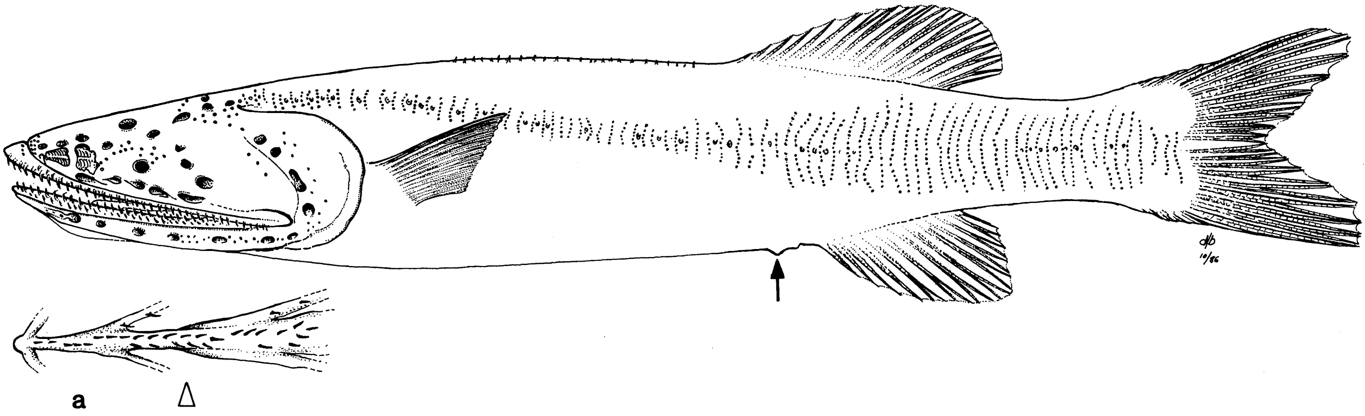

Fig.10. *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71, arrow indicates level of anus; a, teeth on copula (not to scale), triangle indicates level of eye.

D. 14; A. 13; P. 15; principal C. 10+9; procurrent C. 8+7; vertebrae 28+20=48; vertical rows of lateral line neuromasts 39 from under dorsal origin to caudal; trunk canal lateral line organs 86. Measurements in Appendix Table 9.

Body oval in cross section behind head; greatest depth midabdominal. Caudal peduncle much longer than deep. Anus anterior to anal fin origin by distance approximately equal to caudal peduncle depth. Skin around anus damaged, no apparent cavernous tissue. Very slight mid-dorsal ridge from dorsal origin halfway to head; no apparent midventral ridge. No anal lappet flaps, scales or ridges at anal fin base. No pore or pigment patch of subpectoral organ visible.

Head large, depressed anteriorly and compressed posteriorly, wider than deep at level of eyes, deeper than wide at rictus. Head and body profile very slightly rounded from snout to dorsal origin. Nostrils very large, much larger than lateral line pores or eye, with raised anterior rim; nasal organ large, elongate with about 35 fully developed olfactory lamellae on each side of central raphe (Fig. 1e); internasal bridge of skin equal to horizontal diameter of posterior nostril; line between tip of snout and eye passes midway through each nostril; small canal connecting posterior nostril with infraorbital canal of lateral line system. Eye small, with well-developed lens, midway between upper jaw and snout profile; interorbital broad, smooth, convex. Mouth enormous, moderately oblique; dentigerous margin of upper jaw straight posteriorly, convex anteriorly, that of lower jaw concave; rictus approximately 2 eye diameters before posterior tip of premaxilla; posterior end of jaws well before end of gillcover, without spines or processes. Jaw teeth well spaced in 1 or 2 rows; individual teeth relatively long, recurved, non-depressible cones with sharply pointed tips (Fig. 2a); upper jaw teeth 40, in single row beginning about 1 eye diameter behind symphysis and extending along entire length of premaxilla, behind rictus, plus 2 larger canines on either side of symphysis; lower jaw teeth in 2 rows commencing just behind symphysis; outer row of 31-33 smaller canines decreasing in size posteriorly and extending to 1 eye diameter before rictus; inner row of 35-37 canines extending to rictus. Palatal teeth similar to jaw teeth; 2 canines on vomer; palatine-ectotperygoid teeth in 1 row commencing 2 eye diameters behind vomer and extending almost to level of rictus, 28 teeth on one side (broken on other), slightly decreasing in size posteriorly; division between palatine and ectopterygoid indistinguishable. Teeth on copula, pharyngeals and gill arches all similar to jaw teeth except smaller and depressible; copular tooth patch long and slender, with 1 row of teeth anteriorly and 2 rows posteriorly, 18-19 teeth longitudinally; length of copular patch about 1.2 in snout.

Free gill arches 4, small slit about length of eye diameter behind ventral arm of fourth arch; dorsal arm of first arch free, half of dorsal arm of second and all of dorsal arms of third and fourth arches bound in skin of gill chamber. Holobranchs well developed, closely spaced, those on ventral edge of first gill arch about 3 times width of arch (Fig. 3a); holobranchs of fourth arch about four fifths as long as those of first arch; holobranchs present on dorsal arm of all 4 arches; small pseudobranch present, of 3-4 filaments, the second largest and slightly longer than width of first gill arch. Normal gill rakers absent; first arch with 5-6 hypobranchial, 5 ceratobranchial and 4 epibranchial tooth patches evenly spaced plus 1 tooth in angle of arch;

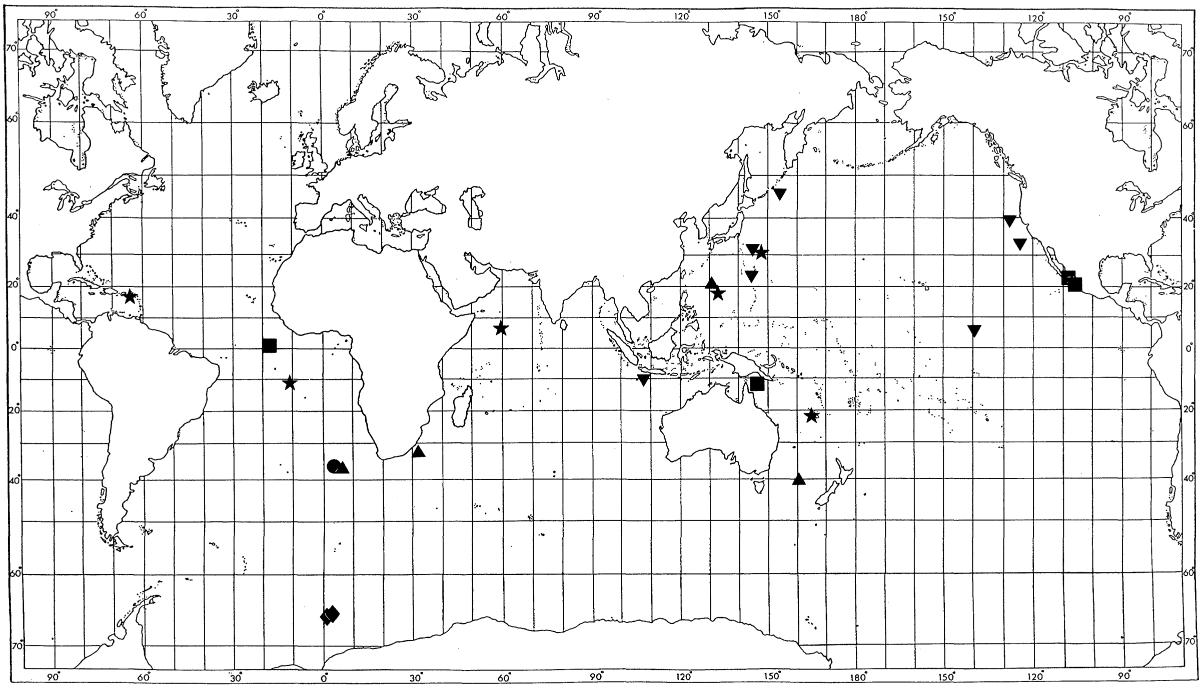

Fig.11. Horizontal distribution of *Procetichthys kreffti* (closed circle), *Cetichthys indagator* (triangle), *C. parini* (inverted triangle), *Notocetichthys trunovi* (diamond), *Danacetichthys galathenus* (star) and *Rhamphocetichthys savagei* (closed square).

hypobranchial patches of 1-2 teeth, ceratobranchial teeth all single and epibranchial patches of 1-3 teeth (Fig. 3a); second arch with 8 small canines on ventral arm, third arch with 3 teeth ventrally, fourth arch edentate; no teeth on medial faces of arches. Dorsal pharyngeals as 2 pharyngobranchial tooth plates on each side of roof of mouth, anterior (third pharyngobranchial) plate with 7-8 teeth arranged in triangular patch, posterior (fourth pharyngobranchial) plate with 15-17 teeth in oval-shaped patch; paired ventral pharyngeals (fifth ceratobranchials) as elongate triangular tooth plates with 19-20 teeth.

No indication of tube pierced by pores in lateral line. Lateral line system complex (Figs 6b, 10), consisting of 86 lateral line organs in longitudinal row from top of gill opening to base of caudal rays; these organs in very shallow groove approximately half an eye diameter wide, with bottom of groove smoother than skin of either side; each lateral line neuromast associated with vertical row of papillate superficial neuromasts; posterior rows longer with more papillae; from row 51 just posterior to anal origin to row 82 just before caudal base, number of papillae range from 13-18 per row with 6-10 papillae dorsal and ventral to main neuromast, except for 3 shorter rows with 8-12 total papillae; rows 83-85 on caudal base with 8-10 papillae each, while last uneven row on caudal rays with 17; rows 40-50 with 4-11 papillae, rows 1-39 with 1-6 total papillae per row; each papilla in a shallow pit of smoother skin; larger papillae, 2-3 times the size of those in vertical rows, in main depression of lateral line, organised approximately every 2 rows in space between rows; 31 larger papillae from opercular opening to row 50, none behind; both larger and smaller papillae with nerve running to opening at tip of papillae and joining lateral line nerve overlying muscle mass under skin; branches of nerve also entering each main lateral line neuromast; although solidified mucous in center of most main neuromasts and some larger papillae, no microstructure evident at 50 times magnification. Lateral line scales narrow and flat in underlying connective tissue. Two parallel rows of superficial neuromasts, similar in size and shape to those of vertical rows of lateral line, the dorsal trunk line, in dorsal midline from level of gill openings to just before dorsal origin, 32/40 papillae per row.

Lateral line system on head of deep cavernous tubes

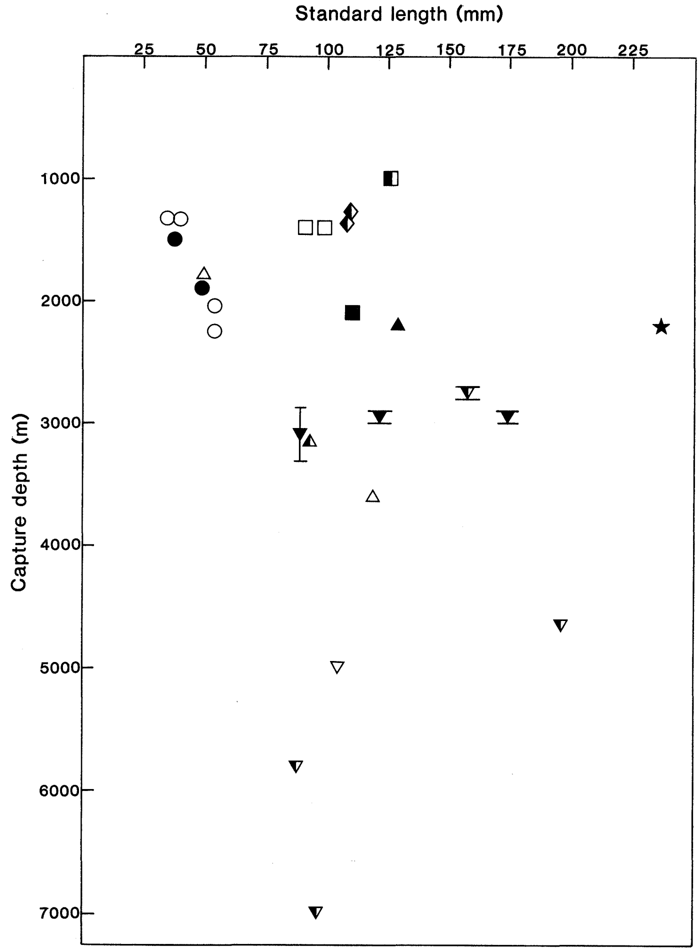

Fig.12. Vertical distributions of *Procetichthys kreffti* (star), *Cetichthys indagator* (triangle), *C. parini* (inverted triangle), *Notocetichthys trunovi* (diamond), *Danacetichthys galathenus* (circle) and *Rhamphocetichthys savagei* (square); open symbols indicate day captures, solid symbols night captures, half solid symbols day/night or unknown time, depths are maximum fishing depths of open nets; closing net captures indicated by vertical bars giving fishing depth limits.

with moderate-sized pores (Fig. 4a); neuromasts large, flat, diamond shaped on floor of canals. Supraorbital canal from snout to behind eye, with 7 pores and 6 neuromasts, 5th pore largest but far from dorsal midline, anterolateral bend after 5th pore joined to main canal with 3 pores and organs, supratemporal pore medially joined to 2nd pore. Infraorbital canal not joined to main canal, with 8 pores and 8 neuromasts, 7th organ not displaced anteriorly, 8th pore behind eye; connection between 1st infraorbital pore and posterior nostril, with neuromast in floor of small joining canal. Mandibular canal with 7-8 pores (skin bridge between anterior 2 pores only partially formed on one side) and 7 neuromasts plus 3 large papillae in floor of elongate 1st pore; preopercular canal not joined to lower jaw canal, with 4-5 pores and 3 neuromasts. Three or 4 irregular rows of superficial neuromasts across front of snout, with 15-20 papillae per row; 15-16 papillate neuromasts from behind posterior nostril to over and behind eye, as superficial accessory line; about 15 papillae around last 3 dorsal canal pores; 3 papillae before upper preopercular pores and about 15 papillae on operculum behind pores; about 15 papillae on posterior lower jaw.

Dorsal and anal fins far posterior; dorsal origin slightly before anal origin. Dorsal with 14 rays, 2 simple rays followed by 11 branched rays and 1 simple ray; anal with 13 rays, 2 simple, 10 branched and 1 simple. Pectoral fin moderate in size, directed obliquely upwards, upper rays longest, all rays branched for about distal third of their length. Caudal fin moderately long, strongly forked with 19 principal rays.

The specimen is a mature female with 2 distinct egg sizes; the larger eggs are 1.9-2.0 mm in diameter, the smaller 0.3-0.5 mm in diameter. The overies are ruptured, protruding through the body wall and the details of ovarian structure and urogenital openings could not be ascertained. No testes or bladder are apparent.

Colour in alcohol dark brown, fin tips light brown; mouth, gill cavities, stomach, intestine and peritoneal lining unpigmented.

Distribution. The only known specimen was captured with an open net fishing to 2200 m in the south Atlantic (Figs 11,12).

Etymology. After Gerhard Krefft of ISH, who has organised the world's largest collection of whalefishes and provided hospitality and encouragment for their study, in recognition of his contributions to the knowledge of deep sea fishes.

Remarks. Other specimens of cetomimids taken in the same haul include *Cetichthys indagator*, *Cetomimus* sp., *Cetostoma regani*, *Gyrinomimus* sp. and *G. grahami*.

Subfamily Cetomiminae Goode & Bean, 1895

Diagnosis. Nasal organ small, olfactory lamellae greatly reduced or absent; no connection between infraorbital canal of lateral line system and posterior nostril; eye degenerate, without lens in specimens over 100 mm; 3-10 rows of jaw teeth, either granular, triangular or elongate, never widely spaced; pseudobranch absent; pectoral rays 17-24; lateral line system on body usually with overlying tube pierced by pores; caudal fin with 12-17 principal caudal rays; peritoneum dark brown.

Ditropichthys Parr, 1934

Ditropichthys Parr, 1934: 21. Type species *Cetomimus storeri* Goode & Bean, 1895 by original designation.

Diagnosis. *Ditropichthys* differs from all other cetomimid genera in having fully developed, club-shaped gill rakers, a pair of thin dermal folds along abdomen and anal lappets connected as an unbroken fold of skin containing lappet scales over base of anal fin.

Description. D. 19-22; A. 15-18; P. 17-21; principal C. 6-8+7-8=13-16, counts approximate as all fins damaged; vertebrae 20-24+16-19=38-42 (n=39); trunk canal lateral line scales and organs 10-13. Size moderate, maximum 131 mm; head moderate to large, 2.9-3.4 in SL, and moderate to wide, width at eye 2.3-3.7 in HL; mouth large, jaws ending about midway between eye and opercular margin; snout rounded and moderate, 2.1-3.1 in HL; dorsal and anal bases moderate, 1.2-2.2 in HL; caudal peduncle short to moderate, 1.8-2.4 in HL and slender to moderate, depth 2.0-3.1 in CPL; anus slightly anterior to close to anal fin origin, distance 1.6-6.0 in CPD.

Nasal organ short and high without lamellae. Eye tiny, 14-31 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores, supraorbital canal with 6 pores joined to main canal with 3 pores; infraorbital canal with 8 pores, last neuromast not displaced out of series, contiguous with main canal, but no connecting skinbridge; mandibular canal with 5-6 pores, not joined to preopercular canal with 5 pores; neuromasts of head large, round, firm. Lower jaw with weakly-developed lateral and ventral spines posteriorly. Jaw teeth tiny, closely set in irregular diagonal rows; vomerine tooth patch elongate to oval; palatine teeth present; ectopterygoid tooth plate elongate, extending about to rictus; copular tooth patch on 1 plate, short to moderate with length 4.6-8.6 in HL, and very broad to moderate, width 2.2-6.2 in length.

Free gill arches 4, with slit behind ventral arm of fourth arch; holobranchs well developed on all 4 arches, present on dorsal arm of first arch. Gill rakers fully developed, club shaped, denticulate, on all 4 arches; similar smaller rakers on medial faces of all 4 arches; no ventral pharyngeal tooth plates.

Lateral line a broad tube pierced by wide pores, without flaps or keels; lateral line scales flat and rectangular to oval. Cavernous tissue extensive around anus only. No subpectoral organ visible. Paired fleshy ridges on abdomen. No diagonal midbody ridges present. Anal lappets long and broad, joined together in solid skin fold extending over anal fin base to about anal ray 13-14; no membranous curtain connecting posterior anal rays. Stomach darkly pigmented.

Etymology. From the Greek *di* - two, *tropis* - keel and *ichthys* - fish, presumably in reference to the folds over the anal fin or the paired abdominal ridges. The gender is masculine.

Remarks. Specimens have been collected in meso- and bathypelagic waters of all three oceans. The genus is monotypic.

Ditropichthys storeri (Goode & Bean, 1895)

Figs 1f, 3c, 4d, 5b, 8b, 9, 13-16

Cetomimus storeri Goode & Bean, 1895: 453, pl. 17(3). Holotype USNM 35634, lost, from the north-western Atlantic, 39°03'N, 70°51'W.

Cetomimus storeri.-Goode & Bean, 1896: 69-70, pl. 21(79) (redescription).-Jordan & Evermann, 1896:550 (redescription).-Brauer, 1906: 252-253, pl. 10(5) (Indian Ocean specimen).-Murray & Hjort, 1912: 613, 681-682, fig. 497 (north-eastern Atlantic specimen).-Parr, 1928: 177, fig. 43 (north-western Atlantic specimen).

Ditropichthys storeri.-Parr, 1934: 21-24, fig. 5 (redescription).-Norman, 1939: 32 (Indian Ocean specimen).-Harry, 1952: 58-59 (2 Bermuda specimens).-Marshall, 1954: 225, 241 (redescription) .-Koefoed, 1955: 3 (north Atlantic specimen).-Rass, 1955: 334-337 (north-western Pacific specimen listed) .-Marshall, 1960: 43, 112 (swim bladder).-Munk, 1965: 22, 26-28, pl. 10(1) (ocular anatomy).-Munk, 1966: 38, 55-56, pl. 15(1) (ocular anatomy).-McAllister, 1968: 98 (hyoid arch).-Craddock & Mead, 1970: 31 (south-eastern Pacific specimen listed).-Marshall, 1971: 144, fig. 50 (lateral line organs).-Kotthaus, 1972: 17 (Indian Ocean specimen); Fitch, 1979: 63-65, fig. 1f (otolith).-Stein, 1985: 190 (north-eastern Pacific specimen listed).

Gyrinomimus bruuni?.-Parin *et al.*, 1974: 114 (Atlantic specimen briefly described).

Material examined. See Appendix Table 3. The following description is based on 26 specimens (26.8-128.5 mm, with an * in Table 3) chosen on the basis of their good condition. The descriptions of such features as fin shape, lateral line pore shape and number of superficial neuromasts is a composite based on different parts of the best specimens. Meristic counts include the range of all specimens examined for which counts were made.

Diagnosis. As for genus.

Description. D. 19-22; A. 15-18; P. 17-21; principal C. approximately 6-8+7-8=13-16, no fins complete enough for exact count; procurrent C. ca. 3-5+3-4; vertebrae 38-42; lateral line scales/organs 10-13. Measurements in Appendix Table 4.

Body oval in cross section, greatest depth at level of pectoral base, becoming compressed posteriorly. Caudal peduncle 2.0-3.1 times longer than deep. Anus usually within 2 mm of anal fin origin. Cavernous tissue strongly developed immediately before anus in roughly triangular-shaped patch joining its fellow from other side in ventral midline, not extending under anal fin. High, thin mid-dorsal keel or ridge from posterior end of head to dorsal origin. Belly with pair of skin ridges/flaps from level of pectoral fin to beginning of cavernous tissue, slightly diverging anteriorly. Body wall below abdominal cavity like

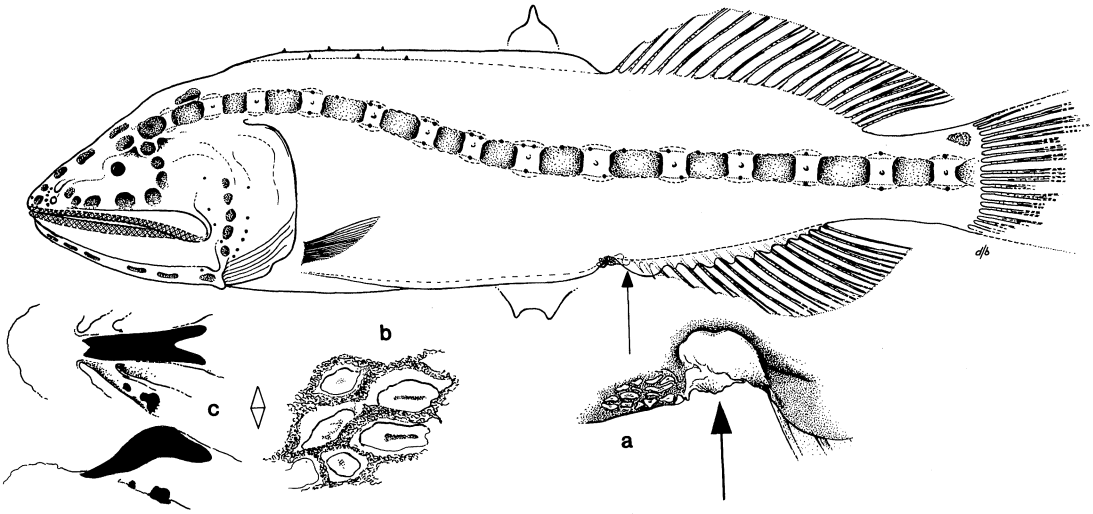

Fig.13. *Ditropichthys storeri*, 131 mm, ISH 1083/71, arrow indicates level of anus; a, b, enlargement of cavernous tissue; c, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye.

truncated triangle in cross section, with apex ventral; thin, solid sheets of muscle laterally between skin and abdominal cavity, ventrally belly keel with 4 separate bundles of muscle running longitudinally and surrounded by white translucent tissue somewhat similar to that found in fishes with indirect luminescent systems (Haneda, 1950); translucent keel extends from cavernous tissue anteriorly to just behind level of pectoral fin base. Very well-developed anal lappet flaps joined together as 1 scalloped flap from anus to base of last 1-5 anal rays, shorter anteriorly and posteriorly; flap supported by weakly ossified scales, flat and elongate, with distal edges making up scalloped edge of flap (Fig. 9); individual scales difficult to count in unstained specimens, numbering approximately 12-17; no indication of scales in belly flaps, which are almost continuous with anal flaps except for interruption of cavernous tissue.

Head very large, deeper than wide, slightly depressed anterior to eye in smaller specimens; head and anterior body profile weakly rounded, outline uneven with bones and pores creating bumps and pits. Nostrils similar to head lateral line pores, midway between tip of snout and eye; anterior nostril round, probably with raised anterior rim in undamaged specimens, half to one third diameter of posterior nostril; internasal skin bridge about as wide as anterior nostril diameter; posterior nostril oval; raphe located entirely in anterior nostril, very short, high, narrow to moderately rounded, lightly pigmented, without lamellae, some specimens with single basal ridge posteriorly (Fig. 1f). Eye small, without lens even in smallest specimens, slightly closer to top of head than upper jaw; interorbital broad, convex and bumpy, narrower in smaller specimens.

Mouth very large, slightly oblique; jaws very slightly concave in undamaged specimens; rictus 2-3 eye diameters before end of premaxilla; posterior end of jaws far before margin of gill cover, closer to level of eye than operculum; lower jaw with weakly-developed lateral and ventral spines posteriorly. Jaw teeth tiny, in a broad band in each jaw, wider anteriorly than posteriorly in irregular diagonal rows, no posterior clumping, extending more than one eye diameter behind rictus in both jaws. Membrane of both jaws very wide and thick, covering most palatal teeth. Vomerine teeth tiny, apparently decreasing in number with increasing specimen size; largest specimens with 5 or fewer teeth, smallest usually with 5-13 teeth, one 32 mm fish with 21 vomerine teeth; patch elongate to oval shaped; in contrast palatine and ectopterygoid teeth increase in number with increasing specimen size; palatine patch elongate, from slightly behind level of vomer to before eye, 1-2 teeth wide in smallest specimens to 5-6 teeth wide in largest; ectopterygoid patch elongate from about level of eye to or slightly before rictus, increasing in breadth (numbers of teeth across) with increasing size; edentate space between palatine and ectopterygoid decreasing with increasing size from half to less than one tenth length of palatine patch as palatine patch increases. Roof of mouth with numerous far-spaced papillae. Copular tooth plate very short and broad, rounded anteriorly and emarginate to lunate posteriorly (Fig. 13c), more elongate and slightly pointed anteriorly in 1 specimen only, domed medially as basibranchials very narrow; teeth tiny, increasing in numbers with increasing size.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of gill chamber. Holobranchs of all 4 arches well developed, closely spaced, those on ventral arm of first arch about equal to bony width of arch; holobranchs of fourth arch as long as or slightly longer than those of first arch; holobranchs present on dorsal arm of all 4 arches. Club-shaped gill rakers covered with tiny teeth present on all 4 arches (Fig. 3c), numbering 3-4+9-11 on first, 3+8-11 on second, 2-3+6-9 on third and 1-3+5-7 on fourth; 1 specimen with single small tooth patch on fifth arch; similar, smaller toothed knobs project medially from all 4 arches, numbering respectively 10-14, 8-12, 7-10 and 4-7; the numbers do not increase with size and as the size of teeth do not increase with increasing size either, smallest specimens with mouths and gill cavities filled with relatively much larger teeth. Dorsal pharyngeals as pair of large, slightly domed tooth plates covered with tiny teeth; anterior plate elongate, about 2 times longer than wide, rounded anteriorly and truncate posteriorly; posterior plate shorter, half to one third length of anterior, truncate to slightly emarginate anteriorly where it meets anterior plate and rounded posteriorly; plates very closely spaced in comparison to other cetomimids. No ventral pharyngeal plates, except for 1 small tooth patch on fifth ceratobranchial of one side in only 1 specimen.

Lateral line a broad tube with 11-14 pores, without flaps or keels; anteriorly pores almost rectangular, 2-3 times longer than wide with skin bridges over lateral line organs and scales narrow; posteriorly pores more oval with skin bridges wider; 10-13 underlying scales rectangular, oval or diamond shaped, flat or slightly concave, without dorsal or ventral projections, first and last scales usually larger (Fig. 5b); lateral line neuromasts large, round, firm. Skin bridges between pores with 1-3 dorsal and 1 ventral papillate neuromasts and usually 1-2 papillae on dorsal margin of some pores; 2-4 papillae at bases of middle caudal rays behind last lateral line pore; 2 mid-dorsal rows, the dorsal accessory lines, of 8-11 superficial neuromasts from level of upper opercular opening halfway to dorsal origin, rows divergent anteriorly becoming one row posteriorly.

Lateral line system of head with shallow canals, large pores and very large neuromasts under skin bridges between pores (Fig. 4b). Supraorbital canal with 6 pores and 5 neuromasts, with lateral bend at pore 5 joined to main canal with 3 pores and organs plus supratemporal pore and neuromast medial to pore 2. Infraorbital canal with 8 pores and 8 neuromasts, joined to main canal at first pore, skinbridge over neuromast 8 damaged in most specimens, apparently incomplete or absent; neuromast 8 not displaced anteriorly or dorsally out of series. Mandibular canal with 5-6 pores and 4-5 neuromasts, pores much smaller than skin bridges, anterior 2 organs small; mandibular canal not joined to preopercular canal with 5 pores and 4 organs. Papillate superficial neuromasts on head arranged 3-5 on snout medial to first supraorbital pore, 3-4 between supraorbital pores and anterior nostril, 1 anteroventral to anterior nostril, 1 posterior to first infraorbital pore, 4-6 from ventral spine of lower jaw behind posterior premaxillary to top of preopercle, 5-6 from angle of subopercle to behind dorsal preopercular pore, and at least 1 on posterior lower jaw.

Dorsal and anal fins far back on body; dorsal longer than anal, dorsal origin and end before and behind those of anal, always more dorsal rays, usually 3 more, range 2-4; in undamaged specimens all but first ray of dorsal and anal branched, middle rays longest. Pectoral low, short, directed posterodorsally, middle rays longest, none branched, last 2 rays very short, apparently fused to last largest ray in largest specimens. Caudal fin rays all broken, no accurate counts of principal rays possible, fin shape unknown.

Ovaries paired, 33 dissected specimens (27.6-131 mm), all but 1 with eggs 0.1-0.15 mm diameter or less, ovaries flacid to rounded, increasing in length with age (Fig. 14); 1 specimen 112 mm with well-rounded ovaries extending forward halfway to pectoral girdle, with eggs of varying sizes from less than 0.1 mm to ca. 0.25 mm diameter, attached to internal wall and folds of ovary, none free in lumen, largest eggs with visible oil drop (Fig. 8b); only this specimen with considerable fat in abdominal cavity. Small, short, median bladder dorsoposterior to ovaries in largest specimens, indeterminate in smaller specimens. Urogenital papilla behind anus and ovarian opening, most distinct in smaller specimens. No testes apparent.

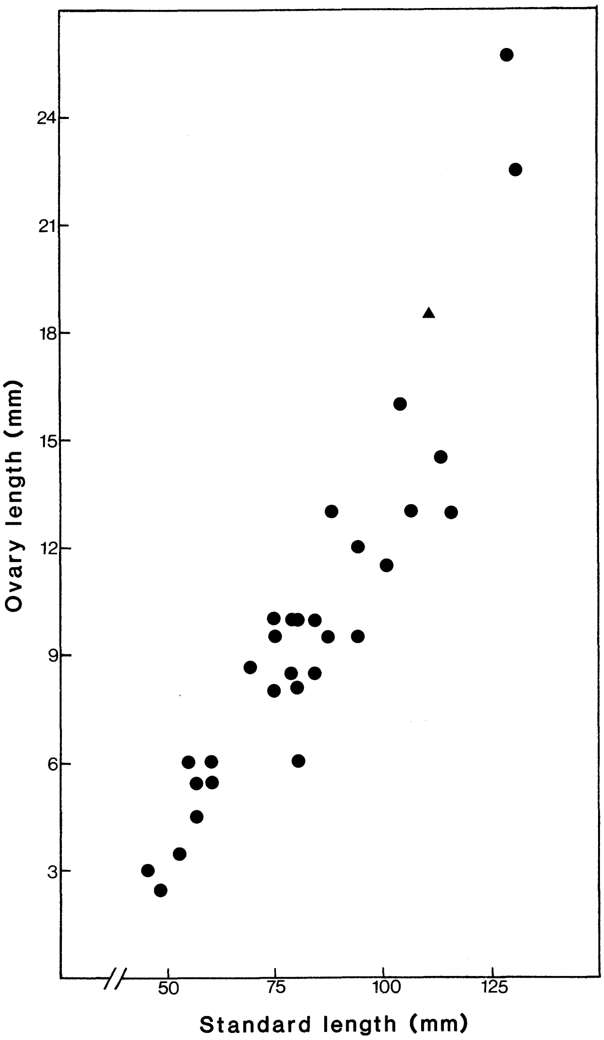

Fig.14. *Ditropichthys storeri* ovary length versus standard length; triangle indicates specimen with eggs more than 0.15 mm diameter.

Colour in alcohol very dark brown; oral and gill cavities very light brown; stomach and peritoneum dark brown, intestine without pigment.

Distribution. More than 80 specimens have been collected in all three oceans, from 41°N to 43°S in the Atlantic and from 45°N to 32°S in the Pacific (Fig. 15). The distributional gaps in the central south Atlantic, south Indian and various parts of the Pacific are presumably due to inadequate sampling. The species appears to have a circumglobal distribution between 45°N and 45°S.

The vast majority of specimens have been taken in nets fishing below 1000 m. Three specimens were taken in closing nets between 1200 and 1550 m, both day and night, and 1 specimen was taken diurnally between 900 and 1100 m; two of these specimens were only 30-40 mm SL (Fig. 16). All specimens over 90 mm were taken with nets fishing to 1550 m or deeper, while four of the six captures shallower than 1000 m (650-877 m) took specimens less than 35 mm. Larger specimens appear deeper dwelling and smaller specimens may undertake a limited vertical migration to 650 m nocturnally.

Etymology. After David Humphrey Storer, author of the 'History of the Fishes of Massachusetts'.

Type specimen. The holotype, USNM 35634, has been missing from the USNM collections since at least 1965 and is presumed lost. Although some Goode and Bean specimens were deposited at MCZ, there is no indication that this specimen was ever registered at MCZ. With such distinctive features as belly ridges and joined anal lappet flaps, there has never been a question as to the identity of the species, even though the holotype apparently has not been re-examined since the original description.

Remarks. Although considerable variation is apparent in the morphometrics of the 26 measured specimens (Table 4), most of this can be accounted for in the great size range measured (27-128 mm) and, even though relatively undamaged and undistorted specimens were used, the difficulty of accurate measurements of soft specimens. Counts of dorsal and anal rays, vertebrae, lateral line scales and gill rakers varied by counts of 5 or less and no variation in morphometrics or meristics could be correlated to indicate more than one species is represented. The extreme counts of 38 and 42 vertebrae were found in only one specimen each of 39 fish x-rayed. Ranges and means of specimens from the Pacific (n = 6), Indian (n = 1), north Atlantic (n = 11) and south Atlantic Oceans (n = 8) were compared and no differences were apparent. The most striking difference found, the elongate copular tooth plate

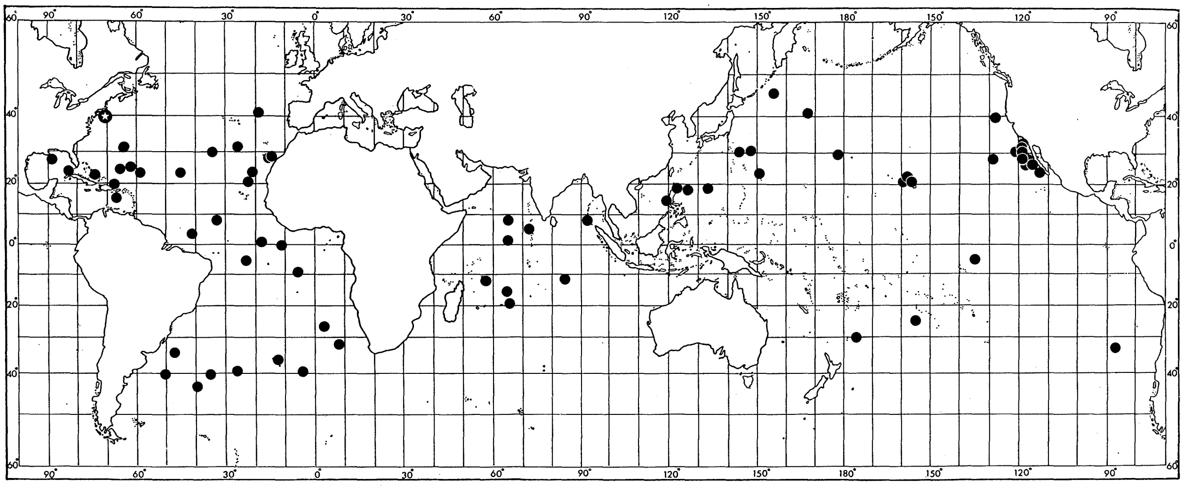

Fig.15. *Ditropichthys storeri* horizontal distribution; symbols may represent more than one specimen, star indicates holotype.

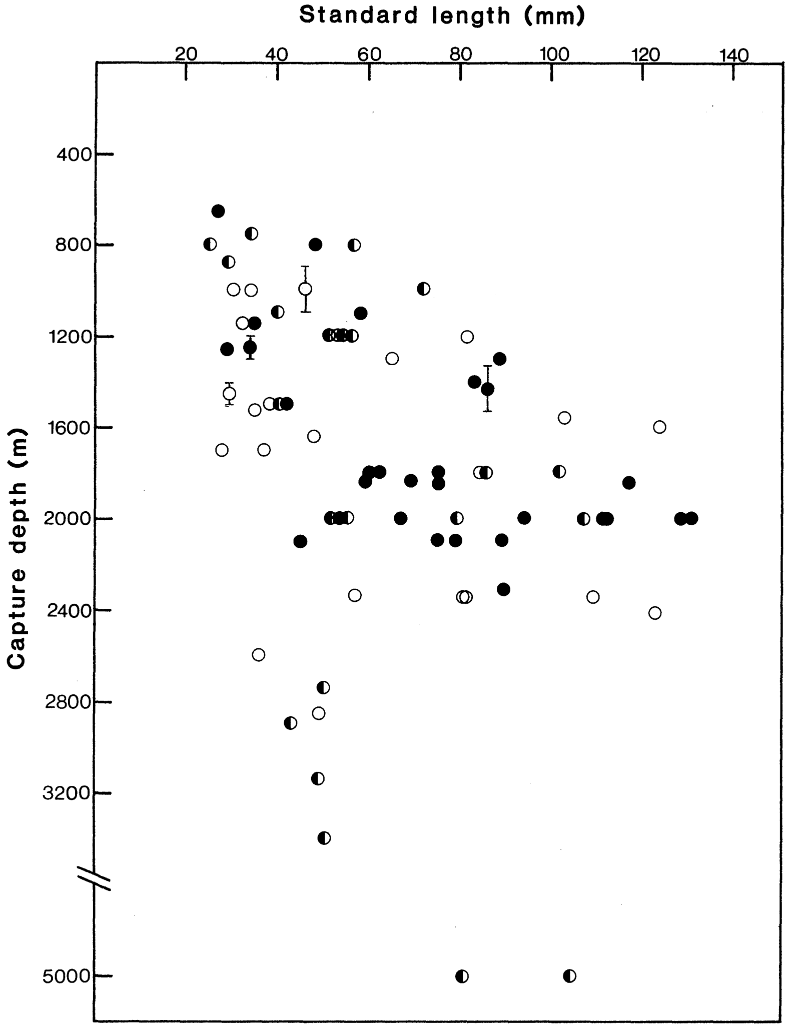

Fig.16. *Ditropichthys storeri* vertical distribution; open symbols indicate day captures, solid symbols night captures, half solid symbols day/night or unknown time, depths are maximum fishing depths of open nets; closing net captures indicated by vertical bars giving fishing depth limits.

of one northeast Pacific specimen, was not correlated with any other difference.

A comparison of morphometric values by size class (Table 4) indicates allometry in a number of features. As with most cetomimids, the eye is relatively larger in small specimens and does not appear to increase in absolute size beyond 1.1-1.3 mm in diameter, while specimens of 40 mm have eye diameters of 0.7-0.9 mm. Similar to the species of *Cetichthys*, the body fills out with flesh with increasing size; body depth and dorsal-anal distance both increase with increasing size, reflecting the tendency for larger specimens to be more robust. No other allometry is striking. The standard deviations of more than 10% of the mean for six of the 17 measurements that lack allometric growth indicate these measurements are too variable to be of great value. In particular, measurements of head, eye and posterior maxillary widths are susceptible to variation from distortion.

Cetichthys n.gen.

Type species. *Cetomimus* (*Psapharocetus*) *indagator* Rofen, 1959.

Diagnosis. *Cetichthys* differs from all other cetomimid genera in having a short ectopterygoid tooth patch, about as long as 1-2 eye diameters and ending far before the rictus, and holobranchs on all 4 gill arches very short and far separated. The lack of palatine teeth and the form of the gill arch tooth plates as short, rounded knobs are shared only with *Notocetichthys*, while the low number of vertebrae (39-43) is shared only with *Ditropichthys* and *Notocetichthys*, and the position of the anus far in front of the anal fin is shared only with *Procetichthys* and *Notocetichthys*.

Description. D. 13-16; A. 12-14; P. 19-24; principal C. 5-7+6=11-13; vertebrae 24-26+15-18=39-43; trunk canal lateral line organs and scales 8-14. Size large, maximum 196 mm; head large to very large, 2.6-3.2 in SL and moderate to wide, width at eye 2.5-5.2 in HL; snout rounded and moderate, 2.7-3.0 in HL; mouth large to very large, jaws ending slightly closer to opercular margin than eye; dorsal and anal bases short, 2.1-4.5 in HL; caudal peduncle moderate to very long, 1.3-2.0 in HL and moderate to deep, depth 2.1-4.0 in CPL; anus far from anal origin, distance 0.8-1.1 in CPD.

Nasal organ short and high without lamellae or ridges. Eye tiny, 25-47 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores; based on *C. parini* only, supraorbital canal with 6 pores joined to main canal with 2 pores, infraorbital canal with 8 pores joined to main canal with last neuromast slightly displaced anteriorly, mandibular canal with 5 pores slightly separated from preopercular canal with 5 pores; neuromasts moderate sized, papillae like, delicate. Lower jaw with weak lateral and ventral spines or projections posteriorly. Jaw teeth short to long, width 1-3 in length, closely set in indistinct diagonal rows; vomerine tooth patch triangular or diamond shaped, flat; palatine teeth absent; ectopterygoid tooth plate very short, ending far before rictus; copular tooth patch on 1 plate, short to long, 3-10 in HL, and moderate to broad, width 3.6-8.8 in length.

Free gill arches 4, with slit behind ventral arm of fourth arch; holobranchs very short and far spaced on all 4 arches, present on dorsal arm of all 4 arches. Gill rakers as round knobs with small teeth on all 4 arches, 3+1+6-9 on first arch; tooth plates present on medial face of all 4 arches; no ventral pharyngeal tooth plates.

Lateral line a broad tube pierced by very wide pores without flaps or keels; lateral line scales large, round, flat. Cavernous tissue weakly developed between anus and anal origin, none elsewhere. No subpectoral organ visible. No paired abdominal ridges or diagonal midbody ridges. A single anal lappet and ridge present or absent; no membranous curtain connecting posterior anal rays. Stomach darkly pigmented.

Etymology. From the Greek, *cetus* (*keto*) - whale and *ichthys* - fish, in reference to the body shape, mouth size and common name. The gender is masculine.

Remarks. A total of 12 specimens have been collected from 45°N to 40°S in the Pacific, in the east and west Indian Ocean and in the Atlantic at 37°S (Fig. 11). Two species are represented.

Key to the Species of *Cetichthys*

1. Lateral line scales 12-14, pores 13-15; anterior 5-7 lateral line pores equal to or smaller than width of scales; caudal peduncle length 4-4.5 in SL; anal base length 10-11 in SL; no anal lappet or ridge at anterior anal base..*C. indagator*

------ Lateral line scales 8-10, pores 9-11; anterior 5-7 lateral line pores wider than width of scales; caudal peduncle length 5-6 in SL; anal base length 7-8.5 in SL; 1 small anal lappet without scale at end of weak ridge at base of anal ray 3.......................................*C. parini*

Cetichthys indagator (Rofen, 1959)

Figs 11, 12, 17

Cetomimus (*Psapharocetus*) *indagator* Rofen, 1959: 255, fig. 1. Holotype: ZMUC P23451, *Galathea* Stn 186 from the east coast of South Africa, 32°33'S, 32°01'E, 3620 m, 1645 hrs, 31 Jan. 1951.

Cetomimus indagator.-Smith, 1961: 566 (South African specimen listed).-Nielsen, 1974: 44 (holotype listed).-Paxton & Bray, 1986:433, fig. 135.1 (redescription).

Material examined. 4(51.5-128.8): ISH 1186/71, 128.8 mm SL, 37°08'S, 5°23'E, South Atlantic Ocean, 0-2200 m, N, 21 Mar. 1971; ZMUC P23451(holotype), 117.7 mm SL, 32°33'S, 32°01'E, South Indian Ocean, 0-3620 m, D, 31 Jan. 1951; LACM 11314-1, 92.5 mm SL, 40°07'S, 161°08'E, South Pacific Ocean, 0-3150 m, DN, 4 Dec. 1966; NSMT(from ORI) P44368, 51.5 mm SL, 20°03'N, 130°05'E, North Pacific Ocean, 0-ca.1750 m, D, 20 Jan. 1985.

Diagnosis. See *C. parini* diagnosis.

Description. The holotype is in reasonable condition, with most of the skin of the lateral line and head canals torn or missing. The ISH specimen is in very poor condition with head and abdomen torn open and the pectoral fins and about one quarter of the skin gone. The LACM specimen is in reasonable condition, but totally faded, without colour. The NSMT specimen is very poor, with smashed head and lost skin.

D. 14-15; A. 12-13; P. 21; principal C. 6-7+6; procurrent C. 5+7; vertebrae 24+17-18=42-43; trunk canal lateral line scales/organs 12-14. Measurements in Appendix Table 5.

Body oval in cross section, greatest depth at level of pectoral base. Caudal peduncle much longer than deep, depth 2.7-4.0 in length. Anus far from anal fin origin, distance about equal to caudal peduncle depth. Cavernous tissue weakly developed anterior to anal fin origin, not reaching anus or ventral midline, most prominent in smallest specimen. Mid-dorsal and midventral keels not apparent. No anal lappet flaps, scales or ridges at base of anal fin. No subpectoral organ visible.

Head very large, compressed, much deeper than wide; in smallest specimen anterior head depressed and concave; head and anterior body profile weakly rounded. Nostrils similar to lateral line head pores, torn in all specimens, closer to tip of snout than eyes; raphe short and high without lamellae, ridges or pigment. Eye small, without lens, about midway between upper profile of head and upper jaw. Interorbital broad and convex; posterodorsal projections above eye most prominent in smaller specimens.

Mouth enormous, slightly oblique; jaws slightly concave; rictus 1-2 eye diameters before posterior end of premaxilla; posterior end of jaws well before edge of gill cover; lower jaw with weakly developed lateral and ventral spines posteriorly, more prominent in smaller specimens. Jaw teeth small, very long in inner row with length more than 3 times width, decreasing to outer row of very short teeth, all depressible orally; teeth closely set in irregular rows, without posterior clumping or grouping; premaxilla with 3 anterior and 3-4 posterior irregular rows, total number of teeth in approximate row 65-130; dentary with 3-4 anterior and 4-9 posterior irregular rows, total number of teeth in approximate row 55-130, numbers and rows increasing with size; dentary teeth extending 1 eye diameter or less behind rictus. Vomerine teeth short, in 1-5 rows forming roughly oval-shaped patch of 7-23 total teeth, numbers increasing with size; no palatine teeth; ectopterygoid tooth patch short, about 1.5 eye diameters long and under or slightly behind eye, teeth short to medium in 2 rows with 12-23 teeth in longest row. Copular tooth plate moderate in length and width, length 4.1-11.7% SL decreasing with increasing size, club shaped with posterior end largest and rounded, anterior pointed; teeth short, in irregular rows, about 3-6 rows across narrowest point and 27-38 rows along length.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of gill chamber. Holobranchs of all 4 arches poorly developed, short and far spaced, those of first arch about 3-4 in width of bony arch, filaments of fourth arch about twice length of those of first arch; separate holobranchs on ventral arm of first arch 27-32, on ventral arm of fourth arch 13-24; holobranchs present on dorsal arm of all 4 arches. Normal gill rakers absent; short, raised,

Fig.17. *Cetichthys indagator* holotype, 117.7 mm, ZMUC P23451; photo J. Fields, AMS.

rounded knobs covered with tiny, depressible teeth on all 4 arches, those in angle elongate and almost club shaped; gill knobs of first arch 3+1+8-9, of fourth arch 1-2+1+5-6; smaller raised tooth plates on medial faces of ventral arms of all 4 arches, numbering 8-9, 7-9, 6-8, 3-5. Dorsal pharyngeals as pair of small, high-crowned tooth plates, anterior plate kidney to oval shaped, much larger than posterior; posterior plate oval shaped; both plates covered with small, depressible teeth much larger than those on gill knobs. No ventral pharyngeal tooth plates.

Lateral line a broad, shallow tube of thin, fragile overlying skin with 13-15 wide pores without flaps or keels; 12-14 underlying scales, round, flat, without projections, interspaces half to 1 scale width between first 5-7 scales, wider than scales posteriorly; skin bridges over organs narrower than scales, usually lost; 1-2 papillae on remaining skin bridges; 2 papillae at bases of middle caudal rays behind last lateral line pore in ISH specimen; 1-2 papillae in dorsal midline behind head, presumed remnants of 2 lost rows of dorsal accessory line of superficial neuromasts.

Lateral line system of head with shallow canals and wide pores; skin bridges over neuromasts forming pores mostly torn; no complete pore/organ counts or superficial neuromast counts possible on any specimen; few remnants present indicate similarity to *Cetichthys parini*. Skin smooth, thin, fragile, lacking scales except in lateral line.

Dorsal and anal fins far back on body; dorsal origin distinctly before anal; dorsal base longer than anal, ending behind anal; anal base non symmetrical, origin elevated on extension of body behind anus; last anal ray base under 2nd or 3rd penultimate dorsal ray; dorsal and anal rays 6-10 longest, none branched. Pectoral fin low, short, directed posteriorly, upper rays longest, none branched. Caudal fin weakly emarginate to rounded, no rays complete.

Ovaries of 2 largest specimens paired, orangish, about 15 mm long, flaccid, with very tiny eggs; bladders paired, about one third length of ovaries in holotype, whitish, as long as ovaries in LACM specimen but hollow and balloon like, without apparent internal structure. No obvious urogenital papilla, urogenital opening immediately behind anus in holotype, perhaps in area before anal fin origin in LACM and ORI specimens.

Colour in alcohol light to dark brown; oral and gill cavities without pigment; stomach and peritoneum dark brown, intestine without pigment. Colour of LACM specimen when freshly caught brown with red-orange on head and dorsally, red-orange in oral and gill cavities.

Distribution. The three larger specimens were taken in the southern hemisphere between 30°-40°S, one in each ocean, and the smallest in the north-west Pacific (Fig. 11).

The three larger specimens were taken in open nets fishing to at least 2200 m, the smallest specimen in an open net with 5000 m of wire out, perhaps fishing to between 1500-2000 m (Fig. 12).

Etymology. From the Latin *indagator* - explorer.

Type specimen. The holotype of *C. indagator*, ZMUC P23451, was re-examined and appears to have an abnormaly shortened anal fin base (Fig. 17).

Remarks. The original description of *C. indagator* is detailed, but some interpretations require emmendation. The only teeth in the roof of the mouth other than those on the vomer are located far behind the vomer under the level of the eye; these are ectopterygoid rather than palatine teeth. The species of *Cetichthys* and *Notocetichthys* are the only cetomimids to lack teeth on the palatine, which is located immediately posterolateral to the vomer and extends posteriorly to the ectopterygoid. Rofen (1959:256) and Harry (1952:63,65) refer to the ectopterygoid teeth of other species of cetomimids as the posterior palatine patch. Rofen (1959:256) described the gill rakers of *C. indagator* as "... small round bony plates covered with gill teeth ...". These structures are not plates, but raised knobs (Fig. 3b) that most closely approach the club-shaped gill rakers of *Ditropichthys* and are unique to species of *Cetichthys* and *Notocetichthys*.

The identification of the small, smashed specimen from south of Japan was somewhat equivocal, but the long caudal peduncle, higher vertebral number and shorter anal fin base were considered decisive.

The dentition of the smallest specimen is prominent, with the individual teeth relatively longer than those of the larger specimens. The length of the copular tooth patch is striking, 11.7% SL, and displays allometric growth in the larger specimens, decreasing to 4.1% SL in the largest; the absolute length of the tooth patch remains constant or even decreases with size, ranging from 6.0-5.2 mm. The other feature that displays allometric growth is eye diameter, with an absolute measurement of 1.0-1.2 mm in all four specimens.

Cetichthys parini n.sp.

Figs 1g, 2b, 3b, 4c, 11, 12, 18

?*Cetomimus* sp.-Stein, 1985: 190 (in part, California specimens listed).

Type material. HOLOTYPE: SIO 53-344, 196.2 mm, Transpac 44/65, north-west Pacific south-east of Kurile-Kamchatka Trench, 45°24'N, 154°11'E, 0-ca.4680 m, 1245-2138 hrs, 16 Sept. 1953.

PARATYPES: 7(87.5-174 mm): OSUO 2552-3, 2(121.6-174 mm), *Golden Fleece* 2499/4, north-east Pacific off California, 39°23'N, 127°57'W, 2900-3000 m, closing net, 2127-0027 hrs, 10 Dec. 1981; SIO 87-9, 157.2 mm, Atom KLS141F, north-east Pacific off California, 32°50'N, 124°7'W, 2700 m, closing net, 28 May 1986; ZIN 47877, 104.2 mm, *Vityaz* 5082, central Pacific, 5°58'N, 139°57'W, 0-ca. 5000 m, 1320-1655 hrs, 16 Sept. 1961; AMS I.27258-001 (from ZIN 47875), 96.0 mm, *Vityaz* 3503, west Pacific, 23°05'N, 144°54'E, 0-ca.7000 m, 14 Oct. 1955; NSMT P60001 (from TH 800403), 88.6 mm, *Kaiyo Maru* Kocnet 9A, north-west Pacific off Bonin Island, Japan, 31°05'N, 147°35'E, 2887-3329 m, closing net, 2000-0800 hrs at depth, 27-28 May 1980; ZIN 47876, 87.5 mm, *Vityaz* 4535, east Indian Ocean off Bali, Indonesia, 10°04'S, 108°E, 0-ca.5800 m, 4 Nov. 1959.

Diagnosis. *Cetichthys parini* differs from *C. indagator*, its only congenor, in having fewer trunk canal lateral line scales and organs (8-9 versus 12-14) and pores (9-10 versus 13-15), vertebrae (39-41 versus 42-43), gill knobs on the ventral arm of the first (7-8, rarely 9 versus 9-10) and fourth (4-6 versus 6-7) gill arches, shorter caudal peduncle (16.7-19.2 versus 24.1-24.7% SL) and longer anal fin base (11.5-14.3 versus 7.1-9.9% SL). In addition *C. parini* has the anterior 5-7 scales of the lateral line further apart, with the interspaces wider than 1 scale width (versus anterior 5-7 interspaces equal to or less than one scale width), a weakly developed anal lappet without a scale at the anterior anal base (versus absent), the copular tooth patch longer and narrower than in specimens of *C. indagator* of similar size and the teeth of the posterior dentary and especially premaxillary grouped into clumps, particularly in specimens less than 130 mm (versus no clumping of posterior jaw teeth).

Description. The holotype is in good condition, although the skin of the lateral line and head canals is torn or missing and the fins are incomplete. The larger OSUO paratype is poor, with a badly smashed head; the smaller OSUO and SIO paratypes are in good condition, with only some of the lateral line missing. All of the ZIN paratypes are in good condition, except for broken jaws, but the NSMT paratype has lost about half the skin. The values of the holotype are followed by the range of values of the paratypes in brackets.

D. 14(13-16); A. 13(12-14); P. ?(19-24); principal C. ?(5-6+6); procurrent C. ?(4-5+4-5); vertebrae 24+15 =39 (24-26+15-17=40-41); trunk canal lateral line scales and organs 8(8-9). Measurements in Appendix Table 5.

Body oval in cross section, greatest depth at level of pectoral base. Caudal peduncle longer than deep, depth 2.1-3.6 in length. Anus far from anal fin origin, distance about equal to caudal peduncle depth. Cavernous tissue weakly developed with little structure, most prominent in smallest specimens, just anterior to anal fin origin, not reaching anus or ventral midline. Low but distinct mid-dorsal and midventral keels in most specimens extending anteriorly from dorsal origin and anus respectively. One anal lappet flap without scale at base of anal ray 3 set at end of very low ridge from anal ray 1 (Fig. 18b). No subpectoral organ visible.

Head very large, slightly compressed and distinctly deeper than wide; in smaller paratypes head anteriorly depressed and strongly concave from jaws to dorsal midline; head and anterior body profile weakly rounded with uneven pits and projections on top of head, bony projections posterodorsal to eyes prominent in smaller paratypes. Nostrils similar to head lateral line pores, torn in all specimens, closer to tip of snout than eyes; raphe short, high, without lamellae or ridges, situated below anterior nostril, weakly pigmented basally in some specimens (Fig. 1g). Eye small, without lens even in smallest specimens, nearer upper profile of head than upper jaw. Interorbital very broad, weakly convex.

Mouth enormous, slightly to moderately oblique; jaws slightly to moderately concave; rictus 2-3 eye diameters before posterior end of premaxilla; posterior end of jaws well before end of gill cover; lower jaw with weakly developed lateral and ventral spines posteriorly, more prominent in smaller paratypes. Jaw teeth small, more elongate in inner row with length sometimes more than 3 times width, decreasing to outer row of very short teeth, all depressible (Fig. 1b); teeth in irregular rows with distinct

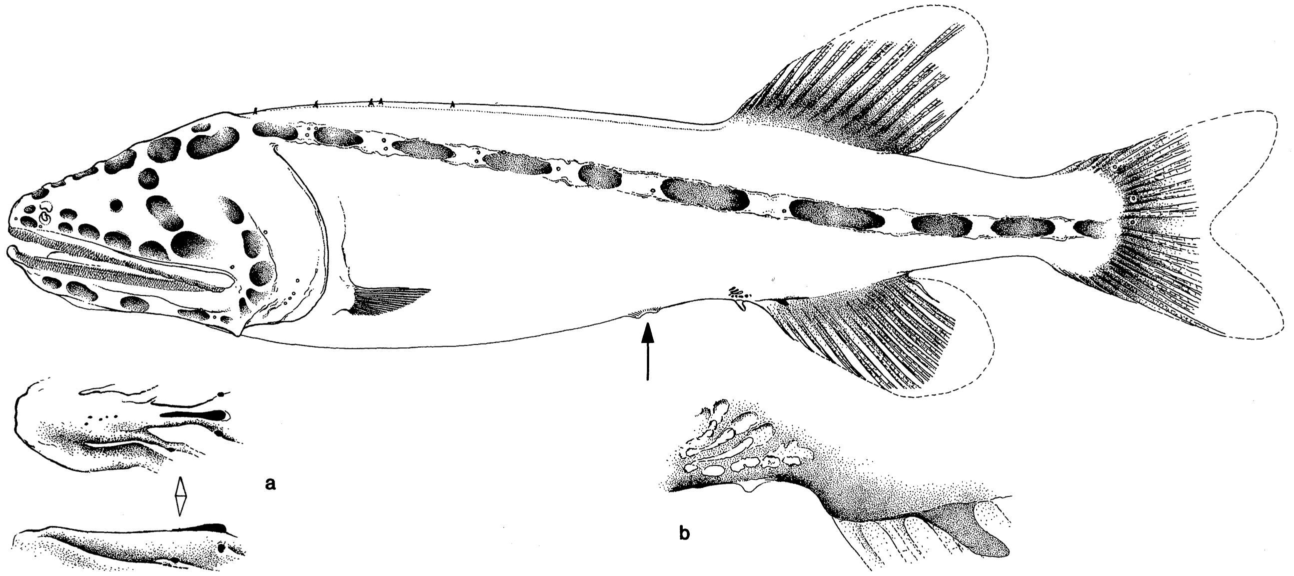

Fig.18. *Cetichthys parini* holotype, 196.2 mm, SIO 53-344, arrow indicates level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, *C. parini* paratype, 87.5 mm, ZIN 47876, showing cavernous tissue and anal lappet, right hand side.

grouping into clumps in posterior jaws of smaller specimens, not as distinct in holotype; premaxilla with up to ?(3-4) anterior and 4(4-6) posterior irregular rows, total number of teeth in approximate row ?(105-145, 3 specimens counted); dentary with up to 5(4-5) anterior and 9(7-8) posterior irregular rows, total number of teeth in approximate row 171/178(95-165, 4 specimens), tooth numbers and rows increasing with specimen size; teeth on dentary extending about 1-1.5 eye diameters behind rictus. Vomerine teeth short, in 3(1-4) rows usually forming an approximate oval-shaped patch totalling 13(9-20) teeth, number not correlated with size; no palatine teeth; ectopterygoid tooth patch short, about 1-2 eye diameters in length, under or slightly behind eye, teeth short to medium, in 2(2-4) rows with 24(13-22) teeth in longest row. Copular tooth plate moderate in length and slender, length 3.5 (4.4-8.9)% SL, decreasing with increasing size, club shaped with posterior end largest and rounded, anterior end pointed (Fig. 18a); teeth short, in irregular rows, about 4(2-5) rows across narrowest point and 32(32-51) rows along length.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of oesophagus. Holobranchs of all 4 arches poorly developed, short and far spaced, those of first arch about 3-4 times in width of bony arch (Fig. 3b); holobranchs of fourth arch about 2 times length of those of first arch; separate holobranchs on ventral arm of first arch 32(27-32), on ventral arm of fourth arch 20(16-21); holobranchs present on dorsal arm of all 4 arches. Normal gill rakers absent; short, raised, rounded knobs covered with tiny depressible teeth on all 4 arches, those in angle elongate and almost club shaped; gill knobs of first arch 3+8(7-9), of fourth arch 2(1-2)+6(4-6); smaller raised tooth plates on medial faces of ventral arms of arches 1-4, numbering 7(5-8), 7(5-6), 6(3-5), and 2(2-3). Dorsal pharyngeals as pair of small, high-crowned tooth plates, anterior plate kidney to oval shaped, distinctly larger than posterior; posterior plate tear-drop, kidney or oval shaped, somewhat pointed medially in some specimens; both plates covered with small, depressible teeth much larger than teeth on gill knobs. No ventral pharyngeal tooth plates.

Lateral line a broad tube, moderately deep in holotype, shallow in paratypes, of thin overlying skin with 9-10 wide pores without flaps or keels; 8-9 underlying scales, round, flat, without projections, interspaces wider than scale width; skin bridges over neuromasts narrower than scales, usually lost; 1-6 papillate neuromasts on some remaining skin bridges; 2-3 papillae at bases of caudal rays behind and above last lateral line pore; dorsal accessory line of superficial neuromasts as 2 mid-dorsal rows of widely-spaced papillae from level of top of gill opening posterior to about halfway to dorsal fin origin, rows close together posteriorly, divergent anteriorly, about 6-8 papillae per row.

Lateral line system of head with cavernous canals in holotype, shallow canals in paratypes, and wide pores (Fig. 4c); skin bridges over neuromasts forming pores mostly complete in holotype, torn in paratypes. Supraorbital canal with 6 pores and 5 neuromasts joined to main canal with 2 pores and 3 neuromasts (last before top of gill slit), with supratemporal pore and neuromast medial to pore 2. Infraorbital canal with 8 pores and 6 lower and 2 upper neuromasts, joined to main canal at 1st pore, last 2 neuromasts and associated pores slightly displaced anterodorsally. Mandibular canal with 5 pores and 4 neuromasts, almost joined to preopercular canal with 5 pores and 4 neuromasts. Papillate superficial neuromasts on head mostly lost?, 1-2 on snout, 1-2 below nostrils, 1 above posterior tip of premaxillary, 1 behind uppermost preopercular organ, 3-4 just above angle of preopercle, at least 2 over last lower jaw pore. Skin smooth, lacking scales except in lateral line, that of holotype thicker, of paratypes thin and fragile.

Dorsal and anal fins far back on body; dorsal origin slightly before anal origin; ends of dorsal and anal opposite; fin rays incomplete. Pectoral fin low, short, directed posteriorly, upper rays longest. Caudal fin weakly to moderately forked in specimens with complete rays.

Ovaries paired, orangish in 2 largest specimens with eggs less than 0.1 mm, increasing in size with age. Bladders paired, whitish and covered with light layer of pigment, rounded with small lobes in largest specimens, attached to dorsal mesentary before end of ovary, 9.5 mm by 3 mm in holotype, much smaller in all others. None of the specimens with fully developed ovaries and presumably all are juveniles. Much of abdominal cavity filled with fat in two largest specimens. Four smallest paratypes with distinct urogenital papillae just before anal fin origin under level of cavernous tissue; no papillae apparent in four largest specimens, urogenital opening just behind anus in holotype. Paired small, dark brown structures in body wall either side of anus visible in most specimens including holotype.

Colour in alcohol light to dark brown; oral and gill cavities without pigment; stomach and peritoneum dark brown, intestine without pigment.

Distribution. The eight specimens range from the eastern Indian Ocean and central Pacific to both sides of the north Pacific (Fig. 11).

The species is apparently the deepest dwelling of all whalefishes. Four captures were made with closing nets, all fishing between 2700 and 3330 m; all other captures were made by open nets fishing to at least 4500 m (Fig. 12). It is perhaps surprising that we have so many specimens of this bathypelagic species.

Etymology. After Nikolai V. Parin, who provided the IOANM (now ZIN) collection of cetomimids for study, in recognition of his contributions to pelagic and deep sea ichthyology.

Remarks. There seems little doubt that *Cetichthys parini* and *C. indagator* are distinct species, with non-overlapping values in meristics (vertebrae and lateral line scales/organs and pores) and morphometrics (caudal peduncle length and anal fin base length (Table 5). One weak anal lappet and curved sections of posterior jaw teeth are both restricted to *C. parini* (versus absent in

C. indagator). There is also a tendency for *C. indagator* to have a higher number of tooth knobs and medial tooth plates on the gill arches and a shorter head and wider caudal peduncle, but the ranges of values overlap in the two species.

Variation within the eight type specimens of *C. parini* is considerable. The most striking difference involves the amount of flesh on the specimens, with the largest, the holotype, appearing heavy and well rounded; flesh on the head reduces the prominence of bony projections, the belly and caudal peduncle are well rounded, and a large amount of fat is present in the abdominal cavity. The largest paratype is also relatively heavy and well-filled out. In contrast the five smaller paratypes, all at least 30% shorter than the largest paratype, appear emaciated, with the head strongly convex between the upper jaw and the dorsal profile, with prominent projections, and the body slender. These differences result in the size-correlated differences of measurements of body depth and caudal peduncle depth (Table 5), that could be a function of gaining condition and laying down fat and muscle with increasing size. Allometric growth is indicated for head length, premaxillary and dentary lengths and snout to pectoral distance, all of which are greater in smaller specimens. Neither the eye diameter nor length of the copular tooth patch appear to increase in size with specimen growth; eye diameter is 1.0-1.2 mm in all specimens, while the copular tooth plate ranges from 6.8-7.9 mm, at least 0.8 mm longer than the absolute measurements of the specimens of *C. indagator*. The increased amount of tissue in the two largest specimens is also correlated with deeper canals of the lateral line system, both on the head and body.

Notocetichthys Balushkin, Fedorov & Paxton, 1989

Notocetichthys Balushkin, Fedorov & Paxton, 1989: 155. Type species *Notocetichthys trunovi* Balushkin, Fedorov & Paxton, 1989 by original designation.

Diagnosis. *Notocetichthys* differs from all other cetomimid genera in lacking vomerine and ectopterygoid teeth, in having the copular tooth patch reduced to a tiny plate behind the level of the eye, cavernous tissue in an area behind the anus with a distinct free posterior margin and prolonged posterior extension as a free, thin flap without any supporting scale, and in having 5-7 diagonal skin ridges along the midbody with each ridge centred on a lateral line scale. *Notocetichthys* is most similar to *Cetichthys*, each lacking palatine teeth and having gill arch tooth plates on short, rounded knobs. The two genera differ in the unique characters described above, and also in the condition of the infraorbital canal (joined to the supraorbital in *Cetichthys*, separate in *Notocetichthys*) and in the number of dorsal and mandibular canal pores (10 and 6-7 in *Notocetichthys* versus 8 and 5).

Description. D. 13; A. 11-13; P. 17?-19; principal C. 5-6+5-6=10-12; vertebrae 24-26+15=39-41; trunk canal lateral line scales and organs 15-16. Size moderate, maximum 109 mm; head large, 3.1-3.2 in SL and moderate to wide, width at eye 3.1-4.2 in HL; snout rounded and moderate in length, 2.5-2.9 in HL; mouth large, jaws ending about midway between level of eye and opercular margin; dorsal and anal fin bases short, 2.7-3.2 in HL; caudal peduncle moderate to long, 1.6-1.7 in HL and deep, 2.2-2.4 in length; anus far from anal origin, distance 0.8-1.0 in CPD.

Nasal organ short and broad with few weak ridges present or absent. Eye tiny, 22-32 in HL, without discernible lens. Lateral line system of head as series of wide canals with apparently large pores (skin damaged), with the following pore counts based on presence of neuromasts: supraorbital canal with 6 pores, apparently joined to main canal with 4 pores, infraorbital canal apparently separate from dorsal canal with 8 pores, last displaced anteriorly, mandibular canal with 6-7 pores, apparently joined to preopercular canal with 5 pores. Lower jaw with apparently weak lateral and ventral spines posteriorly (spines broken). Jaw teeth tiny, height less than 2 times basal width, closely set in indistinct diagonal to vertical rows; vomerine, palatine and ectopterygoid teeth absent; copular tooth patch on 1 plate, tiny, length 29-35 in HL, and relatively broad, width 1.1-2.4 in length, origin behind level of eye.

Free gill arches 4, with slit behind ventral arm of fourth arch; holobranchs long and moderately spaced on all 4 arches, present on dorsal arms of all 4 arches. Gill rakers as round knobs with small teeth on all 4 arches, 2+1+7 on first arch; tooth plates present on medial faces of all 4 arches; no ventral pharyngeal tooth plates.

Lateral line a shallow, broad tube, with wide pores; lateral line scales large, flat and round (first and last scales semirectangular). Cavernous tissue in small well-defined area behind anus with raised, free posterior margin and elongate flap without supporting scale over about third anal ray. Diagonal midbody skin ridges centred on lateral line scales 7-13. No subpectoral organ visible. No paired abdominal ridges. No series of anal lappets with scales, or ridges or membranous curtain associated with anal fin. Stomach pigment brown.

Etymology. From the Greek *noto* - southern, *cetus* (*ketos*) - whale and *ichthys* - fish, in reference to the Antarctic occurrence of the two known specimens.

Remarks. Only two specimens have been collected, in Antarctic waters at 65°S, by nets fishing to a maximum of 1275 and 1360 m depth.

Notocetichthys trunovi Balushkin, Fedorov & Paxton, 1989

Figs 11, 12, 19

Ditropichthys sp.-Trunov, 1985:296, 305 (listed from Lazarev Sea).

Notocetichthys trunovi Balushkin, Fedorov & Paxton, 1989: 156, fig. 1. Holotype ZIN 47696, 107.5 mm, FRV *Volny Veter* Stn 14, Lazarev Sea, Antarctica, 65°20'S, 02°34'E, 0-1360 m over 1370-1400 m bottom, 20 Jan. 1983; paratype ZIN 47697, 109.0 mm, FRV *Volny Veter* Stn 11, Lazarev Sea, Antarctica, 65°17'S, 2°42'E, 0-1275 m over 1285-1300 m bottom, 17 Jan. 1983.

Diagnosis. As for genus.

Description. The two type specimens are in reasonable condition, except most of the skin over the lateral line and head canals is missing.

D. 13; A. 11-13; P. 17?-19; principal C. 5-6+5-6=10-12; vertebrae 24-26+15=39-41; trunk canal lateral line scales and organs 15-16. Measurements in Appendix Table 6.

Body oval anteriorly, greatest depth at level of pectoral base. Caudal peduncle 2.2-2.4 times longer than deep. Anus far from anal origin, distance about equal to caudal peduncle depth. Cavernous tissue well developed in small, diffuse area behind anus extending to level of first anterior anal rays, with posterior edge of area raised and free and with thin, flap-like extension over anal fin similar to very narrow anal lappet but without supporting scale. Low, narrow, diagonal ridges of skin centred on 6-7 lateral line scales from before to behind dorsal fin; ridges expand at lateral line to form skinbridge over neuromast; white vessels inside ridges that expand at ends of ridges to form networks of tiny vessels under dorsal and anal bases and over caudal peduncle. No mid-dorsal or midventral keels apparent. No anal lappet flaps, scales or ridges over anal fin base.

Head very large, deeper than wide with almost straight profile from snout to occiput. Nostrils closer to tip of snout than eye, round, anterior about twice diameter of posterior, skin bridge about as wide as posterior nostril; nasal organ short and broad with few weak ridges present in one specimen, situated below anterior nostril, covered by light brown pigment. Eye small, without discernible lens, closer to top of head than upper jaw.

Mouth large, slightly oblique; rictus 1-2 eye diameters before end of premaxillary; posterior end of jaws closer to level of eye than margin of operculum. Jaw teeth tiny, triangular, height less than 2 times basal width, closely set in indistinct diagonal to vertical rows, depressible orally. No vomerine, palatine or ectopterygoid teeth. Copular tooth plate tiny, 0.9-1.1% SL, on posterior copula about midway between levels of eye and posterior premaxilla, oval to rectangular, width 1.1-2.4 in length, with about 18 tiny teeth set in approximately 3 rows, middle row longest.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of gill chamber. Holobranchs of all 4 arches moderately long and moderately spaced, those of first arch about four fifths as long as bony width of arch; holobranchs of fourth arch about equal to or slightly longer than those of first arch; holobranchs present on dorsal arms of all 4 arches. Normal gill rakers absent; short, raised, rounded knobs covered with tiny teeth on all 4 arches, those in angle elongate and almost club shaped; gill knobs of first arch 2+7-8, second arch 1+8, third arch 1+4, fourth arch 1+6; smaller raised tooth plates on medial faces of ventral arms of all 4 arches, numbering 7, 7, 5, and 4 respectively (only 1 specimen counted). Dorsal pharyngeals as 2 pair of small, high-crowned tooth plates, directed medially rather than ventrally so that anterior plate of right side abuts between anterior and posterior plates of left side; plates roughly dome shaped, posterior half to two thirds size of anterior, both covered with about 4 rows of teeth similar in size and shape to jaw teeth. No ventral pharyngeal tooth plates.

Lateral line a broad, shallow tube with overlying skin mostly lost, anterior skin bridges apparently very narrow;

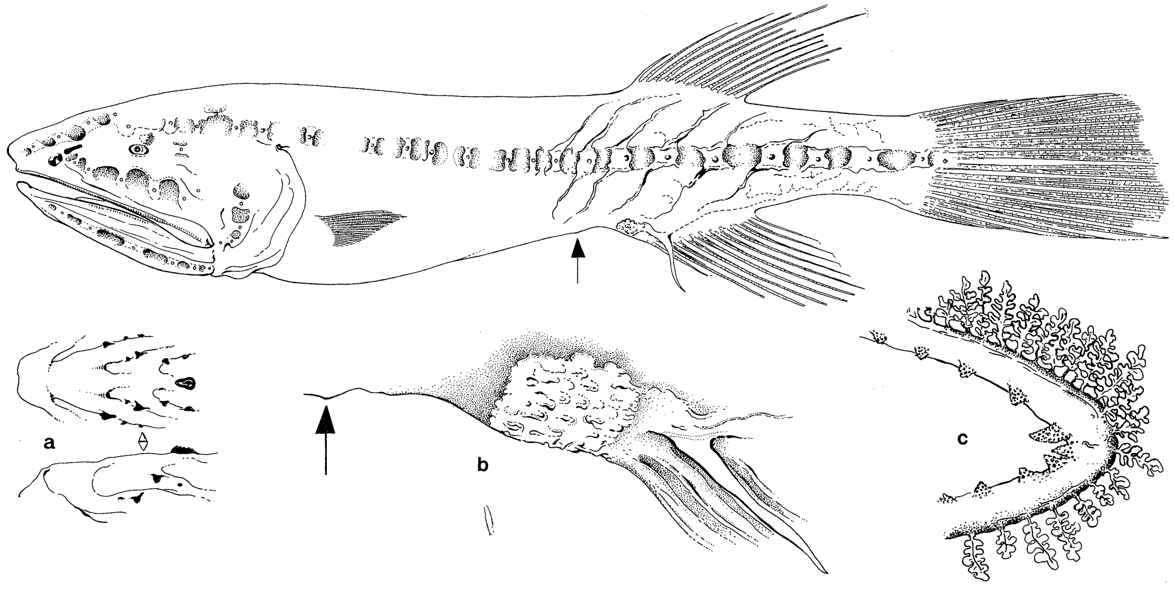

Fig.19. *Notocetichthys trunovi* holotype, 107.5 mm, ZIN 47696, arrow indicates level of anus, dashed lines indicate white "veins"; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, enlargement of cavernous tissue; c, first gill arch, left side (not to scale).

anterior pores almost round, posterior pores longer than wide; 15-16 lateral line scales round and flat (first and last semirectangular) without projections; some anterior scales close together; others wide apart, interspaces as wide as scale posteriorly; no papillate neuromasts observed on lateral line or mid-dorsally; 2 papillae on basal quarter of caudal fin.

Lateral line system of head with wide, shallow canals and moderate to large neuromasts, overlying skin mostly lost. Supraorbital canal with 6 pores and 5 neuromasts, apparently joined to main canal with 4 pores and neuromasts, supratemporal medial to pore 3. Infraorbital canal with 8 pores and 7 neuromasts, the last slightly displaced anterodorsally behind eye, apparently separate from main canal. Mandibular canal with 6-7 pores and 5-6 neuromasts, joined to preopercular canal with 5 pores and 4 neuromasts. No distinguishable papillae on head. Skin smooth, thin and fragile, without scales except in lateral line.

Dorsal and anal fins far back on body; dorsal origin slightly to distinctly before anal origin; both fins exceptionally long rayed, longer than any other cetomimid; middle dorsal and anal rays longest, none branched. Pectoral fin moderately high on body, short, directed dorsoposteriorly; upper 5-6 pectoral rays longest, none branched. Caudal fin weakly forked to emarginate.

Ovaries paired, organish, about 9 mm long in paratype, with tiny eggs less than 0.1 mm diameter. Bladders paired, very thin walled without apparent internal structure, almost as long as ovaries, and about half as wide as long. Possible urogential papilla just before anal fin origin, far behind anus.

In life claret coloured, tips of fins bright orange, belly with bluish tinge, mouth and gill cavities pink (Baleshkin *et al.*, 1989). Colour in alcohol moderate brown to grey brown; oral cavity without pigment, except brown skin flap medial to teeth, gill cavity light brown; peritoneum dark brown, stomach moderate brown, intestine without pigment.

Distribution. The only two specimens come from bathypelagic waters of the Antarctic (Fig. 11). The only other cetomimids known from such southern waters are two species of the genus *Gyrinomimus* (Fedorov & Balushkin, 1983; Fedorov, Balushkin & Trunov, 1987).

Both specimens were collected between the surface and 1400 m (Fig. 12). It is noteworthy that both were caught in pelagic nets fishing less than 100 m off the bottom, indicating that perhaps this species is benthopelagic.

Etymology. After I.A. Trunov of the Atlantic Fisheries and Oceanographic Research Institute, Kaliningrad, who collected the two type specimens.

Remarks. The holotype of *Notocetichthys trunovi* was taken in the same haul as the holotype of *Gyrinomimus andriashevi* (Balushkin *et al.*, 1989).

Danacetichthys n.gen.

Type species. *Danacetichthys galathenus* n.sp.

Diagnosis. This new genus has small, elongate teeth closely set in well-defined longitudinal rows in the jaws and palate, unlike all other cetomimid genera except *Gyrinomimus*. *Danacetichthys* differs from *Gyrinomimus* in the presence of ventral pharyngeal tooth plates on the fifth ceratobranchial, number of free gill arches (4 versus 3), vertebral number (43-46 versus 47-59), shape of lateral line scales (round or widely rectangular and flat versus strap like or narrowly rectangular and curved) and maximum size (54 mm versus 390 mm).

Description. D. 14-16; A. 14-15; P. 21-23; principal C. 13-15?; vertebrae 26-29+15-20=43-46; trunk canal lateral line organs and scales 16-18. Size small, maximum known 54 mm; head very large, 2.7-2.8 in SL and wide, width at eye 2.6-3.8 in HL; snout rounded and moderate, 2.9-3.3 in HL; mouth very large, jaws ending much closer to opercular margin than level of eye; dorsal and anal bases short to moderate, 2.0-3.2 in HL; caudal peduncle short to moderate, 2.0-3.8 in HL, and moderate to deep, 1.3-2.3 in CPL; anus close to anal fin, distance 2.6-6.3 in CPD.

Nasal organ small and low, without lamellae or ridges. Eye small, 15-19 in HL, but with lens well developed or reduced. Lateral line system of head a series of large canals with wide pores, no canals undamaged; supraorbital canal with 6 pores, apparent break between last supraorbital and first main canal pore, main canal with 3-4 pores, infraorbital canal with about 9 pores, the last displaced, not joined to main canal, mandibular canal about 8 pores, unknown if joined to preopercle with about 4 pores; neuromasts tiny and delicate. Lower jaw with weakly developed lateral and ventral spines posteriorly. Jaw teeth elongate, inner row with length more than 3 times basal width, closely set in well defined longitudinal rows; vomerine tooth patch rectangular, ellipsoidal or triangular; palatine and ectopterygoid teeth distinct, latter reaching level of rictus; copular tooth patch short to moderate and broad.

Free gill arches 4 with slit behind ventral arm of fourth arch; holobranchs well developed on all 4 arches; holobranchs on dorsal arm of first arch. Gill rakers as separate, slightly raised, round or ellipsoidal patches of small teeth on all 4 arches (9-10 on first arch), but none on medial faces; ventral pharyngeal tooth plates present.

Lateral line a broad, thin-walled tube pierced by very wide pores; lateral line scales round or widely rectangular, posteriorly close together. Cavernous tissue only at anus. Subpectoral organ present. No paired abdominal ridges or diagonal midbody ridges. No lappets, ridges, folds or membranous curtain associated with anal fin. Stomach lightly to darkly pigmented.

Etymology. *Dana*, the Danish research vessel and from the Greek *cetus* (*ketos*) - whale and *ichthys* - fish, in reference to the fine early collection of 33 whalefishes from the *Dana* Expeditions now at the University of

Copenhagen. The gender is masculine.

Remarks. Six specimens have been collected from the Atlantic, Indian and Pacific Oceans. All the specimens are immature and apparently represent one species.

Danacetichthys galathenus n.sp.

Figs 1h, 3d, 4d, 11, 12, 20

Type material. HOLOTYPE: ZMUC P2340563, 39.3 mm, *Dana* 3613 VI, south-west Pacific off New Caledonia, 22°43'S, 166°06'E, 0-ca. 1330 m, 0530 hrs, 28 Nov. 1928.

PARATYPES: 5(34.0-53.9 mm): NSMT P60002 (from TH 821052), 53.9 mm, *Kaiyo Maru* Kocnet 15(B), north-west Pacific off Bonin Is., Japan, 30°25'N, 147°18'E, 0-2046m, 0808-1657 hrs, 10 June 1982; USNM 200525, 53.5 mm, *Anton Bruun* III APB 7014, Indian Ocean, 7°14'N, 59°53'E, 0-2250 m, 3 m IKMT, 1255-1815 hrs, 16 Aug. 1963; ISH 1944/71, 48.6 mm, *Walther Herwig* 459/71, central Atlantic, 10°57'S, 11°20'W, 0-1900 m, CMBT 1600, 1818-2218 hrs, 7 Apr. 1971; SIO 70-327, 38.1 mm, RV *Melville* Ant. 4-630-12, western Pacific, 18°20'N, 133°29'E, 0-1500 m, 1700-0045 hrs, 9 Sept. 1970; ZMUC P2340564, 34.0 mm, *Dana* 1267 II, western Atlantic, 17°56'N, 64°50'W, 0-ca. 1330 m, 0730 hrs, 14 Mar. 1922.

Diagnosis. As for genus.

Description. The holotype is in good condition, with most of the head and lateral line pores as well as papillate neuromasts visible. The NSMT paratype has some skin rubbed off the head and lateral line, but the fins are remarkably complete. Most of the other paratypes are in fair condition, with much skin missing. The ISH specimen has the abdominal wall torn and the stomach protruding. The fins of the SIO specimen are incomplete. The values of the holotype are followed by the range of values of the paratypes in brackets.

D. 14(14-16); A. 15(14-15); P. 21(21-23); principal C. ?(6-8+7); procurrent C. ?(5-6+?); vertebrae 29+16=45 (26-28+15-20=43-46); trunk canal lateral line scales/organs 17(16-18). Measurements in Appendix Table 6.

Body oval in cross section behind head; greatest depth at level of pectoral base. Caudal peduncle 1.3-2.4 times longer than deep. Anus close to anal fin origin. Cavernous tissue extensive around anus only, in series of grooves running dorsoanteriorly from around anus and preanal area; grooves separated by low skin ridges, extending two thirds distance to lateral line tube (Fig. 20a,b). Short, low mid-dorsal ridge, no belly ridge. No anal lappet flaps, scales or ridges at base of anal fin. Subpectoral organ anteroventral to pectoral base visible in best preserved specimens, details of structure unknown.

Head very large, about as deep as wide posteriorly, somewhat depressed anteriorly; head and anterior body profile weakly rounded or slightly concave anteriorly. Nostrils moderate, about half eye diameter, halfway between eye and tip of snout, with raised anterior rim; nasal organ short and low, with no lamellae or ridges, situated almost entirely in anterior nostril (Fig. 1h); internasal skin bridge one third to one quarter nostril diameter. Eye small, with well-developed (2 specimens) or reduced (4 specimens) lens, slightly closer to upper jaw than top of head; strong bony projection of sphenotic over eye.

Mouth enormous, slightly oblique, jaws relatively straight in undamaged specimens; rictus 1-2 eye diameters before posterior end of premaxilla; posterior end of premaxilla closer to edge of gill cover than level of eye; lateral and ventral posterior spines of lower jaw weakly developed. Jaw teeth tiny, very elongate in inner row with basal width more than 3 times in length, those of outer row about one third length of inner; upper jaw with 3(3-4)

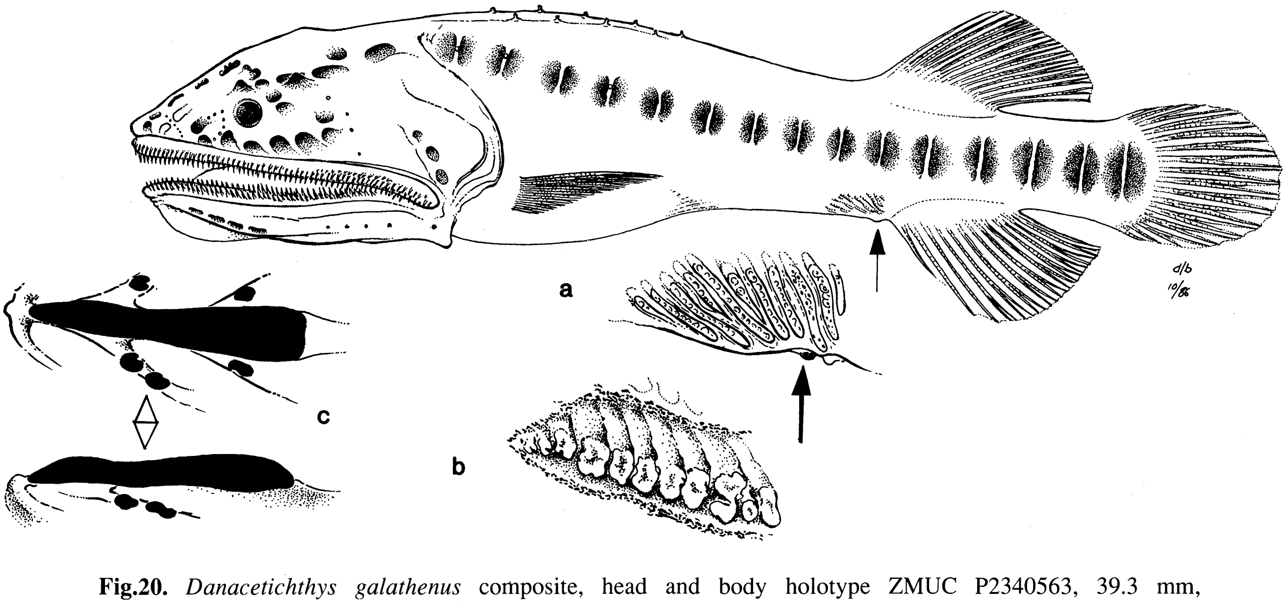

Fig.20. *Danacetichthys galathenus* composite, head and body holotype ZMUC P2340563, 39.3 mm, unpaired fins paratype NSMT P60002, 53.9 mm, arrow indicates level of anus; a, b, enlargement of cavernous tissue; c, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye.

complete rows of teeth and fourth outer row incomplete; 91(93-94 in 2 paratypes) teeth in inner row; lower jaw with 4(3-5) rows of teeth with 71(60-82 in 4 paratypes) in inner row; tooth rows not precise, with some teeth between rows. Vomerine teeth short to moderate, inner teeth longest, in about 3(3-6) rows with 22(15-46) teeth, tooth patch rectangular, ellipsoidal or triangular in shape; palatine teeth moderate to long, inner row longest, in 2-3(2-5) rows with longest row of 16(15-22) teeth; ectopterygoid teeth short to moderate with very small space at end of palatine teeth, in 1(1-2) rows posteriorly and 3(2-4) rows anteriorly with longest row of 38(34-54) teeth, extending about to level of rictus; copular tooth patch short to moderate and wide, pointed anteriorly, rounded posteriorly, broadest posteriorly (Fig. 20c); teeth moderate in length, 7-10(5-13) approximate rows across with about 33(27-40) teeth in length. All teeth depressible towards centre of oral cavity.

Free gill arches 4, with small slit about length of 2 eye diameters behind ventral arm of fourth arch; dorsal arms of arches 1 and 2 free, most of 3 and all of 4 bound together. Holobranchs of all 4 arches well developed and closely spaced, those of first arch about 2.5 times bony width of arch (Fig. 3d); holobranchs of fourth arch about four fifths length of those of first arch; holobranchs absent or present only on ca. 10% of dorsal arm of first arch. Normal gill rakers absent; arch 1 with 2+7(2+7-8) tooth plates, round to elliptical in shape with moderately long, depressible teeth, more than 15 and less than 100 teeth per plate; similar tooth plates on arches 2-4 numbering 1+6(6-8), 1+8(0-1+6-7) and 0+4(3-5), no tooth plates on medial faces of arches. Dorsal pharyngeals as 2 pair of ellipsoid-shaped tooth plates in roof of mouth, posterior about two thirds size of anterior; teeth moderate to long, longest posteriomedially, in indistinct curving rows. Ventral pharyngeal tooth plates of fifth ceratobranchial small and elliptical (triangular to rectangular), covered with small teeth.

Lateral line a broad tube of very thin, fragile overlying skin with 18(17-19) wide pores without flaps or keels, remaining skinbridges much narrower than underlying scales; 17(16-18) underlying scales, round to widely rectangular, flat, without projections, interspaces about half scale width anteriorly, scales almost touching posteriorly; single mid-dorsal row of about 10 papillae from level of top of gill slit to about one third distance to dorsal fin origin, representing dorsal accessory line of neuromasts visible in holotype, presumably rubbed off other specimens.

Lateral line system of head with shallow canals and wide pores, skin mostly torn (Fig. 4d). Supraorbital canal with 6 pores and 5 neuromasts, with fifth and sixth pores large; main canal with 3-4 pores and 3 neuromasts with apparent break between last supraorbital and first main pores; supratemporal pore medial to main pore 2. Infraorbital about 9 pores and 8 neuromasts, last displaced anterodorsally out of series to behind eye, not joined to main canal. Mandibular canal about 8 pores and 7 neuromasts, preopercle about 4 pores, unknown whether joined or not. Group of 5-6 papillate superficial neuromasts on either side of tip of snout, curving row of 10 papillae across internarial bridge of skin, row of 5 papillae between eye and posterior nostril, row of 4-5 widely spaced papillae down preopercle, row of about 20 papillae on posterior half of ventral side of lower jaw.

Dorsal and anal fins far back on body; anal origin under dorsal ray 2-4; ends of dorsal and anal opposite; rays of holotype remarkably complete, middle dorsal and anal rays longest, penultimate 7-8 rays branched at tips. Pectoral fin low, short, directed posteriorly, upper rays longest, no branched rays. Caudal fin weakly rounded (slightly truncate), middle rays longest.

Ovaries of all thin, short, undeveloped, largest paratype with short tubular gonad of orange colour. Paired tubular bladders with transparent walls and connection to dorsal mesentary lateral to ovaries.

Colour in alcohol faded brown; oral cavity light brown; stomach light to dark brown; peritoneum dark brown; intestine without pigment.

Distribution. All six specimens have been taken within 30° of the equator (Fig. 11), in all three oceans.

The species is deeper dwelling than either *Cetostoma* or *Ditropichthys*, as all of the relatively small specimens have been taken with nets fishing to at least 1300 m (Fig. 12).

Etymology. From the Greek *galathenos* - young, in reference to the apparently immature state of all of the type specimens.

Remarks. The six specimens display variation in morphometrics and dentition that is difficult to interpret. The two Atlantic specimens have a much longer caudal peduncle than the other specimens, and have longer dorsal and anal fin bases (Table 6). The three Pacific specimens have more posterior dorsal and anal fin origins than the other specimens. No allometric growth is apparent for any measurement. The most striking differences in dentition are in the number and arrangement of the vomerine teeth. The two smallest specimens have an approximately triangular-shaped tooth patch with the base anterior, about five rows and 19 to 25 total teeth; these specimens come one each from the Pacific and Atlantic Oceans. The other two Pacific specimens, including the largest specimen in the series, have only three rows of vomerine teeth in an approximate rectangle, totalling 15 to 22 teeth. The Indian Ocean and other Atlantic specimen have five to six rows totalling 42 to 46 teeth. Although two or more species may be represented in the series, all are considered one species until more specimens of larger size become available.

Cetostoma Zugmayer, 1914

Cetostoma Zugmayer, 1914: 4. Type species *Cetostoma regani* Zugmayer, 1914 by monotypy.

Diagnosis. *Cetostoma* differs from all other cetomimid genera in having a higher number of dorsal and anal rays (29-37 and 26-34 versus 13-21 and 13-20), elevated dorsal and anal fin bases (versus not elevated) long to very long (versus moderate to very short), 2.6-4.4 in SL (versus 3.8-14.1 in SL), the dorsal fin origin closer to the snout (distance 1.7-2.0 in SL versus 1.3-1.6 in SL), a very long, narrow copular tooth patch as 3 separate dentigerous plates (versus 1 solid plate), the slit behind the fourth gill arch restricted to a tubular hole behind the angle of the arch (versus a slit behind the ventral arm or none), numerous small skin ridges along the belly from the pectoral base to the anus and the posterior anal fin membrane in curtain-like folds.

Description. D. 29-37; A. 26-34; P. 20-21; principal C. 8-9+7-8=(15)17; vertebrae 23-27+23-26=47-53; trunk canal lateral line scales and organs 15-17. Size large, maximum 246 mm; head moderate to large, 3.2-4.5 in SL and narrow, width at eye 3.8-6.3 in HL; mouth large, jaws extending slightly closer to opercular margin than level of eye; snout rounded and moderate, 2.1-3.1 in HL; dorsal and anal bases long, 0.6-1.3 in HL; caudal peduncle short to moderate, 1.6-2.8 in HL and very slender, 2.8-4.7 in CPL; anus close to anal fin origin, distance 1.5-5.1 in CPD.

Nasal organ short, high and narrow without lamellae or ridges. Eye tiny, 15-41 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores, 6 pores in supraorbital canal, main canal apparently separate from supraorbital canal with 3 pores, infraorbital canal separate from main canal with 9 pores, last not displaced dorsally or anteriorly, mandibular canal with 6-7 pores not joined to preopercular canal with 5 pores; neuromasts large, firm, thin and rectangular. Lower jaw with indistinct lateral spine and distinct ventral spine posteriorly. Jaw teeth tiny, in irregular diagonal bands; vomerine tooth patch variable, oval, rectangular, diamond shaped or asymetrically curved; palatine tooth patch long and slender, extending to level of eye; ectopterygoid tooth patch long and slender, extending behind rictus; copular tooth patch on 3 separate plates, very long and slender with length 1.8-2.0 in HL and width 23-44 in length.

Free gill arches 4, with tube-like slit behind angle of arch 4; holobranchs well developed on first 3 arches, small on fourth arch, present on dorsal arm of first arch. Gill rakers as separate tooth plates on first 3 arches, smaller tooth plates on medial face of arch 1, present or absent on medial faces of arches 2-3; no ventral pharygneal tooth plates.

Lateral line a broad tube pierced by wide pores, with moderate flaps over posterior pores; lateral line scales round, rectangular or diamond shaped, flat. Cavernous tissue in small area immediately before anus. Subpectoral organ visible in smallest, faded specimens. Weak, single midventral ridge along belly. Numerous small, longitudinal ridges of skin between pectoral base and anus. No diagonal midbody ridges. Anal lappets numerous, joined basally, about one per ray for length of fin. Stomach pale, without pigment.

Etymology. From the Greek *cetus* (*ketos*) - whale and *stoma* - mouth. The gender is neuter. There have been unjustified emmendations of the name to *Cetostomus* by some authors.

Remarks. More than 150 specimens have been collected in all three oceans, from 38°N to 40°S in the Atlantic and 43°N to 7°S in the Pacific (Fig. 23). The genus is monotypic.

Cetostoma regani Zugmayer, 1914

Figs 3e, 21-25

"New Genus" Murray & Hjort, 1912: 613, 682, fig. 498 (north Atlantic specimen).

Cetostoma regani Zugmayer, 1914: 3-4. Holotype MOM 3215 from the north-eastern Atlantic, 30°45'N, 25°47'W.

Cetomimus regani.-Parr, 1928: 173-176, fig. 42 (north-eastern Atlantic specimen).-Parr, 1929: 23-27, figs 9,

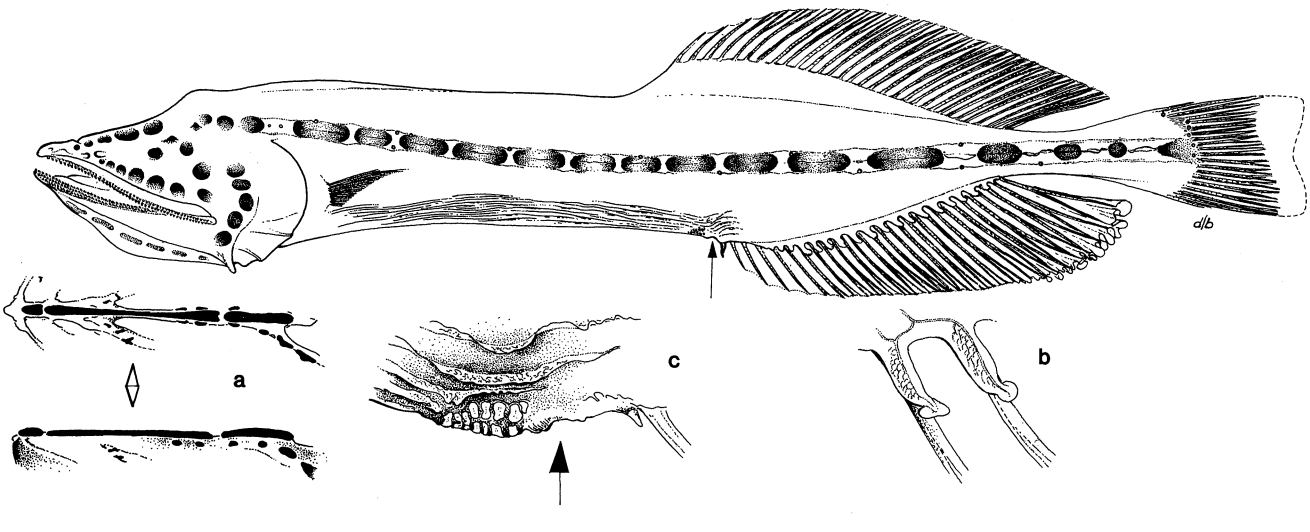

Fig.21. *Cetostoma regani*, 134.0 mm, IOS 10380/5, arrow indicates level of anus; a, copular tooth plates (not to scale), dorsal and lateral views, diamond indicates level of eye; b, anal lappet detail; c, cavernous tissue detail based on ISH 2162/79, 62 mm.

10 (osteology).-Gregory, 1933: 211-212, fig. 92 (osteology repeated from Parr).-Ebeling, 1962: 141 (eastern Pacific specimens listed).-McAllister, 1968: 98 (hyoid arch).

Cetostomus regani.-Parr, 1934: 27-29, fig. 7 (redescription).-Koefoed, 1955: 4-5, pl. II(B) (north Atlantic specimen).-Pearcy, 1964: 87-88 (Oregon specimens listed).-Fitch & Lavenberg, 1968:69 (California specimen).-Kotthaus, 1972: 17, fig. 110 (Indian Ocean specimen, otolith).-Rosen, 1973: 489-492, figs 54, 115 (caudal skeleton, pharyngobranchials).-Herring, 1976: 235-237 (carotenoid pigment).-Fitch, 1979: 63-65, fig. 1e (otolith).

Cetostoma regani.-Harry, 1952:68 (2 Bermuda specimens).-Marshall, 1960: 43 (lack of swimblader) .-Ebeling & Weed, 1973: 397-408, figs 3H, 4F, 5G (osteology, relationships).-Paxton, 1973: 214 (north-eastern Atlantic specimens listed).-Parin *et al*., 1978: 175 (eastern Atlantic specimens listed).-Maurin *et al*., 1978: 80 (north-eastern Atlantic specimens listed) .-Hubbs *et al*., 1979: 10 (California list).-Paxton, 1986: 525, fig. (north-eastern Atlantic specimens).

Cetostomus sp.-Stein, 1985: 190 (north-eastern Pacific specimen listed).

Material examined. See Appendix Table 7. *Cetostoma regani* is apparently the most fragile of all cetomimids; although more than 140 specimens were available, only two specimens had almost all the skin remaining. Complete lateral line pore and scale counts were possible on only five specimens, and only one side of one specimen had the complete number of anal lappet scales over the anal fin. Most specimens had lost all traces of skin and many were broken just behind the head. Dorsal and anal fin rays were counted in all specimens marked * in Table 7; those specimens which were measured are marked **. Vertebrae were counted from x-rays of 40 specimens. The number of tooth patches on the first three gill arches were counted in 17 specimens.

Diagnosis. As for genus.

Description. D. 29-37; A. 26-34; P. 20-21; principal C. (8) 9+(7) 8=(15)17 (8+7 in 1 of 30 specimens counted); vertebrae 47-53; trunk canal lateral line scales/organs 15-17. Measurements in Appendix Table 8.

Body compressed, greatest depth at origin of anal fin. Caudal peduncle 2.8-4.7 times longer than deep. Anus close to anal fin origin. Cavernous tissue immediately around anus, in small adjoining patch in ventral midline anterior to anus. Parallel, thin, transparent ridges of skin running on belly from pectoral base to under first anal fin rays, about 6-10 ridges on each side of ventral midline with dorsalmost ridge about one quarter to one third of way to lateral line (Fig. 21c). No mid-dorsal ridge; weak midventral ridge from level of pectoral base to cavernous tissue. Anal lappets with supporting scales well developed, but easily torn off, beginning under anal ray 4-6 and extending to last 1-3 rays, approximately 1 lappet per ray, but only one complete count of 29 lappets; individual lappets joined at bases but not throughout length; most lappets one third ray length or less (but in 1 LACM specimen 218 mm from the north-east Pacific, lappets more than half ray length), with supporting scales shorter, about half lappet length, ovoid in shape; each lappet with central vessel running length of lappet with many side branches, vessels lateral to lappet scale (Fig. 21c). Subpectoral organ anteroventral to pectoral base visible as darkly pigmented area without apparent pore in 3 faded specimens smaller than 75 mm.

Head moderately large, compressed, deeper than wide posteriorly and somewhat depressed anteriorly; profile from snout to occiput slightly concave, occiput to dorsal origin weakly convex; ventral profile from pectorals to anal weakly concave. Nostrils damaged in almost all specimens, located slightly closer to tip of snout than eye; anterior nostril about half size of posterior with very narrow internasal skin bridge; nasal organ short, high and narrow, without lamellae or ridges, situated mostly in anterior nostril. Eye tiny, with no indication of lens or lens remnant in even smallest specimens, somewhat closer to top of head than upper jaw.

Jaws enormous, angled posteroventrally, upper jaw slightly convex in undamaged specimens; rictus 1-2 eye diameters before posterior end of maxillary; posterior end of jaws somewhat closer to opercular margin than level of eye; posterior lower jaw with indistinct lateral and small, distinct ventral spines. Jaw teeth tiny, triangular, depressible, in indistinct diagonal rows across rounded edges of jaws; dentigerous portions of jaws widest anteriorly, particularly in smallest specimens, posteriormost lower jaw with only 1-2 rows of teeth, extending 1-2 eye diameters behind rictus. Vomerine teeth similar to but smaller than jaw teeth, particularly in large specimens where almost indistinguishable; shape of tooth patch variable, from rectangular to oval to diamond shaped to asymetrically curved as teeth apparently lost with age; palatine teeth intermediate in size between those of vomer and jaws, in approximate diagonal rows in narrow band, beginning at level of vomer in small specimens and anterior to vomer in larger, narrowing posteriorly to end at level of eye; in smallest specimens distance between lateral edge of vomerine patch and palatine teeth about half width of palatine patch, increasing to 1-2 times width of vomerine patch in larger specimens; ectopterygoid tooth band originating slightly before level of eye as 1-2 rows of tiny teeth internal to palatine band and broadening to narrow band behind end of palatine teeth, extending far behind rictus and curving ventrally towards quadrate. Copular tooth patch exceptionally long, more than 10% SL, extending far behind level of eye, in 3 separate patches: first a small oval to rectangular patch usually with tapering posterior extension in larger specimens, a long thin patch extending from just behind first patch to before articulation of second hypobranchials and a third, somewhat rectangular patch shorter than second, extending behind articulation of second hypobranchials (Fig. 21a); 2-5 (usually 3) separate tooth patches on lateral face of second basibranchials ventral to second and third copular tooth patches. Hyoid arch very deep, extending into oral cavity much further than in other cetomimids.

Free gill arches 4, with tiny, tubular slit behind angle of gill arch 4; about half of dorsal arms of arches 1 and 2 free, dorsal arms of arches 3 and 4 bound together in skin of esophagus. Arch 4 with wide flap of skin around angle and posterior third of ventral arm bearing small, moderately spaced holobranchs; holobranchs of first 3 arches well developed and closely spaced, largest anteriorly on ventral arm decreasing in size towards angle (Fig. 3e); short to moderate holobranchs on one third to two thirds of free dorsal arms of arches 1-2, small holobranchs only around angle of arch 3; anterior holobranchs of arch 1 about 2 times bony width of arch; posterior holobranchs relatively larger in smaller specimens. Normal gill rakers absent; arch 1 with 3-5+8-10 tooth plates rectangular to oval shaped and oriented anteroposteriorly with triangular-shaped ventral extension on lateral face of arch on anterior ventral plates; 0-2+8-11 tooth plates on medial face of arch 1, oval or rectangular shaped and oriented dorsoventrally; arch 2 with 2-3+5-7 lateral and 0-1+3-7 medial tooth plates; arch 3 with 0-1+4-7 lateral and 0+0-3 medial tooth plates; arch 4 edentate; number of tooth plates not correlated to specimen size. Dorsal pharyngeals as 2 pair of oval-shaped tooth plates, first with elongate anterior extension, flatter, less domed than those of other cetomimids; second shorter with straight posterior margin; no ventral pharyngeals; all teeth of gill arches similar to jaw teeth but smaller.

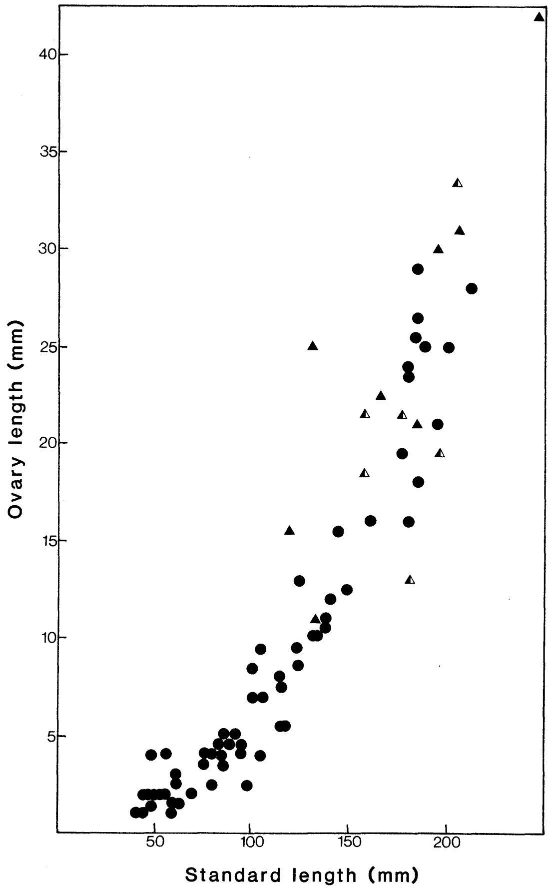

Fig.22. *Cetostoma regani* ovary length versus standard length; triangles indicate egg sizes of 0.1 mm or greater, solid triangles one size class of eggs, half solid triangles with two size classes of eggs.

Lateral line a broad, shallow tube with thin overlying skin, pierced by 16-18 wide pores, anterior pores as wide as canal and rectangular in shape, last 2-3 pores smaller and circular to oval; last 3-4 bridges of skin covering organs and scales between pores with well-developed medial keel of skin, rarely with small posterior flap hanging over pore; skin bridges narrow anteriorly, wide posteriorly; 15-17 lateral line scales oval, rectangular or very rarely diamond shaped, flat, without dorsal or ventral projections, much narrower than interspaces; each scale with very large neuromast overlying central foramen, organ thin, high and rectangular with base oriented anteroposteriorly in lateral line canal. Usually 1-2 dorsal and 1 ventral papillae on undamaged skin bridges and dorsal margins of pores, but not enough complete specimens to determine pattern; 5-6 papillae at base of caudal rays; anterior 2-5 papillae of dorsal accessory line visible on two specimens, widely spaced above gill opening.

Lateral line system of head with shallow, wide canals

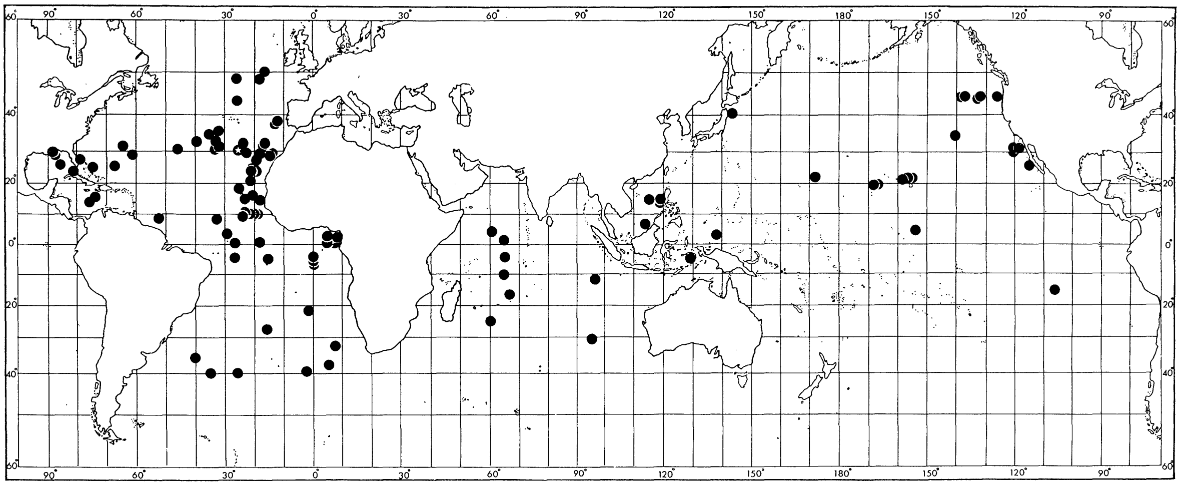

Fig.23. *Cetostoma regani* horizontal distribution; symbols may represent more than one specimen, star indicates holotype.

covered by very thin skin, large pores and very large neuromasts under skin bridges between pores; almost all canal and pore systems torn and damaged in examined specimens, following counts based on two recently caught specimens from the Caribbean: supraorbital canal with 6 pores and 5 neuromasts, fifth pore not close to midline; main canal with 3 pores, first far behind and apparently separate from supraorbital canal, with single supratemporal pore medial to penultimate main pore; infraorbital canal with 9 pores and 8 organs, last far behind eye, not displaced anteriorly or dorsally out of series and not joined to main canal; mandibular canal with 6-7 pores and 5-6 organs, not joined to preopercular canal with 5 pores and 4 organs. Papillate neuromasts very small and unpigmented. Curved row of 5-6 papillae down posterior third of gill cover, vertical row of 4 papillae between posterior tip of premaxilla and fourth preopercular pore, 2 papillae below posterior tip of premaxilla; snouts of all specimens damaged.

Dorsal and anal fins with elevated bases on posterior half of body, very long based; dorsal longer than anal, dorsal origin before and end after those of anal; always more dorsal rays, usually 4 more, range 2-6; first 3-4 rays of each fin heavier and unbranched, all remaining rays branched; unbranched rays shorter, all branched rays subequal in length; membrane between last 10 rays of anal fin thin and extensive with curtain-like folds. Pectoral low, short, directed posterodorsally; all rays except first 2 and last 4-5 branched for about half their length; upper-middle rays longest, last 1-2 rays very short with last ray usually seen only on cleared and stained material. Caudal shape unknown, no fins complete; counts strikingly constant, 9+8 principal rays (8+7 in only 1 of 30 specimens counted).

Ovaries paired, flaccid to rounded in 75 dissected specimens (39.6-246.5 mm), increasing in length with age (Fig. 22). Only 2 specimens with eggs greater than 0.1 mm in

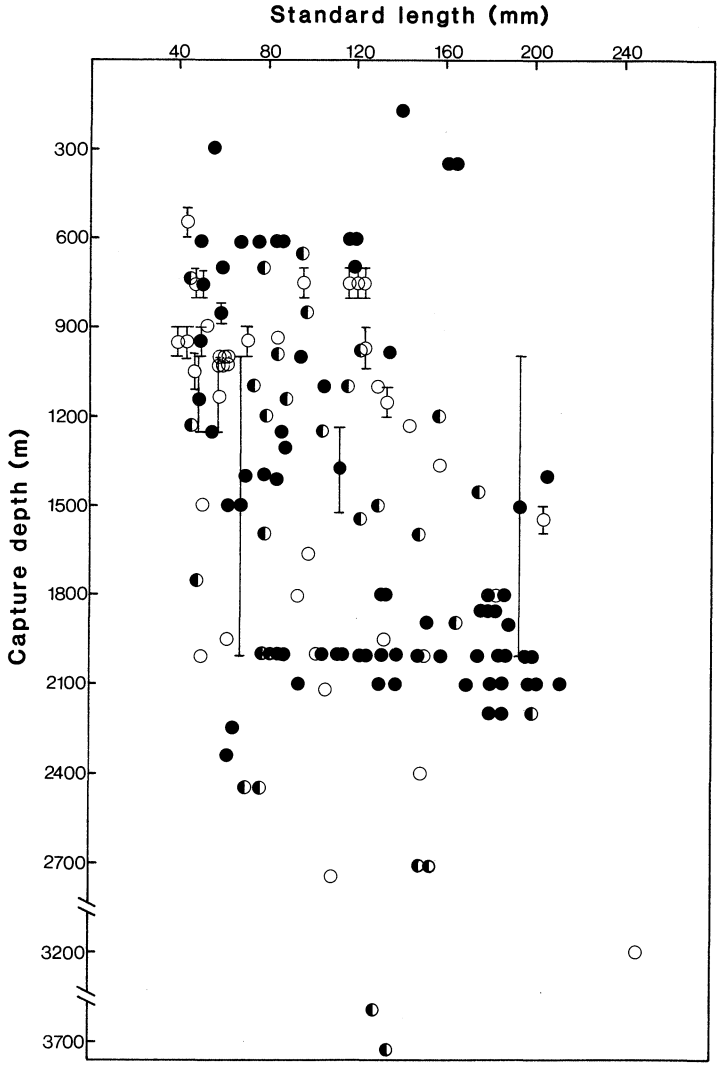

Fig.24. *Cetostoma regani* vertical distribution; open symbols indicate day captures, solid symbols night captures, half solid symbols day/night or unknown time, depths are maximum fishing depths of open nets; closing net captures indicated by vertical bars giving fishing depth limits.

diameter: 131 mm specimen with ovaries 25 mm long by 6 mm wide at anterior end, filled with eggs, all ca. 0.2 mm in diameter and 204 mm specimen with ovaries 33.5 mm by 8.5 mm with few eggs 0.6 mm diameter and most eggs much less than 0.1 mm diameter; of 12 specimens with eggs about 0.1 mm diameter, 7 with all eggs 0.1 mm and 5 with few eggs 0.1 and most much less than 0.1mm; remaining 61 specimens immature or with eggs less than 0.1 mm. Females apparently do not approach maturity before 125 mm; more than one spawning per lifetime is indicated by the presence of two egg sizes in some ovaries and the range of sizes (120-246 mm) with larger eggs. No males found. Bladder indistinct even is small specimens, apparently single, dorsoposterior to ovaries, oval. Distinct urogenital papilla larger than those of other cetomimids at base of first anal ray.

Colour in alcohol light brown on head, light to dark brown on body and fins; oral and gill cavities, stomach and intestine pale, peritoneum very light brown with scattered melanophores. Colour of two fresh specimens reddish-orange head, black body, dorsal, anal and caudal fins black with bright red edges (W.J. Richards, in literature, July 1988).

Distribution. More than 150 specimens have been collected in all three oceans, from 50°N to 40°S in the Atlantic, 15°N to 31°S in the Indian and 45°N to 15°S in the Pacific (Fig. 23). The lack of captures in the central Atlantic between 10° and 30°N is apparently due to a lack of sampling effort (see Fig. 30), as is the dearth of Pacific captures. *Cetostoma regani* has the broadest distribution of any cetomimid.

The 17 diurnal captures with closing nets (by IOS) give the best picture of vertical distribution of any cetomimid (Fig. 24). A normal diurnal distribution between 700 and 1200 metres is indicated. The shallowest diurnal capture (500-600 m) is of one of the smallest specimens (43 mm) and the deepest (1500-1600 m) is of one of the largest (204 mm), indicating a trend for the diurnal depth to increase with increasing size, similar to the picture for *Ditropichthys storeri*. Nocturnally a limited vertical migration to 600 to 700 m is indicated by eight open net captures of specimens less than 125 mm; migration to 110 to 400 m occurs rarely, with only five of 150 specimens taken above 600 m.

Etymology. After C. Tate Regan of BMNH.

Type specimen. The holotype, MOM 3215, is a small specimen in poor condition, with few remnants of skin and no lateral line pores or anal lappets remaining. The fin rays and jaws are broken and the body badly distorted; accurate measurements were impossible for most features. Nevertheless the high number of dorsal and anal fin rays, elongate fin bases and three separate copular tooth plates result in an unquestionable identification.

Remarks. Two specimens with dorsal ray counts of 35 and 37 were labeled as ms holotypes of new species (ZMUC P2340565 and USNM 200530). Dorsal and anal fin ray counts were made on a total of 103 specimens (Fig. 25) and only nine specimens had dorsal ray counts over 34; four of these were collected in the north Atlantic, two in the Indian Ocean and one in the west Pacific. No other feature of morphology, dentition or morphometrics distinguished these nine specimens from other measured specimens with 29 to 34 dorsal rays, although many of the specimens were badly damaged and features of the lateral line system on the head and body could not be detailed for most. The nine specimens represent the tail of a normal bell-shaped curve for the distribution of dorsal rays (Fig. 25) and are considered part of the normal variation of *C. regani*.

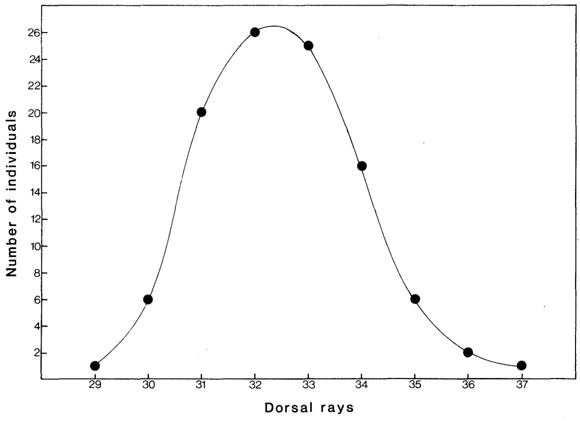

Fig.25. *Cetostoma regani* distribution of dorsal finray numbers in 103 specimens.

Measurements were made on 22 specimens from 48 to 246 mm (Table 6). Analyses of the measurements of three size classes (48-79, n = 5; 96-125, n = 7; 183-246, n = 11) indicate that the relative lengths of the head, jaws and snout to pectoral, dorsal and anal distances are longest in the smallest size class, but not different in the two largest classes, while relative body depth and eye width are greatest in the largest specimens (Table 8). Allometric growth over all three size classes is apparent for eye diameter, dorsal origin to anal origin and caudal peduncle length. The four measured specimens from the Indian and Pacific Oceans did not show significant differences from the 18 Atlantic specimens and only one species of *Cetostoma* is currently apparent.

Gyrinomimus Parr, 1934

Figs 1j, 2c, 3g, 4e, 5c, 7b, 8a, 26

Gyrinomimus Parr, 1934: 29. Type species *Gyrinomimus myersi* Parr, 1934 by monotypy.

Diagnosis. *Gyrinomimus* has elongate, closely-set teeth in distinct rows in the jaws and palate, unlike all other cetomimid genera except *Danacetichthys*. *Gyrinomimus* differs from *Danacetichthys* in the number of free gill arches (3 versus 4), form of gill "rakers" (solid, flat tooth plates covering most of lateral face of arch versus separate, round, domed tooth plates), absence of ventral pharyngeal tooth plates (versus present), vertebral number (47-59 versus 43-46), lateral line scale shape (narrowly rectangular or strap like and curved versus round or widely rectangular and flat) and maximum size attained (390 mm versus 54 mm). *Gyrinomimus* is most similar to *Cetomimus*, differing only in the teeth (elongate in distinct longitudinal rows in all but two species versus short in distinct or indistinct diagonal rows) and the shape of the vomerine tooth patch (rectangular or laterally elongate and flat versus round or elliptical and dome shaped).

Description. D. 14-21; A. 14-20; P. 18-23; principal C. 13-16; vertebrae 26-39+16-24=47-59 (n=105); trunk canal lateral line organs and scales 12-23. Range of measurements based on 60 specimens of at least 8 species in Appendix Table 9. Size very large, maximum attained 390 mm; head moderate to very large, 2.7-3.9 in SL and wide, width at eye 2.0-2.9 in HL; mouth large to very large, jaws ending much closer to opercular margin than to level of eye; snout rounded and moderate in length, 2.7-3.9 in HL; dorsal and anal bases short to moderate, 1.3-2.6 in HL; caudal peduncle short to long, 2.0-4.2 in HL and slender to moderate, 1.1-3.3 in CPL; anus close to anal fin origin, distance 2.0-9.3 in CPD.

Nasal organ small to moderate, mostly in anterior nostril, usually with low lamellae in larger specimens. Eye tiny, 17-61 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores; supraorbital canal with 6-7 pores, separate from main canal of 4-5 pores; infraorbital canal separate from main canal with 8-10 pores, the last displaced anterodorsally out of series; mandibular canal with 6-11 pores, joined to preopercular canal with 1-5 pores; neuromasts moderate in size. Lower jaw with well-developed lateral and ventral spines or projections posteriorly. Jaw teeth long, width at least 3 in length, closely set, usually in distinct longitudinal rows, rarely with both diagonal and longitudinal rows; vomerine tooth patch rectangular or laterally elongate and flat; palatine and ectopterygoid tooth patches slightly separated, latter long and extending to or beyond level of rictus; copular tooth patch in 1 plate, short to long, 2.6-4.9 in HL, and narrow to broad, 1.8-7.6 in length, shield shaped.

Free gill arches 3, no slit behind ventral arm of fourth arch; holobranchs well developed on first 3 arches, tiny to large on fourth arch. Gill rakers as tooth plates on all 4 arches; tooth plates present or absent on medial face of arches; no ventral pharyngeal tooth plates.

Lateral line a broad tube pierced by wide to tiny pores, flaps and keels present or absent; lateral line scales strap shaped or narrowly rectangular, curved, often with terminal projections of 1-3 spines. Cavernous tissue in small area or extensive around anus and often at other areas (along dorsal and anal rays, predorsally, dorsolaterally above pectoral, posterior lateral line). Subpectoral organ present or absent. No paired abdominal ridges or diagonal midbody ridges. Anal lappets present or absent, if present from 3-14 separate lappets over anal base; no other flaps, ridges or membranous curtain associated with anal fin. Stomach darkly pigmented.

Etymology. From the Greek *gyrino* - tadpole and *mimus* - like. The gender is masculine.

Remarks. More than 125 specimens have been collected from all three oceans. *Gyrinomimus* is the most widespread of all cetomimid genera, extending from 52°N in both the Atlantic and Pacific to 59°S in the Atlantic and 72°S in the Pacific.

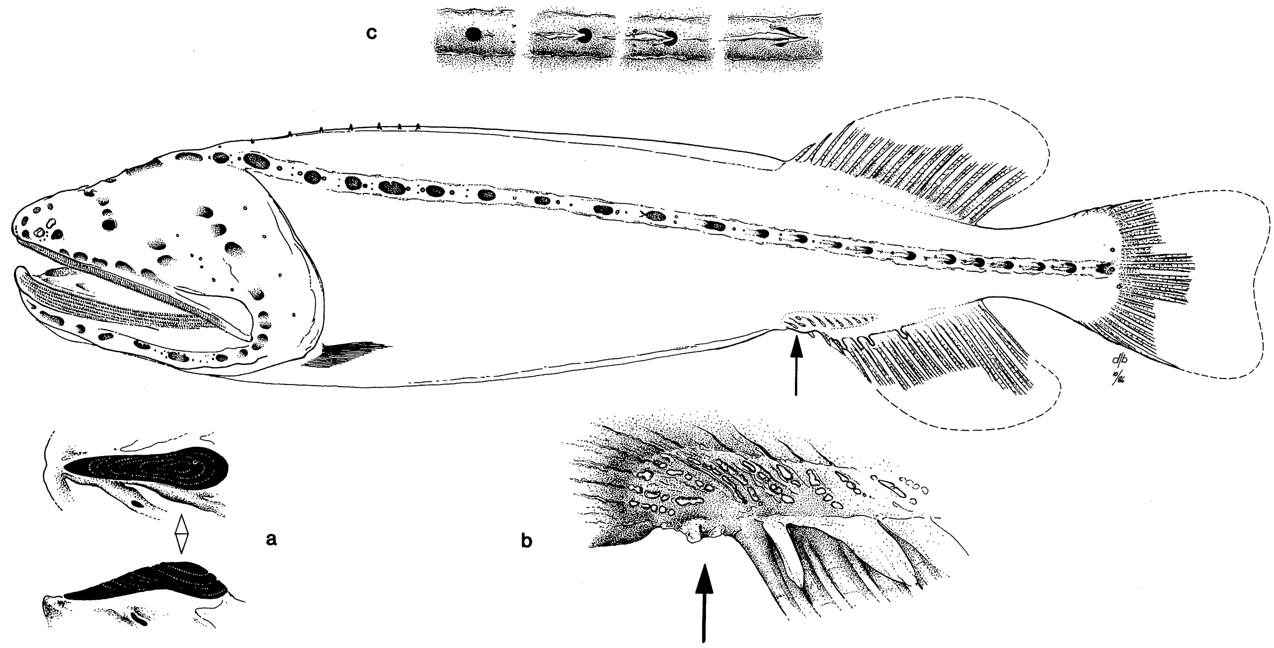

Fig.26. *Gyrinomimus* sp. C, 272.0 mm, LACM 6903-21, arrows indicate level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, detail of cavernous tissue and first anal lappets; c, detail of lateral line pores.

Gyrinomimus contains seven nominal species (Table 1) and is currently being revised. The recognition of *G. notius* and *G. parri* as junior synonyms is based on the fact that tooth rows are added to the jaws and palate with growth and the number of vomerine tooth rows was considered diagnostic in both original descriptions. Variation in other characters is still being studied, but at least four new species await description. Specific characters include presence and number of anal lappets, size of fourth holobranch, distribution of cavernous tissue, number and shape of lateral line pores, shape and number of spines on lateral line scales, number and distribution of tooth plates on the gill arches and number of vertebrae and dorsal and anal rays.

Cetomimus Goode & Bean, 1895

Figs 1k, 2f, 3h, 4f, 7a, 27

Cetomimus Goode & Bean, 1895: 452. Type species *Cetomimus gilli* Goode & Bean, 1895 by subsequent designation of Jordan & Evermann, 1896: 549.

Pelecinomimus Gilchrist, 1922: 56. Type species *Pelecinomimus picklei* Gilchrist, 1922 by monotypy.

Cetomimus (*Psapharocetus*) Harry, 1952: 59. As subgenus, type species *Cetomimus kerdops* Parr, 1934 by original designation.

Diagnosis. *Cetomimus* has no single, derived character to distinguish it from all other genera. Like *Rhamphocetichthys* and *Gyrinomimus*, *Cetomimus* has only three free gill arches. *Cetomimus* differs from *Rhamphocetichthys* in lacking ventral pharyngeal tooth plates, in having a cavernous lateral line system of large canals pierced by wide pores on the head and body and in having a much shorter, rounded snout. *Cetomimus* is most similar to *Gyrinomimus*, differing in the form of the teeth (short in indistinct, diagonal rows versus long in distinct, usually longitudinal rows) and in the shape of the vomerine tooth patch (round or elliptical and dome shaped versus rectangular or laterally elongate and flat).

Description. D. 15-20; A. 13-20; P. 17-23; principal C. 14-16; vertebrae 24-34+15-20=44-54 (n=30); trunk canal lateral line scales and organs 10-24. Range of measurements, based on 15 specimens of at least 6 species in Appendix Table 9. Size large, maximum 256 mm; head moderate to very large, 2.3-3.4 in SL and wide, width at eye 1.9-2.9 in HL; mouth large to very large, jaws ending much closer to opercular margin than level of eye; snout rounded and moderate, 2.5-2.9 in HL; dorsal and anal bases short to moderate, 1.4-2.8 in HL; caudal peduncle very short to moderate, 2.2-4.1 in HL and slender to deep, 1.3-3.6 in CPL; anus close to anal fin origin, distance 3.1-5.5 in CPD.

Nasal organ small to moderate, mostly in anterior nostril, many species with ridges or reduced lamellae on rounded nasal organ. Eye tiny, 13-39 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores; supraorbital canal with 6-7 pores, separate from main canal with 4-5 pores; infraorbital canal separate from main canal with 8-9 pores, last displaced anterodorsally; mandibular canal with 6-9 pores, joined to preopercular canal with 3-4 pores; neuromasts moderate in size. Lower jaw with well-developed lateral and ventral spines or projections posteriorly. Jaw teeth short, width less than 2 in length, closely set in indistinct rows; vomerine tooth patch round or elliptical and dome shaped; palatine and ectopterygoid teeth slightly separated, latter extending to or beyond level of rictus; copular tooth patch on 1 plate, moderately long, 3.0-6.3 in HL and broad, 3.3-5.8 in length.

Free gill arches 3, no slit behind ventral arm of fourth arch; holobranchs well developed on first 3 arches, tiny to large on fourth arch. Gill rakers as tooth plates on all 4 arches; usually no tooth plates on medial face of arches; no ventral pharyngeal tooth plates.

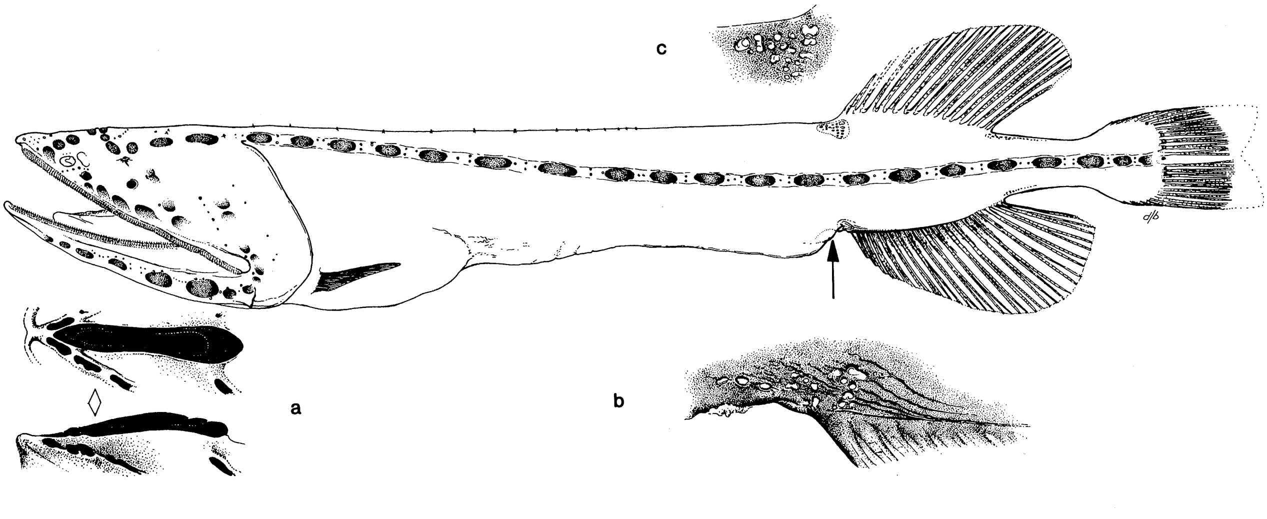

Fig.27. *Cetomimus* cf. *compunctus*, 124.7 mm, ZMUC *Dana* 1208 IV, arrow indicates level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, detail of cavernous tissue before anal fin; c, detail of cavernous tissue before dorsal fin.

Lateral line a broad tube pierced by small to wide pores with flaps and keels present or absent; lateral line scales strap shaped or narrowly rectangular, curved, often terminating in 1 spine. Cavernous tissue in small area or extensive around anus, and often at other areas (along anal and dorsal rays, predorsally, caudal peduncle, isthmus, posterior lateral line, flap on posterior upper jaw). Subpectoral organ present in some species. No paired abdominal ridges or diagonal midbody ridges. No anal lappets with internal scales; skin fold present or absent along anal base; skin ridges associated with anterior anal rays often present; no membranous curtain joining posterior anal rays. Stomach darkly pigmented.

Etymology. From the Greek *cetus* (*keto*) -- whale and *mimus* -- like. The gender is masculine.

Remarks. More than 180 specimens have been collected from all three oceans, extending from 41°N in the Pacific and Atlantic to 40°S in the Atlantic and 57°S in the Pacific.

Cetomimus contains seven nominal species (Table 1) and a revision of the species has just begun. *C. gilli* and *C. picklei* are in the same species group, as are *C. craneae* and *C. compunctus*. Study of variation is required, but at least five new species await description. Recognition of subgenera requires re-evaluation of all species groups. Specific characters include the number and shape of lateral line pores and flaps, distribution of cavernous tissue, size of the fourth holobranch and number of dorsal and anal rays and vertebrae.

Rhamphocetichthys n.gen.

Type species. *Rhamphocetichthys savagei* n.sp.

Diagnosis. *Rhamphocetichthys* differs from all other cetomimid genera in the development of an elongate, pointed snout 5.1-6.2 in SL (versus rounded and 6.5-14.1 in SL) with the upper jaw overhanging the lower, in the lack of a cavernous lateral line system on the head and tooth plates on gill arches 2-4, and in the high number of lateral line scales (31-40 versus 8-24). Unlike all other members of the subfamily Cetomiminae, *Rhamphocetichthys* lacks a lateral line canal pierced by pores on the body and cavernous luminous tissue around the anus, characters shared only with *Procetichthys*.

Description. D. 15-17; A. 15-17; P. 21-24; principal C. 16; vertebrae 27-29+16-17=43-45; trunk lateral line organs and scales 31-40. Size moderate, maximum known 126 mm; head very long, 2.6-2.9 in SL, and narrow, width at eye 6.6-10.1 in HL; mouth very large, jaws ending much closer to opercular margin than to level of eye; snout very elongate and pointed, 1.9-2.2 in HL; dorsal and anal bases short, 2.7-3.8 in HL; caudal peduncle moderate to short, 2.3-3.0 in HL, and very slender, 2.5-4.5 in CPL; anus close to anal fin origin, distance 1.0-4.3 in CPD.

Nasal organ small and high, without lamellae or ridges. Eye tiny, 21-26 in HL, without discernible lens. Lateral line system of head a series of small, widely-spaced superficial neuromasts. Lower jaw with blunt lateral and ventral projections posteriorly. Jaw teeth tiny, triangular in diagonal rows; vomerine teeth at least 5; palatine and ectopterygoid teeth separate, latter extending beyond rictus with enlarged posterior teeth; copular tooth patch on 1 plate, moderate with length 3.6-4.2 in HL and moderate to broad, width 4.6-7.3 in length.

Free gill arches 3, no slit behind fourth arch; holobranchs well developed on all 4 arches, absent on dorsal arm of first arch. Gill rakers as separate plates (4-11 on first arch) of tiny teeth, none on medial face and no tooth plates on arches 2-4; ventral pharyngeal tooth plates on fifth ceratobranchial present.

Lateral line a series of vertical rows of papillate superficial neuromasts, 1-3 per row; no lateral line canal or pores; lateral line scales rectangular and flat. No cavernous luminous tissue. Subpectoral organ present. No paired abdominal ridges or diagonal midbody ridges. Anal lappets separate, 4-9; no ridges, folds or membranous curtain associated with anal fin. Stomach with very light brown pigment.

Etymology. From the Greek *rhamphos* - curved beak, *cetus* (*ketos*) - whale and *ichthys* - fish, in reference to the beak-like snout. The gender is masculine.

Remarks. Only four specimens, which presumably represent one species, have been collected from bathypelagic waters of the Pacific and Atlantic Oceans.

Rhamphocetichthys savagei n.sp.

Figs 1i, 2d, 3f, 4g, 11, 12, 28

Type material. HOLOTYPE: MCZ 60342, 125.7 mm, GRH 1042, Coral Sea, 12°22'S, 146°29'E, 0-ca. 1000 m, 30 Nov. 1981.

PARATYPES: LACM 30034-11, 90.8 mm, *Velero IV* 11733, Gulf of California, Mexico, 20°51'N, 106°28'W, 0-1400 m, 0700-1515 hrs, 8 Nov. 1967; AMS I.26872-001 (exLACM 30042-11), 98.5 mm, *Velero IV* 11764, Gulf of California, Mexico, 23°24'N, 108°17'W, 0-1400 m, 1015-1845 hrs, 15 Nov. 1967.

Other material. ISH 2297/71, 110 mm, *Walther Herwig* 478/71, central Atlantic, 01°04'N, 18°22'W, 0-2100 m, 12 Apr. 1971.

Diagnosis. As for the genus.

Description. The holotype is in good condition except the upper and lower jaws have parted at the ricti and the specimen has been preserved with the mouth wide open and jaws distorted. Both paratypes have faded and torn skin and ruptured abdominal cavity; the larger paratype has lost the anterior tip of one upper jaw. The fourth specimen is in poor condition, with the tips of the upper jaws broken, the ventral body wall torn, the body distorted and skin missing anterior to and under the dorsal fin. Values of the holotype are followed by those, if different, of the paratypes in brackets with those of the fourth specimen following a semicolon.

D. 17(15;15?); A. 17(15); P. 23/24(21-23;22); principal C. 8+8, procurrent C. ?(6+6; ca. 5+5); vertebrae 27+16=43(27-28+16-17=44;29+16=45); lateral line scales and organs 33(31-32;40). Measurements are given in Appendix Table 6.

Body oval in cross section behind head. Greatest depth at pectoral fins. Caudal peduncle 2.5-4.5 times longer than deep. Anus before anal fin by distance equal to one quarter (half to two thirds) caudal peduncle depth. Striated tissue, possibly homologous to cavernous tissue, on lateral line between scales and at caudal base (Fig. 28b). No cavernous tissue around anus. Low mid-dorsal ridge present; small midventral fold from anus anterior to one third of way to head present in one paratype. Anal lappet scales 8-9 (1-3 scars; 5-6 scars) over anterior anal fin bases (Fig. 28c). Subpectoral organ distinct in holotype as dark body beneath skin, anteroventral to pectoral base with possible pore in skin, unclear in faded paratypes.

Head large and very compressed, head width approximately half head depth. Snout greatly elongated, eye about midway between tip of snout and edge of operculum. Head profile smoothly rounded except for bony projection behind eye. Nostrils large, without raised rims, nearer to eye than tip of snout and close to upper jaw; posterior nostril about 50% larger than anterior; internasal bridge of skin about half diameter of anterior nostril; raphe moderate (short), high and narrow or rounded, without lamellae or ridges (Fig. 1i). Eye small, without lens or much apparent structure, midway between upper jaw and profile of snout. Interorbital narrow, convex with bony projection just behind eye.

Mouth enormous; premaxilla evenly concave, extending anteriorly beyond lower jaw; dentary concave posteriorly, anterior tip downturned to fit behind and between anterior tips of premaxillae; approximately one fifth (half) of anterior downturned border of dentary edentate; anteriormost lower jaw with a median soft projection; rictus approximately one eye diameter before posterior tip of premaxilla; jaws extend almost to gill cover; mandible with small blunt lateral projection posteriorly, tip of angular produced into blunt spine ventrally. Jaw teeth granular, in many irregular series on both jaws (Fig. 2d,e); individual teeth tiny with flattened, trapezoidal-shaped base set in jaw socket; upright tooth shorter than base length, arising from lateral edge of base, triangular and laterally compressed; all jaw teeth point towards centre of oral cavity; dentigerous edge of jaws slightly rounded; teeth in approximately diagonal series, with about 75 (65-85;48) series of 3-6(2-5) teeth each in premaxillary and 37(60-64;38) series of 6-9(5-6) teeth on the dentary, extending posteriorly slightly behind rictus. Individual teeth of palate and hypobranchial arches similar to jaw teeth, but most much smaller; vomerine teeth lost, sockets not countable(at least 5 in one paratype), slightly closer to tip of premaxillary than eye; palatine teeth in 1(1-3;1-2) rows, with 6/7(13-15;15) teeth in longest row; edentate space between palatine and ectopterygoid half to two thirds eye diameter; ectopterygoid teeth in 1-1.5 (2-5;1-2) series, 31/32(43;34) in longitudinal row, increasing in size posteriorly, with posterior 3-4 teeth as tiny canines; edentate space (absent; absent) before these 4 posteriormost teeth. Copular tooth patch elongate, 2.1 (1.7-1.9;2.3) in snout, modified dumb-bell shaped with posterior end widest and emarginate (Fig. 28a); 31 (32-36;27) teeth in longitudinal series.

Free gill arches 3, no slit behind fourth; most of dorsal arms of gill arches bound together. Holobranchs long but widely spaced, those on ventral edge of first arch about twice as long as bony width of arch (Fig. 3f); holobranchs of fourth arch as long as those on first arch; no holobranchs on dorsal arm of first arch. Normal gill rakers absent; first arch with 1(3;0-1) epibranchial, 6(6-7;4-5) ceratobranchial and

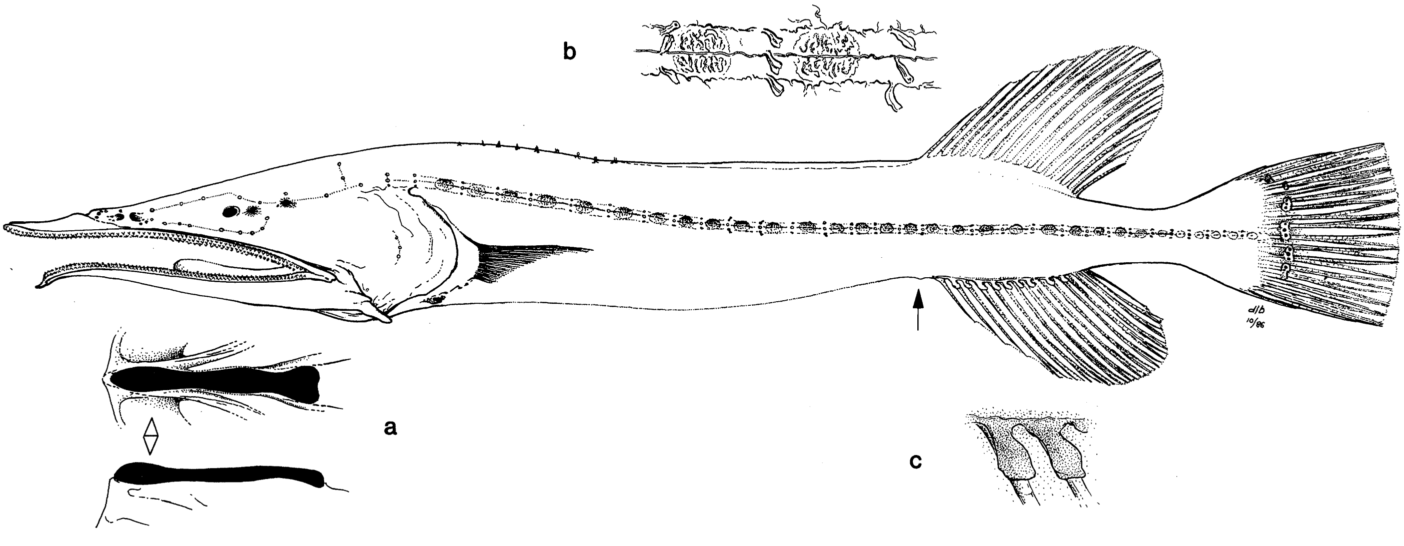

Fig.28. *Rhamphocetichthys savagei* holotype, 125.7 mm, MCZ 60342, arrow indicates level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, detail of lateral line; c, detail of anal lappets.

1-2(0-1;0) hypobranchial lateral tooth plates; 1-7(;1-3) teeth per plate with largest the posteriormost plate of ceratobranchial; no tooth plates on medial face of arch, or on epi-, cerato- or hypobranchials of arches 2-4. Dorsal pharyngeals as 2 pharyngobranchial tooth plates on each side of roof of mouth; anterior (third pharyngobranchial) toothplate elongate and slightly curved, pointed (rounded) anteriorly and rounded posteriorly; 3-6(3-8;2-5) irregular rows of teeth with 12(13-22;12) teeth in longest row; posterior plate short, about 2.5 in length of anterior plate, with 2-4(1-5;2-3) irregular rows of teeth and 6-7(7-11;5) teeth in longest row; paired ventral pharyngeals of fifth ceratobranchials as curved plates with pointed ends, almost twice as long as posterior dorsal plates, with some 2-6 long rows of teeth and 11(14-18;11) teeth in longest row. The dorsal and ventral elements of the hypobranchial tooth plates do not contact as the dorsal pharyngeals are over the space between the copula and ventral pharyngeals.

Lateral line not a broad tube, but a shallow, wide trough with weak folds of skin along dorsal and ventral margins of trough; 33(31-32; ca. 40) scales from top of gill cover to caudal base embedded under skin of bottom of trough; each scale rectangular with central pore through which runs branch of lateral line nerve; skin overlying scale with central neuromast, the main lateral line organ, and single more slender elongate papillae above and below. Free fold of skin originating in dorsal midline behind head and increasing in size to dorsal fin origin; dorsal accessory line of superficial neuromasts as 2 parallel rows of papillae on anterior half of fold, about 9 papillae per row, paired anteriorly and alternating posteriorly. In paratypes, skin faded so small paired nerves visible running length of fold with branch to each neuromast.

No cavernous lateral line system present on head. Superficial neuromasts similar to those in lateral line represent neuromasts found in head canals of other cetomimids, with similar arrangement (Fig. 4g); in some areas a nerve connects a line of neuromasts. Only holotype with discernible head system, paratypes too faded and skin of head of fourth specimen badly torn. Supraorbital line from tip of snout to behind eye with 5 neuromasts, joined to main line with 5-6 neuromasts and supratemporal line with 3 papillae. Two typical lateral line organs with 3 papillae each, presumably with underlying scales, between main line and top of gill slit. Infraorbital line under eye from posterior nostril with 8 neuromasts; line across ventral preopercle with 4 neuromasts, mandibular line with 5-6 neuromasts, line ventrolateral to nostrils with 9 papillae and 2 series across anterior head, one anterior to nostrils with 3 papillae on each side and one at level of anterior nostril with 1 papilla; connections between each branch not clear, total number of neuromasts in all series approximate.

Dorsal and anal fins far back on body; anal origin under third dorsal ray; ends of dorsal and anal bases opposite; tips of most rays broken but posterior rays obviously much longer than anterior rays, longest rays branched at tips in holotype. Pectoral fin low, short, directed obliquely upward with few longest rays branched only at tips; ventralmost 6 rays much shorter than upper rays. Caudal ray ends broken.

Gonads of holotype about 10 mm long, flattened, whitish; gonads of 1 paratype thin and undeveloped, other 2 specimens torn, sex of all specimens indeterminate. Bladder paired, very short and wide, almost round.

Colour in alcohol medium brown (faded in paratypes). Oral cavity light brown, stomach with some light brown pigment, intestine without pigment except posterior one fifth weakly orange in holotype; peritoneum dark brown.

Distribution. With records from the Coral Sea, Gulf of California and central Atlantic (Fig. 11), the species (if only one) is broadly distributed within 25° of the equator.

All four captures were made with open nets fishing to between 1000 and 2100 m (Fig. 12).

Etymology. After Jay M. Savage, who gave the author opportunity and encouragement as a student and developed the midwater trawling programme which collected the two LACM paratypes, in recognition of his contributions in biology.

Remarks. Before the fourth specimen, the holotype, became available the three smaller specimens were considered to represent two species, distinguished by differences in lateral line organ and scale numbers, size and numbers of teeth in the jaws (Fig. 2d,e) and ectopterygoid and size of the edentate area at the tip of the lower jaw. The holotype has the lower number of lateral line organs similar to the Mexican specimens and some lower tooth numbers similar to the Atlantic specimen. At least in some species of *Gyrinomimus*, tooth numbers increase rather than decrease with growth. While it is possible that three species are represented by the four specimens, only one is named until more specimens in undamaged condition are collected.

Other cetomimids collected in the same haul as the ISH specimen include *Cetomimus* sp., *C. compunctus*, *Cetostoma regani* and *Ditropichthys storeri*.

Relationships

The establishment of derived character states for use in a phylogenetic analysis of relationships can be based on outgroup comparisons of related taxa (fossil or Recent) and ontogenetic transformations. For cetomimids, neither fossils nor larvae nor juveniles less than 25 mm are known, and outgroup comparison is the method used to polarise character states.

Family relationships of the Cetomimidae have not been adequately established. Within the last 20 years at least 20 families, mostly in the orders Stephanoberyciformes and Beryciformes, have been hypothesised as relatives of the Cetomimidae (Greenwood *et al.*, 1966; Myers & Friehoffer, 1966; Rosen & Patterson, 1969; Ebeling & Weed, 1973; Rosen, 1973). A full outgroup analysis would include the character states for representatives of these 20 families, but is beyond the scope of the present paper. Virtually every author has considered the Rondeletiidae and Barbourisiidae as the closest relatives of the Cetomimidae, with Rosen (1973) and Ebeling & Weed (1973) justifying their classifications with osteological characters. The outgroup analysis has been restricted to the monotypic *Barbourisia* and the two species of *Rondeletia*; both are the only genera of their respective families.

Genera rather than species of cetomimids are used in the distribution of character states (Appendix Table 10) and the computer analyses that follow. The genera are clearly distinguishable (see the Key to Genera above). While the species composition and relationships within each genus are valid subjects for analysis in their own right, the species revisions of *Gyrinomimus* and *Cetomimus* required for such analyses have not been completed.

Specimens of *Rondeletia* and *Barbourisia* used for morphometrics and other character distributions are listed in Materials and Methods. More complete ranges of meristics were taken from Paxton (1974) for *Rondeletia* and from unpublished data for *Barbourisia.* In the following discussion, characters are described in the order they are given in the generic descriptions and numbered for reference (Table 10; Fig. 29). In all cases but one, characters are restricted to those that could be polarised unequivocally using both outgroup families. The relationships of the two outgroup families to each other are unresolved (Fig. 29). Therefore when a character showed two states, one in each of the two outgroups, it was not used.

Four features, pelvic fins, pleural ribs, gill rakers/tooth plates on the medial side of the fourth gill arch and pyloric caeca, are present in *Rondeletia* and *Barbourisia* and absent in all cetomimids examined. To determine whether these three characters of loss are synapomorphic for the Cetomimidae (at least in relation to *Barbourisia* and *Rondeletia*) requires data from some additional taxa for outgroup comparison. The taxa chosen are the Beryciformes, including the Stephanoberyciforms, with data from Zehren (1979). These characters are considered first.

1. Pelvic fins. All cetomimids lack pelvic fins and pelvic girdles. Pelvic fins and girdles are present in *Rondeletia* and *Barbourisia*, as well as all beryciforms examined by Zehren (1979). The absence of pelvic fins and girdles is a synapomorphy defining the family Cetomimidae.

2. Pleural ribs. All cetomimids lack pleural ribs. Pleural ribs are present in *Rondeletia* and *Barbourisia*, and in all Beryciformes (Zehren, 1979). The absence of pleural ribs is a synapomorphy for the Cetomimidae.

* Pyloric caeca. Pyloric caeca are not found in cetomimids. The number of pyloric caeca in *Barbourisia* ranges from 9-14; 6 are found in *Rondeletia.* No data on pyloric caeca in the Beryciformes are available (Zehren, 1979; Ebeling & Weed, 1973; Woods & Sonoda, 1973). Whether the presence or absence of pyloric caeca is derived cannot be determined with the available data and the character is not utilised in the phylogenetic analysis.

* Medial gill tooth plates arch 4. All cetomimids lack tooth plates on the medial face of the fourth gill arch, whereas these elements are present in both *Barbourisia* and *Rondeletia.* However no data are available on the condition in other beryciform families (Zehren, 1979) and the derived state cannot be determined with the present data.

* Basibranchial tooth plates. One other feature distinguishes all cetomimids from *Rondeletia* and

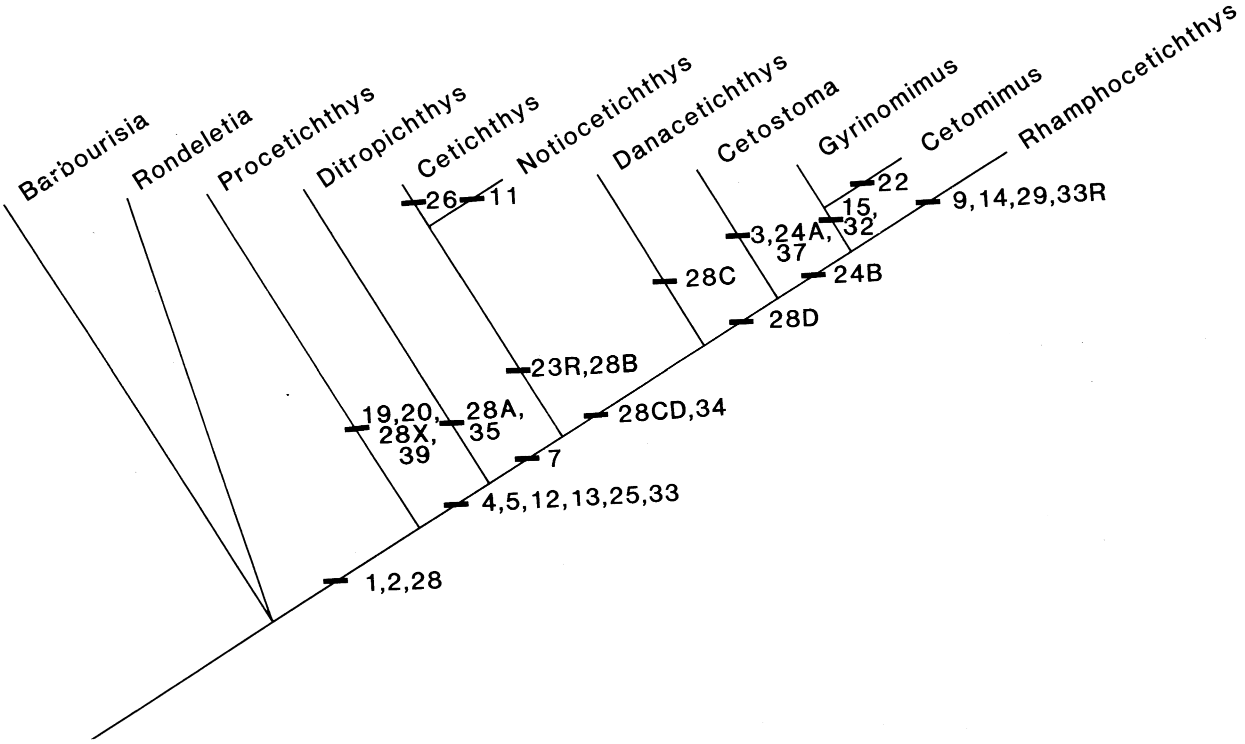

Fig.29. Relationships of the cetomimid genera; numbers refer to apomorphies described in text; letters A-D refer to different states in a transformation series, R to reversals.

Barbourisia. These latter two genera lack basibranchial tooth plates, which are present in all cetomimids. However basibranchial tooth plates are present in the Polymixiidae, Berycidae, Monocentrididae and some Holocentridae and absent in all other beryciforms (Zehren, 1979). The available data do not allow determination of the derived state for this character.

3. Dorsal and anal finray number. The number of cetomimid dorsal and anal finrays ranges from 11 to 37 and can be divided into only two clear states, 11 to 22 and 26 to 37. With both *Rondeletia* and *Barbourisia* falling in the lower range, the higher number is considered the derived state and is autapomorphic for the monotypic *Cetostoma.*

In *Cetostoma* and *Ditropichthys* there are consistently two to four more dorsal rays than anal rays (in *Ditropichthys* the ranges do not overlap), while in all other cetomimid genera the number of dorsal and anal rays are equal or vary inconsistently by one or two rays. While *Barbourisia* always has more dorsal than anal rays, in *Rondeletia* they are equal in number or almost so and the derived state cannot be determined on present evidence for this character set.

4. Pectoral finray number. The number of cetomimid pectoral rays ranges from 15 to 24, with the only clear break between 15 in *Procetichthys* and 17 to 24 in all other genera. The higher number results from the presence of small ventral rays which decrease in size ventrally; these tiny ventral rays are not present in *Procetichthys. Rondeletia* and *Barbourisia* have fewer rays than any cetomimid and lack tiny ventral pectoral rays. The higher pectoral ray number is considered derived.

5. Principal caudal finray number. The number of principal caudal rays in the Cetomimidae ranges from ten (five dorsal plus five ventral rays) to 19 (10+9). With 19 principal rays in *Rondeletia* and *Barbourisia* (as well as most pre-perciform fishes), the reduced number of caudal rays is considered derived and found in all cetomimid genera except *Procetichthys.* The caudal fin is distinctly forked in *Procetichthys* (Fig. 10), and moderately to weakly forked in *Rondeletia* and *Barbourisia.* In almost all other cetomimid specimens, the caudal rays are weak and easily broken, with no caudal fins complete. None of the fins appear strongly forked, however, and seem rounded, truncate, emarginate or weakly forked, suggesting the caudal is not used strongly in propulsion.

6. Total vertebral number. The total number of cetomimid vertebrae ranges from 38 to 59 while in the outgroups, *Rondeletia* has 24 to 27 (n = 19) and *Barbourisia* has 40 to 43 (n = 15). Although the variation is almost continuous within the family Cetomimidae, *Ditropichthys, Cetichthys* and *Notocetichthys* clearly have low ranges with some specimens having less than 40 vertebrae, while *Cetostoma, Gyrinomimus* and *Cetomimus* have ranges that include some specimens with more than 50 vertebrae. The low range is considered primitive and the intermediate values of three genera are included in the derived state with respect to *Rondeletia* and *Barbourisia.*

7. Preanal vertebral number. The cetomimid preanal vertebral number ranges from 20 to 40, with only *Procetichthys* and *Ditropichthys* having the low number of 20 (range 20 to 24). The range in the other cetomimid genera is 23 to 40; *Rondeletia* and *Barbourisia* have nine to 19 preanal vertebrae. The higher number of preanal vertebrae is considered derived. The extensive range of total vertebral numbers in *Gyrinomimus* and *Cetomimus* is correlated with the variation in preanal vertebrae.

Procetichthys and *Cetostoma* have a higher number of anal vertebrae than all other cetomimids (with that of the latter presumably correlated with the higher number of dorsal and anal rays). *Rondeletia* has fewer than 16 anal vertebrae and *Barbourisia* has more than 20; the derived state cannot be determined.

8. Lateral line organ number. The number of lateral line neuromasts, one fewer than the number of lateral line pores in those genera with a lateral line canal, ranges from eight to 86 in the cetomimids, with the higher number of 31 to 86 found in *Rhamphocetichthys* and *Procetichthys.* All other cetomimid genera have eight to 24 neuromasts. The number of neuromasts in *Barbourisia* and *Rondeletia* ranges from 14 to 32, with the number in *Rondeletia* being the number of vertical rows of neuromasts. The higher number of neuromasts is considered derived in the Cetomimidae. The number of lateral line neuromasts is not related to vertebral number.

The lateral line consists of vertical rows of neuromasts in *Procetichthys* and *Rhamphocetichthys* and a canal with single neuromasts covered by a bridge of skin in all other cetomimid genera. Since *Rondeletia* has vertical rows of neuromasts and *Barbourisia* has a lateral line canal, the derived state in the Cetomimidae cannot be determined.

9. Length of snout. The only measurements considered for character analysis were those eight (of 22; Appendix Table 9) for which at least one genus had a range outside all other genera. These eight measurements were taken on six specimens of *Rondeletia* and five of *Barbourisia* (see Materials and Methods).

The snout length ranges from 7.9 to 19.5% SL in the Cetomimidae. The long snout of *Rhamphocetichthys* is distinctive within the cetomimids. *Rondeletia* has a longer snout than *Barbourisia,* thus putting into question which state is derived. However the snout of *Rhamphocetichthys* is elongate and pointed with the upper jaw overhanging the lower, unlike the rounded jaws of all other taxa examined, including *Rondeletia,* and is considered derived.

10. Width of head between eyes. The width between the eyes ranges from 3.2 to 21.6% SL in the cetomimids, with those of *Barbourisia* and *Rondeletia* ranging from 11.8 to 19.9%. The eye widths of *Cetostoma* and *Rhamphocetichthys* were the narrowest measured and are considered derived.

* Lengths of snout to dorsal, dorsal base and anal base. The short snout to dorsal fin origin distance and long dorsal and anal fin bases of *Cetostoma* are outside the ranges of all other taxa measured including *Barbourisia* and *Rondeletia,* are correlated with the high dorsal and anal fin counts and are considered derived. These characters were not utilised in the computer programme, because to do so would in effect be weighting what appears to be a single feature, the increased number of dorsal and anal fin rays (character 3).

* Length of anus to anal origin. The anus is further forward of the anal fin origin in *Procetichthys*, *Cetichthys* and *Notocetichthys* (distance = 5.0-9.9% SL) than in all other cetomimids (0.6-4.3% SL). The outgroup genera display both character states, with the measurements of *Rondeletia loricata* extending into the range of the higher values and the single specimen of *R. bicolor* with an advanced anus (7.2% SL). The softness of the tissue and poorly defined finbases in this genus make the measurements more subjective than most. The derived state is not clear and the character is not utilised in the analyses.

11. Length of copular tooth plate. The length of the copular tooth plate in cetomimids ranges from 0.9 to 15% SL. The negative allometric growth of this element results in the high percentage SL for *Danacetichthys* and some small specimens of *Cetichthys* and precludes the separation of the long copular tooth plate of *Cetostoma* as a distinct character state. However the very short tooth plate in *Notocetichthys* is clearly outside the range of all other genera measured. A copular tooth plate is lacking in both *Barbourisia* and *Rondeletia* and the polarity of the two states of tooth plate length cannot be determined by outgroup comparison. However, the negative allometry apparent in two genera, with a relatively longer tooth plate present in the smallest specimens, is ontogenetic evidence that the short copular tooth plate of *Notocetichthys* is derived.

* Ratio of copular tooth plate length/width. The ratio of copular tooth plate length/width displays two character states, with the long, narrow plates of *Procetichthys* and particularly *Cetostoma* having ratios far exceeding those of all other taxa measured. However the derived state cannot presently be determined, due to the absence of the plate in *Barbourisia* and *Rondeletia* and the lack of any clear indication of allometry.

12. Nasal organ development. The nasal organ of cetomimids is well developed, elongate and has more than 30 lamellae in *Procetichthys*, whereas it is reduced, short and round with none to ten lamellae in all other cetomimids (Fig. 1). In *Barbourisia* the nasal organ is fully developed with up to 30 lamellae and in *Rondeletia* it is moderately large and elongate with 13 to 18 distinct lamellae. The reduced state is considered the derived condition in cetomimids.

13. Eye lens development. A well-developed lens is present in the eye of the outgroup genera *Rondeletia* and *Barbourisia* and is retained as a primitive condition only in the cetomimid genus *Procetichthys*. No lens is present in any other cetomimid over 100 mm SL, but is present or reduced in the small specimens (34-54 mm) of *Danacetichthys*. Ontogenetic reduction and loss of the eye lens is considered the derived state in cetomimids.

14. Cephalic laterosensory system. In *Barbourisia* and *Rondeletia* and all cetomimid genera except *Rhamphocetichthys*, the laterosensory system on the head consists of a series of canals covered by skin that is pierced by large pores. In *Rhamphocetichthys* a series of widely spaced free papillate neuromasts are joined by underlying nerves, in the approximate position of the canals of the other genera. The papillate neuromast system is considered autapomorphic for the monotypic *Rhamphocetichthys*.

15. Supraorbital head canal. The supraorbital head canal is joined to the main head canal in *Barbourisia* and *Rondeletia* and all cetomimid genera except *Gyrinomimus* and *Cetomimus* and questionably *Cetostoma* and *Danacetichthys*, where they are broken into two separate canals. The discontinuous condition is considered derived.

16. Dorsal head canal pore number. The number of pores in the dorsal canal of the head (the supraorbital canal plus the main canal) ranges from eight to 12 in the Cetomimidae with two states: 8-9 and 10-12. The number of dorsal pores in both *Barbourisia* and *Rondeletia* is eight and the higher number in cetomimids is considered derived.

17. Infraorbital head canal. The infraorbital canal is distinctly separate from the supraorbital canal in all cetomimid genera except *Cetichthys*, in which they are joined, and *Ditropichthys*. In *Ditropichthys* the canals are partially joined (a neuromast is present between the two pores, but the covering skinbridge has been lost). In both *Barbourisia* and *Rondeletia* the two canals are joined. Separate canals are considered derived in cetomimids.

The cetomimid number of infraorbital pores ranges from eight to ten, but does not fall into distinct classes; *Rondeletia* has seven infraorbital pores and *Barbourisia* has ten.

18. Last infraorbital neuromast. The last (counting from anteriorly) infraorbital neuromast and two adjoining pores are displaced anterodorsally, so they are not continuous with the rest of the infraorbital canal, in five cetomimid genera. In all other genera plus *Barbourisia* and *Rondeletia* the canal is continuous; the displaced condition is considered derived for cetomimids.

19. Nasal organ infraorbital canal connection. A small pore joins the posterior nasal cavity with the anterior circumorbital canal in *Procetichthys*. The connection is considered autapomorphic for this monotypic genus, as it was not found in any other taxon examined. However two pores are present in the posterior wall of the nasal cavity at the end of the raphe in *Rondeletia*, where they lead to an organ of unknown function, briefly described by Tominaga (1970). The pores in the two taxa are not considered homologous, as the organ behind the nasal cavity in *Rondeletia* is not apparent in *Procetichthys*.

20. Jaw tooth spacing. In *Barbourisia*, *Rondeletia* and all cetomimid genera except *Procetichthys*, the jaw teeth are closely set, with the tooth bases almost touching, or at least less than the basal width of a tooth apart (Fig. 2). The jaw teeth of *Procetichthys* are very widely spaced in one to two uneven rows, with the space between teeth greater than the basal tooth width (Fig. 2a), and this is considered the derived condition.

21. Jaw tooth rows. In *Barbourisia*, *Rondeletia* and most cetomimids the jaw teeth are organised in approximately diagonal rows across the oral surface of the jaws (Fig. 2b, d-f). In *Danacetichthys* and most species of *Gyrinomimus* the jaw teeth are set in distinct longitudinal rows down the length of the jaws (Fig. 2c). In only two undescribed species of *Gyrinomimus* the early teeth formed in juveniles are in

diagonal rows, while teeth added later in life are in longitudinal rows (Paxton, ms). Both outgroup comparison and ontogenetic evidence support the consideration of longitudinal rows as the derived state.

22. Vomer. The vomer displays a variety of conditions, from edentate in *Rondeletia* and *Notocetichthys*, to having two teeth in *Procetichthys*, to having numerous teeth in other genera; the shape of the tooth patch varies from triangular to rectangular, trapezoidal, elipsoidal, oval and round with shape and number of teeth defying objective division into discrete character states. However in *Cetomimus* the vomer projects distinctly ventrally into the oral cavity as a hemispherical dome, becoming more pronouncedly domed in larger individuals. In all other genera including *Barbourisia* and *Rondeletia*, the vomer is flat or only very slightly domed, and the domed vomer of *Cetomimus* is considered derived. The vast majority of species of *Cetomimus* have a vomer that is round in outline, in contrast to the rectangular to oval vomer seen in *Gyrinomimus*.

23. Palatine teeth. The outgroup genera *Barbourisia* and *Rondeletia* and the cetomimids *Cetichthys* and *Notocetichthys* lack palatine teeth. The presence of palatine teeth in all other cetomimid genera is considered derived.

* Ectopterygoid teeth. The ectopterygoid of *Rondeletia* is toothless, whereas the ectopterygoid of *Barbourisia* has a long tooth plate extending to the rictus. All but two cetomimid genera share the long toothplate with *Barbourisia*, whereas that tooth plate is very short in *Cetichthys* and absent in *Notocetichthys*. While one of the states should define a lineage within the cetomimids, the polarity of evolution cannot be determined from the two outgroup genera.

* Copular tooth plate(s). Three separate basibranchial tooth patches are present in *Cetostoma*, whereas a single basibranchial tooth patch is found in all other cetomimids. As both *Barbourisia* and *Rondeletia* have edentate basibranchials, the derived condition for the number of cetomimid basibranchial tooth plates cannot be determined from present data.

24. Fourth gill slit. The fourth gill arch is free, with a large gill slit extending above the angle behind the fourth arch of *Barbourisia*, *Rondeletia* and the cetomimid *Procetichthys*. In most other cetomimids the fourth gill slit is reduced to an opening behind the ventral arm of the fourth arch; in *Cetostoma* the fourth gill slit is further reduced to a small tubular opening behind the angle of the fourth arch (state 24A). In *Rhamphocetichthys*, *Gyrinomimus* and *Cetomimus* the fourth slit is completely closed, with only three free gill arches, and this is considered the most derived condition (state 24B). The unique condition in *Cetostoma* is considered a separate state as part of a transformation series.

25. Pseudobranch. A pseudobranch on the inside of the gill cover is present in *Barbourisia*, *Rondeletia* and the cetomimid *Procetichthys*. Its absence in all other cetomimids is considered derived. With this and the other characters of loss, there is no evidence that the loss occurred more than once.

26. Arch 1-3 holobranchs. The holobranchs or gill filaments of the first three gill arches are well developed and closely set in *Barbourisia*, *Rondeletia* and all cetomimids except *Cetichthys* (Fig. 3). In *Cetichthys* the holobranchs are very reduced and far separated (Fig. 3b) and this is considered the derived condition. In cetomimids the amount of the dorsal arm of the first gill arch bearing holobranchs varies from more than 50% to 0, but the variation is a continum and states are not defined.

27. Arch 4 holobranchs. The holobranchs of the fourth gill arch are well developed, closely set and at least half the length of those on the first arch in the outgroup genera *Barbourisia* and *Rondeletia* and most cetomimids. In *Cetichthys* the holobranchs of the fourth arch are as reduced and widely spaced as those of the first arch. In *Cetostoma*, *Cetomimus* and most species of *Gyrinomimus*, the filaments are closely spaced but reduced in length to less than a quarter of those on the first arch, in some species being almost invisible. The reduced conditions are considered derived.

28. Gill raker form. In *Barbourisia* and *Rondeletia*, the gill rakers are elongate and slightly flattened in shape, typical of rakers in most fishes. In *Procetichthys*, gill rakers have been replaced by individual isolated teeth (Fig. 3a). In *Ditropichthys* the gill rakers are club shaped (Fig. 3c), in *Cetichthys* and *Notocetichthys* low, toothed knobs (Fig. 3b), in *Danacetichthys* domed, rounded tooth plates (Fig. 3d) and in the other four genera flat tooth plates that often fuse with increasing age to form an unbroken patch of teeth (Fig. 3e-h). With elongate the primitive outgroup condition, the other forms are considered a transformation series from club shaped (state 28A), to low knobs (state 28B), to domed plates (state 28C) through to flat plates (state 28D); the isolated teeth of *Procetichthys* are considered derived (state 28X), but not a stage of the transformation series.

29. Arch 2-3 gill "rakers". Gill rakers or their equivalent are present on the second and third gill arches of the outgroup genera *Barbourisia* and *Rondeletia* and all cetomimids except *Rhamphocetichthys*, where their loss is considered derived. The loss of gill tooth plates on the fourth gill arch is usually correlated with the closure of the fouth gill slit, and is not distinguished as a separate character.

30. Medial gill "rakers". In *Barbourisia*, small gill rakers are present on the medial faces of all four gill arches. In *Rondeletia* gill rakers in the form of small tooth plates are present on the medial faces of arches two to four (but not arch 1). Tooth plates are present on the medial faces of arches one to three in four cetomimid genera and absent in all or most species in five genera. The loss of these medial elements from arches two to three is considered derived in the Cetomimidae.

31. Ventral pharyngeal tooth plate. Paired ventral pharyngeal tooth plates are present on the fifth ceratobranchial of both *Barbourisia* and *Rondeletia* (very small in *Rondeletia*) and three cetomimid genera. The loss of these tooth plates in six cetomimid genera is considered derived.

* Lateral line form. The lateral line of *Barbourisia* is a

deep canal with the overlying skin pierced by small pores and supported by scales in the medial wall of the lateral line canal. In *Rondeletia* the lateral line is a series of vertical rows of papillate neuromasts, without underlying scales. Vertical rows of neuromasts with underlying scales are present in two cetomimid genera, with the rest having a shallow or deep canal, large pores and supporting scales. The two character states cannot be polarised on the basis of the outgroup condition.

32. Lateral line scales. In seven cetomimid genera the lateral line scales lie flat in the medial wall of the lateral line canal and are round-oval or rectangular in shape with smooth margins (Fig. 5b). In *Gyrinomimus* and *Cetomimus* the scales are elongate and curved, with the dorsal and ventral edges curved up the sides of the lateral line canal to support the overlying skin; the dorsal and ventral margins have one to many projections (Fig. 5c). *Rondeletia* lacks lateral line scales, while the lateral line scales of *Barbourisia* are curved with dorsal and ventral projections. However these projections are double and supported by numerous cross struts (Fig. 5a). The curved scales of *Barbourisia* do not appear homologous with those of *Gyrinomimus* and *Cetomimus*. While the flat versus curved states cannot be polarised on the basis of the outgroup genera, they are polarised due to their correlation with numerous other derived states in *Gyrinomimus* and *Cetomimus* (Table 10). The different states are objective and easy to define, suggesting a major evolutionary change.

33. Cavernous tissue. Cavernous tissue is lacking in both outgroup genera *Barbourisia* and *Rondeletia* and the cetomimids *Procetichthys* and *Rhamphocetichthys* (although a slight indication is present over the lateral line scales of the latter genus). In all other cetomimid genera cavernous tissue is present at least in bilateral areas anterodorsal to the anus. The presence of cavernous tissue is considered the derived state. In *Ditropichthys* and some species of *Gyrinomimus* and *Cetomimus*, cavernous tissue is also present in at least one other area (fin bases, lateral line, caudal peduncle, abdomen). While cavernous tissue at areas other than close to the anus might be considered a further derived state in a transformation series, it is not done so here because the additional areas are different in different taxa and not all species of the latter two genera have the additional tissue.

34. Subpectoral organ. A subpectoral organ is discernible in five cetomimid genera (only in some species of two of these) and absent in the other four cetomimid genera and *Barbourisia* and *Rondeletia*. The presence of a subpectoral organ is considered the derived state.

35. Paired abdominal ridges. In *Ditropichthys* two flaps of skin extend from near the pectoral base to the anus, supported internally by ridges most developed posteriorly in the ventral wall of the abdomen. No such ridges or paired flaps are present in any other cetomimid or *Barbourisia* and *Rondeletia*. The paired ridges are considered autapomorphic for the monotypic *Ditropichthys*. A single, weak, midventral ridge is present in a few cetomimids and is similar to the mid-dorsal ridge found in many cetomimids. The weak single ridges are not characterised because in a number of cases they seem to be dependent on preservation quality.

36. Anal lappets. Long flaps of skin supported by internal scales hang over the anal fin base in *Ditropichthys* and *Cetostoma*. Separate anal lappets with internal scales are present in *Rhamphocetichthys* and some species of *Gyrinomimus*, while a single lappet without a scale is present in one of the two species of *Cetichthys*. The other four cetomimid genera and both outgroup genera *Barbourisia* and *Rondeletia* lack anal lappets. As the different types of lappets do not appear to represent a clear transformation series, they are combined into a single derived character state. Although the number of lappets and whether they are separate or joined vary among the five cetomimid genera, their position over the anal fin and the usual presence of scales are the basis for considering them homologous.

37. Anal fin membrane. The membrane joining the last ten anal rays is voluminous and curtain like only in the monotypic *Cetostoma* (Fig. 21), where it is considered autapomorphic; it does not occur in any other cetomimid or the outgroup genera *Barbourisia* and *Rondeletia*.

38. Stomach pigment. The wall of the stomach is dark brown in all cetomimids except *Rhamphocetichthys*, where it is light brown and *Procetichthys* and *Cetostoma*, which lack stomach pigment. As both *Barbourisia* and *Rondeletia* have darkly pigmented stomachs, the complete lack of pigment is considered derived within the cetomimids.

39. Peritoneal pigment. The peritoneal lining is light brown in *Cetostoma* and dark brown in all other cetomimids except *Procetichthys*, which lacks peritoneal pigment. The peritoneal lining of *Barbourisia* is dark, that of *Rondeletia* is light brown. The lack of pigment is considered derived within the Cetomimidae.

Discussion. The 39 character sets (Table 10) were analysed by the computer programme PAUP version 2.4 (Swofford, 1985) to produce phylogenies based on parsimony, with the minimum number of evolutionary steps. *Rondeletia* and *Barbourisia* were combined as a single outgroup. The data matrix was manipulated once: characters with two states in one genus were changed from missing to derived for a second analysis. The two runs produced a total of nine trees (one and eight trees respectively).

A combination of the nine trees indicates that unresolved problems involve the relationships of *Cetichthys* with *Notocetichthys* and of the five most derived genera. The cladogram presented as a working hypothesis (Fig. 29) comes closest to two trees (one in each analysis), the only difference being the order of the genera *Cetostoma* and *Rhamphocetichthys*, as discussed below.

The monophyly of the family Cetomimidae is supported by three synapomorphies relative to *Barbourisia*, *Rondeletia* and other families of the Beryciformes, the absence of pleural ribs and pelvic fins and the presence of gill rakers in some form other than elongate and flattened. The establishment of *Procetichthys* as the primitive sister group of all other cetomimids is one of the most unequivocal nodes in the cladogram. The monophyly of the remaining cetomimid genera (here considered a subfamily) is supported by five synapomorphies and the monotypic *Procetichthys* is defined by four autapomorphies.

The genus *Ditropichthys* is placed as the primitive sister group of the remaining seven genera in all analyses, although only one synapormorphy, the higher number of preanal vertebrae (character 7), supports the monophyly of the other genera. The monotypic *Ditropichthys* is defined by the autapomorphic features of paired abdominal ridges and gill rakers in the form of toothed clubs (characters 28A, 35).

The relationship of *Cetichthys* and *Notocetichthys* was not resolved in the computer analyses. In some phylogenies they were in a monophyletic line defined by the gill raker form of toothed knobs (character 28B), while in others the monotypic *Notocetichthys* was separate and more primitive, defined by the single autapomorphy of a short copular tooth plate (character 11). The most parsimonius cladogram includes these two genera in a monophyletic line that is also defined by the loss of palatine teeth (character 23R). This latter synapormorphy is a reversal of the derived condition for the family Cetomimidae of palatine teeth present. *Cetichthys* is defined by the synapomorphic feature of reduced holobranchs.

The monophyly of the remaining five genera is supported by gill raker form (character state 28C,D) and the presence of a subpectoral organ in at least some species of each genus (character 34); every computer analysis placed them in monophyly. However the relationships of each to the other is ambiguous. Only the sister group relationship of *Gyrinomimus* and *Cetomimus* was recognised in all analyses, with the line defined by the form of the lateral line scales (character 32). The shape of the vomerine tooth plate (character 22) defines *Cetomimus*. *Gyrinomimus* lacks a synapomorphic character, as the distinctive longitudinal rows of elongated teeth (character 20) are also found in *Danacetichthys*.

The relationships of the other genera are open to question. Both *Cetostoma* and *Rhamphocetichthys* are highly derivative forms, with each monotypic genus defined by three or four autapomorphies.

The hypothesis chosen for the relationships of the five genera (Fig. 29) is identical to one of the nine trees produced and is supported by the two characters with multiple state changes, gill raker form (28) and fourth arch gill slit (24). *Danacetichthys* is placed as the sister group of the other four genera due to the unique, intermediate form of the gill arch tooth plates (Fig. 3d). This genus is known only from six juvenile specimens. However *Danacetichthys* is not merely the juvenile form of one of the more than ten species of *Gyrinomimus*. Although the jaw teeth are similar to those of *Gyrinomimus*, none of even the smallest specimens of *Gyrinomimus* have gill tooth plates the same as those of *Danacetichthys*, the fourth gill slit is always closed in *Gyrinomimus* and the lateral line scales have dorsal and ventral projections.

Consideration of *Cetostoma* as the sister group of the other three genera is supported by the reduction and closure of the fourth gill slit (character 24). None of the other solutions allowed each line to be defined by at least one synapomorphy. The chosen hypothesis (Fig. 29) is similar to the single tree generated in the first analysis (where characters with two states in one genus were considered missing), differing only in the reversed order of *Cetostoma* and *Rhamphocetichthys*. Such a solution, with *Rhamphocetichthys* as the primitive sister group of the other three genera, requires a reversal of character 24, a reopening of the fourth gill slit in *Cetostoma*, and is rejected because it is less parsimonius. The only reversal evident in the present solution is the loss of cavernous tissue in *Rhamphocetichthys*, and this reversal is required in every tree.

Some comments about the analysis and resulting phylogeny are warranted. One feature restricted to and widely distributed within the family Cetomimidae proved of less value in ascertaining generic relationships than expected. The distribution of anal lappets (character 36) does not define any of the hypothesised monophyletic lines within the family. As lappets are absent in *Procetichthys* and present in *Ditropichthys*, they presumably evolved in the ancestor to *Ditropichthys*. The anal lappets display a labile evolutionary picture, being fully developed and completely joined in *Ditropichthys*, reduced to one in one species of *Cetichthys* and lost in the other species, as well as in *Notocetichthys*, fully developed and partially joined in *Cetostoma*, as separate elements in *Rhamphocetichthys* and some species of *Gyrinomimus* and presumably independently lost in *Danacetichthys*, some *Gyrinomimus* and *Cetomimus*. A classification that required fewer evolutionary changes for this feature would result in many more reversals for other characters. Perhaps the evolutionary labileness will be more explicable when the function(s) of anal lappets are understood.

The characters utilised in the present analysis do not include the less labile osteological features. Clearly further characters and analyses are required to resolve some areas and test the present hypothesis of relationships.

This synopsis recognises six monotypic genera. Two factors influenced the subjective decisions of what level to draw generic limits. The genera *Gyrinomimus* and *Cetomimus* each contain more than ten species. Further, the few available specimens of both *Danacetichthys* and *Rhamphocetichthys* suggest that more than one species may be involved. Finally the fact that the majority of species are known from fewer than ten specimens suggests that more species will be discovered in the future.

Biology

Sight. The eyes of most cetomimids grow very little with increasing size, and with the exception of *Procetichthys*, do not exceed 2.0 to 2.5 mm diameter. The same holds true for female ceratioid anglerfishes, another bathypelagic group (Bertelsen, 1951). The lack of a lens in most adult whalefishes indicates that image formation is not possible, although Munk (1965) concluded that light perception might be possible even in the most degenerated eyes. With a well-formed lens, the eye of *Procetichthys kreffti* presumably is capable of both light detection and image formation, as are the eyes of at least young *Danacetichthys galathenus*.

The remnants of a degenerating lens have been found in two of the smallest specimens of *Cetostoma regani* (40.7 and 50.2 mm), but in other specimens 39.7 mm and over the lens is gone. Similar remnants are present in a 39.5 mm specimen of *Cetomimus* sp. F, but not in other specimens of the genus 45.7 mm and over. No remnants have been discernible in any of the other five genera, including specimens of *Ditropichthys* as small as 26.8 mm and *Gyrinomimus* 51.0 mm. The presence of lens remnants supports the suggestion of Munk (1965), that the eyes are fully differentiated and functional in juvenile whalefishes and degenerate with age. The degeneration presumably would be related to the lack of light in the bathypelagic depths inhabited by adult whalefishes. No specimens smaller than 25 mm have ever been taken.

Olfaction. Marshall (1967) surveyed the olfactory organs of bathypelagic fishes and found two different types of nasal organs. In bathypelagic representatives of a few families (Serrivomeridae, Nemichthyidae, Macrouridae), both males and females have reduced nasal organs. The majority of bathypelagic species studied (all but one family of ceratioid angler fishes, Gonostomatidae) are sexually dimorphic, with males having large nasal organs and females reduced nasal organs and associated areas of the brain. To this list can now be added Eurypharyngidae (Gartner, 1983), Saccopharyngidae (Nielsen & Bertelsen, 1985) and Monognathidae (Bertelsen & Nielsen, 1987). In contrast, almost all mesopelagic and deep benthic fishes have moderate or large nasal organs in both sexes. As all examined cetomimids have been females, all whalefishes except *Procetichthys kreffti* are thus typical bathypelagic fishes with greatly reduced nasal organs in females.

Male cetomimids have yet to be discovered. Gosline (1971:135) suggested, without elaboration, that megalomycterids may prove to be the macrosomatic males of cetomimids. This suggestion will be considered in detail in a future paper on the osteology of the Cetomimidae. Suffice it to say that, while appealing, identification of megalomycterids as male cetomimids would appear to be refuted by, among other features, determination of the 34.5 mm holotype of *Megalomycter teevani* as a female (Myers & Freihoffer, 1966:195).

The limited development of weak olfactory lamellae in some specimens of *Cetomimus* and *Gyrinomimus* (Fig. 1j,k) appears to be size related, as the smallest specimens lack any indication of lamellae. The loss of olfactory acuity presumed by the reduction and loss of lamellae (not necessarily a valid assumption, see for instance Thiesen *et al.*, 1980) which parallels the loss of sight in the dark bathypelagic environment is explicable if food in this environment does not give off many odours. Marshall (1967:69) concluded that in most bathypelagic species "...the olfactory organs and associated brain centres are so reduced that they are most unlikely to help in the finding of food." The loss of both sight and smell is apparently compensated for in cetomimids by one of the widest lateral line systems known in fishes. The lack of a cavernous lateral line in *Procetichthys kreffti* is associated with both a large nasal organ and presence of an eye lens. However *Rhamphocetichthys savagei* lacks a large nasal organ, eye lens and cavernous lateral line.

Mechanoreception. Coombs *et al.* (1988) and Webb (1989) have surveyed the distribution and variety of lateral line systems in fishes. The cetomimids are richly endowed with both wide lateral line canals and large numbers of papillate superficial neuromasts. Coombs *et al.* (1988: 586) point out that it is not unusual to find these two features in combination, and that their evolution may be favoured in low-noise environments. The deep sea cetomimids appear to be a particularly striking example of this correlation.

The head canal pattern of cetomimids is a variation of the standard teleost pattern. The loss of head canals in *Rhamphocetichthys* is combined with their replacement by lines of superficial neuromasts, an event which has occurred independently in many fish groups (Coombs *et al.*, 1988: Fig. 22.14). The loss of the main trunk canal and its replacement by vertical rows of superficial neuromasts, the trunk accessories, has occurred independently in *Procetichthys* and *Rhamphocetichthys*. These monotypic genera are known from one and four specimens respectively and nothing is known of their biology that is different from the other whalefishes to correlate with this lateral line specialisation.

Of the four major head canal types identified in teleosts (Webb, 1989), cetomimids have widened canals without bony walls or roofs (although the orientation of the cupula in the canal, one of the defining characteristics of canal type, has not been determined). While the head canals of *Procetichthys* are relatively the narrowest of the family (Fig. 4), they are covered in skin, not bone.

Primary variations in the head canals of the lateral line system include whether the supraorbital canal is continuous with or separate from the main canal, whether the infraorbital canal is separate from or joined to the main canal and whether the last (posterior) neuromast and its associated pores of the infraorbital series is continuous with the series or displaced anterodorsally. According to the evolutionary relationships proposed in the previous section, each of these three evolutionary events occurred only once in the family. Secondary variations include differences in the numbers of neuromasts and pores in each canal and in the numbers of superficial neuromasts in various lines. Each of these features may vary in a single species of cetomimid.

Three primary differences are apparent in the main trunk canal, the most fundamental being the replacement of the trunk canal with vertical accessory lines of superficial neuromasts in *Procetichthys* and *Rhamphocetichthys* mentioned above. The remaining genera have two basic types of trunk canal which are influenced by the type of lateral line scales in the floor of the canal. In all genera except *Gyrinomimus* and *Cetomimus*, the lateral line scales are flat and two dimensional; the sides of the lateral line canal are unsupported. In many taxa the "canal" consists of very narrow skinbridges barely covering the neuromast and not nearly the width of the scale (Fig. 20). This shallow condition of the lateral line may be related primarily to size; the largest specimens of at least *Cetichthys parini* have more cavernous lateral line canals, as the longest specimens also have more flesh on the head and body.

In *Gyrinomimus* and *Cetomimus* the lateral line scales have lateral extensions which support the lateral walls of a deeper and more cavernous trunk canal (Fig. 5c). These scales not only provide support for the lateral canal wall, but provide wide anchoring points for the roof of the canal. With such anchoring points and lateral walls, the diameter of the canal is thus restricted at the scale and overlying neuromast, in relation to the rest of the canal. Such restriction will increase the velocity of fluid flow past the cupula and increase the receptor response, while the increased volume of fluid in the widened canal increases sensitivity of the neuromasts (Denton & Gray, 1988). However the functional significance of the flaps that partially close off the posterior pores and the median keel on the posterior portions of the canal roof, both of which are most developed in *Gyrinomimus* and *Cetomimus*, has yet to be established.

The highly developed lateral line system of whalefishes is clearly the primary sensory system of these bathypelagic fishes, with both sight and olfaction systems reduced in almost all taxa. Increased sensitivity of the trunk canal presumably accrues with the greater development of a cavernous canal (increased canal depth) with growth. However the size at which this becomes most pronounced, at least in *Cetichthys parini*, is more than 150 mm SL, far beyond the size at which the eye lenses have degenerated. The extreme development of a cavernous trunk canal thus does not exactly correspond to the loss of the eye lens, but does provide an extensive sensory receptor system in adult whalefishes. Such a system must provide for the detection of prey, predators and conspecifics for reproduction. Neither the body shape nor fin development are indicative of rapid swimming in whalefishes (see below), that might jam a sensitive system. The extensive development of wide canals and superficial neuromasts provides the slow-swimming cetomimids with information about the quiet bathypelagic environment.

Respiration. Marshall (1960:171) has demonstrated the considerable reduction in organ systems in bathypelagic fishes when compared to mesopelagic species, including the number and extent of gill filaments. Marshall (1960) related this economy of form with increasing depth to the decreasing amount of available food. An extreme reduction in gill filaments is apparent in *Cetichthys* (Fig. 3b), the deepest dwelling of all cetomimids. Not enough closing net captures are available to determine exact depth ranges to correlate with total gill lamellae of other species. The great reduction in gill lamellae of *Cetichthys* may be related to the increased oxygen carrying capacity of deeper, colder water; or perhaps some type of cutaneous respiration supplements the oxygen supply from the degenerated gills.

Food and feeding. Ebeling & Cailliet (1974) correlated mouth size with living depth in the fish families Myctophidae and Melamphaeidae. They showed that the deeper-dwelling bathypelagic species of each family had larger mouths than the mesopelagic species. Such a generality does not appear to hold within the wholly bathypelagic family Cetomimidae. *Cetichthys* is the deepest dwelling cetomimid, yet the premaxillary length is not longer than that of some specimens of *Danacetichthys*, *Gyrinomimus*, *Cetomimus* or *Rhamphocetichtys* (Table 9), nor does *Cetichthys* apparently reach the maximum total length of any cetomimid to attain the largest absolute mouth. While the capability of taking the largest available meal presumably was the selective advantage resulting in the large mouths found in all cetomimids, extremes of depth apparently do not result in even larger mouth sizes.

Many of the features of whalefishes - exceptionally large mouth, lack of scales, ribs and pelvic fins, long abdominal region with posterior dorsal and anal fins and anus, and weak pectoral girdle with unforked post-temporal - would be advantageous in taking large, single meals such as a large fish. More than 300 specimens were x-rayed, and only five had visible stomach contents. All were of the genus *Gyrinomimus* and had a single relatively large fish in the stomach. Four of these were dissected and in each case the stomach contents consisted of a single myctophid in good to excellent condition, with complete scales in three cases. Each stomach also had other items in good condition (a stomatopod larva; a broken salp barrel and two crustaceans; a salp complete with phronemid amphipod). Net feeding during death throes in the trawl is the most plausible explanation of these largely mesopelagic food items in the stomach (see Hopkins & Baird, 1975 for a review of net feeding in mesopelagic fishes). The size of the fishes ingested (50 mm, 70 mm, 39 mm) relative to the size of the whalefish (125, 150, 150 mm) indicates cetomimids are capable of ingesting fish prey up to almost half their standard length, but normally do not do so.

Few cetomimids contained identifiable stomach contents (only those with obviously distended stomachs were dissected), presumably due to the scarcity of food at bathypelagic depths or regurgitation in the net. A total of 14 specimens representing five genera, including eight specimens of *Cetostoma regani*, contained recognisable stomach contents. All of the stomach contents were crustaceans, ranging from copepods to decapods. The dentition of whalefishes, small, closely-set teeth in all but *Procetichthys*, is presumably related to the crustacean diet, while the food of this latter genus is unknown.

The typical whalefish is heavy bodied with a large head, very poorly developed pectoral fin, low dorsal and anal fins, short and broad caudal peduncle and rounded to emarginate caudal fin. None of these features are correlated with rapid swimming and as hypothesised for many deep sea fishes, cetomimids are probably slow-swimming predators that lie in wait for prey to swim close to the large mouth. The only exception to this might be *Procetichthys*, which has a considerably larger pectoral fin, a distinctly forked caudal fin and a more compressed body. However the large number of superficial neuromasts aligned in vertical rows on the trunk are not typically associated with fast swimming fishes and this species also is most likely a slow swimmer.

Age and growth. Assuming unbiased sampling and similar escape bahaviour in different taxa, there are clearly different maximum sizes in the different genera of cetomimids, with *Ditropichthys* attaining no more than 150 mm and *Gyrinomimus* reaching almost 400 mm. It is likely that the latter genus reaches larger sizes, as none of the examined specimens were reproductively mature. The best representation of size range is available for *Ditropichthys*, with 84 specimens known from 25 to 131 mm SL (Table 4). Allometric growth is apparent in a number of parameters, the most striking feature being the addition of fat and muscle in larger specimens, particularly in *Ditropichthys* and *Cetichthys*, resulting in heavier, deeper bodies. Specimens smaller than 40 mm are unknown for most taxa. No data are available for age estimates.

Reproduction. The vast majority of examined cetomimids have been immature. All examined specimens that were large enough to have gonads identifiable by observation up to 50 times magnification have been females. This has been confirmed by embedding and sectioning gonads of eight medium to large specimens representing five species in four genera. No indication of testicular tissue has been found.

Almost all of the ovaries examined have been filled with eggs 0.1 mm or less in diameter. The largest eggs seen are in the 236 mm holotype of *Procetichthys kreffti*, with eggs 1.9 to 2.0 mm in diameter. A 280 mm specimen of *Gyrinomimus andriashevi* (ISH 952/71) has eggs up to 1.3 mm in diameter, while the largest eggs of 75 dissected specimens of *Cetostoma regani* are 0.6 mm in diameter from a 204 mm specimen. All three of these fishes had smaller eggs in the ovaries, with the latter specimen having only a few 0.6 mm eggs and many eggs much less than 0.1 mm diameter. Five other specimens of *C. regani* had two eggs sizes in the ovary (0.1 mm and much less than 0.1 mm), as did the only specimen of *Ditropichthys storeri* (112 mm) with eggs greater than 0.15 mm (0.25 mm and less than 0.1 mm). At least some species of cetomimids appear to spawn more than once per lifetime, unlike the scenario that has been proposed for an increasing number of bathypelagic fishes. There is no evidence that cetomimids go through a nuptial metamorphosis involving the reduction in feeding and other systems that precedes a single spawning and then death, as proposed for the Anotopteridae, Paralepedidae, Notosudidae, Nemichthyidae, Saccopharyngidae and Monognathidae (Bertelsen & Nielsen 1987:167).

The great disparity in egg sizes found in a single ovary (0.3-0.5 and 1.9-2.0 in *Procetichthys*; 0.2-0.3 and 1.3 in *Gyrinomimus andriashevi*; 0.6 and 0.1 in *Cetostoma regani*), coupled with the range of sizes of *C. regani* with larger eggs (120-246 mm), suggest that the multiple spawnings do not occur in the same spawning season, but are spread over more than one year. It it also possible that the smaller eggs are resorbed upon full maturation. More data are required to comment on seasonality. Two of the three specimens detailed above were taken in southern temperate waters in March (autumn), while the *C. regani* was taken in northern temperate waters at the end of May (spring), with the few remaining 0.6 mm eggs suggesting an earlier spawning. It appears that different taxa have different size eggs at spawning, with *Procetichthys* having at least 2.0 mm eggs, *Gyrinomimus* at least 1.3 mm and *Cetostoma* and perhaps *Ditropichthys* in the 0.5 to 0.6 mm range.

With both males and juveniles/larvae under 25 mm unknown, discussion of reproductive strategies is speculative. However at least some evidence indicates spawning occurs at bathypelagic depths rather than near the surface. All species have ovaries that increase in size with age and usually larger egg sizes are restricted to the largest individuals (see Figs 14, 22); apparently the largest individuals are those most likely to spawn. For those species with a reasonable sample size, it is clear that the largest individuals are the deepest dwelling (Figs 16, 24). Although there may be limited vertical migration of *Cetostoma regani* to 300 m, no individual larger than 160 mm has been taken in waters shallower than 1000 m (Fig. 24). Although a few smaller individual have eggs larger than 0.1 mm, the majority with larger eggs exceed 160 mm, suggesting spawning takes place below 1000 m (admittedly a spawning migration to shallower waters would presumably be brief and likely to be missed). Possibly the fertilised eggs ascend to the epipelagic waters where planktonic food is more abundant, as is the case for the bathypelagic ceratioid anglerfishes, where the larvae are well known from the upper 300 m (Bertelsen, 1951). As the largest ovaries have thousands of eggs (e.g. *Procetichthys kreffti*), and there may be as many as 2800 cetomimids per cubic kilometre of seawater in the richest areas, the lack of identified cetomimid larvae in the numerous plankton tows taken throughout the world is disconcerting. Presumably the larvae are either so unlike the adults they have not been identified or are so fragile they are damaged beyond recognition in the net. However the larva from a 2 mm egg should be relatively robust. Cetomimid larvae may live in the meso- or bathypelagic, and have smaller opportunity to be sampled. There is no indication of internal fertilisation and direct development, the final possibility which would seem to be precluded by the large number of ovarian eggs.

The final mystery concerns the whereabouts of the male whalefishes. A number of possibilities exist. Although gonads of eight specimens have been sectioned and all found to be females, the smallest specimens were a 133 mm *Cetostoma regani* and a 59 mm *Ditropichthys storeri*. It is possible that the species are sequential hermaphrodites and the small males have not been sampled. Another possibility is that cetomimids are so sexually dimorphic that the males are currently placed in another taxon. Gosline's (1971) suggestion that megalomycterids are macrosomatic male cetomimids is thus appealing, but is not supported by the available evidence (one holotype was described as a female, and the finray counts of only one of the four megalomycterid genera match any of the nine cetomimid genera).

Looking at other possible taxa, one finds the statement of Robins (1974), also without elaboration, that some of the mirapinniform fishes are prejuveniles of cetomimids. Bertelsen & Marshall (1984:382) have summarised the differences between the mirapinnatoids and cetomimoids, which include presence versus absence of pelvic fins, jaw size and shape and principal caudal fin ray counts. The largest *Eutaeniophorus* and *Parataeniophorus* specimens known are 53 and 46 mm long respectively (Bertelsen & Marshall, 1984), considerably overlapping the smallest known cetomimid (*Ditropichthys*) at 25 mm. Mirapinnids are certainly not prejuvenile cetomimids and with at least the holotype and only specimen of *Mirapinna essau* identified as a 39 mm juvenile female (Bertelsen & Marshall, 1984), the family is an unlikely candidate for the missing cetomimid males. Other possibilities are that the sex ratio is skewed with few males, or that the males (and gravid females?) live deeper and have not yet been collected.

If male cetomimids are macrosomatic, as is the case with many other bathypelagic families, the possibility exists that the cavernous tissue of females may be involved with the attraction of males, perhaps in pheromone production. Perhaps the anal lappets, associated at least anteriorly with cavernous tissue in all taxa with lappets except *Rhamphocetichthys* (which lacks cavernous tissue), function in some kind of fanning or primitive pumping mechanism, although no distinctive muscles are apparent.

Distribution

Horizontal. A discussion of distribution patterns is severely limited by the small sample size, with six of the eight species considered in this paper represented by fewer than ten captures (Figs 11, 15, 23). Nonetheless a few generalisations are possible, particularly with consideration of 13 species distributions of the genus *Gyrinomimus* (Paxton, ms) and more than 100 captures of *Cetomimus* not identified to species.

The family Cetomimidae is found in all major oceans, from 52°N to 72°S. Whalefishes occur in the Gulf of Mexico and at least the southern portions of the Gulf of California and Okhotsk Sea, but not in the Mediterranean Sea or Bering Sea. The two commonest species, *Cetostoma regani* and *Ditropichthys storeri*, have cosmopolitan distributions between 50°N and 40°S. The Atlantic distribution of *D. storeri* is similar to the tropical-subtropical pattern found for mesopelagic myctophids (Backus *et al.*, 1977:fig. 2), with only one northern capture clearly beyond the boundaries of the region. *C. regani* on the other hand, with a number of captures in the north Atlantic temperate region, clearly has a more extensive distribution than any of the mesopelagic patterns described. While occurring in all three oceans, *Danacetichthys galathenus* has a narrower latitudinal range from 30°N to 22°S, but is only known from six specimens. A similar cosmopolitan distribution with latitudinal range from 29°N to 5°S is displayed by eight specimens of *Gyrinomimus bruuni*, while 12 specimens of the closely related *Gyrinomimus* sp. C range from 52°N to 26°S in two oceans. The seven captures of *Cetichthys parini* are restricted to the central and the north Pacific and tropical east Indian Oceans. Of the two most frequently captured species of *Gyrinomimus*, 23 specimens of *Gyrinomimus* sp. H are restricted to the north Pacific between 39°N and 52°N, while 24 specimens of *G. grahami* have been taken circumglobally in the Southern Ocean south of the Subtropical Convergence between 32°S and 72°S. Although *G. andriashevi* and *Notocetichthys trunovi* have only been taken twice in southern latitudes, each may eventually display similar distribution patterns.

Thus two general patterns of distribution are apparent for whalefishes. The cosmopolitan pattern, which may prove to be the most common for cetomimids, is typical of other bathypelagic species, such as five species of gigantactinid anglerfishes (Bertelsen *et al.*, 1981:figs 64-69) and at least six species of linophrynid anglerfishes (Bertelsen, 1982:table 3). These cosmopolitan species cross numerous water mass boundaries, unlike most mesopelagic species (see Backus *et al.*, 1977). With water masses best developed in the upper 1000 m (Sverdrup *et al.*, 1942:fig. 209B), the deeper dwelling bathypelagic species have weaker boundaries with which to contend. Nevertheless some cetomimids, such as the north Pacific boreal species of *Gyrinomimus* and the subantarctic species, are clearly restricted to areas of one or a few water masses, as are most of the anglerfishes of the genus *Oneirodes* (Pietsch, 1974:91). Bertelsen *et al.* (1981:72) suggested the difference in shape between the more globose *Oneirodes* and the more hydrodynamic *Gigantactis* in part accounted for the different distribution patterns, with the latter actively moving between water masses. Such shape differences are not apparent between the two localised species of *Gyrinomimus* and the other cetomimids, and some other factor must be of more importance.

The species of *Oneirodes* are not found in the unproductive areas of the central water masses (Pietsch, 1974), whereas the gigantactinids show no such restrictions (Bertelsen *et al.*, 1981:68). The majority of cetomimid specimens have been taken relatively close to land masses or islands, particularly in the north Atlantic and Pacific, in the areas of greatest sampling effort. The apparent absence of *Cetostoma* and *Ditropichthys* in the central areas of the north and south Atlantic (Figs 15, 23) clearly reflects the lack of deep trawling in those areas (Fig. 30). Cetomimids appear similar to gigantactinids in having broad geographic distributions that include central water masses.

The presence of two different patterns of distribution within the family Cetomimidae is not surprising, as other bathypelagic fish families show a range of distribution patterns, from the species of *Oneirodes* restricted to one water mass (Pietsch, 1974), to the species of *Saccopharynx* restricted to one ocean (Nielsen & Bertelsen, 1985:202) to the cosmopolitan species of *Gigantactis* (Bertelsen *et al.*, 1981). As with fishes of other oceanic zones, bathypelagic fishes display a range of distribution patterns from restricted to cosmopolitan. When more sampling effort is put into the vast bathypelagic area, and distribution patterns become clearer, a higher proportion of wide ranging species may be found in bathypelagic waters due to the relative weakness of boundaries in deeper waters and the more widespread water masses at those depths.

Vertical. The problem of ascertaining vertical distributions from open net captures has been highlighted in many studies. One is forced to use the deepest point the net reached, which is usually the level at which the net spent the most time, and assume the specimens had the best chances of being caught at that depth, even though the net was open and fishing at shallower depths. To complicate matters the fishing depths of the deepest trawls are often an approximation, as they are beyond the range of depth recorders. It is these approximate deepest possible capture depths which have been plotted for the vertical distributions (Figs 12, 16, 24). Fortunately 28 of the 259 specimens reported here were taken in closing nets, providing for three of the eight species some confirmation of living depths.

All cetomimids studied to date are bathypelagic in habitat, with captures below 1000 m. Two species, *Ditropichthys storeri* and *Cetostoma regani*, also live in mesopelagic waters between 600 to 1000 m, at least as juveniles and small adults. The latter species occasionally (4% of specimens) extends into the upper 500 m with one specimen taken at 110 m. There is a strong indication of vertical migration for the smaller specimens of both species. All of the six specimens of *D. storeri* taken above 1000 m were taken in night hauls, during a trawl which included both day and night hours or where time data were not available, as were 15 of the 16 specimens of *C. regani* trawled at 700 m or above. The nocturnal closing net captures below 1000 m clearly show that not all specimens vertically migrate and the small numbers indicate migration is an unusual phenomenon. Both species show a trend for larger individuals to inhabit deeper water, confirmed at least for *C. regani* with a 1500 to 1600 m closing net capture of a 200+ mm individual. It is not clear whether the large number of both species taken in the 2000 to 2200 m range reflects actual living depths or the large number of trawls taken at those depths, particularly by ISH. The vast majority of closing net trawls taken on the RV *Discovery* by IOS were taken above 1500 m, although more than 150 fished to below 1500 m (Merrett, *in litt.*, Aug. 1988) and caught few cetomimids. Nevertheless, as both species have vertical ranges that extend above the bathypelagic zone, the two species with the broadest vertical range also have the widest horizontal distribution; none of the 13 species of *Gyrinomimus* studied have as wide a geographic distribution as *Ditropichthys* or *Cetostoma*.

The other six species detailed in this paper are represented by only 25 specimens. All but the species of *Cetichthys* have been taken in trawls fishing from 1000 to 2300 m deep. The four closing net captures of *C. parini* between 2700 and 3200 m confirm this genus as the deepest dwelling of all cetomimids. Grey (1957:311-312) listed 17 species of bathypelagic fishes found below a depth of 2000 m. *C. parini* is the only cetomimid that can unequivocally be added to this list due to closing net captures. However *C. indagator* and *Procetichthys kreffti* have only been taken in open nets fishing below 2000 m, and can provisionally be added.

The vast majority of whalefishes have been taken in midwater trawls fishing well off the bottom. However, the holotype of *Gyrinomimus grahami* was taken in a bottom trap at 2400 m and the two type specimens of *Notocetichthys trunovi* were taken in two separate trawls within 100 m of the bottom at 1200 to 1400 m. Some cetomimids may be benthopelagic some of the time.

Abundance. Due to the previous paucity of specimens, whalefishes have always been considered very rare. The accumulation of more than 500 specimens requires a reanalysis of this idea. With a centre of distribution below 1000 m (Fig. 12), many species are clearly below the sampling levels of most midwater fish surveys. For instance the Atlantic mesopelagic survey of Backus *et al.* (1977) utilised 1022 midwater trawls, but only 69 of 2254 trawling hours were spent below 1000 m.

One of the most extensive collections of bathypelagic fishes is that of the Institut für Seefischerei in Hamburg (ISH), collected in the Atlantic and Antarctic by the fisheries research vessels *Walther Herwig* and *Anton Dohrn* between 1966 and 1986. A large commercial herring trawl with a circumference of 1600 meshes (MT 1600) was utilised for most catches (Krefft, 1974; Post, 1987). This trawl has head and foot ropes of 70 to 80 m with a potential mouth area of 20 x 30 m or 600 m^2 (Stehmann, *in litt.*, Oct. 1986; Post, 1987). Although Post (1970: 165) used ca. 700 m^2 as the mouth opening, and Post (1987) 600 m^2, both Gjosaeter & Kawaguchi (1980:28) and Hulley (1986:229) used 300 m^2 in their calculations of mesopelagic fish abundances. Hulley (*in litt.*, 3 Feb. 1988) argues that the effective mouth opening at 3.5 knots must be much closer to 300 than 600 m^2, and 300 m^2 is utilised in the calculations below. Other trawls with 1000 meshes and 1216 meshes have been used less frequently by ISH. Krefft (1974), Tesch (1982) and Post (1987) have summarised data for these collections.

The ISH collections include 170 cetomimids taken in 60 trawls. Of these, 145 specimens or 85% were taken in 49 trawls that fished to a maximum of 1800 to 2600 m. To give a better appreciation of whalefish abundance and distribution, the 89 ISH trawls fished at least to 1800 m are mapped and the 49 trawls positive for cetomimids indicated (Fig. 30). The most striking feature is the 1971 cruise between Buenos Aires and Hamburg, where at least one cetomimid was taken in every trawl fished to 1800 m or below. Other cruises were not as successful, with later cruises in 1979 and 1982 having a combined positive trawl rate of only 25% for the 36 trawls fished at least to 1800 m. Nonetheless the total positive capture rate of 55% for the 89 deep trawls clearly shows that cetomimids are not rare at those depths.

Some of the individual catches are even more surprising. One subantarctic trawl to 2600 m at 54°S captured eight specimens of *Gyrinomimus grahami*; the ovaries were not running ripe and some type of spawning aggregation is not indicated. Four to six specimens of *Cetostoma regani* were taken in four different ISH trawls. Between four and six different species of cetomimids were taken in the same ISH trawl on seven of the 19 deep trawls of the 1971 cruise (no other cruise took more than two species per trawl and then only once). The number of cetomimid specimens per trawl ranged from one to eleven specimens, with the 1971 deep trawls averaging 5.2 specimens per trawl. While the south Atlantic appears to be richer in whalefishes than the north Atlantic (with a phenomenal 91% positive deep trawls between 0°-40°S), it seems that cetomimids may be one of the commonest bathypelagic fish families below 1800 m in all areas.

Parin (1985) has estimated that some 200 species representing 27 families live in the bathypelagic and abyssopelagic zones. Of these the ceratioid anglerfish families Oneirodidae and Linophrynidae with about 50 and 25 species respectively, are the largest bathypelagic families (although other families, such as the Myctophidae, are larger, very few species are bathypelagic). With an estimated 35 species, the Cetomimidae appears to have the second largest number of bathypelagic species.

Not enough work with large closing nets has been done at these depths to determine relative abundances. However if one assumes the vast majority of whalefishes live at or below 1800 m (in the 1971 *Walther Herwig* cruise 99 cetomimids were taken in 19 trawls below 1700 m and seven specimens taken in 58 trawls from 50-1600 m), some approximation of abundance can be reached by calculating the amount of water filtered when the trawl is at depth. The calculation, 300 m^2 mouth opening x 6160 m (3.5 knots for one hour at depth, Krefft, 1974:228) divided by 5.2 (the average number of specimens per deep trawl) gives one whalefish every 355,000 m^3 of water between 1800 to 2300 m in the south Atlantic, where the richest tows have been made. While this figure indicates approximately 70 m between individuals, a total abundance of more than 2800 whalefishes per cubic kilometre of seawater, at least between 1800 and 2500 m in the south Atlantic, is a much higher number than previously appreciated.

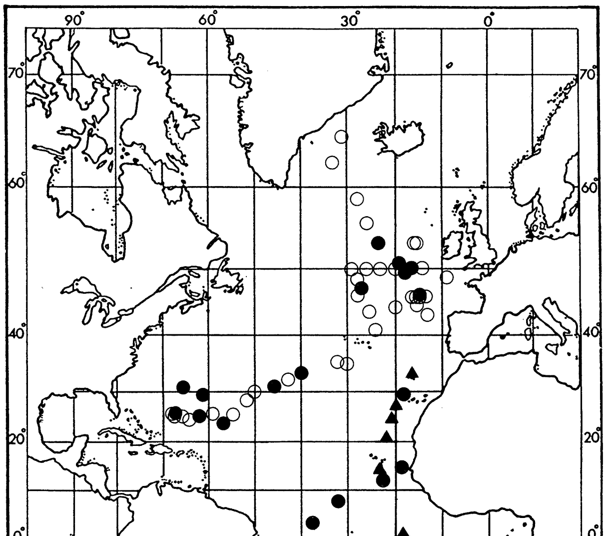

Fig.30. ISH commercial midwater trawls 1968--1986 fished to below 1750 m; solid symbols represent trawls positive for cetomimids; triangles represent one 1971 cruise.

The most abundant whalefishes are clearly *Cetostoma regani* and *Ditropichthys storeri*, with 141 and 77 specimens collected respectively. No other species of cetomimid is nearly that common; the next most commonly collected are two temperate/polar species of *Gyrinomimus* with 20 to 25 specimens each. The abundance of *C. regani* and *D. storeri* is not solely related to their occurrence in the mesopelagic zone, and therefore easier capture, for more than 100 and 70 specimens respectively have been taken by trawls fishing to 1000 m or deeper. In terms of population size and breadth of distribution, these two highly divergent and unrelated species of whalefishes are by far the most successful of the family.

With six of the eight species considered in this paper represented by less than ten specimens, and four by less than five specimens, it seems probable that additional species of whalefishes exist and have not been captured.

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APPENDIX

Table 3. *Ditropichthys storeri* material examined; * specimens included in counts and measurements Table 4; ** specimens cleared and stained.

	Inst.	Reg.No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
1.	ISH	1083/71(1)	131	39°19'S	03°15'W	SAtl	0-ca.2000	N	19/3/71
2.	ISH	1575/71	128.5*	27°14'S	02°56'E	SAtl	0-2000	N	1/4/71
3.	USNM	200526	124	12°09'S	58°35'E	Ind	0-1600	D	26/8/64
4.	MCZ	43331	123	15°57'S	64°46'E	Ind	0-2407	D	5/6/64
5.	ISH	743/71(1)	116.5*	40°18'S	35°07'W	SAtl	0-1850	N	9/3/71
6.	ISH	607/74	112	07°55'N	32°41'W	NAtl	0-ca.2000	N	21/7/74
7.	AMS	I27264-001	112**	36°49'S	12°17'W	SAtl	0-2000	N	17/3/71
8.	ISH	531/76	109	42°58'S	39°53'W	SAtl	0-2350	D	7/1/76
9.	ISH	1083/71(2)	107						
10.	SIO	53-340	104	41°12'N	168°17'E	NPac			10/9/53
11.	ZIN	47882	104			NPac	0-5000		23/5/53
12.	TH	831588	102.5	23°03'N	150°17'E	NPac	0-1577	D	2/6/83
13.	ISH	773/79	101.5	25°31'N	62°00'W	NAtl	0-1800	ND	6/4/79
14.	LACM	44682-1	94.5			NPac			12/11/79
15.	ISH	3446/71	94	39°55'S	26°02'W	SAtl	0-ca.2000	N	11/3/71
16.	OSUO	2513	91.8	39°46'N	128°00'W	NPac	0-2315	N	11/12/81
17.	ISH	2897/71(1)	88.5*	20°27'N	21°58'W	NAtl	0-2100	N	18/4/71
18.	LACM	30599-1	87.8*	33°22'N	118°02'W	NPac	0-1300	N	12/9/68
19.	SIO	64-39	86.0	28°32'N	118°17'W	NPac	0-1800	ND	11/2/64
20.	TH	790081	86	30°16'N	144°35'E	NPac	1329-1541cl	N	11/6/79
21.	AMS	I18816-001	84.4*	33°22'N	118°02'W	NPac	0-1800	D	11/10/68
22.	AMS	I21143-001	84	21°25'N	158°25'W	NPac			1/16/76
23.	AMS	I18821-001	83**	31°40'N	118°39'W	NPac	0-1400	N	4/2/69
24.	ISH	364/79	81.3*	23°46'N	58°59'W	NAtl	0-1200	D	28/3/79
25.	ISH	127/76(1)	81.0*	40°20'S	50°02'W	SAtl	0-2350	D	19/11/75
26.	ISH	127/76(2)	81						
27.	SIO	64-24	80.5	23°54'N	113°39'W	NPac			4/2/64
28.	ZIN	47878	80.3*	45°16'N	156°13'E	NPac	0-5000		23/1/53
29.	ISH	2950/71	79	23°47'N	20°59'W	NAtl	0-2100	N	19/4/71
30.	ZIN	47881	79.0*	19°50'N	68°14'W	NAtl	0-2000		3/2/73
31.	ISH	905/79(1)	75.2*	24°41'N	66°20'W	NAtl	0-1800	N	18/4/71
32.	ISH	2897/71(2)	75.0*						
33.	ISH	743/71(2)	74.6*						
34.	LACM	44681-1	71.5			NPac	0-1000		24/10/74
35.	ISH	743/71(3)	69.0*						
36.	ISH	1580/68	66.9	34°01'S	47°39'W	SAtl	0-2000		15/2/68
37.	LACM	9730-30	65**	30°50'N	118°39'W	NPac	0-ca.1300	D	5/1/66
38.	SIO	78-189	62.3	30°57'N	120°46'W	NPac	0-1800	N	13/8/75
39.	ISH	905/79(2)	60.0*						
40.	ISH	743/71(4)	59.0*						
41.	MCZ	50691	58	23°02'N	45°33'W	NAtl	0-1100	N	17/10/73
42.	ISH	127/76(3)	57						
43.	ZMUC	P2340007	56.9*	14°37'N	119°52'E	NPac	0-ca.800		17/6/29
44.	ZMUC	P2340008	55.5*	00°31'S	11°02'W	SAtl	0-ca.2000		4/3/30
45.	LACM	9661-8	55.2	27°18'N	115°19'W	NPac	0-ca.1200	D	16/6/67
46.	LACM	44391-1	55.1	27°48'N	88°45'W	NAtl	0-ca.2000		30/7/59
47.	ISH	995/71	54.3*	36°49'S	12°17'W	SAtl	0-2000	N	17/3/71
48.	LACM	8988-33	54.0	28°54'N	118°10'W	NPac	0-?1200	N	6/5/65
49.	AMS	I18826-001	53.3*	21°25'N	158°25'W	NPac	0-1200	D	9/12/73
50.	LACM	9350-28	51.6	29°30'N	118°25'W	NPac	0-ca.1200	ND	28/8/65
51.	SIO	63-540	50.8	32°27'S	08°49'E	SAtl	0-3400	DN	6/6/63
52.	SIO	60-232	50	04°59'S	135°19'W	SPac	0-2750		1/7/60
53.	TH	800405	49	30°34'N	147°31'E	NPac	0-3156	ND	3/6/80
54.	MCZ	43337	49	07°55'N	64°55'E	Ind	0-2850	D	23/5/64

	Inst.	Reg.No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
55.	IOS	5809	48.1*	28°06'N	14°05'W	NAtl	0-800	N	6/11/65
56.	ZMUC	P2340006	48.0*	30°08'S	176°50'W	SPac	0-ca.1650	D	14/12/28
57.	SIO	78-61	46.6	21°25'N	158°25'W	NPac	900-1100cl	D	24/5/71
58.	LACM	30179-9	46.5			NPac			28/5/68
59.	ISH	2296/71	44.7*	01°04'N	18°22'W	NAtl	0-2100	N	12/4/71
60.	CAS(SU)	63730	43	32°12'N	64°36'W	NAtl			13/9/30
61.	MCZ	50690	43	33°50'S	87°41'W	SPac	0-2900	ND	17/1/66
62.	SIO	70-327	41.5	18°20'N	133°29'E	NPac	0-1500	N	9/8/70
63.	MCZ	60394	41			NAtl			
64.	IOS	3661	40.2*	41°N	19°W	NAtl	0-1500		14/3/58
65.	ZIN	47879	40.1*	11°55'S	84°11'E	Ind			
66.	ZIN	47880	40	04°50'S	23°27'W	SAtl	0-1100		13/1/72
67.	SIO	63-425	38.2	27°46'N	129°15'W	NPac	0-1500	D	2/4/62
68.	SIO	70-332	37.4	18°14'N	127°16'E	NPac	0-1700	D	12/8/70
69.	MCZ	43338	36	19°24'S	65°30'E	Ind	0-2600	D	8/6/64
70.	SIO	70-336	35.1	18°50'N	124°10'E	NPac	0-1525	D	19/8/70
71.	SIO	70-112	35.1	24°39'S	155°00'W	SPac	0-1150	N	3/10/69
72.	AMS	I21144-001	34	21°25'N	158°25'W	NPac			2/5/78
73.	IOS	11261	34	31°32'N	25°26'W	NAtl	1200-1300cl	N	7/7/85
74.	UMML	14840	34	23°39'N	82°45'W	NAtl	0-777		20/1/64
75.	LACM	32747-1	33.4	21°25'N	158°25'W	NPac	0-1000	D	16/12/70
76.	LACM	32740-6	32.9	21°25'N	158°25'W	NPac	0-1150	D	21/9/70
77.	SIO	68-490	32.7	28°57'N	178°09'E	NPac			22/9/68
78.	LACM	32749-6	30.0	21°25'N	158°25'W	NPac	0-1000	D	1/3/71
79.	IOS	10380	29.5	29°54'N	34°15'W	NAtl	1400-1500cl	D	18/6/81
80.	UMML	9724	29	15°00'N	67°05'W	NAtl	0-877		17/11/60
81.	USNM	200527	28.7	01°50'N	65°06'E	Ind	0-1250	N	27/5/64
82.	ISH	1330/79	27.6*	31°11'N	63°27'W	NAtl	0-ca.1700	D	19/4/79
83.	MCZ	60738	26.8*	03°39'N	41°38'W	NAtl	0-ca.650	N	16/7/83
84.	BOC	2134	25	22°43'N	74°23'W	NAtl	0-ca.800		29/3/27

Table 4. Morphometrics of 26 specimens of *Ditropichthys storeri* as % SL: average (minimum-maximum) standard deviation.

SL	26.8-27.6	40.1-60.0	69.0-88.5	116.5-128.5	26.8-128.5	
n	2	11	11	2	26	
HL	29.7(29.1-30.2)0.78	31.7(29.7-33.9)1.35	32.6(30.9-34.9)1.50	31.3(31.0-31.6)0.42	31.8(29.1-34.9)1.44	(n=23)
SnL	9.5(9.4-9.7)0.21	11.6(9.7-14.4)1.25	11.3(9.9-12.8)0.85	11.7(11.2-12.2)0.71	11.3(9.4-14.4)1.11	
PmL	19.9(19.2-20.5)0.92	21.0(19.3-23.4)1.28	21.2(19.7-22.6)0.96	21.3(20.6-21.9)0.92	21.0(19.2-23.4)1.11	
LJL	20.6(19.8-21.4)1.13	22.0(20.7-232)0.99	21.9(20.8-23.3)0.82	20.6(20.3-20.9)0.42	21.7(19.8-23.3)0.99	(n=25)
Pm-Op	13.4 (n=1)	12.0(10.2-13.0)1.25	13.0(10.1-16.4)1.75	12.5(12.4-12.5)0.07	12.5(10.1-16.4)1.48	(n=25)
ED	1.9(1.8-1.9)0.07	1.7(1.4-2.2)0.27	1.3(1.1-1.5)0.13	1.1(1.0-1.1)0.07	1.5(1.0-2.2)0.34	
EW		10.9(8.7-12.6)1.43	11.5(10.2-12.1)0.71	13.4(12.8-14.0)0.85	11.4(8.7-14.0)1.35	(n=20)
HW	8.8(8.2-9.4)0.85	15.4(13.3-17.3)1.29	15.7(13.8-17.3)1.02	15.5(14.8-16.2)0.99	14.9(8.2-17.3)2.21	(n=23)
PmW		12.8(11.4-14.8)1.22	13.9(12.3-16.6)1.68	13.8(12.9-14.7)1.27	13.3(11.4-16.6)1.42	(n=20)
BD	20.5(17.2-23.9)4.74	22.8(20.7-24.4)1.19	25.0(20.2-27.9)2.09	26.9(25.4-28.4)2.12	23.9(17.2-28.4)2.47	
D-A	12.7(11.9-13.4)1.06	15.7(12.0-18.3)1.78	16.7(14.2-19.2)1.38	19.1 (n=1)	16.1(11.9-19.2)1.99	(n=25)
CPD	4.6(4.1-5.1)0.71	6.0(4.7-7.0)0.67	6.4(5.5-7.5)0.61	6.7(6.7-6.8)0.07	6.1(4.1-7.5)0.78	
CPL	13.4(12.3-14.5)1.56	15.7(13.5-18.3)1.27	15.1(13.6-16.2)0.76	15.5(15.2-15.9)0.49	15.3(12.3-18.3)1.17	
Sn-P	33.1(29.5-36.6)5.02	34.5(32.0-37.8)1.72	35.2(33.5-37.0)1.39	32.7(32.6-32.9)0.21	34.5(29.5-37.0)1.94	(n=25)
PL	10.1(8.6-11.6)2.12	11.3(9.2-15.0)1.92	10.8(9.7-12.6)0.90	9.1(8.2-10.0)1.27	10.5(8.2-15.0)1.15	(n=18)
Sn-D	64.9 (n=1)	64.7(63.2-66.6)1.15	66.1(64.6-68.7)1.26	65.0(64.0-66.0)1.41	65.2(63.2-68.7)1.27	(n=23)
DB	24.3(23.6-25.0)0.99	23.6(22.0-26.6)1.32	24.0(20.9-26.1)1.33	24.6(23.4-25.8)1.70	23.9(20.9-26.6)1.28	
Sn-A	62.7 (n=1)	67.1(62.4-70.7)2.28	68.0(66.5-69.2)0.98	68.3(67.3-69.3)1.41	67.4(62.4-70.7)2.01	(n=23)
AB	16.5(16.4-16.7)0.21	16.8(15.1-19.8)1.35	17.1(15.9-19.1)1.02	16.3(15.8-16.9)0.78	16.9(15.1-19.8)1.11	
An-AO	1.7(1.5-1.8)0.21	1.8(1.0-2.7)0.49	2.3(1.0-3.7)0.85	3.5(2.7-4.3)1.13	2.1(1.0-4.3)0.81	
D	20(20)0	20.2(19-22)0.98	20.4(19-22)0.86	20(19-21)1.41	20.3(19-22)0.88	
A	17 (n=1)	17.1(16-18)0.83	17.0(16-18)0.45	16.0(15-17)1.41	17.0(15-18)0.73	(n=25)
P		19.1(18-21)0.99	19.1(18-21)0.86	17.5(17.18)0.58	18.9(17-21)1.03	(n=24)
Vert	39 (n=1)	39.7(39-41)0.75	39.6(38-41)0.88	40(39-41)1.0	39.7(38-41)0.84	(n=25)
LLSc	12 (n=1)	11.9(11-13)0.57	11.2(10-13)0.92	13 (n=1)	11.8(10-13)0.80	(n=22)

Table 5. Morphometrics, as % SL, and meristics of specimens of *Cetichthys*. * indicates holotype; ** indicates damage or distortion; LJT = lower jaw teeth.

	Cetichthys indagator				*Cetichthys parini*							
Inst.	ISH	ZMUC	LACM	NSMT	SIO	OSU	SIO	OSU	ZIN	AMS	NSMT	ZIN
Reg. No.	1186/71	P23451*	11314-1	P44368	53-344*	2552	87-9	2553	47877	I.27258-001	P60001	47876
SL	128.8	117.7	92.5	51.5	196.2	174	157.2	121.6	104.2	96.0	88.6	87.5
HL	31.2	31.9	33.5	**	33.4	31.6	32.3	32.1	38.4	36.7	36.1	38.5
SnL	11.3	11.0	11.4	11.5	12.3	**	10.9	12.0	13.0	12.7	13.4	14.3
PmL	22.9	22.9	26.5	**	23.5	22.7	24.3	25.9	28.2	26.3	28.1	29.4
LJL	21.4	22.9	27.2	26.4**	22.8	20.7	25.2	24.8	29.1	25.6	28.2	29.6
Pm-Op	9.1	10.3	7.5	**	10.4	10.1	8.4	7.5	10.2	8.6	7.6	9.1
ED	1.3	1.3	1.1	1.9	0.7	**	0.8	0.9	1.2	1.3	1.0	1.1
EW	**	10.6	8.6	**	12.8	**	10.1	12.7	11.1	9.4	10.5	7.4
HW	14.9**	16.0	18.1	12.8**	19.0	18.7	13.4	17.8	19.8	16.1	17.0	16.8
PmW	10.6	9.4	14.3	**	16.3	16.6	9.5	14.1	15.5	10.8	12.6	12.2
BD	**	22.6	22.0	14.6	25.0	22.4	20.1	21.4	22.0	20.3	20.1	21.0
D-A	**	24.0	21.6	15.9	20.6	17.5	15.9	16.4	19.2	18.2	12.9	17.7
CPD	8.5	8.3	9.0	6.2	7.9	7.6	6.9	7.0	7.2	6.4	5.0	6.2
CPL	24.5	24.1	24.1	24.7	16.7	19.1	17.3	19.1	19.2	18.8	18.1	19.2
Sn-P	**	35.3	36.8	32.8	35.6	33.0	34.3	33.2	38.9	36.9	36.9	40.3
PL	**	8.8	10.6	7.0	6.5	5.5	6.2	5.2	7.9	**	9.0	8.6
Sn-D	63.3	70.3	65.1	61.0	69.6	67.5	68.6	66.0	74.0	68.2	68.5	69.7
DB	13.0	11.7	14.8	17.1	15.6	13.9	14.6	14.2	13.9	14.3	14.4	16.3
Sn-A	**	72.4	69.7	61.6	70.3	71.6	69.3	71.5	72.0	69.2	66.5	67.5
AB	9.3**	7.1	7.9	9.9	14.2	11.5	12.7	13.8	13.2	13.2	13.2	14.3
An-AO	**	8.9	8.1	6.2	8.8	7.9	8.3	8.6	8.5	7.0	5.0	7.0
CopL	4.1	4.8	5.6	11.7	3.5	4.4	4.6	6.2	7.4	7.3	8.9	8.8
CopL/W				3.6			6.6			5.9	8.8	
D	14	14	14	15	14	14	16	14	15	13	13	16
A	**	13	12	13	13	12	14	13	14	13	13	14
P	**	21/21	21/?	21/?	?/?	20?/19?	22/22	19/19	23/24	22?/21?	21/21?	23/?
C	12	13	12	**	**	12	11	11	12	12?	12	12?
Vert	25+17=42	25+17=42	25+18=43	25+18=43	24+15=39	26+15=41	25+16=41	25+16=41	24+16=40	25+16=41	24+17=41	24+16=40
LLSc	14?/?	13/13	14/13	13?/?	8/8	9/?	9/9	10?/?	?/?	9/?	?/?	9/?
GRArch1	3+9	3+9/10	3+9	3+10	3+8	3+7	3+9	3+7	3+7/8	3+9	3+8	3+8
GRArch4	1+6	2+7	1/2+7	1+7	2+6	1+5	2+6	1+4/5	1/2+5	1+5	2+5	2+5
LJT		108/112	112		171/178	150		170	113/120	119		95

Table 6. Morphometrics, as % SL, and meristics of specimens of *Notocetichthys*, *Danacetichthys* and *Rhamphocetichthys*. * indicates holotype; ** indicates damage or distortion; Vom T = vomerine teeth.

	Notocetichthys trunovi		*Danacetichthys galathenus*						*Rhamphocetichthys savagei*			
Inst.	ZIN	ZIN	NSMT	USNM	ISH	ZMUC	SIO	ZMUC	MCZ	AMS	LACM	ISH
Reg. No.	47697	47696*	P60002	200525	1944/71	P2340563*	70-327	P2340564	60342*	I.26872-001	30034-11	2297/71
SL	109.0	107.5	53.9	53.5	48.6**	39.3	38.1	34.0	125.7	98.5	90.8	110
HL	31.3	31.9	36.5	36.6	37.4	37.7	37.0	35.3	35.1	34.9	38.3	34.5
SnL	12.5	10.8	12.6	12.1	11.3	12.7	11.3	11.5	16.8	16.2	18.1	17.7
PmL	22.3	21.1	30.2	31.4	29.0	30.8	30.7	29.4	25.8**	28.2	31.3	30.5
LJL	20.6	21.2	29.9	32.1	27.6	31.0	29.9	28.8	24.2**	28.2	34.9	28.2
Pm-Op	8.3	9.8	7.8	9.2	**	10.9	7.8	7.4	8.7	5.5	5.2	3.6**
ED	1.4	1.0	2.2	2.4	2.1	2.0	2.4	2.1	1.4	1.6	1.7	1.4
EW	10.2	7.6	13.9	10.3	**	9.9	12.6	12.6	5.3	5.2	4.7	3.2
HW	12.9	11.4	21.2	16.4	**	14.5	22.0	21.2	8.0	13.2	11.5	7.5
PmW	10.7	13.8	16.7	**	**	6.4**	12.9	11.8	8.8**	7.5	8.0	7.7
BD	18.9	26.0	22.6	17.0	**	17.3	21.9	21.5	12.8	**	13.9	**
D-A	19.8	20.5	13.7	11.4	14.8	12.0	15.5	14.7	10.3	9.9	10.2	10.1**
CPD	8.3	8.4	7.6	8.4	7.6	5.9	8.9	7.6	4.7	3.3	3.4	3.4
CPL	18.2	20.2	10.4	12.5	15.4	9.9	11.5	17.4	11.6	14.7	15.4	13.9
Sn-P	34.8	35.3	36.4	36.6	**	38.7	37.8	35.3	37.0	**	40.2	**
PL	7.7	11.9	13.4	8.2**	**	**	**	9.7	9.7	12.2	8.0	8.7
Sn-D	68.5	69.7	73.3	68.0	**	73.5	73.2	67.6	73.6	71.6	72.4	73.6
DB	11.7	11.7	13.9	12.7	16.9	14.0	13.9	17.4	13.3	10.9	11.3	9.8
Sn-A	74.3	71.0	74.4	70.3	**	77.4	76.4	63.2	75.7	74.7	72.0	74.5
AB	9.9	10.6	12.8	11.6	17.1	12.2	13.1	17.1	12.5	10.3	10.5	9.1
An-AO	9.9	8.1	2.0	1.9	2.1	2.3	2.1	1.2	1.1	2.6	3.3	1.8
CopL	0.9	1.1	10.2	14.6	10.3	15.0	13.9	10.0	8.4	9.6	9.3	8.7
CopL/W	1.1	2.4	5.5	5.6	4.5	4.5	5.9	3.7	5.0	7.3	4.9	4.6
D	13	13	15	15	16?	14	13+?	15	17	15	15	15
A	11	13	14	14	15	15	12+?	14	17	15	15	15
P		19/17	22/21	?/?	22/?	21?/?	21?/?	21?/23	23?/24	21/?	22/23	22/22
C	10	12	14	14?	13	?	?	15?	16	16	17	16
Vert	26+15=41	24+15=39	28+15=43	28+16=44	26+20=46	29?+16=45?	29+15=44	26+19=45	27+16=43	27+17=44	27+17=44	29+16=45
LLSc	16/?	15	18/18	?/?	17?/?	17/17?	?/?	18?/16?	33	32	31/32	40
GRArch1	2+8	2+8	2+7	2+8	2+7	2+7	2+7	2+7	1+7/8	3+7	3+7	0/1+4/5
Vom T	0	0	15	42	46	22	19	25	?	?	?	?

Table 7. *Cetostoma regani* material examined; ! holotype; * specimens with dorsal counts included, Fig. 25; ** specimens included in measurements Table 8 and Fig. 25; *** specimens cleared and stained; + plus length of missing head, specimens not included in vertical distribution Fig. 24.

	Inst.	No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
1.	ISH	894/82	246.5**	49°52'N	16°52'W	NAtl	0-3200	D	19/6/82
2.	ISH	1695/71	211.0**	21°35'S	02°00'W	SAtl	0-2100	N	3/4/71
3.	LACM	9571-3	206.8**	31°21'N	120°46'W	NPac	0-ca.1400	N	16/1/66
4.	IOS	10376/38	204.0**	33°21'N	33°35'W	NAtl	1500-1600cl	D	29/5/81
5.	ISH	2896/71(1)	200.0**	20°27'N	21°58'W	NAtl	0-2100	N	18/4/71
6.	ISH	1442/71(1)	199.0**	33°00'S	07°50'E	SAtl	0-2000	N	30/3/71
7.	SIO	51-90	198.2*	25°48'N	114°46'W	NPac	0-2200	ND	21/3/51
8.	ISH	2949/71(1)	196.4**	23°47'N	20°59'W	NAtl	0-2100	N	19/4/71
9.	ISH	609/74	ca.195	07°54'N	32°43'W	NAtl	0-ca.2000	N	21/7/74
10.	IOS	8959(1)	194.1**	28°47'N	15°02'W	NAtl	1000-2000cl	N	31/7/76
11.	ISH	2098/71	188.4**	05°30'S	16°28'W	SAtl	0-1900	N	9/4/71
12.	ISH	626/68(1)	188.0**	12°07'N	23°08'W	NAtl	0-ca.2000	N	30/1/68
13.	ISH	1082/71	185.0**	39°19'S	03°15'W	SAtl	0-ca.2000	N	19/3/71
14.	ISH	1189/71(1)	185*	37°08'S	05°23'E	SAtl	0-2200	N	21/3/71
15.	ISH	2896/71(2)	ca.185						
16.	ISH	3033/71(1)	ca.185*	32°47'N	16°24'W	NAtl	0-1800	N	22/4/71
17.	ISH	1494/79	183.2**	28°41'N	60°54'W	NAtl	0-ca.1800	D	20/4/79
18.	ISH	740/71(1)	182.6*	40°18'S	35°07'W	SAtl	0-1850	N	9/3/71
19.	ZMUC	P2340005	181.0*	23°47'N	20°59'W	NAtl	0-2100	N	19/4/71
20.	ISH	740/71(2)	ca.180*						
21.	ISH	3033/71(2)	ca.180*						
22.	ISH	1189/71(2)	ca.180*						
23.	ISH	740/71(3)	177						
24.	ZIN	47886	175.6	30°51'S	94°47'E	SInd	0-1465		23/9/76
25.	ISH	858/71(1)	ca.175	39°55'S	26°02'W	SAtl	0-ca.2000	N	11/3/71
26.	ISH	2949/71(2)	170.1*						
27.	ISH	2449/79(1)	165.4	35°24'N	31°53'W	NAtl	0-350	N	29/4/79
28.	MCZ	41339	164.4*	28°47'N	87°57'W	NAtl	0-1900		16/7/60
29.	ISH	2449/79(2)	161.3*						
30.	ISH	2991/71	158.0	27°18'N	19°44'W	NAtl	0-2000	N	20/4/71
31.	ISH	589/82	157.5*	47°52'N	27°08'W	NAtl	0-1370	D	13/6/82
32.	HUMZ	78240	157*	40°35'N	142°31'E	NPac	0-1195		13/9/78
33.	ISH	2708/71	ca.152*	14°05'N	23°12'W	NAtl	0-1900	N	16/4/71
34.	ZMUC	P2340000	151*	25°11'N	20°57'W	NAtl	0-ca.2000	D	25/10/21
35.	OSUO	1516	150.0*	44°48'N	138°30'W	NPac	0-2700	ND	25/7/66
36.	ISH	689/76	149*	36°18'S	40°06'W	NAtl	0-2400	D	9/1/76
37.	ISH	858/71(2)	148.5*						
38.	IOS	4711(1)	148*	30° 00'N	23°00'W	NAtl	0-1600		3/9/61
39.	OSUO	1515	145.6*	44°38'N	137°38'W	NPac	0-2700	ND	26/7/66
40.	ISH	376/82	ca.144*	43°22'N	25°59'W	NAtl	0-1230	D	9/6/82
41.	ISH	2325/79	140.7*	34°20'N	35°24'W	NAtl	0-170	N	28/4/79
42.	ISH	2896/71(3)	138.3*						
43.	ISH	1442/71(2)	137.4*						
44.	SIO	64-535	136.6			EPac			
45.	ISH	2162/79(1)	134.3	32°59'N	39°41'W	NAtl	0-1950	D	27/4/79
46.	IOS	10380/5	134.0*	30°04'N	33°56'W	NAtl	1100-1200cl	D	17/6/81
47.	ISH	3033/71(3)	133.4*						
48.	ISH	626/68(2)	131.4*						
49.	OSUO	1995	131*	44°32'N	132°12'W	NPac	0-3724	D	1/6/70
50.	ISH	2949/71(3)	130.0*						
51.	BOC	2132	130*	24°11'N	75°37'W	NAtl	0-ca.1500		22/3/27
52.	SIO	78-56	129.7	21°25'N	158°25'W	NPac	0-1100	D	30/8/73
53.	LACM	36047-5	125.5*	05°03'S	129°41'E	SPac	0-960	N	1/5/75
54.	ISH	626/68(3)	124.9						
55.	IOS	8607(1)	124.6**	09°03'N	23°08'W	NAtl	700-800cl	D	22/8/74
56.	IOS	6662/34(1)	124.0*	10°49'N	19°57'W	NAtl	900-1040cl	D	20/2/68

	Inst.	No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
57.	ZIN	47883	ca.122	05°29'N	153°57'E	NPac	0-1000		26/2/75
58.	ZIN	47885	ca.121*	03°08'N	08°54'E	NAtl	0-1550		1/1/76
59.	IOS	7824/17	120.8	10°57'N	20°03'W	NAtl	700-800cl	D	8/3/72
60.	ISH	2633/71(1)	120.1	10°52'N	22°09'W	NAtl	0-608	N	15/4/72
61.	OSUO	1996	120.1*	44°25'N	132°13'W	NPac	0-3655	ND	1/6/70
62.	AMS	I18819-001	120***	10°51'N	19°55'W	NAtl	0-700	N	17/2/68
63.	ISH	2633/71(2)	117.0						
64.	MCZ	60396	117.0**	26°44'N	79°23'W	NAtl			7/8/78
65.	IOS	10523/3(1)	117*	05°32'S	00°31'E	SAtl	700-800cl	D	10/5/82
66.	OSUO	2328	116.5*	44°43'N	125°48'W	NPac	1250-1500cl	N	25/5/75
67.	SIO	70-95	116.0	31°37'N	120°19'W	NPac	0-ca.1100		22/3/70
68.	ISH	3102/71	112.0	27°14'S	02°56'W	SAtl	0-2000	N	1/4/71
69.	ISH	519/74	111.4**	14°11'N	18°28'W	NAtl	0-ca.2000	N	18/7/74
70.	USNM	200530	106.7**	03°55'N	60°08'E	NInd	0-2120	D	18/8/63
71.	ISH	626/68(4)	105.9*						
72.	MCZ	42844	104.9*	02°41'N	28°56'W	NAtl	0-ca.1100	N	28/2/63
73.	OSUO	29	104.9*	44°18'N	125°30'W	NPac	0-1250	ND	15/8/61
74.	ISH	954/68	ca.101*	04°43'S	26°39'W	SAtl	0-2000	D	4/2/68
75.	SIO	69-20	100.8**	06°33'N	114°16'E	NPac			24/4/68
76.	ZMUC	P2340004	98.4*	29°11'N	14°14'W	NAtl	0-ca.1666	D	27/3/30
77.	UMML	20001	97*	00°30'N	05°05'E	NAtl	0-850		23/5/65
78.	IOS	8607(2)	96.1**						
79.	UMML	18352	95	23°43'N	81°47'W	NAtl	0-650		21/1/64
80.	ISH	170/68	94.9*	32°34'N	16°53'W	NAtl	0-1000	N	20/1/68
81.	ISH	2295/71	93.5*	01°04'N	18°22'W	NAtl	0-2100	N	12/4/71
82.	MCZ	60395	93.5*	13°40'N	76°40'W	NAtl			8/10/66
83.	ISH	626/68(5)	87.8*						
84.	SIO	69-334	87.7*	14°57'S	106°06'W	SPac	0-1300	N	
85.	ZMUC	P2340565	87.3*	12°02'S	96°43'E	SInd	0-ca.1150	DN	11/10/29
86.	ISH	2633/71(3)	86.5*						
87.	SIO	68-442	86	19°49'N	168°45'W	NPac	0-1250	N	27/8/68
88.	ISH	2633/71(4)	84.9*						
89.	SIO	69/24	84.6	17°04'S	67°08'E	SInd	0-936	D	25/8/68
90.	ZIN	47884	83.5*	15°11'N	74°11'W	NAtl	0-1000		2/3/73
91.	USNM	200531	83.5*	25°52'S	60°00'E	SInd	0-1420	N	5/9/63
92.	UMML	34423	82.2*	26°00'N	86°00'W	NAtl	0-2000		9/5/88
93.	UMML	34423(2)	80.3*						
94.	LACM	44683-1	79.9						1/8/70
95.	ZIN	PLEBEDEV	79.0	08°29'N	52°24'W	NAtl	0-1200		29/2/64
96.	IOS	4711(2)	79*						
97.	LACM	9747-36	78.5**	32°25'N	117°57'W	NPac	0-ca.1400	N	15/4/66
98.	ZMUC	P2340001	77.5	14°37'N	119°52'E	NPac	0-ca.700	N	17/6/29
99.	SIO	68-442	77.4	22°10'N	171°57'E	NPac		D	17/9/68
100.	MOM	HIR.3215	ca.77!	30°45'N	25°47'W	NAtl	0-2000		8/8/12
101.	MCZ	41343	ca.77	28°50'N	88°08'W	NAtl	0-2450		13/7/60
102.	ISH	2633/71(5)	ca.76*						
103.	LACM	32744-1	75.7	21°25'N	158°25'W	NPac	0-110		7/7/70
104.	SIO	78-57	73.2	21°25'N	158°25'W	NPac	0-1100		26/5/74
105.	IOS	10523/12	71.0*	04°53'S	00°25'E	SAtl	895-1000cl	D	12/5/82
106.	LACM	34279-1	69.2	32°25'N	117°53'W	NPac	0-1400	N	21/1/70
107.	IOS	8959(2)	68.7**						
108.	OSUO	28	68.4*	34°36'N	140°32'W	NPac	0-2450		5/3/65
109.	MCZ	43333	68	04°01'S	65°00'E	SInd	0-615	N	30/5/64
110.	USNM	200528	65.5*	10°01'S	64°19'E	SInd	0-2250	N	2/6/64
111.	SIO	78-69	62.6	21°25'N	158°25'W	NPac	0-1500	N	29/9/72
112.	IOS	10150/1(1)	62.5*	26°01'N	20°21'W	NAtl	0-1035	D	8/10/79
113.	ZMUC	P2340002	62.1*	15°22'N	115°20'E	NPac	0-2333	N	20/5/29
114.	ISH	2162/79(2)	62.0*						
115.	ZMUC	P2340003	61.2*	03°41'N	137°53'E	NPac	0-ca.1000	D	12/7/29

	Inst.	No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
116.	IOS	10150/1(2)	60.2*						
117.	SIO	78-63	59.9	21°25'N	158°25'W	NPac	0-ca.700	N	23/5/72
118.	IOS	10150/1(3)	59.2*						
119.	IOS	6662/16	58.8*	11°01'N	19°50'W	NAtl	810-890cl	N	16/2/68
120.	IOS	10150/1(4)	58.3*						
121.	LACM	32749-1	57.8	21°25'N	158°25'W	NPac	0-1000	D	1/3/71
122.	IOS	7803/2	57.1*	18°09'N	25°12'W	NAtl	1015-1250cl	D	19/2/72
123.	MCZ	42843	55.7	00°17'N	27°31'W	NAtl	0-ca.300	N	19/2/63
124.	USNM	200529	55*	01°50'N	65°06'E	NInd	0-1250	N	27/5/64
125.	LACM	32748-1	53.3	21°25'N	158°25'W	NPac	0-900	D	16/12/70
126.	IOS	6662/7	51.7*	11°09'N	19°46'W	NAtl	710-800cl	N	14/2/68
127.	ISH	1862/79	50.8*	30°43'N	46°14'W	NAtl	0-2000	D	25/4/79
128.	BOC	4899	50.5*	37°43'N	12°07'W	NAtl		N	7/9/59
129.	AMS	I18825-001	50.2	21°25'N	158°25'W	NPac	0-ca.1500	D	7/4/70
130.	IOS	10382/6	49.9**	32°37'N	31°44'W	NAtl	900-1000cl	N	21/6/81
131.	ISH	2633/71(6)	49.2*						
132.	IOS	7824/13	48.9**	10°45'N	20°05'W	NAtl	1000-1250cl	N	7/3/72
133.	IOS	10523/13	48.7*	04°55'S	00°22'E	SAtl	995-1100cl	D	12/5/82
134.	SIO	70-347	47.8	14°20'N	119°47'E	NPac	0-1750	DN	19/9/70
135.	IOS	6662/34(2)	47.7**						
136.	IOS	10523/3(2)	47						
137.	UMML	19988	ca.46	02°47'N	08°45'E	NAtl	0-740		16/5/65
138.	BOC	4900	45*	37°33'N	12°57'W	NAtl		D	19/9/59
139.	UMML	20009	ca.45	03°15'N	04°47'E	NAtl	0-1230		25/5/65
140.	IOS	10233/27	44.1*	32°03'N	31°33'W	NAtl	900-1010cl	D	16/9/80
141.	IOS	10523/1	43.4*	05°25'S	00°31'E	SAtl	500-600cl	D	10/5/82
142.	AMS	I18818-001	43.0*	21°25'N	158°25'W	NPac			
143.	CAS	SU65867(1)	ca.42	32°12'N	64°36'W	NAtl			5/7/30
144.	CAS	SU65867(2)	ca.41						
145.	SIO	68-447	40.7	19°11'N	168°44'W	NPac		DN	29/8/68
146.	IOS	11261/15	39.6*	31°14'N	25°19'W	NAtl	900-1000cl	D	28/6/85
147.	ISH	3033/71(4)	133+						
148.	ISH	268/68	125+	29°23'N	18°10'W	NAtl	0-ca.2000	N	22/1/68
149.	ISH	798/73	109+	48°30'N	18°00'W	NAtl	0-2750	D	26/9/73
150.	ISH	1116/79	93+	25°08'N	67°39'W	NAtl	0-1800	D	12/4/79

Table 8. Morphometrics of 22 specimens of *Cetostoma regani*, as % SL: average (minimum-maximum) standard deviation.

SL(mm)	47.7-78.5	96.1-124.6	183.2-246.5	47.7-246.5	
n	5	6	11	22	
HL	29.7(27.4-31.4)1.65	25.4(23.6-26.5)1.07	24.0(22.3-26.0)1.09	25.9(22.3-31.4)2.67	(n=19)
SnL	11.3(8.7-12.5)1.33	9.0(7.9-10.0)0.69	8.4(7.9-9.1)0.39	9.5(7.9-12.5)1.47	(n=17)
PmL	21.2(18.0-23.5)2.01	16.8(15.4-18.6)1.17	17.0(15.4-18.2)0.88	17.9(15.4-23.5)2.24	(n=21)
LJL	22.0(19.2-24.7)1.76	17.8(16.8-19.4)0.97	17.5(15.9-19.3)1.03	18.6(15.9-24.7)2.23	
Pm-Op	8.2(7.6-8.8)0.40	8.1(7.4-8.8)0.41	8.4(7.4-9.9)0.84	8.2(7.4-9.9)0.63	(n=18)
ED	1.7(1.4-2.1)0.25	1.2(0.8-1.3)0.20	0.7(0.6-0.9)0.12	1.2(0.6-2.1)0.46	(n=16)
EW	5.6(4.4-7.4)0.99	4.7(4.3-5.6)0.54	5.8(5.3-6.3)0.39	5.5(4.3-7.4)0.83	(n=15)
HW	8.8(8.2-9.6)0.59	7.2(6.6-8.3)0.59	7.8(7.4-9.3)0.54	7.9(6.6-9.6)0.81	(n=21)
PmW	5.7(4.1-7.9)1.42	4.7(4.0-5.2)0.52	5.7(4.4-6.9)0.75	5.4(4.0-7.9)1.01	(n=20)
DB	10.9(9.6-12.4)1.13	11.6(10.4-12.7)0.78	12.8(10.9-15.0)1.11	12.0(9.6-15.0)1.32	(n=19)
D-A	11.2(10.4-12.5)0.92	14.7(11.4-17.1)1.75	18.1(16.8-19.9)1.04	15.5(10.4-19.9)3.03	(n=21)
CPD	3.3(2.8-4.0)0.39	4.2(3.2-4.8)0.57	4.2(3.1-5.1)0.67	4.0(2.8-5.1)0.69	
CPL	11.9(10.0-13.9)1.35	12.6(11.1-14.8)1.17	14.3(13.1-15.5)0.79	13.3(10.0-15.5)1.50	
Sn-P	31.5(28.4-33.1)1.67	26.7(24.4-27.5)1.00	25.9(22.8-28.3)1.53	27.3(22.8-33.1)2.77	(n=21)
PL	7.8(6.3-8.8)0.92	7.2(5.3-9.8)1.19	6.9(5.8-7.4)0.59	7.3(5.3-9.8)1.19	(n=15)
Sn-D	58.1(55.3-60.1)1.79	53.8(51.1-55.7)1.39	53.0(50.5-56.4)1.82	54.4(50.5-60.1)2.67	
DB	30.2(28.1-32.5)1.55	36.3(33.3-38.1)1.58	35.5(32.9-37.2)1.24	34.5(28.1-38.1)2.74	
Sn-A	63.3(59.0-65.9)2.28	58.3(56.4-60.7)1.35	58.5(51.8-61.6)2.48	59.5(51.8-65.9)2.99	
AB	25.1(22.4-27.6)2.06	31.3(30.0-32.8)1.12	29.4(26.9-35.2)2.20	29.1(22.4-35.2)2.86	(n=21)
An-AO	1.6(1.3-2.2)0.31	1.6(1.1-2.1)0.30	1.5(1.0-1.8)0.27	1.6(1.0-2.2)0.30	(n=20)
CopL	15.5(n=1)	11.9(n=1)	13.1(11.8-14.1)1.28	13.2(11.8-14.3)1.43	(n=8)
CopL/W		44.0(n=1)	25.6(23.0-29.0)2.80	28.7(23.0-44.0)7.32	(n=7)
D	32.2(30-33)1.17	34.0(32-35)1.41	32.5(31-34)0.81	32.9(30-35)1.32	(n=21)
A	29.5(29-31)0.87	30.5(29-32)0.96	28.4(26-30)1.11	29.3(26-32)1.37	(n=20)

Table 9. Ranges of morphometrics, as % SL, and meristics of the genera of the Cetomimidae.

	Procetichthys	*Ditropichthys*	*Cetichthys*	*Notocetichthys*	*Danacetichthys*	*Cetostoma*	*Gyrinomimus*	*Cetomimus*	*Rhamphocetichthys*
n(SL)	1(236.5)	26(26.8-128.5)	12(51.5-196.2)	2(107.5-109.0)	6(34.0-53.9)	22(47.7-246.5)	60(51.0-358.5)	15(44.5-209.6)	4(90.8-125.7)
HL	30.2	29.1-34.9	31.2-38.5	31.3-31.9	35.3-37.7	22.3-31.4	25.8-36.6	29.2-43.1	34.9-38.1
SnL	11.2	9.4-14.4	10.9-14.3	10.8-12.5	11.3-12.7	7.9-12.5	7.1-13.9	10.8-15.5	16.2-19.5
PmL	25.0	19.2-23.4	22.7-29.4	21.1-22.3	29.0-31.4	15.4-23.5	20.9-31.2	22.6-36.4	25.8-32.0
LJL	25.4	19.8-23.3	20.7-29.6	20.6-21.2	27.6-32.1	15.9-24.7	20.6-30.7	23.4-38.8	28.2-34.9
Pm-Op	5.7	10.1-16.4	7.5-10.4	8.3-9.8	5.3-7.6	7.4-9.9	3.5-7.1	4.1-11.3	5.2-8.7
ED	1.1	1.0-2.2	0.7-1.9	1.0-1.4	2.0-2.4	0.6-2.1	0.5-1.9	0.8-2.3	1.4-1.7
EW	12.3	8.7-14.0	7.4-12.8	7.6-10.2	9.9-13.9	4.3-7.4	10.2-15.5	10.8-21.6	3.2-5.3
HW	9.5	8.2-17.3	13.4-19.8	11.4-12.9	14.5-22.0	6.6-9.6	8.1-15.1	9.7-22.6	7.5-13.2
PmW	13.1	11.4-16.6	9.4-16.6	10.7-13.8	11.8-16.7	4.0-7.9	7.4-18.2	5.6-24.7	7.5-8.8
BD	13.5	17.2-28.4	14.6-25.0	18.9-26.0	17.0-22.6	9.6-15.0	13.0-29.7	13.0-35.5	12.8-13.9
D-A	15.3	11.9-19.2	12.9-24.0	19.8-20.5	11.4-15.5	10.4-19.9	8.4-21.1	11.9-24.6	9.8-10.3
CPD	7.6	4.1-7.5	5.0-9.0	8.3-8.4	5.9-8.9	2.8-5.1	4.8-6.7	4.0-8.9	3.3-4.7
CPL	20.7	12.3-18.3	16.7-24.7	18.2-20.2	9.9-17.4	10.0-15.5	7.7-18.4	8.2-14.4	11.6-15.4
Sn-P	31.7	29.5-37.0	32.8-40.3	34.8-35.3	35.3-38.7	22.8-33.1	26.2-36.4	31.4-43.7	37.0-40.2
PL	11.0	8.2-15.0	5.2-10.6	7.7-11.9	8.2-13.4	5.3-9.8	3.4-9.4	5.2-15.8	8.0-12.2
Sn-D	66.4	63.2-68.7	61.0-74.0	68.5-69.7	67.6-73.5	50.5-60.1	65.7-78.0	67.0-79.3	71.6-75.7
DB	15.6	20.9-26.6	11.7-17.1	11.7	12.7-17.4	28.1-38.1	11.3-21.8	13.4-20.7	9.8-13.3
Sn-A	70.1	62.4-70.7	61.6-72.4	71.0-74.3	63.2-77.4	51.8-65.9	62.2-79.0	69.7-79.7	72.0-76.6
AB	12.7	15.1-19.8	7.1-14.3	9.9-10.6	11.6-17.1	22.4-35.2	11.0-20.9	10.5-20.5	9.1-12.5
An-AO	7.2	1.0-4.3	5.0-8.9	8.1-9.9	1.2-2.3	1.0-2.2	0.6-3.1	0.7-2.5	1.1-3.3
CopL	9.4	3.5-7.3	3.5-11.7	0.9-1.1	10.0-15.0	11.8-14.3	2.5-11.8	4.9-9.9	8.4-9.6
CopL/W	13.9	2.2-6.2	3.6-8.8	1.1-2.4	3.7-5.9	23-44	1.8-7.6	3.3-5.8	4.6-7.3
D	14	19-22	13-16	13	14-16	29-37	14-21	15-20	15-17
A	13	15-18	12-14	11-13	14-15	26-34	14-20	13-20	15-17
P	15	17-21	19-24	17-19	21-23	20-21	18-23	17-23	21-24
C	19	13-16	11-13	10-12	13-15?	(15)16-17	13-16	14-16	16-17
Vert	48	38-42	39-43	39-41	43-46	47-53	47-59	44-54	43-45
LLOr	86	10-13	8-14	15-16	16?-18	15-17	12-23	10-24	31-40
GRArch1	4+11-12	3-4+9-11	3+7-10	2+7-8	2+7-8	3-5+8-10	1-4+2-10	1+3-5	1-3+4-8

Table 10. Character state distribution in the Cetomimidae and outgroup genera *Barbourisia* and *Rondeletia*. Derived character states for computer analyses are marked *.

	Barbourisia	*Rondeletia*	*Procetichthys*	*Ditropichthys*	*Cetichthys*	*Notocetichthys*	*Danacetichthys*	*Cetostoma*	*Gyrinomimus*	*Cetomimus*	*Rhamphocetichthys*
1. Pelvic Fins	+	+	—*	—*	—*	—*	—*	—*	—*	—*	—*
2. Pleural Ribs	+	+	—*	—*	—*	—*	—*	—*	—*	—*	—*
3. D+A Rays	15-22	13-16	13-14	15-22	12-16	11-13	14-16	26-37*	14-21	13-20	15-17
4. P Rays	13-14	9-11	15	17-21*	19-24*	17-19*	21-23*	20-21*	18-23*	17-23*	21-24*
5. Principal C Rays	19	19	19	13-16*	11-13*	10-12*	13-15?*	15-17*	13-16*	14-16*	16*
6. Total Vertebrae	40-43	24-27	48*	38-42	39-43	39-41	43-46*	47-53*	47-59*	44-54*	43-45*
7. Preanal Vertebrae	16-19	9-12	20	20-24	24-26*	24-26*	26-29*	23-27*	26-40*	24-34*	27-29*
8. Lateral Line Organs	26-32	14-26	86*	10-13	8-14	15-16	16?-18	15-17	12-23	10-24	31-40*
- Lateral Line Form	CA	PA	PA	CA	CA	CA	CA	CA	CA	CA	PA
9. Snout Length % SL	11.5-12.7	16.2-21.8	11.2	9.4-14.4	10.9-14.3	10.8-12.5	11.3-12.7	7.9-12.5	7.1-13.9	10.8-15.5	16.2-19.5*
10. Eye Width % SL	11.8-14.8	18.4-19.9	12.3	8.7-14.0	7.4-12.8	7.6-10.2	9.9-13.9	4.3-7.3*	10.2-15.5	10.8-21.6	3.2-5.3*
- Snout to D Origin % SL	60.2-67.3	71.9-77.4	66.4	63.2-68.7	61.0-74.0	68.5-69.7	67.6-73.5	50.5-60.1*	65.7-78.0	67.0-79.3	71.6-75.7
- D Base % SL	23.6-31.4	17.0-22.9	15.6	20.9-26.6	11.7-17.1	11.7	12.7-17.4	28.1-38.1*	11.3-21.8	13.4-20.7	9.8-13.3
- A Base % SL	16.5-21.6	16.8-19.7	12.7	15.1-19.8	7.1-14.3	9.9-10.6	11.6-17.1	22.4-35.2*	11.0-20.9	10.5-20.5	9.1-12.5
- Anus - A Origin % SL	1.6-3.3	3.4-7.2	7.2	1.0-4.3	5.0-8.9	8.1-9.9	1.2-2.3	1.0-2.2	0.6-3.1	0.7-2.5	1.1-3.3
11. Cop. Tooth Plate Len. % SL	—	—	9.4	3.5-7.3	4.1-12.0	0.9-1.1*	10.0-15.0	11.8-14.3	2.5-11.8	4.9-9.9	8.4-9.6
- Cop. Tooth Plate Len./Wid.	—	—	13.9	2.2-6.2	3.6-8.8	1.1-2.4	3.7-5.9	23-44	1.8-7.6	3.3-5.8	4.1-7.3
12. Nasal Organ Devel.	++	+	++	—*	—*	—*	—*	—*	—*	—*	—*
13. Eye Lens Devel.	+	+	+	—*	—*	—*	+,—*	—*	—*	—*	—*
14. Head Canals	+	+	+	+	+	+	+	+	+	+	—*
15. Supraorbital Canal	1	1	1	1	1	1	2?*	2*	2*	2*	0
16. Dorsal Canal Pores	8	8	10*	9	8	10*	10?*	9	10-12*	11-12*	0
17. Infraorb. Canal	J	J	S*	J/S*	J	S*	S*	S*	S*	S*	0
18. Last Infraorb. Displaced	—	—	—	—	+*	++*	++*	—	++*	++*	0
19. Nasal-Infraorb.	—	—	+*	—	—	—	—	—	—	—	—
20. Jaw Teeth	CL	CL	W*	CL	CL	CL	CL	CL	CL	CL	CL
21. Jaw Tooth Rows	D	D	—	D	D	D	L*	D	L*	D	D
22. Vomer	Flat	Flat	Flat	Flat	Flat	—	Flat	Flat	Flat	Dome*	Flat
23. Palatine Teeth	—	—	+*	+*	—	—	+*	+*	+*	+*	+*
- Ectopt. Tooth Plate	Long	—	Long	Long	Short	—	Long	Long	Long	Long	Long
- Cop. Tooth Plates	—	—	1	1	1	1	1	3	1	1	1
24. 4th Gill Slit	+	+	+	+	+	+	+	Red*	—**	—**	—**
25. Pseudobranch	+	+	+	—*	—*	—*	—*	—*	—*	—*	—*
26. Holobr. Arches 1-3	L	L	L	L	S*	L	L	L	L	L	L
27. Holobr. Arch 4	L	L	L	L	S*	L	L	S*	L,S*	S*	L
28. Gill Raker Form	EL	EL	TE*	CL*	KN**	KN**	DP***	PL****	PL****	PL****	PL****
29. Gill "Rakers" Arches 2-3	+	+	+	+	+	+	+	+	+	+	—*
30. Medial Gill "Rakers"	+	+	—*	+	+	+	+	+	+,—*	+,—*	—*
31. Ven. Pharyn. Tooth Pl.	+	+	+	+,—*	—*	—*	+	—*	—*	—*	+
32. Lateral Line Scales	C,E	—	FL	FL	FL	FL	FL	FL	C,E*	C,E*	FL
33. Cavernous Tissue	—	—	—	AN+*	AN*	AN*	AN*	AN*	AN,AN+*	AN,AN+*	—
34. Subpectoral Organ	—	—	—	—	—	—	+*	+*	+,—*	+,—*	+*
35. Paired Abdom. Ridges	—	—	—	+*	—	—	—	—	—	—	—
36. Anal Lappets	—	—	—	+*	+,—*	—	—	+*	+,—*	—	+*
37. Anal Fin "Curtain"	—	—	—	—	—	—	—	+*	—	—	—
38. Stomach Pigment	+	+	—*	+	+	+	+	—*	+	+	Red
39. Peritoneal Pigment	+	Red	—*	+	+	+	+	Red	+	+	+