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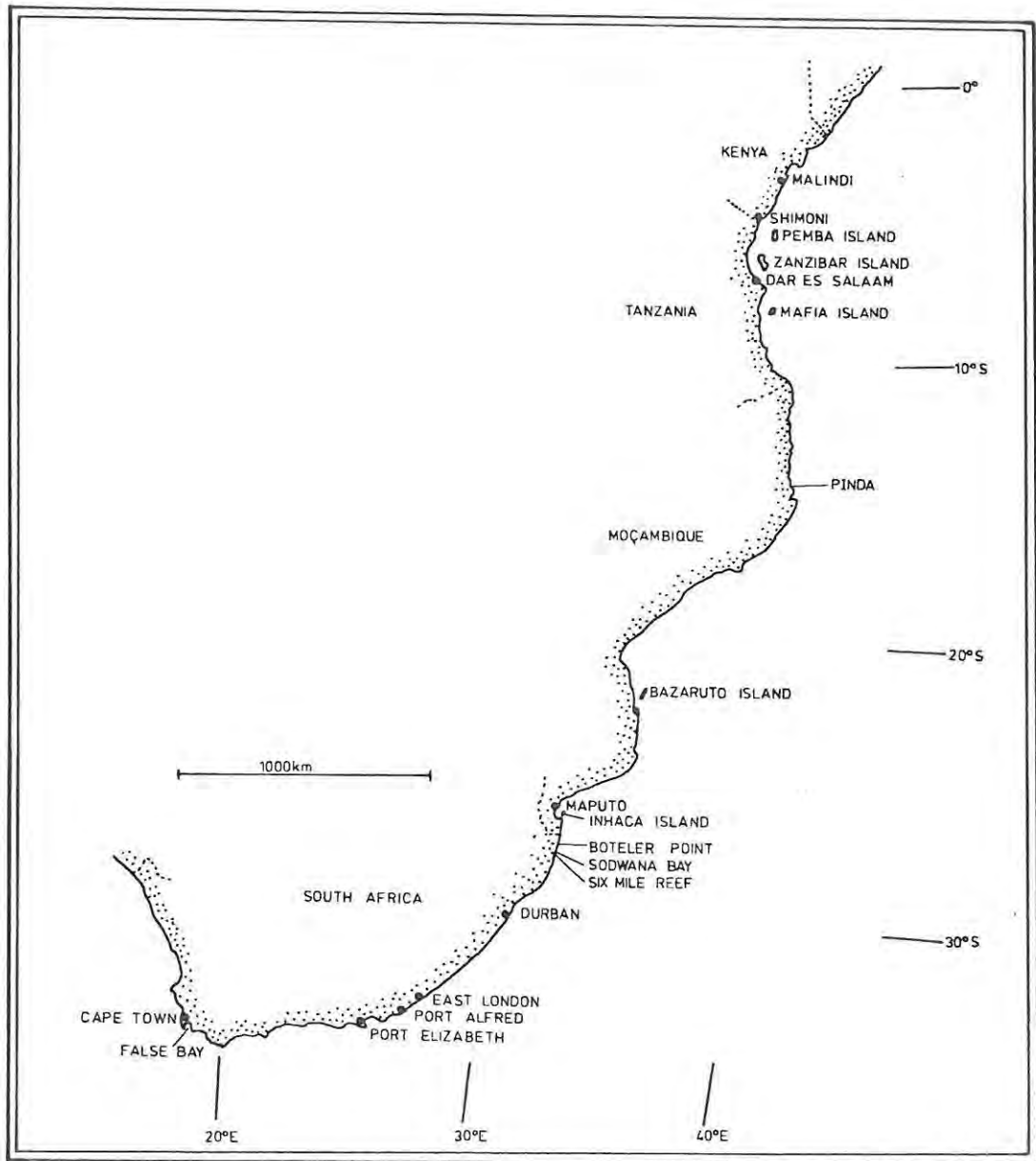
THE TAXONOMY AND OSTEOLOGY OF
FISHES OF THE FAMILY TRIPTERYGIIDAE
(PERCIFORMES: BLENNIOIDEI) OF
SOUTH AFRICA.

Dissertation Submitted in Partial
Fulfilment of the Requirements for the
Degree of
MASTER OF SCIENCE
of Rhodes University

by

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January, 1979.



MAP OF EAST AND SOUTH COASTS OF AFRICA SHOWING COLLECTION AREAS

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ABBREVIATIONS

ANSP = Academy of Natural Sciences of Philadelphia; BMNH = British Museum (Natural History); BPBM = Bernice P. Bishop Museum; QVM = Queen Victoria Museum, Launceston, Tasmania; RUSI = J.L.B. Smith Institute of Ichthyology, Rhodes University; SAM = South African Museum; USNM = former United States National Museum, specimens in National Museum of Natural History, Smithsonian Institution; S.L. = standard length.

Other abbreviations are explained in the text.

ACKNOWLEDGEMENTS.

Most postgraduate studies are the result of the guidance, help and advice of many people, and this one is no exception. I must firstly thank Dr.R. Winterbottom and Mrs.M.M. Smith for initiating this project. Secondly, I wish to acknowledge the financial support of the University Research Division of the C.S.I.R., the Research Committee of Rhodes University, and Mrs.M.M. Smith. Without Mrs. Smith's generous financial assistance this study would not have been possible.

To Dr.V.G. Springer of the Smithsonian Institution I am grateful for the guidance, advice and information he has provided over the past two years. I also acknowledge a particularly great debt to Mr. Paul Skelton for guiding me through the intricacies of fish osteology. He has always been willing to discuss problems, provide relevant literature, and criticise my writing. His criticism and enthusiasm have been of tremendous value to this study.

Early in the study Dr. Eugenie Clark, University of Maryland, made a manuscript copy of her revision of the Red Sea Tripterygiidae available to me. This manuscript provided me with invaluable guidelines.

Mr.W.G. Saul (Academy of Natural Sciences of Philadelphia) and Dr.W.C. Frehofer (California Academy of Sciences) very kindly checked much of Fowler's tripterygiid type material for me.

I am further indebted to a number of people and Institutions which provided specimens on loan or as gifts: Dr.D.F. Hoese (Australia) Dr.W. Klausewitz (Germany), Dr.J. Moreland and Dr.J. Ruck (New Zealand), Dr.A.A. Ramos (Spain), Dr.J.E. Randall (Hawaii), Dr.V.G. Springer, the Academy of Natural Sciences of Philadelphia, the British Museum (Natural History), the Hebrew University of Jerusalem, and the South African Museum.

The colour plates were made from colour slides taken by Dr.J.E. Randall, who kindly permitted me to make use of them.

Miss.E.M. Tarr executed the excellent illustrations for the systematic accounts and Mr.R.E. Stobbs was responsible for the colour plates and innumerable radiographs. The electron microscope unit of Rhodes University provided the electron micrographs.

I also want to record my thanks to Dr.B.R. Davies and Dr.P. Heemstra for their contributions in discussion, and in criticising the manuscript. Particular thanks are due to Dr.M.N. Bruton for steering this project through its final stages.

Last, but not least, I am indebted to the J.L.B. Smith Institute of Ichthyology for the use of facilities, and the Albany Museum for the time to write up this study.

RESUME.

This study is divided into two parts. The first deals with the taxonomy of the South African fishes of the Tripterygiidae. The second part describes the osteology of one genus of the family, and draws comparisons with the other genera discussed in this study.

Five genera of Tripterygiidae are recognized from South African waters. Cremnochorites, a monotypic genus, is described as new. The single species, C. capensis, has been recorded only from the southern and south-eastern coast of South Africa. It is distinguished from other genera by a combination of features which includes scalation, dorsal and anal fin spine counts, and various osteological characters. Three genera, Norfolkia Fowler, Helcogramma McCulloch & Waite, and Enneapterygius Rüppell occur throughout most of the Indo-Pacific. A single species of Norfolkia, N. springeri Clark (in press) is found in Zululand. Two species are ascribed to Helcogramma, H. obtusirostre (Klunzinger) and H. fuscopinna sp.n. Parallels are drawn between two species of Tripterygion Risso, T. tripteronotus and T. delaisi from the Mediterranean. The two South African Helcogramma species show similar depth preferences to the two Tripterygion species, resulting in similar morphological differences between the two species of each pair. The genus Enneapterygius Rüppell is divided into two genera, Enneapterygius and Scoliosolen gen.n. The division is based on the form of the supraoccipital sensory canal and associated osteological characters. Scoliosolen has a crescent-shaped supraoccipital canal and cranial osteology

similar to the majority of other tripterygiid genera, whereas Enneapterygius has a 'U'-shaped supraoccipital canal which curves around the first dorsal fin, a comparatively long, concave supraoccipital bone which extends anteriorly between the parietal and between the posterior ends of the frontals. Two species are referred to Scoliosolen, S. abeli (Klausewitz) and S. conspicuus (Clark), and two new species are described for Enneapterygius, E. pulcherrimus and E. triangulus.

A literature survey revealed little consistency in ascribing species to any particular genus. Thus, throughout this study an attempt is made to define the genera so that future confusion can be avoided. In the light of these definitions an assessment is made of the original descriptions of a large number of species to determine which of the species can be ascribed to Norfolkia and to Helcogramma. This has been possible to a lesser degree for Enneapterygius and Scoliosolen, for the major external feature separating these two genera, the shape of the supraoccipital sensory canal, is described only for Red Sea (Clark, in press) and South African species (this study). This study places four species in Enneapterygius, and six in Scoliosolen.

To provide a firmer foundation for defining the genera, an investigation was made of the osteology of Scoliosolen conspicuus. Enneapterygius was originally chosen for the osteological study as it is reputedly the largest genus of the family, and thus likely to be the most generalized. Once comparisons had been made with other Enneapterygius species, it became apparent that this genus had to be divided into two genera, Enneapterygius and Scoliosolen.

It is not known whether Scoliosolen is the largest genus, but it is likely to be one of the largest once a complete survey of the species originally ascribed to Enneapterygius has been undertaken.

Finally, an osteological comparison is made of the five genera which occur in South African waters to provide firmer bases for the generic definitions. Only those characters which appear to be constant within a genus are used. Reference is made to a number of genera which do not occur in South African waters, to ensure that the characters chosen cannot be applied to other genera.

INTRODUCTION.

Blenoid fishes with three dorsal fins, the tripterygiids, or "three-fin blennies" of Böhlke and Chaplin (1968) are generally small, cryptically coloured, benthic dwellers which prefer vertical rock faces, nooks, crannies and the undersides of ledges as habitats (Zander & Heymer, 1970, 1976; pers. obs.) They are all marine. Of the more than 100 species in some 16 genera (Böhlke & Chaplin, 1968) the great majority are known from the Indo-Pacific, where they are widely distributed between the northern and southern temperate regions. While most species occupy the intertidal and immediate subtidal zones, they are common at 18m depth on the Zululand coast (pers. obs., 1977) and occur to at least 25m in the Mediterranean (Zander & Heymer, 1970). Moreland (pers. comm., 1977) states that "some live on the continental shelf and one is known only from 120 - 600m on soft grey mud" off New Zealand.

Tripterygiids were first placed in the family Blenniidae by Günther (1861). Although some taxonomists retained this grouping (Weber, 1909; McCulloch & Waite, 1918), others recognized the close relationship of the tripterygiids and clinids, and placed these two groups into the family Clinidae (Regan, 1912; Herre, 1939; de Beaufort & Chapman, 1951; Klausewitz, 1960; Schultz, 1960). More recent classifications (Scott, 1957; Rosenblatt, 1960; Greenwood et al., 1966; Böhlke & Chaplin, 1968; Clark, in press.) recognize the Tripterygiidae as separate from the Clinidae. A recent study of Böhlke & Robins (1974) of a new Atlantic "clinid" fish with four dorsal fins (Haptoclinus apectolophus Böhlke & Robins) proposes to reunite the tripterygiids with the Clinidae.

Springer (pers.comm., 1978), currently working on diagnoses of the blennioid fishes, considers the following characters sufficiently diagnostic to separate the tripterygiids from the clinids: some clinids are ovoviparous and males have intromittent organs; no tripterygiid is ovoviparous and males lack intromittent organs; all clinids, except a single naked one, have scales with radii in all fields, whereas tripterygiids have scales with radii only in the anterior field. Tripterygiids also have a distinct gap between the first and second dorsal fins, which is not present in the clinids. In this study the familial status of the Tripterygiidae is considered valid.

The taxonomy of tripterygiid genera and species is by and large uncertain, and with the exception of Clark's (in press.) revision of the Red Sea species, there is little up-to-date literature which can be used for the identification of Indo-Pacific species. Even Clark's revision is of limited general application because of the reputedly high degree of endemism of Red Sea fishes.

The major problem lies with the inconsistency in the choice of genera to which species have been allocated. A few examples will serve to illustrate the problem. Jordan & Snyder (1902) placed Japanese species of the family into four genera: Enneanectes Jordan & Evermann, Enneapterygius, Gillias Evermann & Marsh and Tripterygion. In 1946, Fowler described seven new species of Enneapterygius, none of which appear to be referable to that genus. In 1958 Fowler considered Enneapterygius only as a sub-genus of Tripterygion and referred all his Indo-Pacific species to that

genus. De Beaufort & Chapman (1951) placed all the Indo-Pacific species in Tripterygion. Schultz (1950, 1960) recognised Forsterygion Whitley & Philipps, Tripterygion, Notoclinus Gill, Helcogramma McCulloch & Waite and Lepidoblennius Steindachner. The genus Brachynectes was described by T.D. Scott (1957), and he provided a key for Australian genera which included Lepidoblennius, Helcogramma, Gillias, Brachynectes, Notoclinops Whitley, Verconectes Whitley, Vauclusella Whitley and Tripterygion. Gillias was placed in synonymy with Enneanectes by Rosenblatt (1960). However, E.O.G. Scott (1977) considered Enneapterygius, Enneanectes, Notoclinops, Trianectes McCulloch & Waite, Verconectes and Vauclusella all as synonyms of Tripterygion, and recognised only Brachynectes, Forsterygion, Gillias, Helcogramma and Tripterygion as valid for Tasmanian species of the family. Lal Mohan (1971) provided a key for the Tripterygiidae of the eastern and central Indian Ocean, which includes Gillias, Tripterygion and Helcogramma, but no diagnoses.

The taxonomy of the family is further hampered by much unpublished data and undescribed material. Neither Rosenblatt's (1959) revisionary study of the family, nor Ruck's (1975) study of the osteology of Forsterygion have appeared in print. Moreland has some 30 undescribed species from New Zealand (pers.comm.). It must be pointed out that this problem does not exist in the Caribbean and eastern tropical Pacific, for which Rosenblatt (1960) revised the genus Enneanectes, or in the Mediterranean and north-eastern Atlantic, for which Zander, Heymer & Wirtz recently revised Tripterygion (Zander, Heymer & Wirtz, in press; Wirtz, pers.comm.).

This study was initially undertaken to revise the South African Tripterygiidae. Since no keys for the Indian Ocean tripterygiids other than that of Lal Mohan (1971) was available, and the only key to the genera of the family is that of Rosenblatt (which is unpublished), the task was not easily accomplished. Clark, however, made available a copy of her manuscript of the revision of the Red Sea Tripterygiidae which helped in the identification of a number of species.

A review of the literature revealed the inconsistencies referred to above, and it became clear that definitions of the genera within the family was a prime requisite. This resulted in the generic diagnoses given in the first part of the study, where characters were so selected that fishes of one genus could not be referred to any other genus. Although this is a statement of the obvious, it must be born in mind that only Clark's recent study (in press) provides clear diagnoses for three of 14 or more Indo-Pacific genera. For all other Indo-Pacific genera the original descriptions must be consulted, and few of these provide any comparisons with other genera. The earlier genera, such as Lepidoblennius Steindachner, 1867, Tripterygion Risso, 1810 and Enneapterygius Rüppell, 1835, were not compared to any others; Helcogramma McCulloch & Waite, 1918 was distinguished only from Tripterygion, and Norfolkia Fowler, 1953 was compared only to Gillias (= Enneanectes). Brachynectes is "separated from other Australian genera in having the second dorsal fin shorter than the third" (Scott, 1957: 131). Schultz (1960) provides a

fairly detailed key for the genera he recognised. The descriptions of Gilloblennius Whitley & Phillips, 1939, and Forsterygion Whitley & Phillips, 1939, are brief in the extreme and the genera are distinguished only from Tripterygion. Vanclusella Whitley, 1931, was distinguished from both Enneapterygius and Tripterygion.

The distinction between genera is an entirely arbitrary one, and reflects artificial boundaries selected to distinguish a particular level of divergence between groups of animals. In other words generic grouping is a measure of the proximity of relationship of a group of species, such that the species of a particular group are more closely related to each other than to any other group of species. Since the generic category is arbitrary, the naming of new genera must be objectively exercised. Smith-Vaniz (1976) notes that a lack of objectivity may lead to the unwarranted proliferation of generic names, and he consequently makes greater use of the sub-generic status than some ichthyologists.

Such discipline can only be exercised when dealing with a complete taxon, e.g. a family which this study does not do. However, cognisance has been taken of the need for objectivity, and where new genera are described, the criteria adopted have been those used by other workers who have described tripterygiid genera.

The confusion regarding the validity particularly of Indo-Pacific genera of the Tripterygiidae, which, it is believed, has resulted largely from the lack of comparative generic diagnoses, has been adequately exemplified above. It was consequently decided to extend

this study beyond the taxonomy of South African tripterygiids, and include the comparative osteology of the genera which occur in South African waters, and thereby to provide a broader base for generic definitions.

As it is unlikely that Ruck's (1975) osteology of Forsterygion will be published, it was necessary to describe the osteology of one genus with which salient features of the other South African genera could be compared. Thus, the generic definitions finally given in this study are based both on the external morphological characters by which a genus may be diagnosed, and the osteological characters which distinguish the various genera from one another.

PART I - THE TAXONOMY OF THE TRIPTERYGIIDAE OF SOUTH AFRICA.

METHODS AND MATERIALS.

The bulk of the specimens form part of ichthyocide collections made along the coast of Zululand in northern Natal, in July, 1976 and June, 1977 by members of expeditions from the J.L.B. Smith Institute of Ichthyology, Rhodes University, Grahamstown (including J.E. Randall in 1977). Specimens from the Transkei were collected by J.L.B. and M.M. Smith in the 1950's, and by members of the Institute between 1974 and 1976. The Smiths also collected the specimens from East Africa. T.H. Fraser obtained specimens from Inhaca in 1972, and R. Winterbottom and A.E. Louw those from False Bay, Cape Province, in 1975. The types of Gillias capensis were collected in shrimp trawls in False Bay in 1908. Non-South African Tripterygiidae were loaned or donated by a number of persons and institutions (See Acknowledgements).

393 specimens were examined, of which 212 were radiographed.

The methods of taking external measurements and counting fin rays follow those outlined by Hubbs & Lagler (1958), except as noted below.

All elements of the dorsal, anal and caudal fins were counted following Springer (1968), Rosenblatt (1960) and Clark (in press). The caudal fin of Tripterygiidae invariably consists of seven dorsal and six ventral segmented principal rays, of which the

outer two on either side are unbranched and the remainder are branched only once. A variable number of dorsal and ventral unsegmented procurrent rays is also present.

The following measurements and counts were made:

1. standard length;
2. head length;
3. horizontal eye diameter;
4. snout length (lips do not affect this measurement).
5. upper jaw length;
6. caudal peduncle depth and length;
7. snout angle (measured as shown below, by means of two small pieces of perspex, hinged at one end. The head of the fish is placed in the angle formed by the two arms, and the instrument is then laid against a simple protractor to read off the angle to the nearest degree. This parameter is equivalent to the 'angle of head profile' of Zander & Heymer (1970);

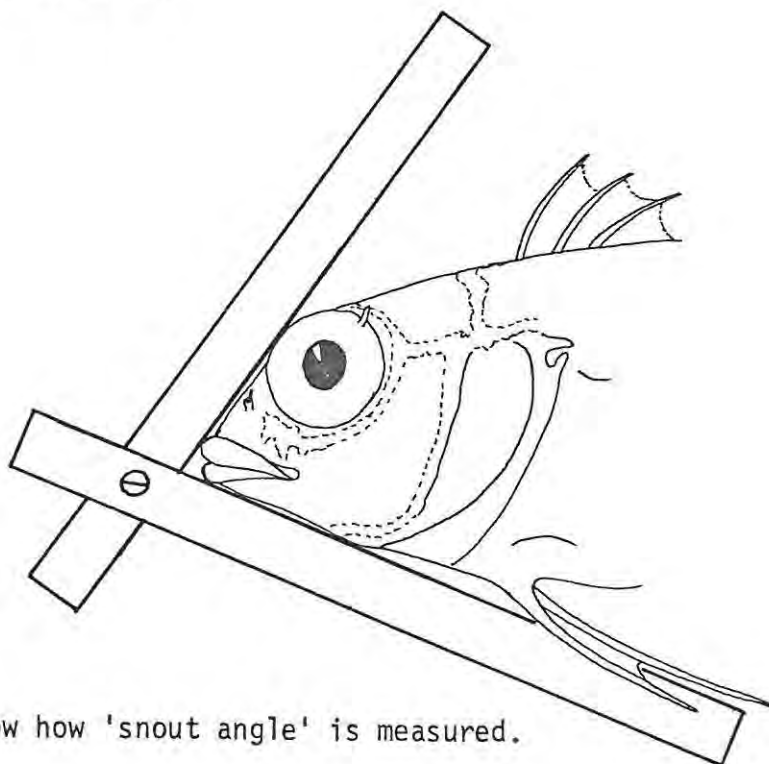


Diagram to show how 'snout angle' is measured.

8. counts for all fins except pelvic fins are recorded (in all known tripterygiids species the pelvic fins consist of one short, hidden spine and two or three undivided, segmented rays united by a membrane for part of their length. All South African species have two rays, of which the inner is always longer. Pectoral ray counts, although given, vary so little between species and genera - 13-16, normally 14 or 15 - that they are not considered to be of any particular diagnostic value. Caudal fin ray counts are given because of variation in number of procurrent rays;
9. the number of caudal and precaudal vertebrae was determined from radiographs (see page 96) for the definition of the first caudal vertebra);
10. lateral line counts (where the lateral line is divided into two portions, they are referred to as 'anterior' and 'posterior series');
11. counts of total lateral scales were made from the first scale in the pectoral fin axil to the last scale on the caudal peduncle (scales on the base of the caudal fin were excluded from the count), and
12. counts of transverse scales were made from the base of the first dorsal fin fin. (Small irregularly interspersed scales are frequently found between the normal scales at the base of the dorsal and anal fins which can result in inconsistency. The small scales are excluded from the counts).

Scales from cleared and stained specimens were mounted on slides and photographed through a compound microscope. Approximately 100 scales from 25 specimens were photographed, and only representative photomicrographs were selected to show certain generic differences in scale structure.

The descriptions are written in a semi-staccato style, instead of the highly staccato style usually employed in taxonomic descriptions, to make reading a little easier.

TAXONOMIC ACCOUNTS.

Prior to this study three species of Tripterygiidae were recorded from South African waters (Smith, 1949): Enneapterygius obtusirostre (Klunzinger), E. pusillus Rüppell, and Gillias capensis (Gilchrist & Thompson). The identification of E. pusillus was considered doubtful by Smith, (1949) who thought it may have been a misidentified E. obtusirostre. It was recorded by Norman (1922) and Fowler (1934) gave a description of one specimen taken in Natal. The colouration as described by Fowler suggests it may be E. triangulus (see below). This study recognises five genera and eight species of Tripterygiidae from South African waters.

A new genus, Cremnochorites, is described for Gillias capensis, as this species cannot be referred to any of the other recognised genera. At present C. capensis appears to be monotypic and endemic to South Africa. Two species are referred to Helcogramma McCulloch & Waite, viz. H. obtusirostre (Klunzinger) and H. fuscopinna sp.n., and a single species to Norfolkia, N. springeri Clark (in press). The genus Enneapterygius Rüppell is split into two genera on the basis of the form of the supraoccipital canal and associated osteological differences: Enneapterygius and Scoliosolen gen.n. Two new species, E. pulcherrimus and E. triangulus are described for Enneapterygius, and two species, S. abeli (Klausewitz) and S. conspicuus (Clark, in press) are referred to Scoliosolen.

Key to the South African genera of Tripterygiidae.

- 1a. Four spines in first dorsal fin, two spines in anal fin,
head scaled 2
- 1b. Three spines in first dorsal fin, one spine in anal fin,
head naked 3
- 2a. Small, denticle-like ctenoid scales on snout, inter-
orbital nape and cheeks, 21-22 pored scales in anterior
series of lateral line Cremnochorites gen.n.
- 2b. Snout and interorbital naked, ctenoid scales on cheeks
and nape, smaller than body scales, 16-17 pored scales
in anterior series of lateral line Norfolkia Fowler.
- 3a. Supraoccipital sensory canal crescent-shaped (figure 1A)
..... 4
- 3b. Supraoccipital sensory canal 'U'-shaped (figure 1B)
lateral line divided into an anterior series of pored
scales and a posterior series of notched scales
..... Enneapterygius Rüppell.
- 4a. Lateral line a single series of pored scales running
to below the third dorsal fin Helcogramma McCulloch & Waite.

4b. Lateral line divided into an anterior series of pored scales and a posterior series of notched scales

..... Scoliosolen gen.n.

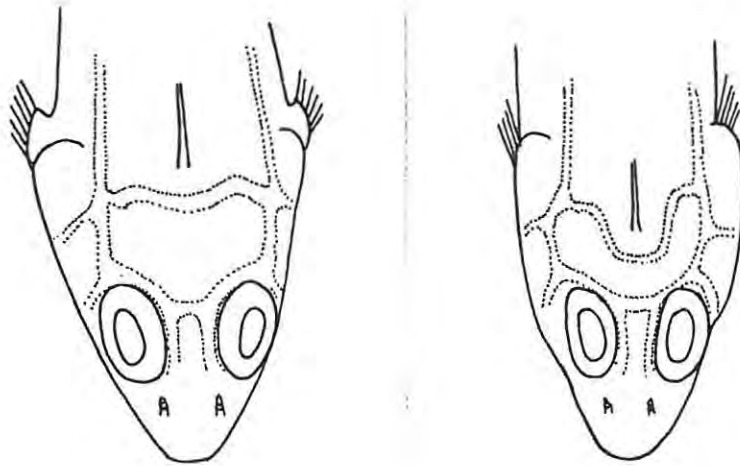


FIGURE 1A B

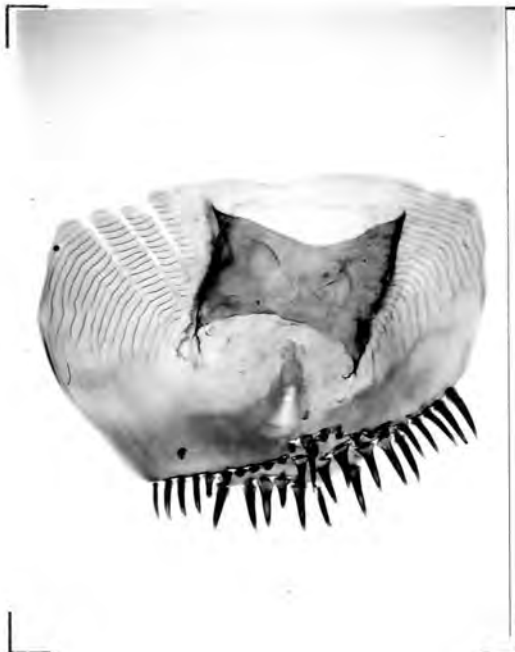
Diagram of crescent-shaped (A) and 'U'-shaped (B) supraoccipital sensory canal.



A



B



C



D

Examples of body scales (A,B) and pored lateral line scales (C,D) of Cremnochorites capensis.

Genus Cremnochorites gen.n.

Type species Tripterygium capense Gilchrist & Thompson, 1908.

General Description.

The first dorsal fin has four soft spines, the second 14-15 soft spines, the third 10-11 segmented rays of which some may be branched once and the last is usually double. The first dorsal fin is lower than the second. The anal fin has two short soft spines and 21-22 undivided segmented rays, the last is usually double. The pectoral fins have the upper rays branched once, and the lower rays simple and thickened. The lateral line is discontinuous, comprising an anterior series of pored scales running to below the anterior of the third dorsal fin, and a posterior series of notched scales extending from below the posterior end of the anterior series onto the caudal peduncle.

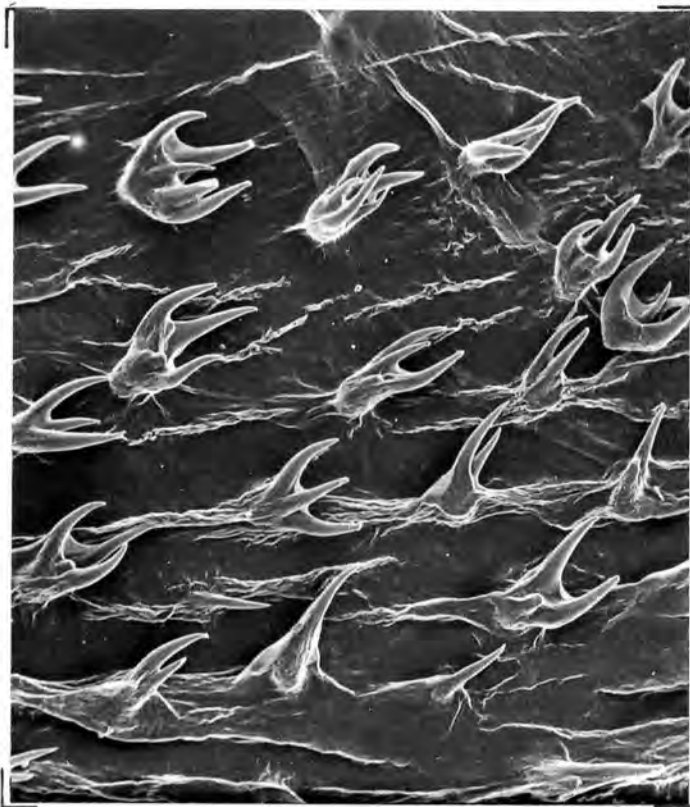
The body is heavily scaled, all scales having relatively large irregular ctenii (Plate 1 A-D). The scales on the abdomen have few ctenii. A few cycloid scales occur around the vent and at the base of the pelvic fins. Scale rows are somewhat irregular. The head and pectoral fin bases are heavily covered with ctenoid scales; those on the posterior edge of the opercle are about half the size of the body scales, decreasing in size anteriorly to small denticle-like scales with a few, large ctenii below the eye and on the cheeks (Plate 2 A,B).

The scales on the head and particularly on the cheeks, appear to be situated on small pedestals, creating the appearance of shark denticles. Small denticle-like spines are found on the nape and

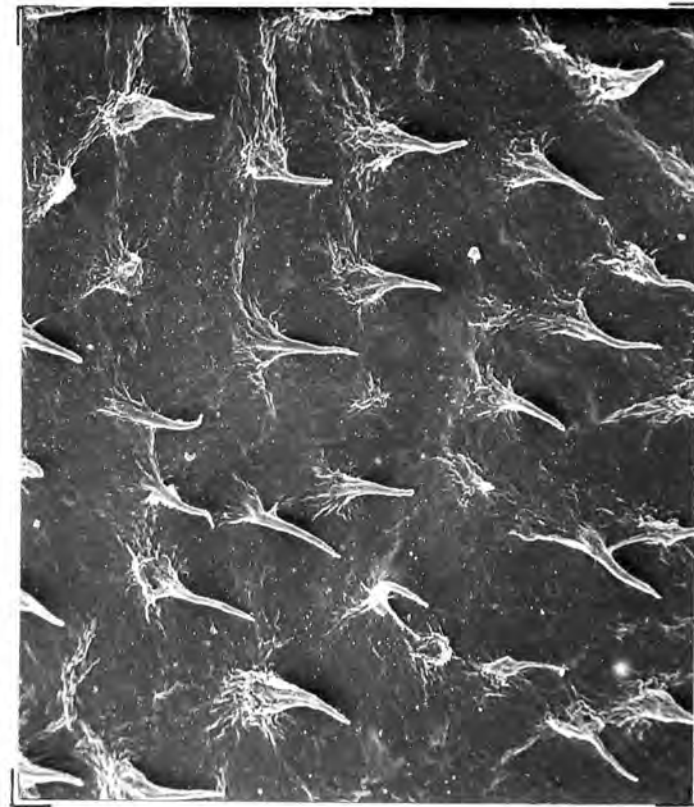
PLATE 2. Stereoscan photographs of head scales of Cremnochorites capensis.



A Cheek scales - 40X



B Portion of skin from perimeter of eye - 80X



C Portion of skin from throat (papillae shrivel during vacuum coating) - 80X

All examples from a 70 mm specimen.

the interorbital area affixed to the cranial bones. There is a ring of 'ctenii' around the perimeter of the eye and on the posterior end of the maxilla (Plate 2B). The skin of the throat is papillose with single 'ctenii' or spines embedded in the papillae (Plate 2C). (The term 'throat' is here used for the area between the lower jaw bones and the posterior edge of the branchiostegal membranes, which are united across the isthmus.) The postero-dorsal edge of post-temporal is serrated; the interorbital is concave, with a ridge over each orbit, and there is a transverse depression behind the orbits. The head is broad with a rounded profile. Large multifid orbital tentacles are present, with similar, small tentacles on the posterior edge of the anterior nostrils. Both jaws have slightly recurved conical teeth, a patch in front and a single row at back of the jaw. The teeth are unequal in size in the lower jaw, but the upper jaw has a row of large teeth with an inner band of small teeth. The vomer has a single row of slightly recurved conical teeth which continues onto the palatines.

Discussion.

C. capensis was originally described in Tripterygium (=Tripterygion) by Gilchrist & Thompson (1918). It was later transferred to Gillias Everm. & Marsh (1899) by Barnard (1927) and retained there by Smith (1949). Rosenblatt (1960) placed Gillias in synonymy with Enneanectes Jordan & Evermann. (Enneanectes is restricted to the eastern tropical Pacific and the western tropical Atlantic). Rosenblatt did not refer Indo-Pacific species in Gillias to any other genus, but merely stated that "none of the Australian or South African species referred to Gillias has anything to do with that genus". (1960:3). Clark (in press) suggested

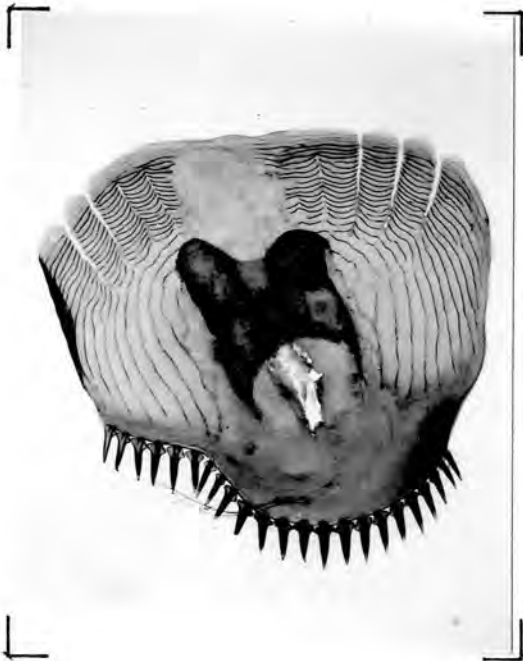
180



A



B



C



D

Examples of body scales (A,B) and pored lateral line scales (C,D) of Norfolkia springeri.

that C. capensis be referred to Norfolkia Fowler for these taxa share four first dorsal fin spines, two anal fin spines and a scaled head. Cremnochorites, differs however, from Norfolkia in a number of characters: palatine teeth are present in Cremnochorites, and absent in Norfolkia; lateral line counts are reversed, 21-22 pored + 15-16 notched scales for the former compared with 13-17 pored + 21-23 notched scales for Norfolkia. The head scales of Cremnochorites are quite unlike those of any other tripterygiid (Plate 2).

The scales on the nape and opercle resemble the body scales but are smaller. The cheek scales (Plate 2A) are very firmly attached. Their posterior margins are raised and have very strong, long ctenii giving the impression of multipronged denticles. A band of 'ctenii' with one to five spines are embedded in skin surrounding the iris (Plate 2B). The skin of the throat is papillose and there are single 'ctenii' embedded in the papillae (Plate 2C). These scales and 'scale ctenii' all stain with alizari red.

Body scales of the species in the two genera are also very different. Those of Cremnochorites (Plate 1) are heavily ctenoid and the ctenii are generally unequal in size. Pored lateral line scales frequently have 2-3 rows of ctenii in the center of the row. Scale foci are close to the posterior edge of the scale and the radii are thus comparatively long. In Norfolkia (Plate 3A-D) ctenii are smaller, more or less equal in size and always in a single row. Scale foci are further away from the posterior edge of the scale and the radii are consequently relatively shorter.

There are also significant osteological differences between the two genera which will be dealt with in Part II. The differences

noted above are considered sufficient to warrant the placing of C. capensis in a separate genus.

Cremnochorites capensis is the only species which can be ascribed to this genus. It has been taken in False Bay, Cape, Skoenmakerskop (near Port Elizabeth), Eastern Cape, and off Port Alfred, Eastern Cape, South Africa. The four type specimens were taken in shrimp trawls, two at 5 fms (10 m) and two at 14 fms (28 m), and the other specimens at 1-8 m below low spring tide. With the exception of the types, for which there are no other collection data, all other specimens were taken from relatively sheltered, vertical, seaweed covered rock faces. One specimen from Port Alfred was taken in a gully at 15 m depth.

Etymology:- Cremnochorites is derived from the Greek kremnos (a cliff), and chorites (native or country man). It is thus named because it has only been found associated with vertical rock faces. The gender is masculine.

Cremnochorites capensis (Gilchrist & Thompson) Figure 2.

Tripterygium capense Gilchrist & Thompson, 1908:140; Thompson, 1918:151, False Bay, Cape, South Africa.

Gillias capensis Barnard, 1927:827.

Gillias capensis Smith, 1949:359.

Material examined.

- (a) 3 Syntypes, SAM 9900, females (46-53 mm S.L.), 10-28 m depth, False Bay, Cape, South Africa, Collected in a shrimp trawl;
- (b) 1 Syntype, SAM 9901, male (54,7 mm S.L.), collected with (a);

- (c) RUSI 7384, 1 fish (49,3 mm S.L.), False Bay, Cape, South Africa, no data;
- (d) RUSI 75-22/1, 8 fishes (46,9-61 mm S.L.), cliff with Pyura sp., 6-8 m depth, False Bay, Cape, coll. R. Winterbottom et al., November, 1975;
- (e) RUSI 75-21/1, 1 fish (80 mm S.L.), sheltered bay with vertical rock walls, 2-3 m in depth, Platboom, Cape, South Africa, coll. R. Winterbottom et al., November, 1975;
- (f) RUSI 76-7/1, 12 fishes (26,9-55,6 mm S.L.), from vertical rock wall, 4 m depth, Skoenmakerskop, Eastern Cape, South Africa, coll. R. Winterbottom et al.,
- (g) RUSI 77-7/1, 2 fishes (18,5 & 41,7 mm S.L.), same as (f), 5 m depth, coll. M. Christensen et al., February, 1977.

Total 29 specimens, all which were radiographed.

Description:

dorsal fins, IV+XIV-XV+10-11, usually IV+XIV+11, first dorsal lower than second, rays except first and last branched once, last ray double;

anal fin, II,21-22, usually II,21, last ray normally double;

pectoral fins, 16, lower 8 thickened and simple, uppermost sometimes simple, remainder branched once;

caudal fin, 6+7+6+5;

lateral line, anterior series of 21-24, usually 22-23, pored scales, posterior series of 17-20, usually 19, notched scales;

lateral series, 36-37;

transverse series, 5/11;

vertebrae, 10 precaudal, 27-28 caudal;

head 3,3-3,7, depth about 4 in S.L.; eye 3,0-3,6, upper jaw 2,0-2,4, snout 3,6-4,4 in head; peduncle depth 0,9-1,1 in peduncle length;

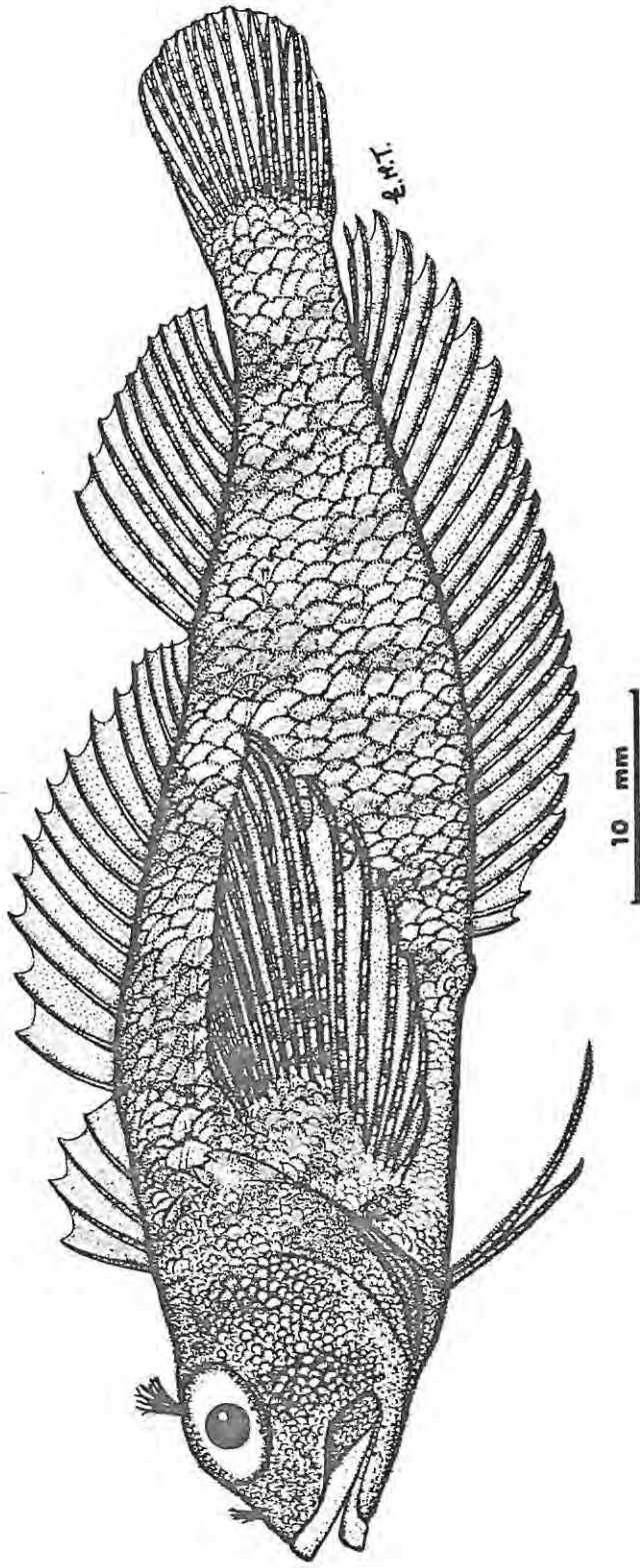


FIGURE 2 CREMNOCHORITES CAPENSIS (GILCHRIST & THOMPSON), MALE

snout angle 71° - 76° .

The balance for the description is given in that for the genus.

The only sexual dimorphism noted consist of a single, conical papilla at the posterior of the vent in males, whereas females have a 'rosette' around the vent (figure 3), which sometimes protrudes a short distance. Although these features appears to be common to many tripterygiids, it cannot always be distinguished.

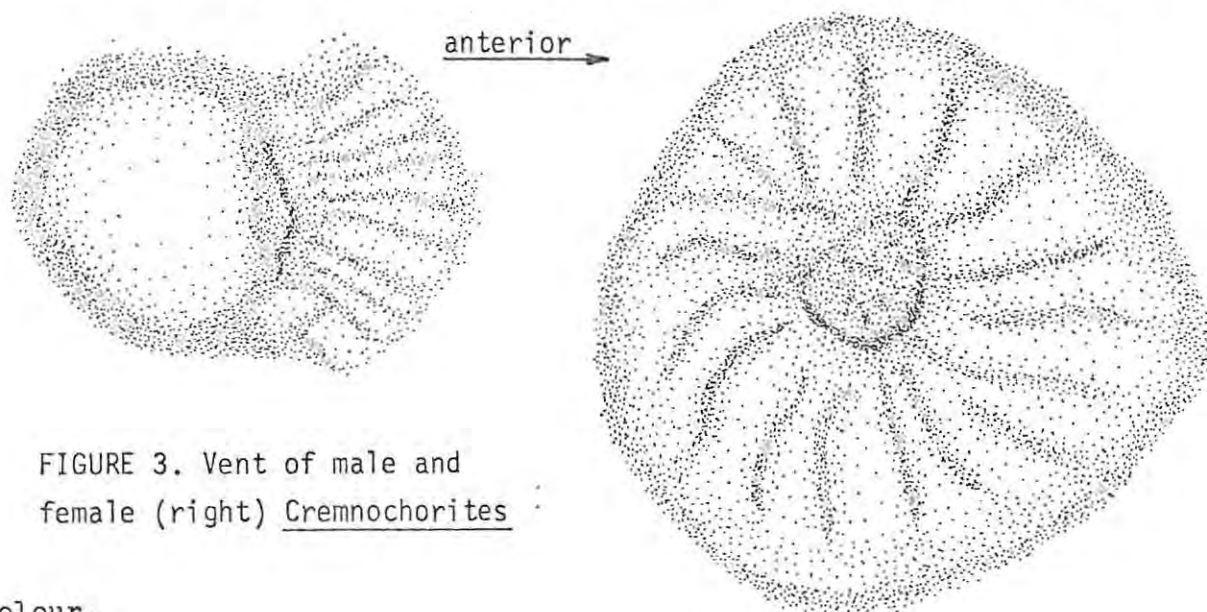


FIGURE 3. Vent of male and female (right) Cremnochorites

Colour.

In preservative these fishes are generally grey with a pale belly. There are six irregular, vertical, dark bars on the body above the midline which may divide into eight or more bars below the midline. The lower body bars may alternate with the upper bars. The penultimate bar is continuous across the caudal peduncle, and the ultimate bar lies at the base of the caudal fin. A dark bar extends across the nape and continues onto the preopercles. Another bar runs from below the midline of the eye to the corner of the mouth. There is an irregular dark blotch on the lower portion of the opercle. The orbital tentacles are dusky. The anal and caudal fins have irregular small dark blotches. The first dorsal fin is dark,

while the second and third have dusky margins. Neither the pelvic nor pectoral fins are pigmented, although there are two short dark bars on each pectoral fin base.

Males have dusky branchiostegal membranes, and a more darkly pigmented head than females.

Live fishes are rust-coloured, and the irregular blotching renders them cryptic in brown and purple algae.

Genus *Norfolkia* Fowler.

Norfolkia Fowler, 1953:263. Type species *Norfolkia lairdi*.

Fowler, 1953 (= *N. squamiceps* McCulloch & Waite, 1916).
by original designation.

The following generic diagnosis is based on that given by Clark (in press), with modifications from the data for South African specimens of *Norfolkia*.

Diagnosis.

The first dorsal fin has four soft spines, the second 13-15 soft spines, and the third 9-11 undivided, segmented rays. The last ray is usually double. The anal fin has two soft spines and 19-22 undivided, segmented rays, except for the last ray which is usually double. The pectoral fins consist of 15-16 rays; the lower 6-7 are simple and thickened, the uppermost 0-3 undivided, and the remainder divided once. The caudal fin has 7+6 principal rays, and 5-7 dorsal and 5 ventral procurrent rays. An orbital tentacle with a serrated margin is present, as is a smaller tentacle on the anterior nostril which also has a serrated margin.

The body and head behind the eyes is heavily scaled. The scales are ctenoid, except for a few cycloid scales on the pectoral fin bases and on the base of the caudal fin, as well as small cycloid scales on the abdomen and around the vent.

The lateral line is divided, with an anterior series of 13-18 pored scales ending below the posterior third of the second dorsal fin, and a posterior series of 18-24 notched scales which runs from 2-3 rows below the end of the anterior series onto the caudal peduncle. (A few unnotched scales are sometimes present at the beginning of the posterior series. These were included by Clark (in press) in this series and can result in very variable counts.)

There are 10 precaudal and 26-28 caudal vertebrae. The vomer has a single band of small conical teeth, while the palatines are edentate.

Discussion.

Norfolkia is characterized by the following combination of characters: head behind the eyes scaled, except for the lower portion of the preopercle; four spines in the first dorsal fin; two spines in the anal fin, and a discontinuous lateral line. Clark (in press) has pointed out that there are similarities between Norfolkia and the more heavily scaled species of Enneanectes, but the latter genus has lower dorsal and anal fin counts (dorsal III+X-XIII+7-10, anal II,14-17) and a broad black bar across the caudal peduncle, which is not present in any known Norfolkia species. The number of spines in the first dorsal and anal fins is constant within a genus.

Species which have been or should be placed in this genus are:

- (a) Tripterygion brachylepis Schultz, 1960:291, described from one specimen taken at Bikini Atoll, Pacific Ocean, in 6-8 m depth;

- (b) Tripterygium clarkei Morton, 1887 (1888):xlvii,78, Tasman Straits;
- (c) Norfolkia lairdi Fowler, 1953:264, fig.12, Norfolk Island, Australia;
- (d) Norfolkia springeri Clark, (in press), Gulf of Aqaba, Red Sea;
- (e) Gillias squamiceps McCulloch & Waite, 1916:449, fig.1, Lord Howe Island, Great Barrier Reef;
- (f) Tripterygion striaticeps Ramsay & Ogilby, 1888:419, Port Jackson, New South Wales, and
- (g) Norfolkia thomasi Whitley, 1964:192, Heron Island, Great Barrier Reef.

T. clarkei and T. striaticeps were placed in Norfolkia by Whitley (1964). In the original description of T. clarkei, Morton (1887) recorded three spines in the first dorsal fin and makes no mention of a scaled head. Norfolkia has four spines in the first dorsal fin and T. clarkei thus cannot be referred to Norfolkia. (Neither Morton (1887) nor Fowler (1953) recorded the number of anal fin spines for T. clarkei. Furthermore the species was named after Clarke's Island and therefore the spelling clarkii used by Whitley (1964) and Fowler (1953) is incorrect). Of the two species, T. striaticeps was considered by Fowler possibly to be the closest to N. lairdi, the type species, but he did not refer this species to Norfolkia. As T. striaticeps was originally described with three first dorsal fin spines and one anal fin spine, (Ramsay & Ogilby, 1888), it is also not referable to that genus. Gillias squamiceps was placed in Norfolkia, and N. lairdi in synonymy with N. squamiceps by Whitley (1964). Apart from the fact that Whitley's (1964) synonymy was based on an undescribed species, which he considered as N. lairdi (Allen et al., 1976), the two species agree in original description in all characters except anal fin counts (II,19 for N. lairdi and 22-23 (presumably II+20-21) for N. squamiceps),

and number of scales from dorsal fin base to anterior lateral line series (1 1/2 and 2 1/2). The total lateral scale count is not given for N. lairdi, nor is the posterior lateral line series count given for N. squamiceps.

N. thomasi and N. springeri are valid species.

Thus the species though by Whitely (1964) to be N. lairdi is still undescribed. There is also an undescribed tripterygiid, illustrated in Doak (1972), which appears to belong in Norfolkia.

T. clarkei and T. striaticeps are not referable to Tripterygion and, with two spines in the anal fin, do not belong in Helcogramma either (see later). No suggestions can be made at present as to which genus these two species should be referred.

Norfolkia springeri Clark. Figure 4.

Norfolkia springeri Clark (in press), Gulf of Aqaba, Red Sea.

As the original description of this species is based on only six specimens, a description is repeated here, based on non-Red Sea specimens.

Material examined:

- (a) RUSI 6514, 1 fish (40 mm S.L.),
- (b) RUSI 6515, 3 fishes (32,5-38,5 mm S.L.),
- (c) RUSI 76-10/1, 3 fishes (30,4-35,3 mm S.L.), rock arch over sand, 13 m depth, Sodwana Bay;
- (d) RUSI 76-16/2, 1 fish (30,4 mm S.L.),

- (e) RUSI 6517, 2 fishes (31,4-40,3 mm S.L.), reef with coral sand, 12-14 m depth, Sodwana Bay;
- (f) RUSI 6516, 2 fishes (38,8 & 44,5 mm S.L.), pool 0-3 m depth, 2,5 km south of Boteler Point;
- (g) RUSI 76-8/3, 5 fishes (28,9-32,7 mm S.L.), gully at 15 m depth, Sodwana Bay;
- (h) RUSI 76-9/1, 5 fishes (27,9-41 mm S.L.), reef with coral, 15 m depth, Sodwana Bay;
- (i) RUSI 76-12/1, 1 fish (16,8 mm S.L.),
- (j) RUSI 76-13/1, 2 fishes (27,6 & 31,1 mm S.L.), reef at 15 m depth, Sodwana Bay;
- (k) RUSI 76-23/1, 6 fishes (19,7-40,8 mm S.L.), pool 0-2 5 m depth, Hulley Point, all above from Zululand, South Africa, coll. R. Winterbottom et al., July 1976;
- (l) (to be sent to BPBM), 7 fishes (27-43 mm S.L.), reef with coral, 10-12 m depth, Sodwana Bay, Zululand, South Africa, coll. J.E. Randall, 21 June, 1977;
- (m) RUSI 74-90/1, 1 fish (32,6 mm S.L.), reef off Barreira, 0-3 m depth, Inhaca Island, Mocambique, coll. T.H. Fraser, 1973, and
- (n) RUSI 7386, 1 fish (34 mm S.L.), reef at 0-2 m, Shimoni, Kenya, coll. JLB. & M.M. Smith, November, 1954.

Total 40 specimens, all of which were radiographed.

In the description below, Clark's data for six type specimens of N. springeri from Aqaba is given in parenthesis.

Description:

dorsal fins, IV+XIII-XIV+9-11, usually IV+XIII+10 (IV+XIII+XIV+10-11, usually IV+XIII+11), height first dorsal equal to, or lower than second dorsal;

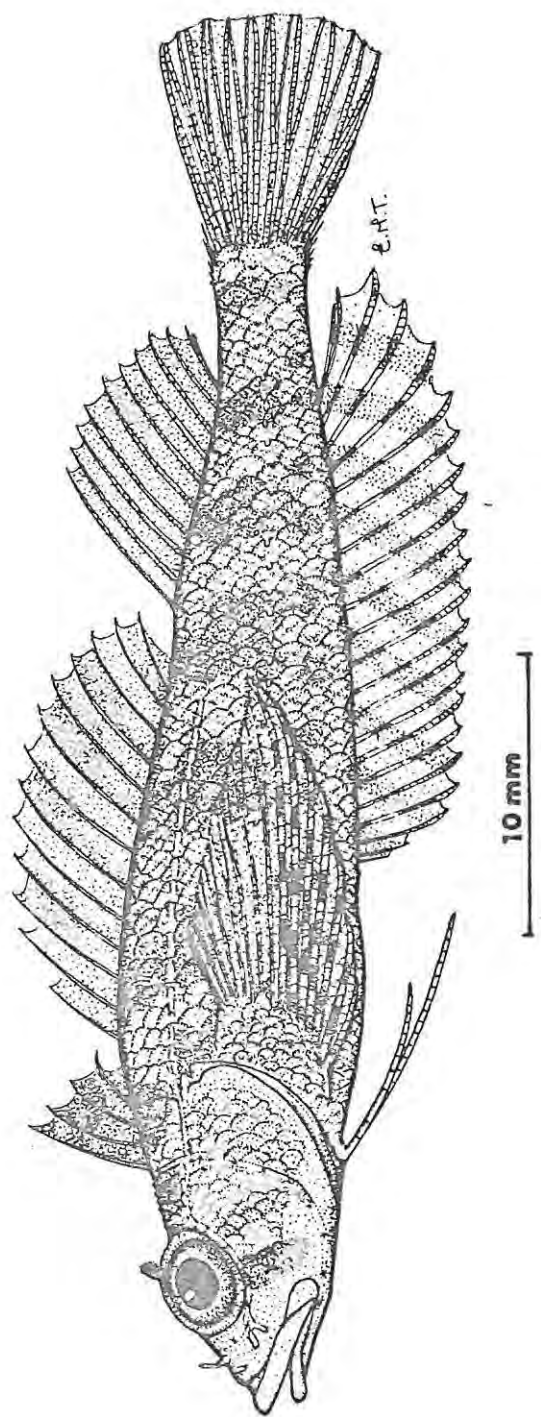


FIGURE 4 NORFOLKIA SPRINGERI CLARK, MALE

anal fin, II,18-19, usually II,19 (II,19);

pectoral fins, 16 rays, lower 7 thickened and unbranched, upper 1-2 unbranched, remainder branched once (3 unbranched +6-7 branched once +6-7 thickened and unbranched);

caudal fin, 6+7+6+5;

lateral line, anterior series 15-17, usually 17(16-17), pored scales to under the last third of the second dorsal fin, posterior series of 18-24, usually 22 (21-24, usually 23) notched scales commencing one or two scales before end of anterior series, three scale rows down, and ending at the base of the caudal fin;

lateral series, 32;

transverse series, 3/8 (Clark does not give a transverse scale count, but the illustration of the holotype of N. springeri shows a count of 3/6);

vertebrae, 10 precaudal, 26 caudal (11+25);

head 3,0-3,5 (3,5-3,6), depth about 5,7 in S.L.; eye 3,1-3,7, upper jaw 2,1-2,6, snout 3,7-4,7 in head; peduncle depth 1,0-1,4 in peduncle length; snout angle 58°-59°.

The body, head and pectoral fin bases are heavily scaled. The interorbital area, snout, and the areas below the eyes and throat are naked. A finely serrated tentacle is present on the eye and the anterior nostril. The pelvic fin rays are not united by a membrane. Clark (in press) records a membrane of about 20% of the length of the longest ray for her Red Sea specimens.

Colour.

No sexual dichromatism was noted. In preservative the whole body is dusky with 6 irregular, dark, vertical bars from dorsal-fin base to midline. The last bar is on the caudal peduncle and the second and third last continue to the anal fin base. There are

8 to 12 (10 according to Clark for Red Sea specimens) narrow, dark bars along the lower half of the body which continue nearly to the anal fin base. These are very clear in small individuals but tend to coalesce in larger fishes forming indistinct, wider bars. The anal fin has 9 bars, which are darker than the body bars, and appear vertical when the fin is folded, but run obliquely forward when the fin is extended. The caudal fin is dusky and faintly barred in large specimens, but has 4 very irregular dusky bars in small individuals. The first dorsal fin is very dark with one or two inverted black half-moons on the edge of the membrane between the spines 1 & 2 and 2 & 3. This pattern could be restricted to males. The second and third dorsal fins of small specimens have indistinct dusky bars continuous with the body bars, but these fins are entirely dusky in large specimens. The pectoral fins have 4-5 irregular, vertical, dusky bars.

Clark's Aqaba specimens tend to have more bars on the body and fins. Presumably, this additional bar on the fins is retained in larger specimens. Her illustration of the species shows six very distinct bars on the caudal fin, which are absent in non-Red Sea specimens. The head of non-Red Sea specimens is dusky with an oblique dark bar running from lower edge of the eye to behind the angle of the mouth. There are small dark blotches on the lower jaw, and a black tip on the nasal tentacle. The orbital tentacle is entirely black. Pigmentation at the base of anal fin and on the belly is pale, while the throat, pelvic fins and branchiostegal membranes are mainly unpigmented with a few small melanophores on the branchiostegals.

In life these fishes are russet brown and are very similar in appearance to Cremnochorites capensis.

Discussion.

There are a few small but significant differences between Red Sea N. springeri and non-Red Sea specimens. These may be summarized as follows:

	<u>Red Sea</u>	<u>Non-Red Sea</u>
(a) Third dorsal rays	10-11	9-11
(usually)	(11)	(10)
(b) Posterior lateral		
line series	21-24	18-24
(usually)	(23)	(22)
(c) Transverse scales	3/6	3/8
(d) Body bars	7	6
(e) Anal fin bars	10	9
(f) Caudal fin bars	present	very faint to absent

(Also see table IV-VII)

The differences in number of dorsal fin rays may be due to the small sample from the Red Sea. The disparity in transverse scale counts could be important, but that of Red Sea specimens was taken from the illustration of the holotype, and need not be accurate. The differences in marking may also be important, but it may be a regional colour variation. Furthermore, the distribution of the species along the east coast of Africa appears to be

discontinuous for the Red Sea specimens were taken only in the Gulf of Aqaba. Since the Red Sea is an area which has enjoyed the attention of ichthyologists for a very long time, it is felt that if the species was present in the southern Red Sea, it would have been collected by now.

When larger samples of this species become available, particularly from the Red Sea, and if the difference in colour pattern, and the apparent difference in transverse scale counts are shown to be consistent, it may become necessary to consider the Aqaba and non-Red Sea groups as two separate sub-species of Norfolkia springeri.

Genus Helcogramma McCulloch & Waite.

Helcogramma McCulloch & Waite, 1918:51.

Type species Helcogramma decurrens McCulloch & Waite, 1918, by original designation, from St. Vincent Gulf, South Australia.

Diagnosis

The first dorsal fin has three soft spines, the second 10-16 soft spines, and the third 6-12 undivided, segmented rays. The last ray is usually double. The anal fin has a single soft spine and 14-21 undivided, segmented rays, except for the last ray which is usually double. The pectoral fins consist of 15-17 segmented rays, of which the lower 6-7 are simple and thickened, the uppermost 1-5 undivided, and the remainder divided once. The caudal fin has 7+6 principal rays, and 8-10 dorsal and 7-10 ventral procurrent rays. Small, simple orbital and anterior nasal tentacles are present.

The lateral line consists of a continuous series of 10-27 pored scales curving down behind the pectoral fin base and continuing along the midside to end below the second or third dorsal fins, or may continue onto the caudal peduncle.

The head is naked, except in a few species which have the nape scaled. The body, except for abdomen and pectoral fin bases has ctenoid scales. The scales have small, even sized ctenii.

A band of 2-3 rows of conical teeth is present on the vomer and anterior ends of the palatines; both jaws have slightly recurved conical teeth in setiform bands in front, decreasing to a single row of teeth at the sides of the jaw. The teeth in the outer rows are enlarged.

Discussion

This genus is distinguished by the combination of 3 first dorsal fin spines, one anal fin spine and the lateral line of a single series of pored scales. The following species possess this combination of characters, and should accordingly be referred to this genus.

- (a) Helcogramma capidata Rosenblatt, in Schultz et al., 1960:297, pl. 121.c., Kapingamaragi Atoll, Caroline Islands, Pacific Ocean;
- (b) Helcogramma chica Rosenblatt, in Schultz et al., 1960:294, fig. 114, Hull Island, Phoenix Islands, Pacific Ocean;
- (c) Tripterygion ellioti Herre, 1944:49, India;
- (d) Enneapterygius fuligicauda Fowler, 1946:188, fig. 52, Riu Kiu Islands;
- (e) Enneapterygius fuscipectoris Fowler, 1946:186, figs. 50,51, Riu Kiu Islands;
- (f) Helcogramma fuscopinna sp.n., Sodwana Bay, Zululand, South Africa;
- (g) Enneapterygius hudsoni Jordan & Seale:419, fig. 101, Samoa;
- (h) Enneapterygius inclinatus Fowler, 1946:190, fig. 55, Riu Kiu Islands;
- (i) Ennantergygius macrobrachium Fowler, 1946:189, fig. 53, Riu Kiu Islands;
- (j) Tripterygium obtusirostre Klunzinger, 1871:498, Red Sea;
- (k) Enneapterygius personatus Fowler, 1946:185, fig. 49, Riu Kiu Islands;
- (l) Tripterygium philippinum Peters, 1868:269, Luzon, Philippines;
- (m) Enneapterygius quadrimaculatus Fowler, 1946:189, fig. 54, Riu Kiu Islands;
- (n) Helcogramma shinglensis Lal Mohan, 1971:219-223, Gulf of Mannar, India;

- (o) Helcogramma steinitzi Clark, (in press), Red Sea;
- (p) Tripterygion trigloides Bleeker, 1858:220, Biliton, Indonesia, and
- (q) Enneapterygius vexillarius Fowler, 1946:192, fig. 56, Riu Kiu Islands.

The type specimens of personatus, fuscipectoris, fuligicauda, quadrimaculatus, inclinatus and vexillarius were checked by Mr. W.G. Saul, of the Academy of Natural Sciences of Philadelphia, to ascertain whether they agree with the original descriptions.

The type of macrobrachium was lost prior to 1956 (Böhlke, pers. comm.). Schultz (1960) considered fuligicauda and macrobrachium as male and female of the same species and synonymized the species with Tripterygion hemimelas. T. hemimelas is referable to Enneapterygius (or Scoliosolen, see later) since it has a divided lateral line. The lateral line of Helcogramma is single. Schultz (1960) may however be correct in considering them male and female of a single species. Fowler (1946) did not sex his type specimens and macrobrachium was described from a single specimen; fuligicauda from three specimens. Since the type of macrobrachium is now missing and the differences in fin counts given in the original descriptions are of similar magnitude to those separating other Helcogramma species, the two species are here accepted as valid.

The South African species of Helcogramma.

Two species are known from South African waters. H. obtusirostre is known from the Red Sea to as far south as the Transkei. This species has also been recorded from the Seychelles (Smith & Smith, 1963). Randall (pers. comm., 1977) has suggested that H. obtusirostre is widespread in the western Indian Ocean, and represents a species complex. Colouration of individuals from different localities varies considerably, and this study shows that colouration also changes with depth.

The second species, H. fuscopinna, is described as new. It also has a wide distribution and is known from East African where J.L.B. and

M.M. Smith collected a number. The five species of Helcogramma known from the western and central Indian Ocean are all very similar in meristics and general colouration.

For the two South African species extensive comparisons are made, since they are to a certain extent sympatric. The evidence presented here suggests that, similar to two Mediterranean species of Tripterygion, T. tripteronotus and T. delaisi, the two South African species have particular depth preferences.

H. obtusirostre is essentially a shallow water dweller, whereas H. fuscopinna occupies deeper water, although there is an overlap between the two. There are also morphological features which, it is suggested, are determined by depth.

Key to the South African species of Helcogramma.

1. 20-21 anal rays, usually 14 spines in second dorsal fin, usually 11 rays in third dorsal fin, distinct blue white line with numerous fine black stipples running from upper lip, below eye to posterior edge of preopercle in large (30 mm S.L.) specimens, body bars indistinct to absent
.....Helcogramma fuscopinna sp.n.
2. 18-19 anal rays, usually 13 spines in second dorsal fin, usually 10 rays in third dorsal fin, no stipple line below eye, body bars irregular but distinct.....
.....Helcogramma obtusirostre (Klunzinger)

Helcogramma fuscopinna sp.n. Figure 5, Plate 4.

Material examined

Type series

- (a) Holotype, RUSI 954, Male (37,6 mm S.L.) reef at 8 m depth
Sodwana Bay, Kwazulu, South Africa, coll. M.S. Christensen,
June, 1977;
- (b) 2 paratypes, RUSI 955, 1 male, 1 female (36,5 & 40 mm S.L.)
from same collection as holotype;
- (c) 1 paratype, RUSI 956, male (37,5 mm S.L.), Bazaruto Island,
Moçambique, coll. J.L.B. & M.M. Smith, September, 1954;
- (d) 5 paratypes, BPBM 21164, 3 males, 2 females (31,5 - 41,3 mm
S.L.), reef at 8 m depth, Sodwana Bay, Kwazulu, South
Africa, coll. J.E. Randall, June, 1977;
- (e) 2 paratypes, USNM 218482, 1 male, 1 female (40,5 & 31,5 mm
S.L.), patch reef at 10 m depth, Sodwana Bay, Kwazulu,
South Africa, coll. R. Winterbottom et al., July, 1976;
- (f) 2 paratypes, BMNH 1978-5.30:1-2, 2 males (34,1 & 40 mm S.L.),
same as (e).

Non-type series

- (g) RUSI 75-13/1, 15 fishes (26-37,4 mm S.L.), and
- (h) RUSI 76-8/4, 20 fishes (19,6-42,4 mm S.L.), reef at 15 m
depth, Sodwana Bay, Kwazulu, South Africa, coll.
R. Winterbottom et al., June, 1976;
- (i) RUSI 7733, 1 fish (34,1 mm S.L.), Pinda, Moçambique;

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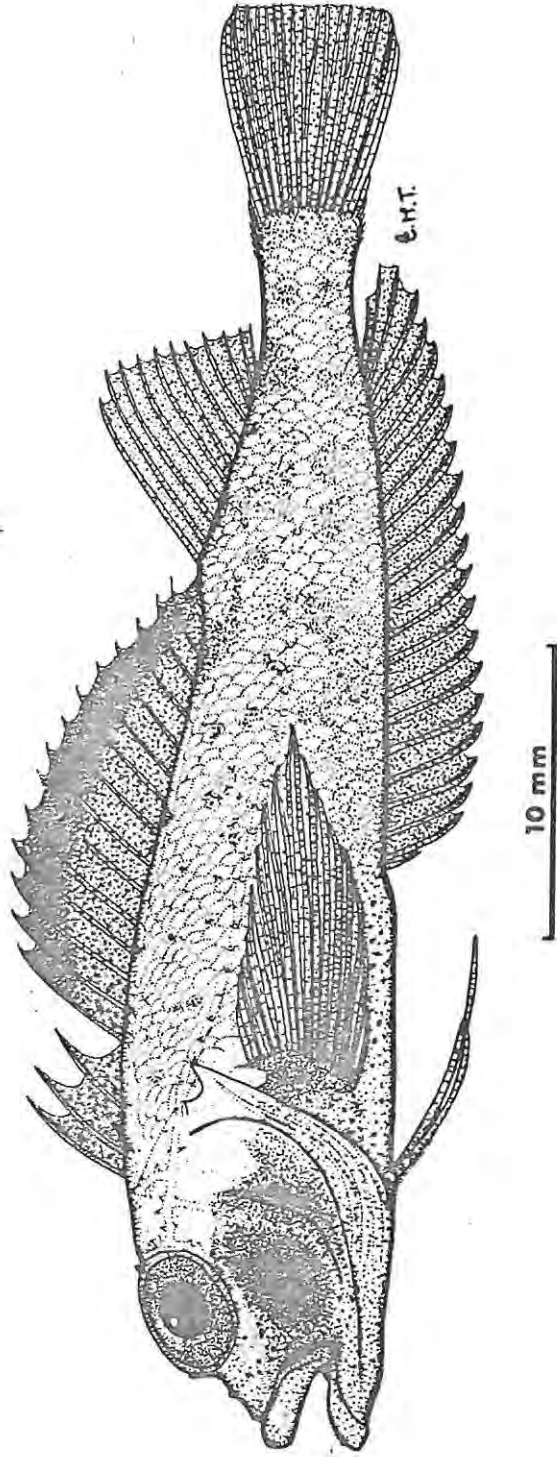


FIGURE 5 HELCOGRAMMA FUSCOPINNA SP. N. HOLOTYPE, MALE 37,6 mm S.L., RUSI 954

- (j) RUSI 7764, 5 fishes (32-41,7 mm S.L.), Bazaruto, Moçambique;
 - (k) RUSI 7731, 1 fish (32,9 mm S.L.);
 - (l) RUSI 7737, 4 fishes (25,1-32,6 mm S.L.);
 - (m) RUSI 7765, 7 fishes (25-32,7 mm S.L.), Mafia, Tanzania, and
 - (n) RUSI 7732, 5 fishes (24-28,4 mm S.L.), Shimoni, Kenya,
- all collected by J.L.B. & M.M. Smith between October, 1952
and November, 1954.

Total 75 fishes, of which 30 were radiographed. (The type series will be extended prior to the publication of this species name by the inclusion of specimens from St. Brandon's Shoals, which are being awaited from the Smithsonian Institution.)

Description:

dorsal fins, III+XIII-XV+10-11 (holotype III+XIV+II), usually III+XIV+II, first dorsal slightly lower than, or equal to, second dorsal, slightly higher in males than in females;

anal fin, I,19-21 (holotype I,21), usually 21 rays;

pectoral fins, 16-17 rays, upper ray undivided, lower 7 rays thickened and undivided, remainder divided once;

caudal fin, 9-10+7+6+9-10;

lateral line, 22-28 (holotype 25), usually 24-25, pored scales curving down behind pectoral fin and ending below anterior half of third dorsal fin;

lateral series, 38-41 (holotype 40), usually 39;

transverse series, 6/10;

vertebrae, 10 precaudal, 26-28, usually 27, caudal,

PLATE 4



Helcogramma fuscopinna sp. n., male
above, female below.

head 3,2-3,7, depth about 4,6 in S.L.; eye 2,6-3,1, upper jaw 2,0-2,4, snout 2,9-4,2 in head; peduncle depth 1,2-1,6 in peduncle length; snout angle 68° - 73° .

The head, nape, abdomen and pectoral fin bases are naked. The body scales are ctenoid and do not extend to the bases of the first and second dorsal fins, leaving a naked strip down either side of these fins. Small, simple orbital and anterior nasal tentacles are present. The pelvic fin rays are united by a membrane for half to third of their length.

Colour (Plate 4.)

Freshly caught adult males have an orange-pink body against which the dusky anal and first two dorsal fins are conspicuous. Scales generally have a row of small melanophores along the posterior edge. Small dusky rosettes are scattered over body, generally more densely below the midline. In very darkly pigmented specimens a row of five or six grey-white blotches with small black stipples above and below the midline stand out. These sometimes form faint vertical bands. In these specimens there may also be two pairs of white blotches on either side of the dorsum at the posterior ends of second and third dorsal fins, in the latter instance forming a saddle on the caudal peduncle. A distinct blue white line with very fine black stipples extends from the upper lip on either side of the midline, below the eye to the posterior edge of the preopercle. This line may be continued as two or three 'spots' on the opercle and upper pectoral fin base. Below this line, the lips, head, throat and chest are

heavily stippled with dusky to black spots and rosettes. Above the line there are very few melanophores. The orbital tentacle is black; whereas the nasal tentacle is unpigmented. The nape and interorbital area is pinkish. The orange-pink fades in preservative, as does the blue-white of the eye-line. The first two dorsal fins are heavily stippled; the stippling on third dorsal is lighter and occurs mainly on the edge of the fin. The anal fin is darkly pigmented, and the caudal fin is slightly darker than the third dorsal, but not as dark as the second. Melanophores decrease in size from the fin base to the margin of the fin and grade from dark brown at the base to black at the margins. The lower half of the pectoral fins is darker than the upper, and there is an oblique white blotch on the mid-pectoral fin base. The melanophores on the lower portions of the base tend to coalesce, forming a large dark blotch. The pelvic fins are finely stippled, and are darker basally than distally. Females and juveniles range from having virtually no melanophores in small specimens to larger females with the lower half of the body very lightly dusted with small melanophores and with dusky margins on the anal and first two dorsal fins. There are also small stipples on the lower portion of the pectoral fin base, mid-opercle, below the eye and on the snout and nape. The orbital tentacle is dark. There may be white blotches at the posterior ends of the second and third dorsal fins.

Etymology:- The name is derived from the combination of the Latin fuscus (dark coloured) and pinna (fin), referring to the dark dorsal and anal fins. The name is to be treated as a noun in apposition.

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TABLE I

Comparative features of five species of Helcogramma
from the Western and central Indian Ocean.

	<u>H. ellioti</u> ? specimens	<u>H. fuscopinna</u> 75 specimens	<u>H. obtusirostre</u> 106 specimens	<u>H. shinglensis</u> 4 specimens	<u>H. steinitzi</u> 88 specimens.
Second dorsal fin spines (usual number)	13	13-15 (14)	12-14 (13)	12,13	12-14 (13)
Third dorsal fin rays (usual number)	8-10*	10-11 (11)	9-11 (10)	9	10-12 (11)
Anal fin rays (usual number)	16-19* (18)	19-21 (20-21)	17-20 (18-19)	20	19-21 (20)
Lateral line scales (usual number)	24	22-28 (24-25)	19-29 (22-24)	20-22	21-27 (25)
Head in S.L. (mean)	2,9-3,2	3,2-3,7 (3,4)	3,2-4,1 (3,6)	3,0-3,8	3,1-3,5
Eye in head (mean)	3,3-3,4	2,6-3,1 (2,9)	2,8-3,6 (3,2)	2,7-3,0	
Snout angle (mean)	"nearly* vertical"	68-73°	73-80°		
Scalation: (a) nape	naked	naked	naked	naked	scaled
(b) at base of D ₁ & D ₂		naked	naked	naked?	scaled
water depth taken	inter- tidal	5-8m	0-8m	inter- tidal	0+m

Data for H. ellioti from Herre (1944) and Lal Mohan (1971). (The figures flagged with an asterisk were taken from Herre, the others from Lal Mohan. Lal Mohan gives dorsal fins III+XIII+11, anal fin I, 20 in his key which disagrees with the original description).

Data for H. steinitzi from Clark (in press).

Discussion

There are five species of Helcogramma recorded from the western and central Indian Ocean. viz. H. ellioti (Herre), H. fuscopinna sp.n., H. obtusirostre (Klunzinger), H. shinglensis Lal Mohan, H. steinitzi Clark (in press). The salient comparative features of these five species are given in Table I.

Herre (1944) provides a very detailed description of the colour pattern of H. ellioti. The males of this species are brilliant blue on the ventral half of the head and trunk where the other species are dark-brown to black. H. ellioti males also have a brilliant blue anal fin and lighter blue caudal and dorsal fins, and a bright blue ocellus outlined in golden-red on the pectoral fin base. This unusual colour pattern and the lower number of rays in the third dorsal fin (according to Herre, see above), distinguishes H. ellioti from the other species. H. steinitzi is the only one of the five species with a scaled nape. There appear to be few features to distinguish H. shinglensis from H. obtusirostre. Lal Mohan's (1971) description of the former species is based on three specimens. The colour description bears similarities to that of H. obtusirostre and it is possible that these are the same species. H. fuscopinna is the only one of the five species with 14 spines in the second dorsal fin. It is similar in colour to H. steinitzi but lacks a scaled nape. H. fuscopinna certainly differs from H. obtusirostre in colouration, relative eye size, and snout length (see below). H. fuscopinna is also the only species which appears to live in deeper water than any of the other Helcogramma species.

Helcogramma obtusirostre (Klunzinger, 1871) Plate 5.

Tripterygium obtusirostre Klunzinger, 1871:498, Red Sea.

Clark (in press) has redescribed this species, as well as several other tripterygiids from the Red Sea. A description is given here for the purposes of comparison. The data has been taken from South African specimens.

Description:

dorsal fins, III+XII-XIV+9-11, usually III+XIII+10, first dorsal fin lower than second dorsal fin, slightly higher in males than in females;

anal fin, I,17-20, usually 19 rays;

pectoral fins, 16-17 rays, upper 1-2 rays undivided, lower 7 rays thickened and undivided, remainder divided once;

caudal fin, 8-10+7+6+8-10;

lateral line, 19-29, usually 23-24 pored scales curving down behind the pectoral fin and ending below the anterior half of the second dorsal fin;

lateral series, 38-43, usually 40;

transverse series, about 6/6;

vertebrae, 10 precaudal, 25-27, usually 26, caudal;

head 3,2-4,1, depth about 4,5 in S.L.; eye 2,8-3,6, upper jaw 2,1-2,7; snout 2,8-3,9 in head, peduncle depth 1,1-1,7 in peduncle length; snout angle, 70°-80°.

PLATE 5



Helcogramma obtusirostre (Klunzinger),
male above, female below.

The body scales are ctenoid. The head, nape, abdomen and pectoral fin bases are naked, as are the areas at the base of the first two dorsal fins. Small, simple orbital and anterior nasal cirri are present. The pelvic fin rays are united by a membrane for about half their length.

Colour (Plate 5.)

Live males have rich, dark brown to black bodies which are irregularly barred and blotched with pale brown and silver-blue. The lower portion of the head and throat are black as is the center of the pectoral fin base. The nape is dark red, and there is a patch of red on either side of the midline on the upper lip. The snout and the interorbital area are dark olive-green. The dorsal and ventral corners of the pectoral fin base are crimson. There is a bright, electric-blue line from the lower lip, through the corner of the mouth nearly to the posterior edge of the opercle. Except for the proximal halves of the pelvic fins, which are crimson, and the first dorsal fin, which is variably light to dark brown, the other fins are generally pale pink and dotted with brown to black melanophores.

Females are considerably less pigmented and have a whitish body and head, with light and dark brown rosettes scattered over the dorsum. The rosettes form faint bands on the body below the midline, and irregular blotches on cheeks, lower lip and pectoral fin bases.

In preservative the whole body of males is darkly spotted with melanophores except the snout, the upper portion of the head, nape, abdomen, base and proximal half of the pelvic fins. In some the abdomen is lightly pigmented. There are two unpigmented areas on either side of the upper lip. The central portion of the upper lip, isthmus and lower portion of the face is very heavily pigmented. The opercles, preopercles and branchiostegal membranes are darkly spotted. There are 2-3 pale saddle-bands on the body extending from dorsum to midline, but there may be less distinct bands between the saddle bands. The first band extends from middle of the second dorsal fin, the second is at posterior end of the second dorsal fin and the third lies at the posterior end of the third dorsal fin. The area around the first dorsal fin is less pigmented than the rest of the body. The third dorsal and caudal fins are unpigmented. The anal fin is dusky with dark tips to the rays, and the distal half of each pelvic fin ray is dark to black. The first and second dorsal fins are dusky with darker edges. There is a black triangle at the mid pectoral fin base, with an unpigmented area below this triangle. The ventral half of each pectoral fin is dusky. In less pigmented individuals the saddle-bands on the body become broader and more distinct.

Females and juveniles are considerably less pigmented. Between the dorsum and midline there are 10-12 indistinct irregular vertical brownish bars, and 13-14 from midline down, which do not reach anal-fin. The last 5-6 bars are continuous across the body. Below the midline is a series of irregular white blotches between some

of the lower bars. The isthmus and pectoral fin bases are lightly dusted with melanophores. Two irregular brown bands run obliquely from the antero-ventral corner of the eye onto the upper lip on either side of the midline. The first two dorsal fins have dusky edges, the anal fin 8 faint vertical dusky bars, and the lower half of the pectoral fins are lightly spotted. The caudal, first dorsal and pelvic fins are generally unpigmented. Large females sometimes show a lighter rendering of the male colour pattern.

Discussion

Most species attributed to Helcogramma appear to be very similar both in meristics and colour patterns. Fin counts fall into a relatively small range and frequently the meristic differences amount to a single fin element. Some species, such as H. steinitzi, H. chica and H. quadrimaculatus, differ only in the extent of the scalation.

This degree of similarity between species is not restricted to Helcogramma, but is also present in other genera. The meristic characters of the Mediterranean Tripterygion tripteronotus and T. delaisi (= xanthosoma, Wirtz, pers. comm.) overlap to such an extent that they are separated readily only on breeding colours and ecological factors. (Zander & Heymer, 1970). Enneanectes pectoralis can be distinguished from E. jordani only by the presence of cheek scales and lack of barring on the caudal fin (Rosenblatt, 1960).

The two South African Helcogramma species can usually be separated on dorsal and anal fin counts and on colouration (Plates 4 & 5). However, reference to figure 11 and tables IV-VIII shows there is an overlap in most of the meristic counts and morphometric measurements of H. fuscopinna and H. obtusirostre. But H. obtusirostre undergoes significant change in colouration with water depth.

Fishes inhabiting relatively deep water may differ from others of the same species, or of closely related species which inhabit shallow water in several ways (Rosenblatt, 1963). In deep water forms, the amount of melanin is reduced, fins are higher and more delicate, the skin covering fins and scales is thinner, the body is less robust and usually more strongly laterally compressed, and the eyes are larger.

Rosenblatt (1963) illustrates these differences with the clinid genus Gibbonsia. G. erythra and G. elegans have similar geographic ranges. G. erythra occurs in deeper water than G. elegans, but the latter species has a greater bathymetric range. Deep water representatives of G. elegans differ from shallow water representatives in many of the same ways that G. erythra differs from shallow water G. elegans. It is suggested that the bathymetric variation in G. elegans be regarded as phenotypic (Rosenblatt, 1963). The scorpaenid, Scorpaena guttata also displays differences between deep and shallow water forms, but in this instance the differences are genotypic. Differentiation in this species has not proceeded to the specific level.

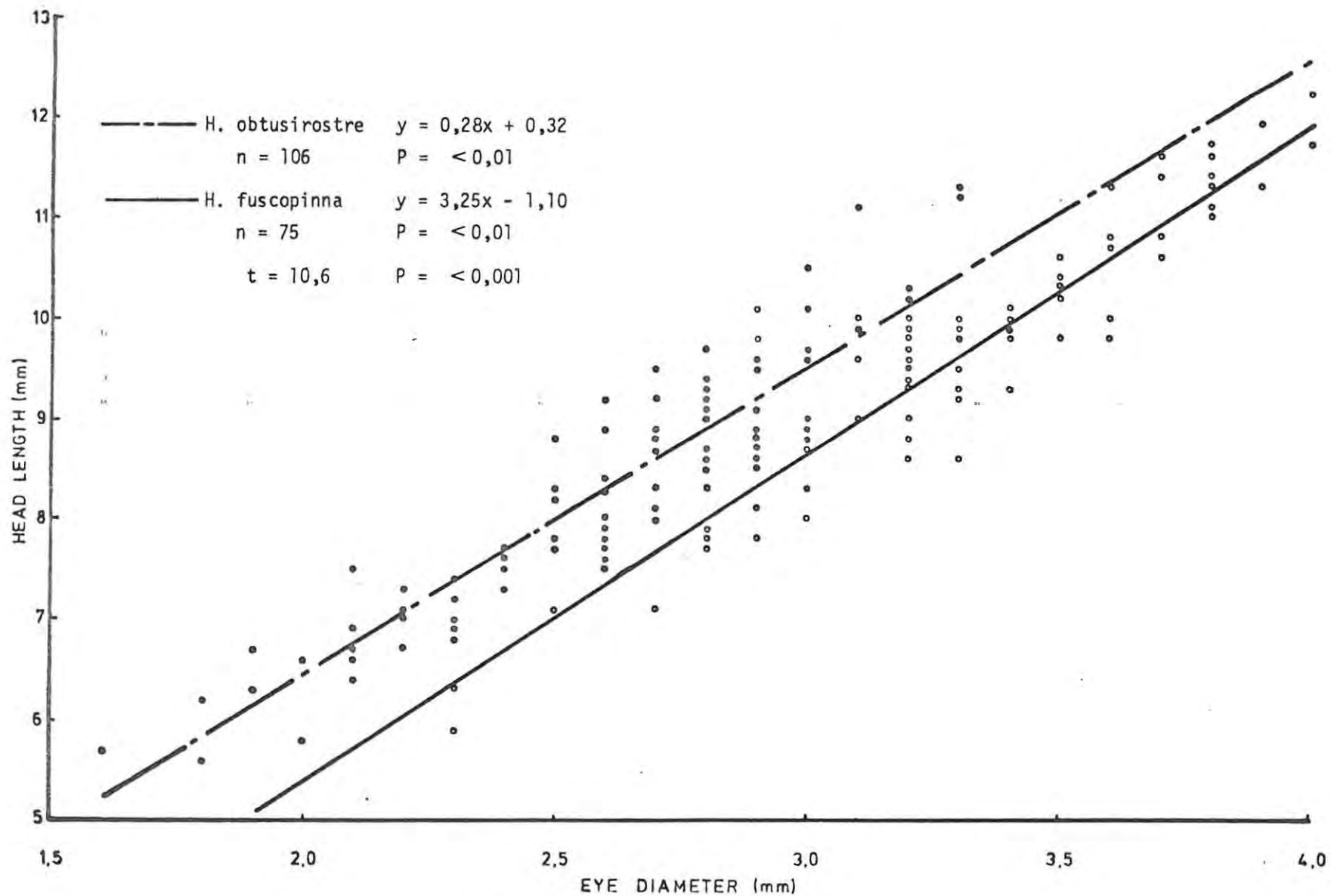


FIGURE 6 Relationship between head length and eye diameter of Helcogramma fuscopinna and H. obtusirostre

In South African waters H. obtusirostre has not been taken in depth greater than 8 m while H. fuscopinna has not been taken in depth less than 5 m. (H. fuscopinna specimens from East Africa were taken in less than 5 m - M.M. Smith, pers. comm.). There is no variation in colouration in specimens of H. fuscopinna taken at 5 m and at 15 m. H. obtusirostre specimens taken at 8 m differ considerably in colouration from those taken at 0-3 m. The colouration of shallow water H. obtusirostre is as described above. Specimens taken at 8 m have considerably less pigmentation, and are very similar in overall colour pattern to H. fuscopinna.

The two South African Helcogramma species may well illustrate some of the trends referred to by Rosenblatt (1963). H. fuscopinna and deep water H. obtusirostre have less pigmentation than shallow water H. obtusirostre. H. fuscopinna also has relatively larger eyes (mean 2,9 in head) than H. obtusirostre (mean 3,2 in head) (table 5, figure 6). There is no difference in eye size between shallow and deep water specimens of either species.

The difference in eye size between those two species was also found by Zander & Heymer (1970) when comparing Tripterygion tripteronotus and T. delaisi in the Mediterranean. T. delaisi, which has a relatively large eye, is a deep water dweller which occurs at 3-25 m (preferentially at 6-8 m), and T. tripteronotus, with a relatively smaller eye, is a shallow water dweller. It is found preferentially at 0-2 m, and has never been taken at depths greater than 6 m.

It may then be inferred that the decrease in pigmentation with increasing depth of H. obtusirostre is phenotypically determined, whereas the eye size of the two species is genotypically determined.

Genus Enneapterygius Rüppell, 1835.

Enneapterygius Rüppell, 1835:2.

Type species Enneapterygius pusillus Rüppell, 1835, by original designation, Red Sea.

Clark (in press) states that some 30 species are referable to this genus. A survey of the literature indicates that the number is somewhat less - about 24 species, including the six new species described by Clark from the Red Sea.

Four species are recognized from South African waters, and these can be divided into two groups. According to the form of the supraoccipital sensory canal. In two species it is crescent-shaped, and in two it is 'U'-shaped. Clark (in press) also makes note of this feature in two Red Sea Enneapterygius species.

An investigation of the osteology of Enneapterygius (described in Part II) showed that significant osteological features are associated with the different forms of the supraoccipital canal. The two groups within Enneapterygius were found to differ osteologically to a similar or greater degree from each other than Enneapterygius, sensu lato, differs from other genera. It was thus considered logical to divide the genus into two genera, based on the form of the supraoccipital canal and associated osteology, and to describe a new genus for those species with a crescent-shaped supraoccipital canal.

It will also be shown in the section dealing the comparative osteology of various genera that there are features over and above those associated with the supraoccipital canal which separate the

two genera. Since only Clark (in press) describes the form of the supraoccipital canal, only Red Sea and South African Enneapterygius species can be allocated to either of the two genera.

Diagnosis of the genus Enneapterygius.

The first dorsal fin has three soft spines, the second 11-14 soft spines, and the third, 8-11 segmented rays. The last ray is usually double. The anal fin comprises one short, soft spine and 17-22 segmented rays, again with the last ray usually double. The lateral line is divided into an anterior series of 9-15 pored scales which ends below the second dorsal fin, and a posterior series of 21-28 notched scales which continues from one or two scale rows below the end of the anterior series onto the caudal peduncle. The supraoccipital sensory canal is 'U'-shaped, curving around the first dorsal fin. Ctenoid scales cover most of the body except the abdomen and pectoral fin bases, which are naked. The head and nape are also naked. The vomer has one to three rows of coniform teeth; the palatines are edentate. There are 10 precaudal and 24-27 caudal vertebrae.

Discussion.

Four species can at present be referred to this genus: E. pusillus Rüppell, the type species, E. pallidus Clark (in press), and two new species, E. pulcherrimus and E. triangulus, which are described here.

The first two species do not occur in South African waters, and descriptions or diagnoses are consequently not provided. Norman (1922) records (without description) E. pusillus from Natal which may be E. pulcherrimus. Fowler (1934) provides a description for

a single specimen of E. pusillus from Zululand, but the description, particularly of the colouration, fits E. triangulus and not E. pusillus. Clark's meristic data (in press) for E. pusillus and E. pallidus are given in tables IV-VII, and the data for the four species are summarized in table II.

The two South African species can be distinguished as follows:

- (a) First dorsal fin lower than second, distinct black pre-anal triangle, body with about six dark blotches, sometimes forming half bars below the midline, anal fin with six dark bars, pelvic fins unpigmented Enneapterygius triangulus sp. n.
- (b) First dorsal fin higher than second, no preanal triangle, no bars on body or anal fin, multicoloured when alive with dusky belly and proximal 2/3 of pelvic fins black
..... Enneapterygius pulcherrimus sp. n.

Enneapterygius triangulus sp. n. Figure 7.

Material examined

Type series

- (a) Holotype, RUSI 6317, female (24,8 mm S.L.), large rock pool 0-3 m, Six Mile Reef, S. of Sodwana Bay, Zululand, South Africa, coll. R. Winterbottom et al., July, 1976;
- (b) 1 paratype, RUSI 6518, male (24,7 mm S.L.), from same collection as holotype;
- (c) 3 paratypes, RUSI 6519, 1 male, 2 females (17,8-25,7 mm S.L.), 0-2 m, same as (a);
- (d) 2 paratypes, (to be donated to BPBM), 1 male, 1 female (25,0 & 25,6 mm S.L.), from same collection as (c);

- (e) 1 paratype, RUSI 6520, male (23,5 mm S.L.), reef at 8 m, and
 (f) 1 paratype, RUSI 6521, male? (27,1 mm S.L.), reef at 11-13 m,
 Jesser Point, Kwazulu, South Africa, coll. M.S. Christensen
et al., June, 1977.

Total 9 specimens, all of which were radiographed.

Description:

dorsal fins, III+XI-XIII+9-10, usually III+XII+9-10 (holotype III+
 XII+9);

anal fin, I,18-19 (holotype I,18);

pectoral fins, 14 rays with upper 1-3 undivided, lower 7 thickened
 and undivided, remainder divided once;

caudal fin, 7-8 dorsal, 6-7 ventral procurrent rays, 7+6 principal
 rays;

lateral line, anterior series 13-15 (holotype 13) pored scales
 ending under the last third of the second dorsal fin and
 followed two scale rows lower by posterior series of 21-22
 (holotype 22) notched scales;

vertebrae, 10 precaudal, 24-26 caudal;

lateral series, 33;

transverse series, 3/3;

head 3,4-3,9, depth about 4 in S.L.; eye 3,0-3,7, upper jaw 2,9-
 3,2, snout 3,0-3,5 in head; peduncle depth 1,1-1,3 in peduncle
 length; snout angle 76° - 78° .

The first dorsal fin is the same height or slightly lower than the
 second. Small, simple orbital and anterior nasal tentacles are
 present. The head and abdomen are naked, and the body scales
 extend to a line between the upper angle of the pectoral fin base
 and the origin of the anal fin. All other characters are as

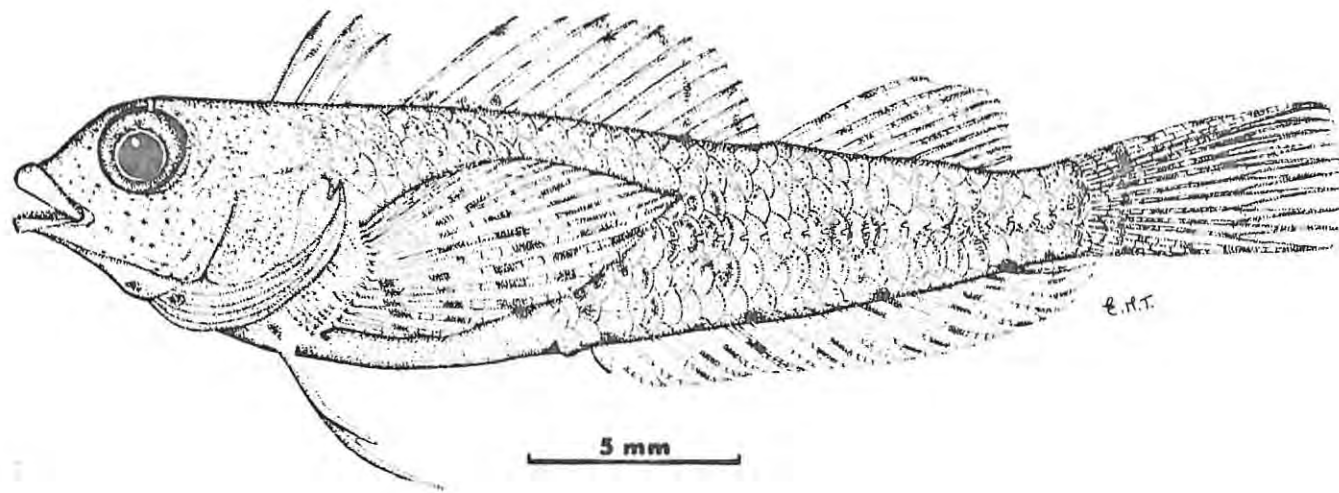
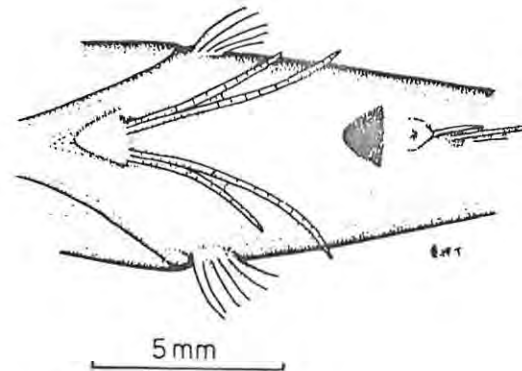


FIGURE 7 A (ABOVE) ENNEAPTERYGIUS TRAIINGULUS SP. N.
HOLOTYPE, FEMALE 24,8 mm S.L., RUSI 6317
B (RIGHT) TRIANGULAR PRE-ANAL MARK OF
e. TRIANGULUS



6317

described for the genus. No sexual dimorphism was noted.

Colour (in preservative)

No live or freshly dead specimens were seen. The body is irregularly pigmented with dark brown to black melanophores, the pigment normally occurring on the posterior edges of the scales. The heaviest pigmentation occurs along the midline and forms a row of irregular dark blotches, the darkest making a bar at the base of the caudal fin. This bar may be divided ventrally to form an inverted 'Y'. The head is lightly spotted with small clusters of melanophores on the cheeks. The lower half of the pectoral fin bases have clusters of melanophores forming narrow bars. There is a dark blotch on either side of the midline on the throat and near the base of the branchiostegals. The abdomen is unpigmented, except for a conspicuous black triangle, which has its apex anterior, and lies just anterior to the anus (figure 7B). The caudal and pectoral fins each have 4-5 irregular, faint dusky bars, with the pigmentation on the rays only, giving the fins a spotted appearance. At the anal fin base, are 5-6 irregularly spaced dark spots which are continued as 'bars' across the fin. Pigmentation occurs only on the rays so that when the fin is extended these spots form a dotted line running from the basal spot obliquely forward. The first dorsal fin is irregularly dusky, while the second may have four broad, irregular bars, and the third three broad irregular bars. There is considerable variation in the intensity of pigmentation in different individuals, though all have a spotted appearance and all have the distinct preanal triangle. No sexual dichromatism was evident.

Etymology:- The species is named for the distinct black pre-anal triangle.

Discussion. This species can be distinguished from the other species referred to this genus by its colouration and higher number of pored scales in the anterior lateral line series (table II).

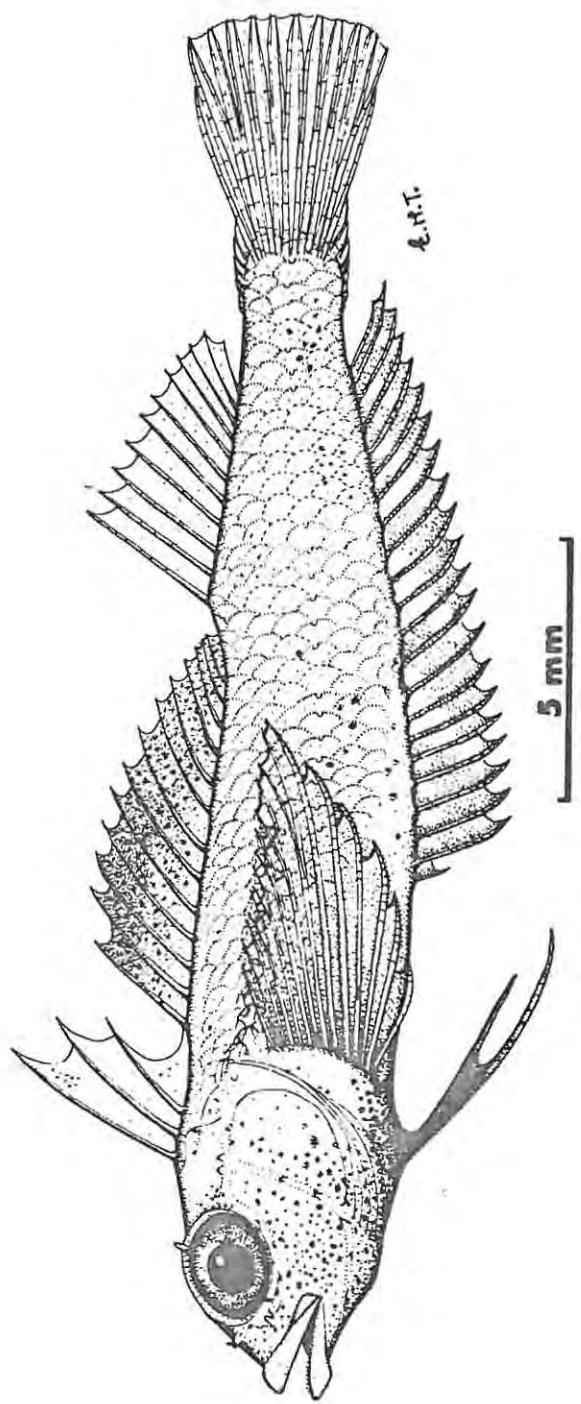


FIGURE 8 ENNEAPTERYGIUS PULCHERRIMUS SP.N. HOLOTYPE, MALE 21,7 mm S.L., RUSI 6522

Enneapterygius pulcherrimus sp. n. Figure 8. Plate 5.

Material examined

Type series

- (a) Holotype RUSI 6522, male (21,7 mm S.L.), rocky reef with corals and sponges, 11-13 m depth, Sodwana Bay, Zululand, South African, coll. M.S. Christensen et al., 17 June, 1978;
- (b) 2 paratypes, RUSI 6523, females (21,6 & 24,5 mm S.L.), rocky reef with corals, 15 m depth, Sodwana Bay, Zululand, South Africa, coll. R. Winterbottom et al., 28 July, 1976;
- (c) 6 paratypes, RUSI 6524, 4 males, 2 females (19,5-22,5 mm S.L.), large rock with sponges surrounded by sand 15 m depth, Sodwana Bay, Zululand, South Africa, coll. R. Winterbottom et al., 25 July, 1976;
- (d) 5 paratypes, RUSI 6525, 2 males, 3 females (17,3--22,9 mm S.L.), sand gully with rock walls, 15 m depth, Sodwana Bay, Zululand, South Africa, coll. R. Winterbottom et al., 26 July, 1976;
- (e) 2 paratypes, (to be donated to USNM), 1 male, 1 female (16,3 & 19,5 mm S.L.), from same collection as holotype, and
- (f) 3 paratypes, (to be donated to BPBM), males (20,1-21,7 mm S.L.), from same collection as holotype.

Total 19 specimens, all of which were radiographed.

Description:

dorsal fins, III+XII-XIV+10-11, usually III+XIII+10-11 (holotype III+XIII+11), first dorsal fin higher than second, more so in males than in females;

50a

PLATE 6



Enneapterygius pulcherrimus sp. n.,
male above, female below.

anal fin, I,20-21, usually I,21 (holotype I,21);
 pectoral fins, 14-15 rays, normally 14, with upper 3-4 unbranched,
 lower 6-7, normally 6, thickened and unbranched, remainder
 branched once;
 caudal fin, 7-8 dorsal, 6-8 ventral procurrent rays, 7+6 principal
 rays;
 lateral line, anterior series of 12 pored scales, first 3 dip down
 over pectoral fin base and remainder continue straight along
 body, posterior of 26 scales, 2 scale rows below anterior series;
 vertebrae, 10 precaudal, 26-27 caudal;
 lateral series, 29 or 30;
 transverse series, 1/2;
 head 3,6-3,9, depth about 4,9 in S.L.; eye 3,0-3,4, upper jaw
 2,0-3,3, snout 3,3-4,1 in head; peduncle depth 1,0-1,4 in peduncle
 length; snout angle 72° - 77° .

The body, except for the head, nape, abdomen and pectoral fin
 bases are covered with ctenoid scales. The scales do not continue
 to the bases of the dorsal or anal fins. Small, simple orbital
 and anal tentacles are present. Other characters are as
 described for the genus.

Colour (Plate 5).

Alive, these fishes are a most beautiful array of reds, green,
 yellow, orange, black and brown. The background colour of the
 body of males is pale cream to white. The scales on the upper
 half of the body are edged with a thin, deep orange line and have
 a few scattered orange and yellow-green spots. On the lower half
 there are 10 orange blotches of coalesced spots along the body,
 with a few small irregular dark, silver-grey spots in between.
 The centre of the abdomen is covered anteriorly with dusky to black
 rosettes, followed posteriorly by a cluster of pale red blotches and then a

'V' (apex anterior) of dusky to black spots just anterior to the anus. The top of the head is laced with subcutaneous green and cream pigment, and has small red surface spots. The 'eyebrows' and orbital tentacles are spotted with crimson. The snout and lips are pale yellow with small orangy-red spots. The cheeks are marked with interspersed black, yellow and red spots. The spotting on the opercle is less intense and lacks yellow. The branchiostegal membranes are pale with black spots. The chin has a few red and black spots. The distal halves of the lower pectoral rays are yellow, while the tips of the upper (divided) rays are pale yellow, and the edges of the mid-upper rays are orange. There is an orange blotch on the proximal half of lower rays, although the lowest ray is unpigmented. Some rays have a green spot at the base. The lower portion of the pectoral fin base carries a large circular, orangy-red mark with a green centre. The first dorsal fin is heavily spotted with light red, the colour being nearly solid between the spines but lighter on the membrane between spine 3 and the dorsum. There are also a few small melanophores on the fin, particularly between the tips of rays 1 and 2. The second dorsal fin is heavily pigmented with dusky to black spots and a few interspersed red spots. The proximal third of each spine is crimson. The fin carries three silvery-transparent vertical bands at spines 5, 9 and 13. The posterior of the fin is edged with a thin silvery-white band. The third dorsal fin is pale to transparent with the rays edged in orange, and there are three completely transparent vertical bars at rays 3 and 6 and at the posterior most point of the fin. In addition there is some black distally between the first two rays. The pelvic fin base and surrounding skin is mottled with deep red and black. Proximally the rays are black, but distally they are covered with small red spots, and the membrane between them is black. Dorsally the

TABLE II

Comparison of selected characters of four species of Enneapterygius.

	<u>E. pusillus</u> 48 specimens	<u>E. pallidus</u> 4 specimens	<u>E. pulcherrimus</u> 19 specimens	<u>E. triangulus</u> 9 specimens.
Second dorsal fin spines (usual number)	11-14 (12)	13-14	12-14 (13)	11-13 (12)
Third dorsal fin rays (usual number)	8-11 (10)	10-11	10-11	9-10
Anal fin rays (usual number)	17-21 (19)	21-22	20-21 (21)	18-19
Lateral line: anterior series (usual number)	8-11 (10)	10-11	12	13-15
posterior series (usual number)	26-28 (26)	28?	26	21-22 (22)
Relative height of D ₁ and D ₂	D ₁ >D ₂	D ₁ <D ₂	D ₁ >D ₂	D ₁ ≤D ₂
Vertebrae: precaudal	11-12	11-12	10	10
caudal (usual number)	23-26 (24)	26-28 (28?)	26-28 (27)	25-26 (26)
live colouration	Multicoloured, no spotting, no preanal Δ	not known, few melanophores no preanal Δ	Multicoloured, no spotting, no preanal Δ	not known, but spotted, distinct preanal Δ

The data for E. pusillus and E. pallidus were taken from Clark (in press). Vertebral counts are not comparable with counts given in this study (see p.95)

caudal fin has dark orange-edged rays with pale orange membranes, and ventrally the fin is pale yellowish-green. The base of this fin is greenish dorsally and has black rosettes on the lower half. The anal fin has a series of pale red blotches at the base of the rays, but the rays are distally unpigmented. There is however fairly intense black and red spotting on the membranes. The colour on the fin decreases posteriorly, and last the 3-4 rays are nearly unpigmented.

Females and immature males show less intense colours and lack the melanin of mature males.

In preservative all pigment except the melanin disappears, leaving the body pale cream in colour with scattered black spots and the black base of the pelvic fins.

Discussion

There appear to be two other species closely related to E. pulcherrimus: E. pusillus Rüppell and E. pallidus Clark (in press). E. pusillus and E. pulcherrimus have similar overall colour patterns, although all E. pusillus specimens examined have a series of eight short dark vertical bars on lower midside not present in E. pulcherrimus. The former species has a lower count for the anterior lateral line series (8-11 vs 12) and a lower average number of anal fin rays - 17-19 compared to 20-21 for E. pulcherrimus (table II).

The colour pattern of live E. pallidus is not known. This species bears greater similarity to E. pulcherrimus in meristics than does E. pusillus.

Differences lie only in the number of scales in the lateral line

(10-11+21 compared to 12+26 for E. pulcherrimus). E. pusillus also lacks the high first dorsal fin of the South African species.

Etymology

The name is derived directly from the Latin adjective and is given for the very beautiful colouration of the fishes of this species.

Genus Scoliosolen gen. n.

This genus is described for those species of Tripterygiidae which are similar to Enneapterygius in external morphology except in the form of the supraoccipital sensory canal.

General characteristics

Like Enneapterygius, there are three soft spines in first dorsal fin, one soft spine in anal fin, and a lateral line divided into an anterior series of pored scales and a posterior series of notched scales. The second dorsal fin has 11-13 soft spines, and the third dorsal fin 8-11 segmented rays, of which the last is usually double. The anal fin has 15-18 segmented rays, bar the last which is usually double. The anterior series of the lateral line has 8-18 pored scales and extends to below the second dorsal fin. The posterior series has 19-23 notched scales, starts one scale row below the end of the anterior series and continues onto the caudal peduncle. The supraoccipital canal is the shape of a posteriorly concave, open crescent (figure 2). The body has ctenoid scales, the head and nape are naked, but the abdomen has ctenoid scales in at least one species which can be referred to this genus, Enneapterygius conspicuus. This species also has a single row of cycloid scales on the pectoral fin base. The vomer bears a single row of small coniform teeth. The South African species also have 3-5 teeth on each palatine. There are 10 precaudal and 22-26 caudal vertebrae.

Discussion

Six species of Enneapterygius can be transferred to Scoliosolen. All are recorded by Clark (in press) from the Red Sea, and two of these are found in South African waters. The six species are

E. abeli (Klausewitz), E. altipinni Clark (in press), E. cinctus Clark (in press), E. conspicuus Clark (in press), E. destai Clark (in press), and E. obscurus Clark (in press). No assessment can be made of other Enneapterygius spp. since no authors other than Clark describes the shape of the supraoccipital canal.

The two species which occur in South African waters are E. abeli and E. conspicuus. Since E. abeli appears to be common in both the Red Sea and Zululand waters it is selected as the type species for the genus Scoliosolen.

Etymology

The name is derived from the Greek skolios (curved), and solen (a channel) in reference to the shape of the supraoccipital caudal. The gender is masculine.

The two South African species are distinguished as follows:

- a. body with four irregular, dark transverse bars, anal fin with 16 or 17, usually 16, raysScoliosolen conspicuus (Clark)
- b. body without bars and bright yellow when alive, males with black head, anal fin 17 to 19, usually 18, rays
.....Scoliosolen abeli (Klausewitz)

Scoliosolen conspicuus (Clark) Figure 9.

Enneapterygius conspicuus Clark (in press), Red Sea.

The species was described from five specimens which were lost en route from Israel to the U.S.A. (Clark, in press). There are small differences between the specimens described by Clark and the

material examined in this study, and these are noted below. This redescription is based entirely on the South African specimens. Clark's data for the original five types are shown in parenthesis.

Material examined.

- (a) RUSI 74-82/1, 4 fishes (18,9-24 mm S.L.), coral reef off Barreira Vermelha, Inhaca Island, Moçambique, coll. T.H. Fraser, 5 December, 1970;
- (b) RUSI 74-90/1, 1 fish (23,6 mm S.L.), same as (a);
- (c) RUSI 76-9/3, 1 fish (21,9 mm S.L.), reef with coral, 15 m depth, Sodwana Bay, Zululand, South Africa, coll. R. Winterbottom et al., 25 July, 1976;
- (d) RUSI 6527, 2 fishes (18,5 & 21,6 mm S.L.), Shimoni, Kenya, coll. J.L.B. & M.M. Smith, November, 1952;
- (e) RUSI 76-1031, 2 fishes (24,1 & 24,9 mm S.L.), rock arch with coral and sponges over sand, 13 m depth, Sodwana Bay, Kwazulu, South Africa, coll. R. Winterbottom et al., 24 July, 1976, and
- (f) RUSI 6526, 1 fish (20,5 mm S.L.), reef with coral and sponges, 14-17 m depth, Sodwana Bay, Kwazulu, South African, coll. M.S. Christensen et al., 18 June, 1977.

Total 11 specimens, all of which were radiographed.

Description:

dorsal fins, III+XI-XII+8-10, usually III+XI-XII+9 (III+XII-XIII+8-9),
 first dorsal equal to or slightly lower than second dorsal;
 anal fin, I,16-17, usually I,16 (I,15-17);
 pectoral fins, 14-15, usually 15 rays with upper 1-3 and lower 7

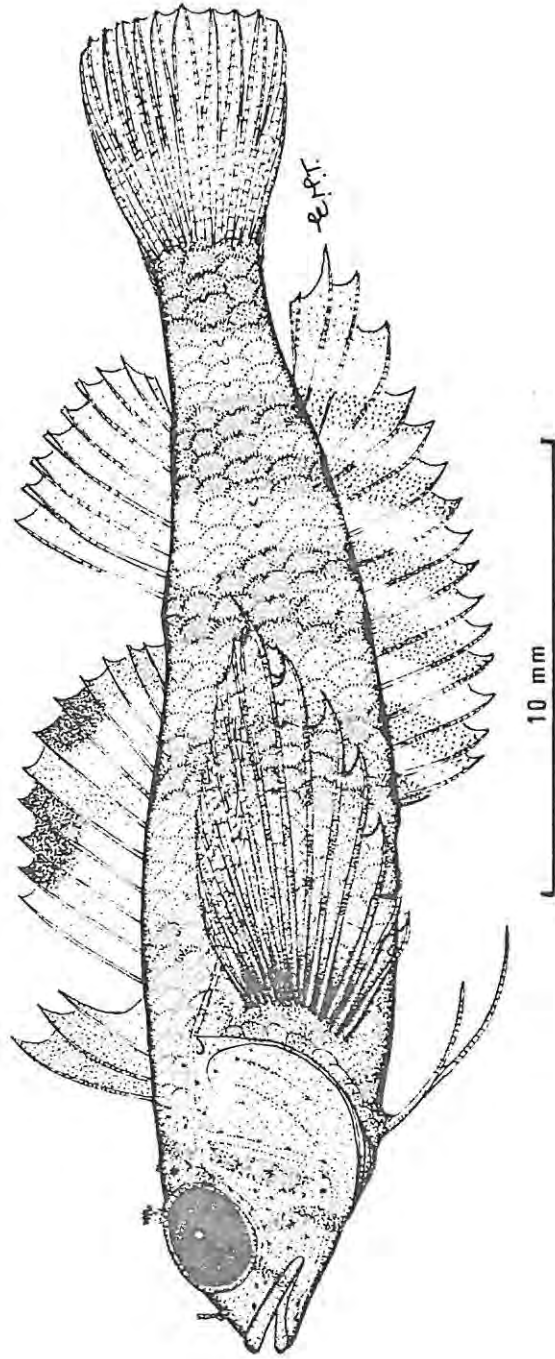


FIGURE 9 SCOLIOSOLEN CONSPICUUS (CLARK), MALE

unbranched, remainder branched once (upper 3 and lower 4 unbranched);
 caudal fin 6-8+7+6+5-6;
 lateral line, anterior series of 11-12, usually 12 (12-13) pored scales, followed one scale row lower by posterior series of 20-22, usually 22, notched scales;
 vertebrae, 10 precaudal, 22-23 caudal;
 transverse series, 3/6;
 lateral series, 29-30;
 head 3,3-3,6 (3,2-3,6), depth about 3,7 in S.L.; eye 3,0-3,3
 upper jaw 2,5-4,0, snout 3,8-4,8 in head; peduncle depth 1,0-1,5 in peduncle length; snout angle 71° - 73° .

The head and nape are naked, while the body, including the abdomen is covered with ctenoid scales. There is a single row of nine thin cycloid scales on the pectoral fin base, running parallel to the edge of the opercle, from the top of the pectoral fin base to the base of the pelvic fins. Both orbital and anterior nasal tentacles are present. The nasal tentacles are narrow and long, have a serrated margin and reach the edge of the orbit. The orbital tentacles are as long as the nasal tentacles, but two to three times as wide, and also have a serrated margin. The pectoral fins are long; the longest ray extending to below the first ray of the third dorsal fin. There is no membrane between the pelvic fin rays.

Colour.

No live or freshly dead specimens were seen.

The side of the body is marked with four conspicuous vertical dark bands which are usually divided ventrally, and may continue onto the anal fin as 5-7 oblique dark bars. The first band extends from the middle of the base of the second dorsal fin, the second from the

TABLE III

Summary of selected meristic data of Scoliosolen destai and S. conspicuus.

	<u>S. destai</u> (Red Sea - 87 spec.)	<u>S. conspicuus</u> (Red Sea - 5 spec.)	<u>S. conspicuus</u> (S.A. - 11 spec.)
Second dorsal fin spines (usual number)	11-13 (12)	12-13 (12)	11-12
Third dorsal fin rays (usual number)	8-9 (9)	8-9 (9)	8-10 (9)
Anal fin rays (usual number)	15-17 (16)	15-17	16-17 (16)
Lateral line:			
anterior series (usual number)	8-12 (10-11)	12-13	11-12 (12)
posterior series (usual number)	19-23 (21-22)	22	20-22 (22)
Vertebrae:			
precaudal (usual number)	10-11 (11)		10
caudal (usual number)	23-26 (24-25)		22-23 (23)

Red Sea figures taken from Clark (in press).

junction of the second and third dorsal fins, the third from the base of the posterior half of the third dorsal fin, and the fourth is on the caudal peduncle. The last bar may be considerably darker than the other, particularly ventrally. There are also one or two less distinct vertical dusky bands on the midside of the body under the pectoral fin. A black pre-anal spot is present. The anterior half to two-thirds of the body and head are dusted with melanophores. The abdomen is unpigmented in females. There are irregular bars on the lower portion of the head and base of the pectoral fin. The pelvic fins are unpigmented. The first dorsal fin is dusky, darker in males than in females, the second dorsal has a dusky edge and faint dusky bars in females, but has a partial black edge in males. There are faint, irregular dusky bars on third dorsal fin, the lower half of the pectoral fins and the base of the caudal fin.

Discussion.

Clark (in press) was unsure whether the five specimens described by her represented a new species or were merely large adults of Enneapterygius destai, another new species from the Red Sea. The description above of conspicuous essentially agrees with Clark's description of conspicuous and not with that of destai. The only meristic difference between the two species is the number of pored scales in the anterior lateral line series (table III). But, Clark does not describe the scalation of either conspicuous or destai. The abdomen of South African conspicuous is entirely covered with ctenoid scales, and it has a single row of cycloid scales on the pectoral fin base. Both these features are absent in destai (Springer, pers. comm.). The two species also differ in colour pattern. The body bars of conspicuous are vertical and very distinct, whereas those of destai, except the bar on the caudal peduncle, are faint and oblique. The peduncular bar of destai is dark and

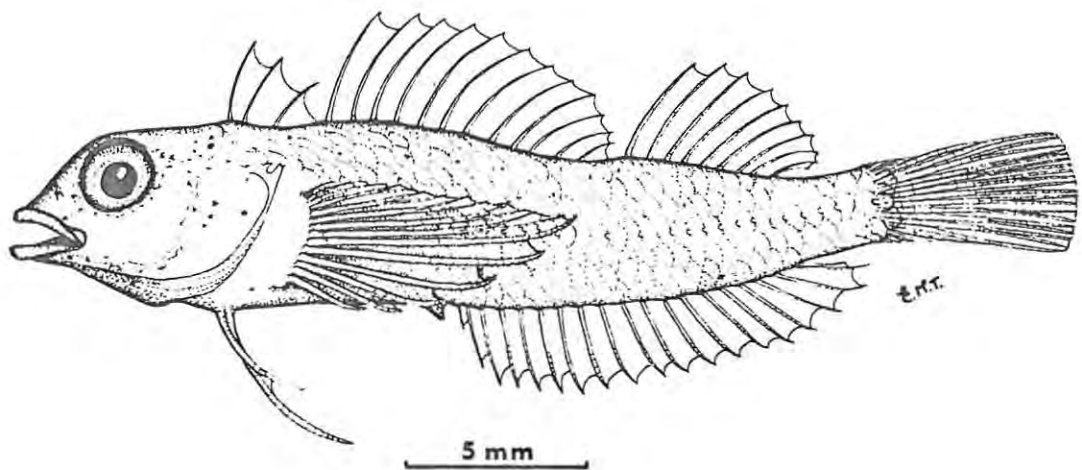
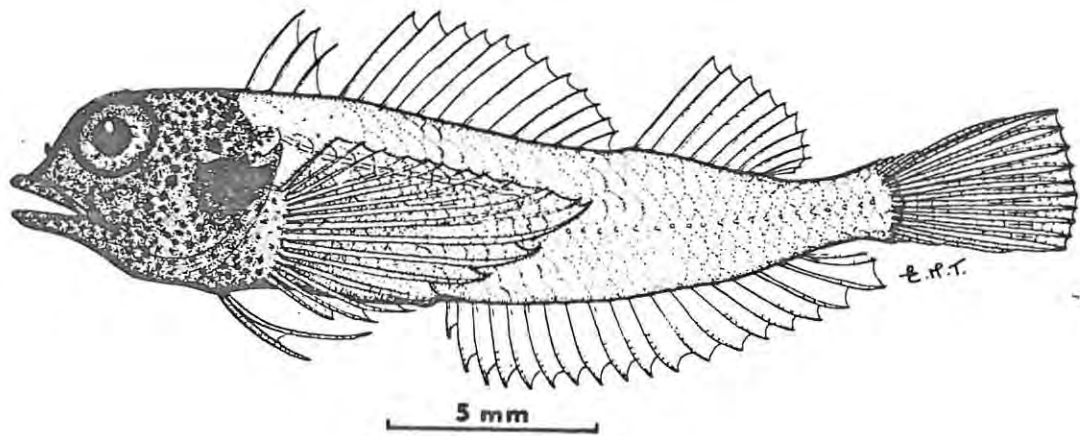


FIGURE 10 SCOLIOSOLEN ABELI (KLAUSEWITZ), MALE (ABOVE) AND FEMALE (BELOW)

constricted in the centre giving the impression of an hour-glass. The two species are thus clearly distinct.

The small differences in meristics between Red Sea and non-Red Sea conspicuous are probably due to the small number of specimens available (table VIII).

Scoliosolen abeli (Klausewitz) Figure 10.

Tripterygium abeli Klausewitz, 1960:11-13, Red Sea.

(Types held in Natur-Museum und Forschungs-Institut Senckenberg).

This species is common in Zululand waters and in the Red Sea, and has been selected as the type species of Scoliosolen. As this species has been redescribed by Clark (in press), and is sufficiently distinct from the other species placed in this genus, a diagnosis only is given here. Morphometric and meristic data for the species are given in Tables I-IV and Figures 6-8.

Diagnosis.

dorsal fins, III+XI-XIII+8-10, usually III+XII+9; anal fin, I,17-10, usually I,18; lateral line, anterior series 12-14 pored scales, posterior series 20-22 notched scales; vertebrae, 10 precaudal, 24-26 caudal. The head, abdomen and pectoral fin bases are naked. The body has ctenoid scales which cover the nape, and extend to the dorsal fin bases. Ventrally the scale line extends from the mid-pectoral fin axil to the second ray of the anal fin. Small, simple anterior nasal and orbital tentacles are present. Each palatine has 3-5 teeth. Other characters are as given for the genus.

Colour.

Live fishes are a bright yellow which fades in preservative. Males have the head, nape, pectoral and pelvic fin bases and anterior portion of the abdomen densely covered with black spots and rosettes,

the most intense black being along the upper jaw. In large males the head is nearly solid black and the body may show irregular vertical bars of darker yellow-orange. Darkly coloured males will also have scattered melanophores on the nape, the antero-dorsal portion of body, as well as a narrow, black edge to the membrane of the first two dorsal fins. Large females may have a few scattered melanophores on the antero-dorsal portion of body, nape, snout, opercle and upper portion of the pectoral fin base.

General comments on tripterygiid taxonomy.

In this portion of the study two new genera and three new species tripterygiids have been described for South African waters.

The first new genus, Cremnochorites, was described for Gillias capensis, since this species could not be placed in any other genus after Rosenblatt (1960) placed Gillias in synonymy with Enneanectes. The second new genus, Scoliosolen, was described as a result of the decision to divide Enneapterygius into two genera. The division is based on the form of the supraoccipital sensory canal and associated osteology. A detailed description of the osteology follows in the next section of the study. It is believed that this division is valid because the degree of difference between the two groups of Enneapterygius is at least of the same magnitude as those which separate many other genera.

An evaluation was made from the literature of which species should be referred to three of the five genera dealt with in this study.

Cremnochorites appears to be monotypic. It is believed that seven species can be referred to Norfolkia and 17 to Helcogramma. It has not been possible to make the same evaluation for Enneapterygius or

Scoliosolen because only Clark's (in press) recent revision of Red Sea Tripterygiidae describes the shape of the supraoccipital canal. Consequently only Red Sea and South African species have been referred to either of these genera.

The literature survey has also revealed a few anomalous species which do not appear to belong in any of the genera dealt with in this study or any of the other genera accepted as valid for the Indo-Pacific. (The Indo-Pacific region as used here excludes the tropical eastern Pacific ocean.) There are three species which have the combination of three first dorsal fin spines, two anal fin spines and a divided lateral line. These are Tripterygium clarkei Morton, Tripterygium striaticeps Ramsay & Ogilby (both from Australian waters and referred to in the section dealing with Norfolkia), and Tripterygium bapturnum Jordan & Snyder, from Japan. The only other genera with the above combination of characters are Enneanectes and Tripterygion. Tripterygion is reputedly endemic to the Mediterranean and northeastern Atlantic (Clark in press), whereas Enneanectes is accepted as a New World genus (Rosenblatt, 1960). These three species may be referable to Enneanectes, which means that either the genus is more widespread, or that a new genus must be described to accommodate them. They may also be placed in a sub-genus of Enneanectes. Until such time as specimens of these three species are studied no further suggestions can be made as to their generic placing.

Another species of tripterygiid, as yet undescribed, which is fairly common on the East African coast and around a number of western Indian Ocean islands, defies generic placing at present. This species has all the external characters necessary to place it in Scoliosolen viz. three first dorsal fin spines, a single anal fin spine, a

divided lateral line, and a crescent-shaped supraoccipital canal. Yet, it differs osteologically from Scoliosolen conspicuus and S. abeli. These two species have palatine teeth, entirely separate ascending and articular processes on the premaxilla, and, in the caudal skeleton a single broad epural and a long neural spine on the second preural centrum (NPU₂). The undescribed species lack palatine teeth, has partially fused ascending and articular processes, two epurals and a short NPU₂.

Here again it is possible that sub-genera for both Scoliosolen and Enneapterygius will have to be erected. This will only be possible when complete revision of these two genera are undertaken.

It is felt that these examples reinforce the argument raised at the beginning of this study - that genera must be very clearly defined, and that such definitions must be based on both external and internal morphology. Colette and Chao (1975) employed a wide variety of external and internal morphological features to provide clear definitions of the genera and species of the bonitos (Sardini, Scombridae). Smith-Vaniz (1976) has defined the genera of the sabre-toothed blennies (Nemophini, Blenniidae) in much the same way.

This taxonomic account is now followed by a detailed description of the osteology of Scoliosolen and a comparison of particular characters of the five genera dealt with in the first part of this study. Finally, definitions of the five genera are provided, based on external morphology as well as osteology.

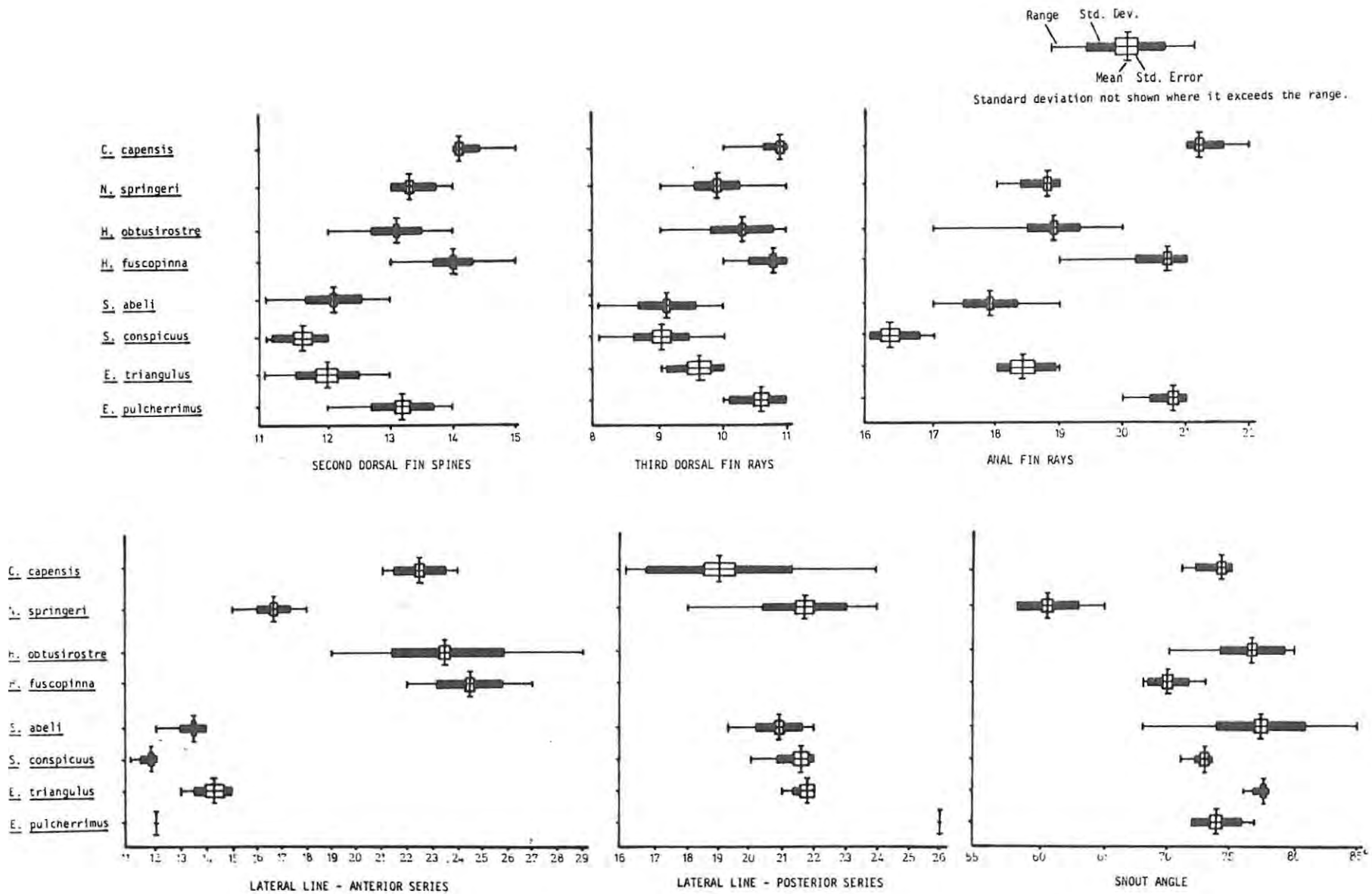


FIGURE 11 RANGES, MEANS, STANDARD DEVIATIONS AND STANDARD ERRORS OF MORPHOMETRIC DATA OF SOUTH AFRICAN SPECIES OF TRIPTERYGIIDAE

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TABLE VII. FREQUENCY DISTRIBUTION OF VERTEBRAL COUNTS.

SPECIES	Precaudal					Caudal vertebrae.							
	9	10	11	12	13	22	23	24	25	26	27	28	
<u>Cremnochorites capensis</u>	23										13	10	
<u>Norfolkia springeri</u>	30								2	25	3		
<u>N. springeri</u> (Red Sea)			4						4				
<u>Helcogramma obtusirostre</u>	30								2	25	3		
<u>H. obtusirostre</u> (Red Sea)			3			1	2	1					
<u>H. fuscopinna</u>	12									3	8	1	
<u>H. steinitzi</u>				5	2			9					
<u>Scoliosolen abeli</u>	1*	19						4	15	1			
<u>S. abeli</u> (Red Sea)			8	4		1	7	2	1				
<u>S. conspicuus</u>	10					2	8						
<u>Enneapterygius pulcherrimus</u>	13									2	10	1	
<u>E. pallidus</u> (Red Sea)			2	1								3	
<u>E. pusillus</u> (Red Sea)			14	12			1	12	6	1			
<u>E. triangulus</u>	12							1*	3	8			

Red Sea figures from Clark, in press.

* Anomalous vertebrae

TABLE VI. SUMMARY OF MORPHOMETRIC DATA.

(Mean values are given in parenthesis)

SPECIES	Head in S.L.	Eye in head	Jaw in head	Snt. in head	P.D. in P.L.	Snout Angle.
<u>Cremnochorites capensis</u>	3,2-3,7 (3,5)	3,0-3,6 (3,3)	2,0-2,4 (2,3)	3,6-4,2 (4,0)	0,9-1,1 (1,0)	71°-75° (74°)
<u>Norfolkia springeri</u>	3,0-3,5 (3,3)	2,9-3,7 (2,4)	2,1-2,6 (2,4)	3,6-4,7 (3,9)	1,0-1,4 (1,2)	58°-65° (60°)
<u>Helcogramma obtusirostre</u>	3,2-4,1 (3,6)	2,8-3,6 (3,2)	2,1-2,7 (2,4)	2,8-3,9 (3,3)	1,1-1,7 (1,3)	70°-80° (77°)
<u>H. fuscopinna</u>	3,2-3,7 (3,4)	2,6-3,1 (2,9)	2,0-2,4 (2,1)	2,9-4,2 (3,5)	1,2-1,7 (1,4)	68°-73° (70°)
<u>Scoliosolen abeli</u>	3,3-3,8 (3,6)	2,9-3,7 (3,3)	2,4-3,0 (2,7)	3,0-4,2 (3,4)	1,2-1,6 (1,4)	68°-85° (77°)
<u>S. conspicuus</u>	3,3-3,6 (3,5)	3,0-3,3 (3,1)	2,5-4,0 (2,8)	3,8-4,8 (4,2)	1,0-1,5 (1,2)	71°-73° (73°)
<u>Enneapterygius pulcherrimus</u>	3,6-3,9 (3,8)	3,0-3,4 (3,2)	2,6-3,3 (2,9)	3,3-4,1 (3,6)	1,0-1,4 (1,2)	72°-77° (74°)
<u>E. triangulus</u>	3,4-3,9 (3,7)	3,0-3,7 (3,3)	2,9-3,2 (3,0)	3,0-3,5 (3,4)	1,1-1,3 (1,2)	76°-78° (78°)

Jaw = upper jaw.

Snt. = snout.

P.D. = peduncle depth.

P.L. = peduncle length.

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TABLE V. FREQUENCY DISTRIBUTION OF SNOUT ANGLE.

SPECIES	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85°	
<u>Cremnochorites</u> <u>capensis</u>														3	1	1	3	4	3	2									
<u>Norfolkia springeri</u>	7	3	8			4		3																					
<u>Helcogramma obtusirostre</u>													1	1		3	1	4	3	8	4	6	3						
<u>H. fuscopinna</u>										7	12	2	3	2	2														
<u>Scoliosolen abeli</u>										1		1				3	3		6	1	5	7	2	4	1			1	
<u>S. conspicuus</u>														1	2	5													
<u>Enneapterygius</u> <u>pulcherrimus</u>															4	2	1	2	2	1									
<u>E. triangulus</u>																				1		5							

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TABLE IV. FREQUENCY DISTRIBUTION OF MERISTIC DATA

SPECIES	FINS: D1		D2					D3				ANAL									
	III	IV	XI	XII	XIII	XIV	XV	8	9	10	11	I	II	15	16	17	18	19	20	21	22
<u>Cremnochorites capensis</u>		26				23	3		2	24		25								21	4
<u>Norfolkia springeri</u>		43			32	11		5	37	1		43			8	35					
<u>N. springeri</u> (Red Sea)		6			4	2			1	5		6				6					
<u>Helcogramma obtusirostre</u>	106			1	90	15		3	64	39	106				1	13	90	2			
<u>H. fuscopinna</u>	75				4	68	3		14	61	74						2	16	56		
<u>Scoliosolen abeli</u>	87		6	70	11			5	68	14	84				14	67	3				
<u>S. conspicuus</u>	11		4	7				1	9	1	11			8	3						
<u>S. destai</u> (Red Sea)	57	2	8	45	6			18	39		57			6	49	2					
<u>Enneapterygius pulcherrimus</u>	19			2	16	1			8	11	19								3	16	
<u>E. triangulus</u>	9		1	7	1				4	5	9					5	4				
<u>E. pallidus</u> (Red Sea)	3				2	1					3	3								1	2
<u>E. pusillus</u> (Red Sea)	48		2	23	13	2		2	14	25	3	48			4	9	28	3	1		

	Lateral line - anterior series																			posterior series														
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	16	17	18	19	20	21	22	23	24	25	26	27
<u>Cremnochorites capensis</u>															5	5	9	3					1	5	2	2	2	1	2		1			
<u>Norfolkia springeri</u>							1	9	16	1															1	1	1	3	12	3	1			
<u>N. springeri</u> (Red Sea)								5	6																			2	2	6	1			
<u>Helcogramma obtusirostre</u>											2	5	5	20	22	13	8	12	4	1	2													
<u>H. fuscopinna</u>															4	7	17	17	7	2	1													
<u>Scoliosolen abeli</u>					3	28	35																			1	5	15	4					
<u>S. conspicuus</u>					2	8																					1	2	6					
<u>S. destai</u> (Red Sea)	1	1	33	20	1																					1		12	16	8				
<u>Enneapterygius pulcherrimus</u>						14																												
<u>E. triangulus</u>						1	2	3																				1	4					
<u>E. pusillus</u> (Red Sea)	3	12	23	2																														

Red Sea figures from Clark, in press.

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PART II - OSTEOLOGY.

To date only one detailed study of tripterygiid osteology has been made. Ruck (pers. comm., 1977) described the osteology of Forsterygion in 1975, but that study has not been published, and is likely to remain unpublished. Reference is made to aspects of tripterygiid osteology in Gosline (1963, 1968), Springer (1968), and Clark (in press). There is a single detailed study of the osteology of the Blenniidae (Springer, 1968), and a number of other references to blenniid osteology (e.g. Makushok, 1958; Stevens, 1963, and Smith-Vaniz & Palacio, 1974). These studies, and Springer & Freihofer's (1976) study of Pholidichthyes leucotaenia Bleeker (Pholichthyidae) have all provided extremely useful guideline for this part of the study. In some instances there is considerable between blenniid and tripterygiid osteology, and these similarities similarly have been pointed out in the text. But, as no complete description of tripterygiid osteology is available, it was necessary to describe the osteology of one genus. Only then could various genera be compared with each other.

Enneapterygius conspicuus was originally selected for the description for two reasons. The genus is reputedly the largest in the family, and it is thus reasonable to assume it is the most generalized. The species was chosen purely for the size of the of the individuals - they are larger, and consequently easier to handle than any of the other Enneapterygius species available. Only when the various South African species of Enneapterygius were compared to select characters consistent in the various species, did the significance of the differences in osteology associated with the two distinct forms of supraoccipital sensory canal become apparent. It thus became clear that Enneapterygius had to be divided into two genera.

METHODS AND MATERIALS.

All specimens came from ichthyocide collections. They were cleared and stained by the enzyme/alizarin red technique as outlined in Mallory (1973). Drawings were made using a stereomicroscope with a drawing tube. The cleared and stained material is listed below.

The osteological nomenclature used in this study has been taken from a number of sources, which are cited in the text.

South African material:

Cremnochorites capensis (Gilchrist & Thompson), RUSI 75-22/1, 2 males (30 & 35 mm S.L.), False Bay, Cape, South Africa; RUSI 76-7/1, 1 male (36 mm S.L.), Skoenmakerskop, Eastern Cape, South Africa;

Enneapterygius pulcherrimus sp. n., RUSI 6500, 1 female (24 mm S.L.), Sodwana Bay, Zululand, South Africa;

Enneapterygius triangulus sp. n., RUSI 6519, 1 female (20 mm S.L.), Sodwana Bay, Zululand, South Africa;

Helcogramma fuscopinna sp. n., RUSI 76-8/2, 2 males, 2 females (32-44 mm S.L.), Sodwana Bay, Zululand, South Africa;

Helcogramma obtusirostre Rüppell, RUSI 74-348, 1 male (33 mm S.L.), Chaka's Rocks, Natal, South Africa; RUSI 76-19/1, 1 male (27 mm S.L.), Sodwana Bay, Zululand, South Africa, 2 males, 2 females (35 & 40 mm S.L.), Coffee Bay, Transkei;

Norfolkia springeri Clark, RUSI 76-8/3, 1 male (31 mm S.L.), RUSI 76-9, 1 female (34 mm S.L.), RUSI 76-11/1, 1 female (26 mm S.L.), all from Sodwana Bay, Zululand, South Africa;

Scoliosolen abeli (Klausewitz), RUSI 76-8/1, 2 females (19 & 24 mm S.L.), Sodwana Bay, Zululand, South Africa;

Scoliosolen conspicuus Clark, RUSI 76-10/1, 1 male (25 mm S.L.),
Sodwana Bay, Zululand, South Africa.

Non-South African material:

Brachynectes fasciata Scott, QVM 1976/5/35, 1 female (35 mm S.L.),
Queen's Beach, Tasmania;

Enneanectes altivelis Rosenblatt, ANSP 126726, 1 male (17 mm S.L.),
Les Saints, St. Batholemey, West Indies;

Enneanectes pectoralis (Fowler), ANSP 126720, 1 male (24 mm S.L.),
Little St. Vincent, Grenadines, West Indies;

Enneapterygius pusillus Rüppell, USNM 205806, 1 female (20 mm S.L.),
El-Tur, Sinai Peninsula, Israel;

Gilloblennius tripenne (Forster), RUSI 6507, 1 male (88 mm S.L.),
New Zealand;

Lepidoblennius haplodactylus Steindachner, RUSI 6512, 1 male (54 mm
S.L.), Tuross Heads, New South Wales, Australia;

Notolinops segmentatum Whitley, RUSI 7930, 1 female (28,5 mm S.L.),
New Zealand;

Notoclinus compressus Hutton, RUSI 7931, 1 male (48 mm S.L.),
New Zealand;

Norfolkia squamiceps (McCulloch & Waite), RUSI 6508, 1 male (44 mm
S.L.), Norfolk Island, Australia;

Tripterygion tripteronotus (Risso), BMNH no number, 1 male (48 mm S.L.),
Banyuls-sur-Mer, France;

Vauclusella annulata (Ramsay & Ogilby), RUSI 6509, 1 female (28 mm
S.L.), Clovelly, New South Wales, Australia, and

Vauclusella rufopileum (Waite), RUSI 6510, 1 female (31 mm S.L.),
Lord Howe Island, Great Barrier Reef.

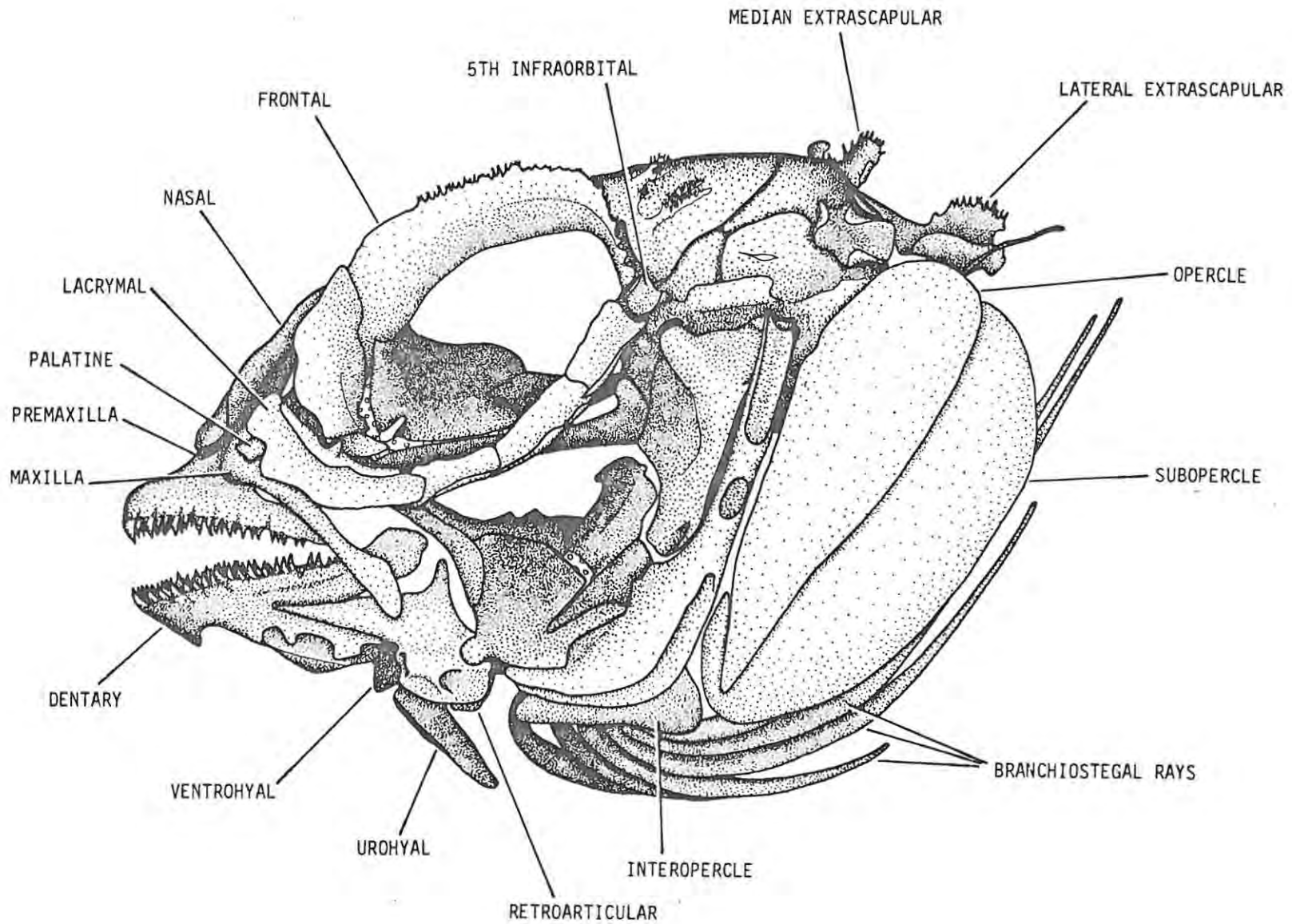


FIGURE 12 LATERAL VIEW OF ARTICULATED SKULL

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THE OSTEOLOGY OF SCOLIOSOLEN CONSPICUUS (CLARK).

The description of the osteology of Scoliosolen conspicuus is divided into three sections:

- 1 - neurocranium and branchiocranium.
- 2 - vertebral column and unpaired fins, and
- 3 - pelvic and pectoral girdles and fins.

Salient features of the osteology of Scoliosolen abeli are compared with S. conspicuus.

Section 1 - Neurocranium and Branchiocranium.

Figure 12 shows an articulated skull of S. conspicuus in lateral view to provide orientation for the descriptions of individual bones.

NEUROCRANIUM (Figures 13-15).

General characteristics. In dorsal view the neurocranium comprises a short, broad brain case, large orbits separated by a narrow interorbital area and bounded anteriorly by a pair of relatively wide lateral ethmoids. The brain case consists of a series of thin plates which have overlapping or synchondral joints with each other. Two prominent lateral bulges run the length of the brain case. These are formed predominantly by the walls of the horizontal semicircular canal in the pterotics.

The ventral surface of the neurocranium is formed by the vomer, lateral ethmoids, parasphenoid, basioccipital, exoccipitals, pterotics, intercalars, prootics and sphenotics. There is a

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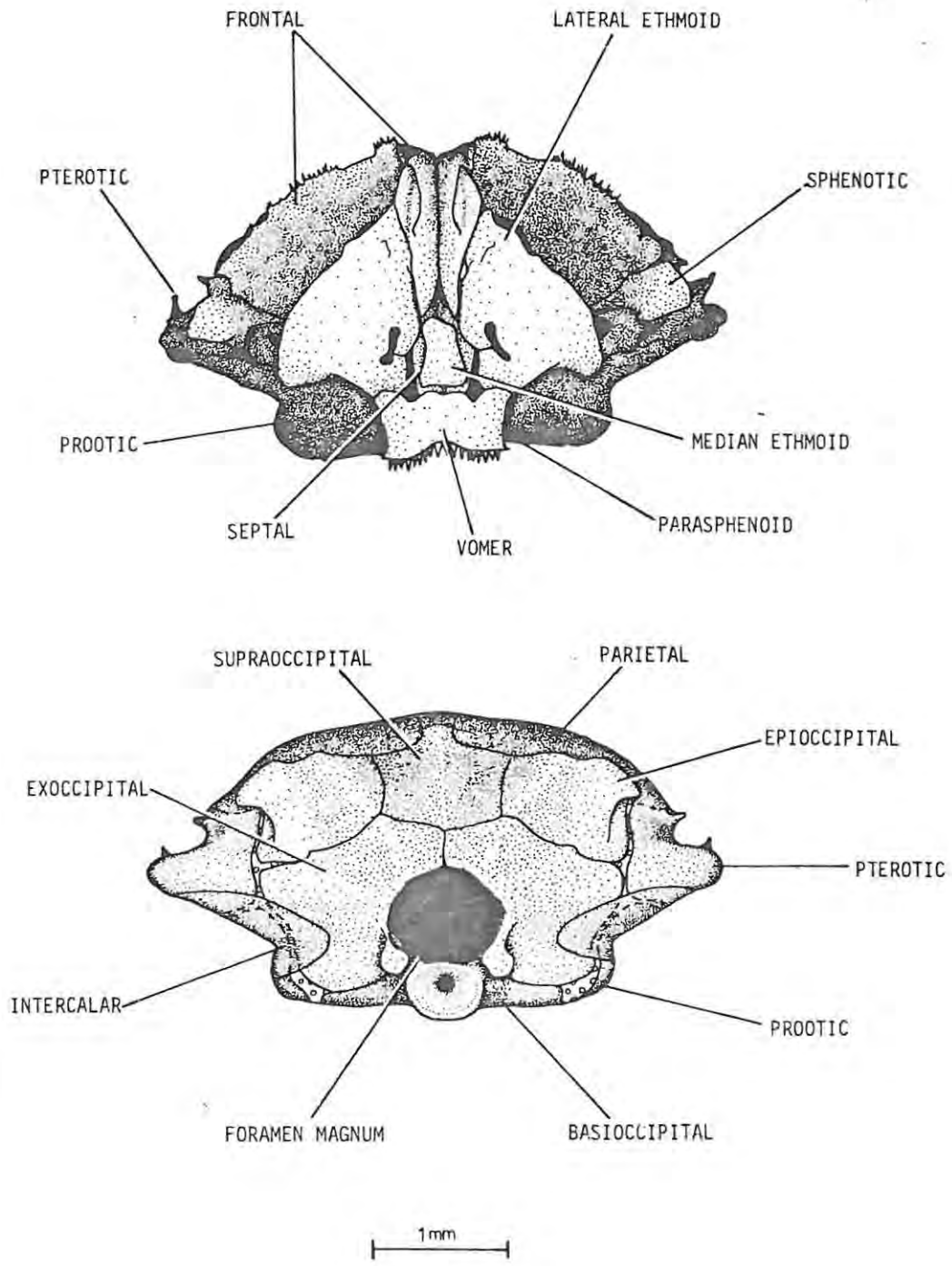


FIGURE 15 ANTERIOR AND POSTERIOR VIEWS OF NEUROCRANIUM

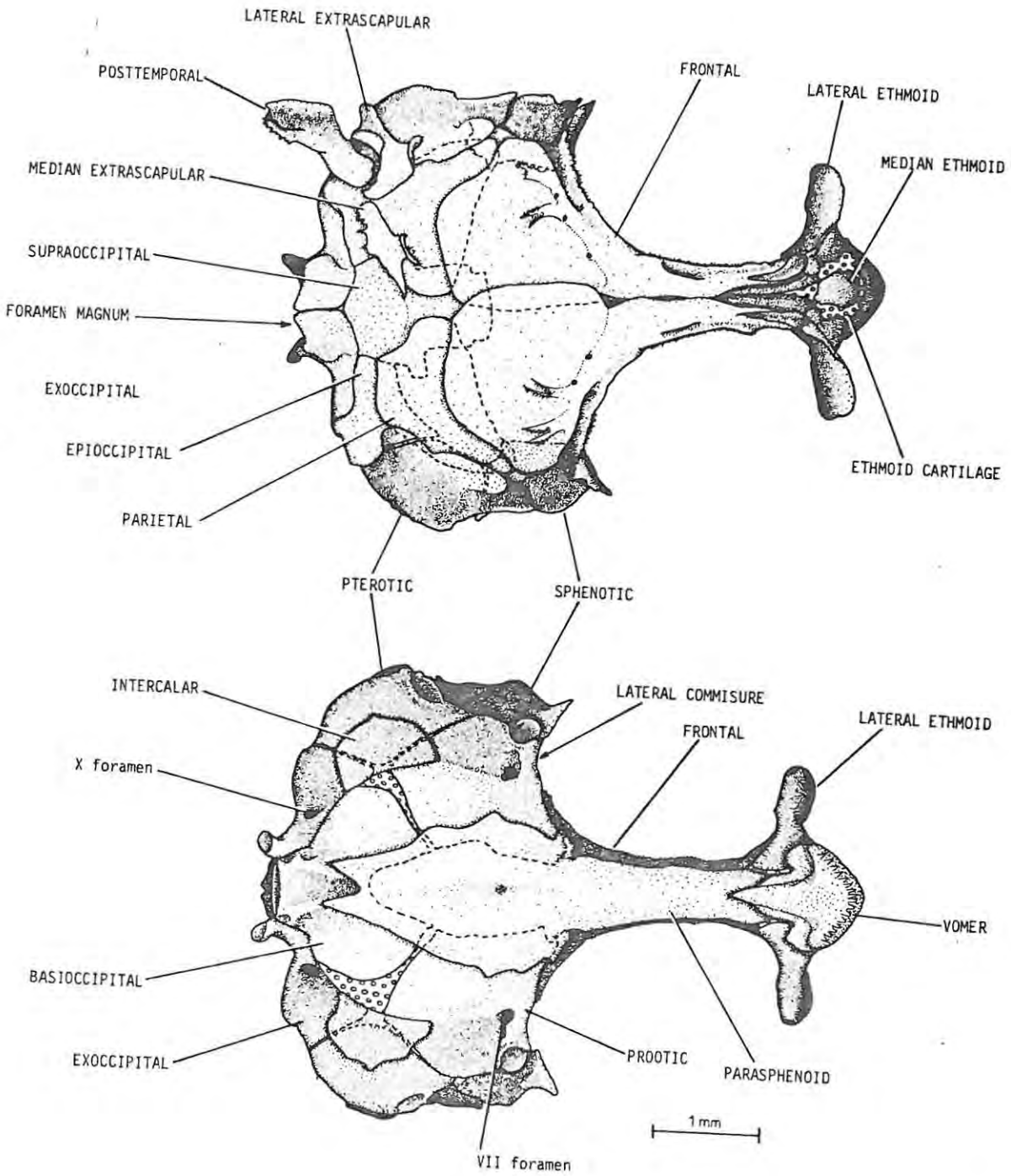


FIGURE 14 DORSAL AND VENTRAL VIEWS OF NEUROCRANIUM

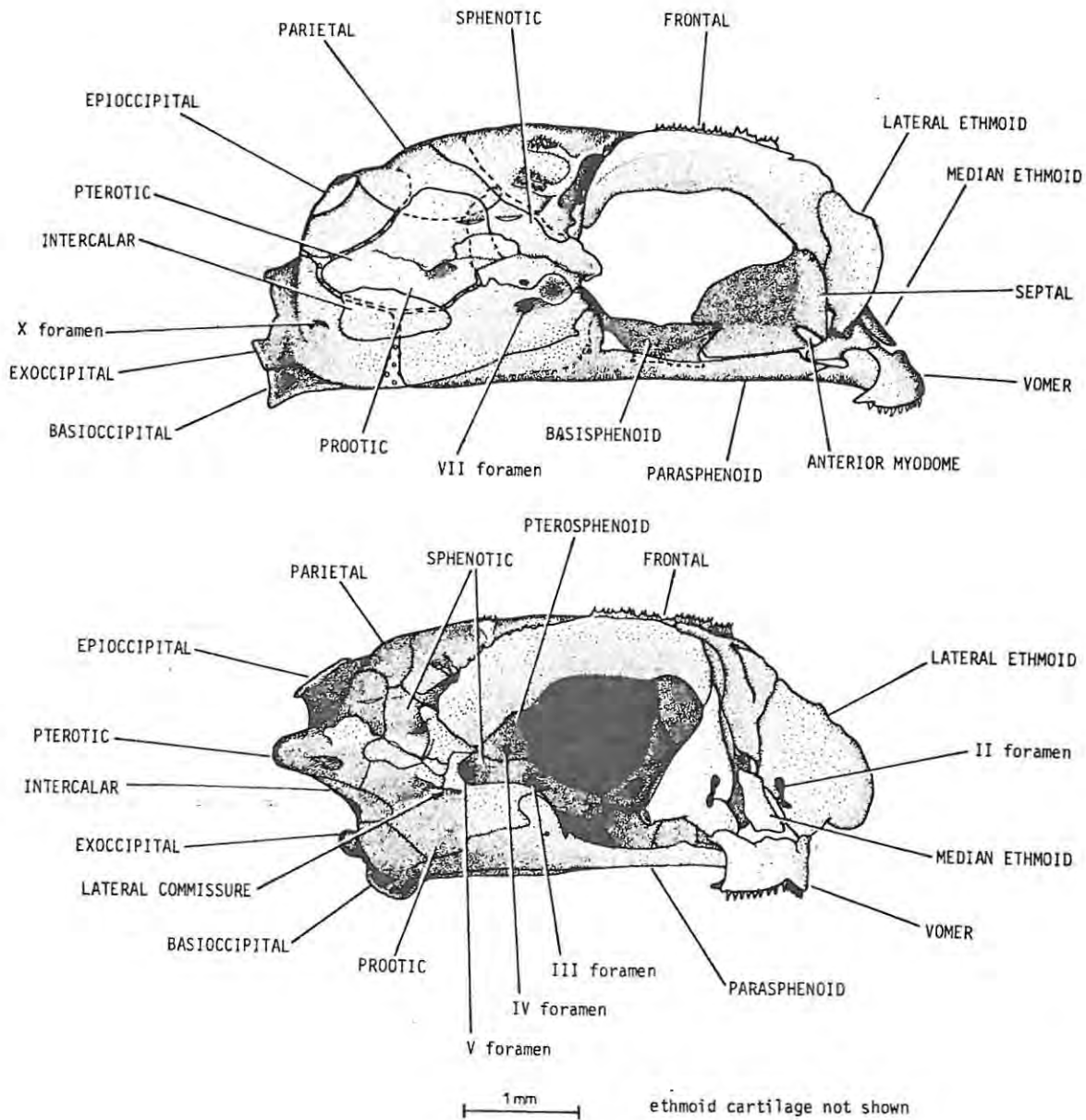


FIGURE 13 LATERAL AND ANTEROLATERAL VIEWS OF NEUROCRANIUM

median gap between the anterior edge of the basioccipital and the overlapping posterior edge of the parasphenoid. The two longest pairs of eye muscles (the rectus internus and rectus externus) pass through this gap to originate on the ventral surface of the basioccipital just anterior to the condyle (Winterbottom, 1974).

In lateral view the neurocranium is roughly trapezoidal. The orbits are rounded and bounded by the posterior surfaces of the lateral ethmoids, the ventral surfaces of the frontals, the pterorsphenoids, median extensions of the prootics and sphenotics and the anterior dorsal margins of the parasphenoid. They are partially separated dorsally by the ventral margins of the frontals, and ventrally by the basisphenoid and septal (Springer & Freihofer, 1976) which together extend along the entire length of the orbit.

Viewed posteriorly the neurocranium is seen to be compressed, and the lateral bulges of the pterotics are conspicuous. The posterior surface of the brain case is formed by the posterior portions of the basioccipital, exoccipitals, supraoccipital and epioccipitals (Patterson, 1974).

The neurocranium is treated in five sections following Patterson (1974) and Collett & Chao (1975). These are the ethmoid region, the orbital region, the otic region, the occipital region, and the parasphenoid. Collett & Chao (1975) used only four divisions, including the parasphenoid in a basicranial region. These authors also include the supraoccipital and intercalars in the otic region of the neurocranium. In this description, following Patterson (1974), these bones are treated with the other components of the occipital region. The parasphenoid is treated separately.

Ethmoid Region. This region is composed of the median ethmoid, lateral ethmoids, the vomer, the ethmoid cartilage, and the nasals which lie over the median ethmoid.

Median Ethmoid. This median ossification has been variously referred to as the 'ethmoid' (Collett & Chao, 1975), the 'mesethmoid' (Makushok, 1958; Patterson, 1974); and the 'median ethmoid' (Springer, 1968; Springer & Freihofer, 1976). Springer's (1968) nomenclature is followed here.

It is an irregular, flat bone with slightly convex surfaces which covers most of the anterior surface of the ethmoid cartilage. It lies between the lateral ethmoids, the most anteroventral extensions of the frontals and anterior dorsal edge of the vomer.

Lateral Ethmoid. The paired lateral ethmoids form the posterolateral walls of the ethmoid region and the anterior wall of each orbit. Each is a broad, fan-shaped, laterally projecting bone with an anteriorly convex surface. The frontals overlap each lateral ethmoid dorsally. Ventrally the median margin of each is expanded anteriorly and posteriorly to form a triangular concavity on the ventromesial surface which cups the ethmoid cartilage laterally. The ventral margins of these concavities suture with the dorsolateral margins of the vomer. The mesial margins of these bones abut the anterior margins of the septal.

A condyle on the ventrolateral corner of each, the lacrymal articulation facet of Barel et al. (1976), articulates with their respective lacrymals. The ventral margin of the laterally extending wing of each lateral ethmoid is slightly convex and articulates with the anterior ends of the palatines.

The olfactory foramen perforates each bone ventromedially. There is a suture line between the foramen and the mesial margin of bone. In S. abeli the suture line is absent.

Vomer (Figures 13-15). The median vomer is 'T'-shaped with an anteriorly convex crosspiece bordered by a dorsally extending flange, and a posteriorly tapering stem. The flange is elevated laterally and overlaps the ventromesial portion of the lateral ethmoids. The stem is dorsally convex and accommodates the anterior end of the parasphenoid.

The vomers of both S. conspicuus and S. abeli bear a single row of about 18 coniform teeth along the anterior margin.

Ethmoid cartilage and anterior mydome.

The ethmoid cartilage is a large median cartilage bounded by and attached to the posterior surface of the median ethmoid, the ventromesial surfaces of the lateral ethmoids, the dorsal surface of the vomer, the dorsal surface of the anterior end of the parasphenoid, and the anterior and ventral surfaces of the septal. The cartilage has two projection, one extending dorsoposteriorly and the other posteriorly. The anterior mydome lies at the origin of the posterior projection. It forms a small semi-spherical cavity partially bounded by a notch at the anteroventral corner of the septal.

Nasal (Figure 16). The two nasals are elongate, trough-shaped bones open on their upper surfaces. The anterior end of each is flattened into a shallow spoon-shaped basin. Approximately one third of the way from the posterior end of each nasal the lateral margin of the trough bends outwards. The sensory canals which

extend the length of each nasal are continuous with the supraorbital canals of the frontals.

Orbital Region.

The orbits are surrounded by the lateral ethmoids, the frontals, pterosphenoids, portions of the sphenotics and prootics, and a series of five infraorbitals. The left and right orbits are partially separated by median ventrally extending margins of the frontals, and by the basisphenoid and septal. Each eye is bounded anteriorly and posteriorly by a pair of separate, concave sclerotic bones. These are not illustrated.

Frontal. Most of the dorsal surface of the neurocranium is covered by two large frontals. Anteriorly these are narrow and arched and abut each other, forming a narrow inter-orbital area. The posterior portion of the frontals are broad and blade-like. Mesially they overlap each other irregularly. Posteriorly they overlap the parietals and supraoccipitals. Laterally the blade-like portions curve ventrally and overlap the dorsal margin of the sphenotics. The inner ventrolateral margin of each frontal overlaps the dorsal margin of a pterosphenoid

Along its outer edge above the orbits each frontal has a thin low ridge which is fringed with small tooth-like projections for its anterior half and posterior third. Close to the sphenotics the edge loses its toothed appearance and becomes scalloped.

The supraorbital sensory canal runs along the lateral edge of each frontal to open anteriorly above the junction between the frontals and lateral ethmoids. The canal is enclosed except for the

posterior end, of length about half the width of the blade-like portion of the bone. The canal continues from the frontal onto the anterior of the sphenotic where it divides into the infraorbital and pterotic canals.

There is a narrow slit-like opening into each canal above the orbit close to the lateral edge of the bone. Behind the orbit two posterior branches of the canal open on the dorsal surface of each frontal. Two low fringed ridges extend from either side of the mouth of each branch. Two or three smaller pores also perforate the posterior wall of the posterior portion of the canal.

There is some variation in the ornamentation of the frontals and the position of the pores of the supraorbital canal. The frontals of S. abeli have short fringed portions close to the sphenotics. There are two pores over each eye of S. abeli, and five or six branch canals opening on the dorsal surface of each frontal. These branches decrease in length toward the midline and lack the fringing at the mouths of the branches.

Basisphenoid (Figure 13). This is a complex median bone which consists of a posterior meningost and an anteroventral belophram (Springer, 1968). The meningost has two short lateral projections forming the arms of a broad 'Y' which are firmly ankylosed to the median processes of the prootics. The belophram is flat dorsally and bifurcates ventrally so that viewed anteriorly it forms an inverted 'Y'. Anteriorly it is pointed and fits into a 'V'-shaped notch in the posterior margin of the septal. The ventral margins rest in the concave dorsal surface of the parasphenoid.

Septal. This autogenous de novo ossification of the anterior part of the interorbital septum was first described by Springer & Freihofner (1976) for Pholidichthyes leucotaenia. These authors have discussed at length the possibility that the septal is a modified beryciform orbitosphenoid (ibid : 34,35), and concluded that it is not. (One of the characteristics of the perciform fishes is the loss of the orbitosphenoid).

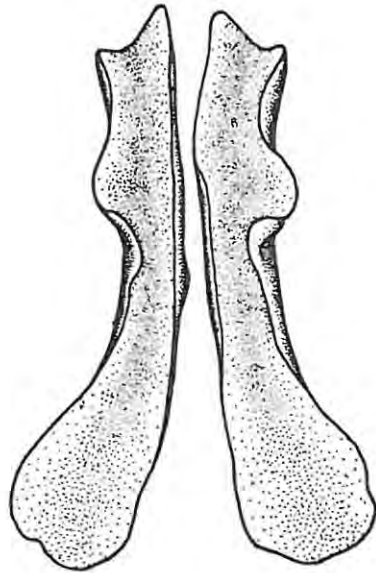
The septal was subsequently identified in the tripterygiid genera Forsterygion (Ruck, 1976) and in Gilloblennius (Springer, per. comm.). It appears to be present in most of the genera of the Tripterygiidae, and its presence or absence seems to be consistent within a genus.

Anteriorly and ventrally the septal divides into two laterally extending flanges. Anteriorly these flanges cup the anterodorsal portion of the ethmoid cartilage, and abut the mesial margins of the lateral ethmoids. Ventrally the two flanges cover the dorsal surface of the posterior extension of the ethmoid cartilage. At its anteroventral corner is a rounded notch bordered by the closure of each pair of flanges. This notch partially bounds the anterior myodome.

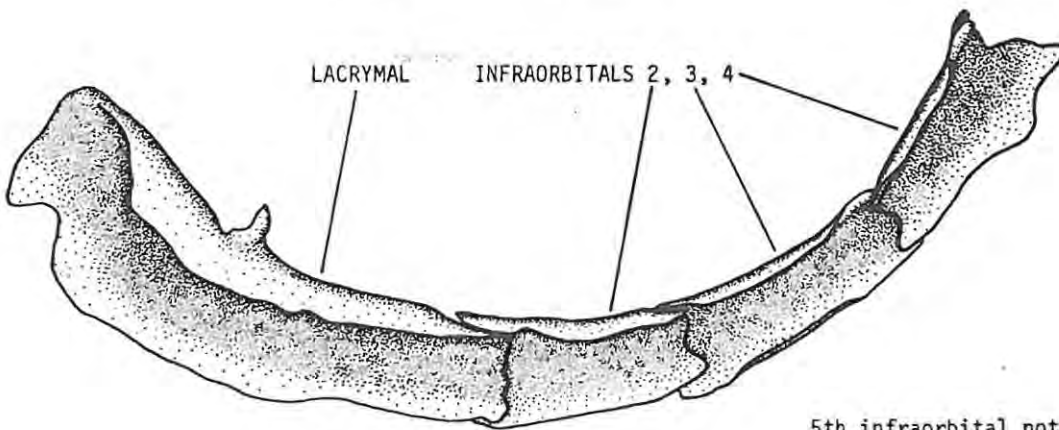
There is a 'V'-shaped notch in the posterior margin of the septal of S. conspicuus which accomodates the pointed anterior end of the basisphenoid. The septal and basisphenoid of S. abeli abut each other.

Pterosphenoid. These are flat bones which lie between the median margins of the prootics and the ventral margins of the frontals in the orbits. Medially they border the orbital fontanelle (Barel, et al., 1976-see below), and join the median processes of the sphenotics for a short distance. Each bears a foramen near its center for

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NASALS



5th infraorbital not shown

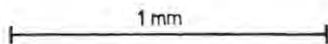


FIGURE 16 NASALS AND INFRAORBITALS

nerve IV (Patterson, 1974).

The orbital fontanelle is the opening between the orbits and the braincase. It is bounded dorsally and dorsolaterally by the frontals, laterally by the pterosphenoids, and ventrally by the median processes of the prootics. A membrane attaches to the inner edges of these bones, enclosing the front of the brain. Midventrally the membrane has a large perforation, providing passage for the olfactory and optic tracts.

Infraorbitals (Figures 12,16). The series of dermal bones extending from the lateral ethmoid, below the orbit to the posterior margin of the orbit has variously been referred to 'circumorbitals' (Springer, 1968), 'suborbitals' (Harrington, 1955; Makushok, 1958; Collette & Chao, 1975), and 'infraorbitals' (Nelson, 1969; Barel *et al.*, 1976; Smith-Vaniz, 1976). The last named term is used in this description.

There are five infraorbital bones. The anteriormost, the lacrymal, is approximately twice the length and one-and-a-half times the width of the second, third and fourth infraorbitals. These latter three bones are about equal in size. The posteriormost is very small (about one sixth of the fourth) and firmly attached to posterior surface of the postorbital wing of the sphenotic. All the bones are 'C'-shaped in section, and form a laterally open trough for the infraorbital sensory canal.

Each lacrymal articulates with the respective lateral ethmoid by means of a shallow concave process on its ventromesial surface.

Otic Region.

This region encloses the otic chambers inside the skull and is formed by the sphenotic, prootic, pterotic, epioccipital and parietal.

Prootic. The prootics join with all the ventral bones of the brain case. Dorsally each prootic is synchondrally joined to a pterotic and sphenotic. Along its entire ventral margin each is overlapped by the parasphenoid. Posteriorly the prootics join the exoccipitals synchondrally, and posterodorsally they are overlapped by the intercalars.

Anteriorly a median process from each prootic ankylose in the midline. The bridge thus formed forms the only osseous portion of the roof of the posterior myodome. The oculomotor nerve (III) (Patterson, 1974) passes through a foramen in a deep depression on the anterior surface of prootic process.

Anterodorsally the prootic forms the ventral portion of the anterior myomandibular articulation socket. (The dorsal portion of this socket is formed by the sphenotic.) Ventral and median to the socket is the lateral commissure which partially conceals the foramina for the V (anterior foramen) and VII (posterior, smaller foramen) complex of nerves.

Anteriorly, on the floor of the brain case, open, cone-shaped pockets in the prootics accommodate the anterior portion of each sagitta.

Sphenotic (Figures 13-15). These are complex bones which lie at the anterolateral corners of the brain case. Dorsally they are narrowly overlapped by the frontals, posteriorly by the parietals

and pterotics, and ventrally they abut the prootics.

A laterally extending shelf along the horizontal midline of each bears the junction between the pterotic and infraorbital sensory canals. Posteriorly the shelf is continuous with that of the pterotics. At its anterior end this shelf forms a dorsoventrally extending flange referred to by Barel et al., (1976) as the 'post-orbital wing' of the sphenotic. The fifth infraorbital is firmly attached to the posterior surface of the wing. Below the anterior end of the shelf the sphenotic forms the dorsal portion of the anterior hyandibular articulation socket. A narrow canal (possibly passage for a blood vessel) passes diagonally forward through the bone posterior to the socket.

A shallow, concave channel housing the anterior vertical semicircular canal extends dorsoventrally along the internal surface of each sphenotic. The channel occupies the posterior half of the bone and is separated from the anterior half by a low ridge which continues along the internal surface of the prootics. The channels are continuous along the surfaces of the prootics and parietals.

Parietal (Figures 13-15). The parietals are convex, roughly kidney-shaped bones, which lie either side of the median supra-occipital. Anteriorly each parietal is broadly overlapped by a frontal, and anteroventrally each overlaps a sphenotic for a short distance. The remainder of the lateral margin of each is broadly covered by its respective pterotic. Medially the parietals overlies the lateral margins of the supraoccipital and posteriorly they overlap the epioccipitals.

The shallow channel of the anterior vertical semicircular canal referred to above runs diagonally backwards along the internal

surface of each parietal as far as its suture with the supraoccipital.

Epioccipital (Figures 13-15). Terminology here follows Patterson (1974), who introduced this term for the bone usually referred to as the 'epiotic' in teleosts.

The epioccipitals are roughly dome-shaped and occupy the posterolateral corners of the dorsum of the neurocranium. The internal perimeter of the bone is roughly ring-like. Posteroventrally each is synchondrally joined to an exoccipital, and medially and laterally to the supraoccipital and pterotics respectively. Anteriorly the epioccipitals are broadly overlapped by the parietals.

Each has a large lateral wing which dorsally forms the articulation surface for the dorsal arm of the posttemporal. On the internal surface of the bone is a large, deep concavity which is occupied by the posterior ampullary chamber. A tube for the posterior vertical semicircular canal curves upward and forward from the concavity and exists against the 'roof' of the epioccipital. A tube for the horizontal semicircular canal opens in the anterior wall of the concavity.

Pterotic. Each pterotic is an irregularly shaped bone with a heavy-bodied, domed ventral portion which forms much of the lateral edge of the neurocranium, which is separated by a deep groove from a thin blade-like dorsal portion. Posterodorsally each pterotic abuts an epioccipital, and posteroventrally each abuts an exoccipital. Along most of the ventral margin each pterotic is covered by an intercalar. Dorsally and anteriorly the blade-like portions overlap the parietals and sphenotics respectively.

Anteriorly the lateral bulge of the pterotic extends as a shelf which is continuous with the sphenotic shelf. Just posterior to its junction with the sphenotic the shelf curls dorsally as a thin crest to form a short open canal in which the pterotic sensory canal lies. Below the shelf, at the anterior of the domed portion of the bone is a shallow lateroventrally concave articulation facet for the posterior hyomandibular condyle.

The tube for the horizontal semicircular canal lies in the domed portion of the pterotic. The anterior end of the tube opens into a second (see above) concavity (accommodating the external ampullary chamber) which occupies most of the anterior internal surface of the ventral portion of the pterotic.

Occipital Region.

This region is comprised of the supraoccipital, basioccipital, exoccipital and intercalar bones. The descriptions of the lateral and median extrascapulars are included here.

Intercalar. These are relatively large, irregularly shaped, simple bones which lie below the domed portion of the pterotics. They entirely cover the synchondral joints between the pterotics and exoccipitals, and pterotics and prootics.

Exoccipital. The paired exoccipitals form the major portion of the posterior base of the skull. Ventrally they are separated by and synchondrally joined to the basioccipital. The posterior edges of these bones form the sides and roof of the foramen magnum, where they suture with each other mid-dorsally. The median supraoccipital abuts each exoccipital for a short distance on

either side of their median joint. Lateral to the suture with the supraoccipital each exoccipital is synchondrally joined to its epioccipital. Dorsolaterally each sutures with a pterotic, and anteriorly they form broad synchondral joints with their prootics. Ventroposteriorly each exoccipital forms a cone-shaped condyle which articulates with the first vertebrae. The vagus foramen passes through these bones mid-ventrolaterally,

Internally, a ridge runs anteriorly along the posterior ventrolateral surface of each exoccipital and continues onto the basioccipital. The posterior portion of each sagitta is located between this ridge and the lateral wall of the exoccipital. A small asteriscus is located in a shallow concavity just dorsal to the posterior end of each sagitta. A smaller, button-shaped lapillus lies above the anterior end of each sagitta.

The floor and posterior wall of the concavity which houses the posterior ampullary chamber (see above) is formed by the exoccipital. The internal entrance to the vagus foramen lies dorsal to this concavity.

Supraoccipital (Figure 15). This is a simple median bone of which most of the lateral and anterior margins are overlapped by the parietals and frontals respectively. The posterolateral edges are synchondrally joined to the epioccipitals and the posterior margin sutures with the exoccipitals. A low ridge extends across the supraoccipital.

Basioccipital (Figures 13-15). The median basioccipital lies at the ventroposterior base of the skull. There is a deep wide notch in the centre of its anterior margin which is overlapped by the notched posterior end of the parasphenoid. At its posterior end the bone is thickened and expanded to form the basioccipital condyle. The condyle forms the floor of the foramen magnum. Anterolaterally the basioccipital forms broad synchondral joints with the pterotics, and laterally with the exoccipitals.

A median gap between the overlapping margins of the basioccipital and parasphenoid allows for the passage of two pairs of rectus eye muscles. A groove to accommodate these muscles extends from the gap to the anterior margin of the condyle where the muscles originate.

Lateral extrascapular. The paired lateral extrascapulars are irregularly shaped bones which are closely attached to the surface of the brain case. Laterally they lie over the junction between the pterotics, epioccipitals and exoccipitals. Each curves around the epioccipital wing and extends mesially to cover the joint between the epioccipital and parietal. The edges of the lateral extrascapulars curl away from the skull to form a shallow channel which houses the junction between the pterotic, supra-temporal, preopercular and cephalic lateralis sensory canals.

The median end of the posterior edge of each lateral extrascapular of S. conspicuus is fringed with tooth-like projections. Those of S. abeli are smooth, and do not extend median to the epioccipital wings.

Median extrascapular. The name used by Harrington (1955) for the paired dermal bones lying median to the lateral extrascapulars on the dorsal surface of the skull is used here. These are also shallow, trough-shaped bones which are closely attached to the neurocranium. They lie over the posterior margin of the parietals, and carry the supraoccipital sensory canal across the posterior of the braincase.

The posterior margin of each median extrascapular is about five times longer than the anterior margin, and is fringed with tooth-like projections.

Each median extrascapular of S. abeli extends over the anterior of the supraoccipital to meet its opposite at the midline of the neurocranium.

Parasphenoid.

The parasphenoid is a long, thin, shallow trough-shaped bone that extends for most of the ventral length of the neurocranium.

Anteriorly it is relatively narrow and the anterior end is cupped in the stem of the vomer. At its midlength it is twice as wide as it is anteriorly, and at the point where it widens it gives rise to two small dorsolaterally extending parasphenoid descending processes (Patterson, 1974). The anterior margins of these processes curve into the orbits to overlap the anteroventral ends of the prootics. Two small arterial foramina penetrate the parasphenoid at the bases of these processes.

From a maximum width at a point roughly two-thirds of the way from

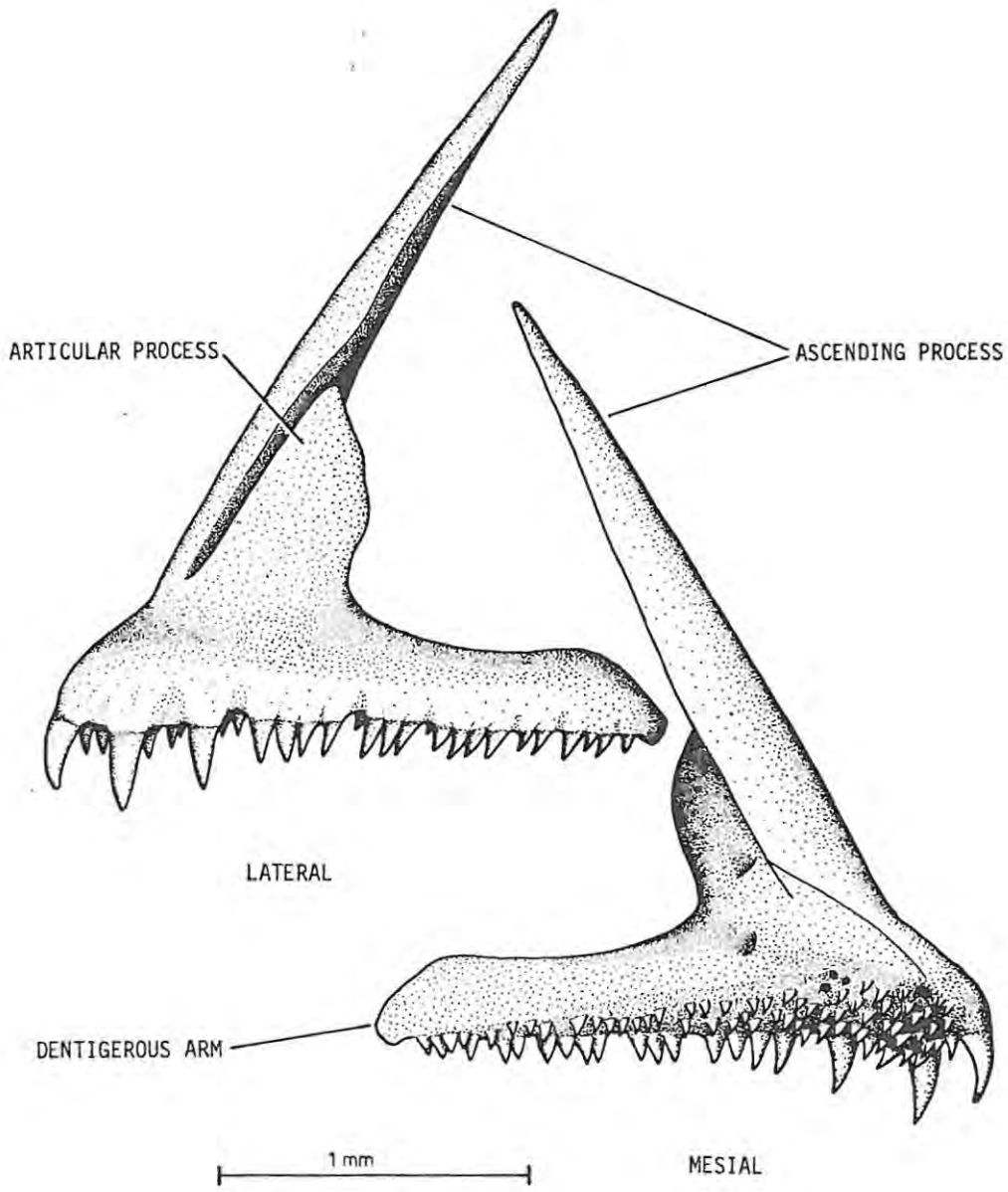


FIGURE 17 LEFT PREMAXILLA

its anterior end the bone tapers posteriorly. The posterior end is deeply notched and overlies the notched anterior end of the basioccipital. Anterior to the basioccipital the lateral margins of the parasphenoid broadly overlap the entire median margins of the prootics. There is a shallow furrow along the midline of the central portion of the posterior half of the bone.

The upper surface of the anterior half supports the velopharynx, the septum, and the posterior portion of the ethmoid cartilage.

BRANCHIOCRANIUM.

The branchiocranium is treated in six sections: mandibular arch, palatine arch, suspensorium, opercular series, hyoid arch, and branchial arches.

Mandibular Arch.

The mandibular arch includes the upper and lower jaws comprising the maxillae, premaxillae, dentaries, angulars and retroarticulars. Both dentaries and premaxillae are toothed.

Premaxilla (Figure 17). These each consist of a ventral portion, the dentigerous arm (Barel *et al.*, 1976), and two processes on the dorsal anterior end of the dentigerous arm. The dentigerous arm is laterally convex. The anteriormost dorsal process, the ascending process, is slightly longer than the dentigerous arm, and is triangular in section. Immediately posterior to and separated from the ascending spine by a narrow gap is a shorter, blade-like articular process, which thickens at its base just anterior to the junction between the dentigerous arm and the spine.

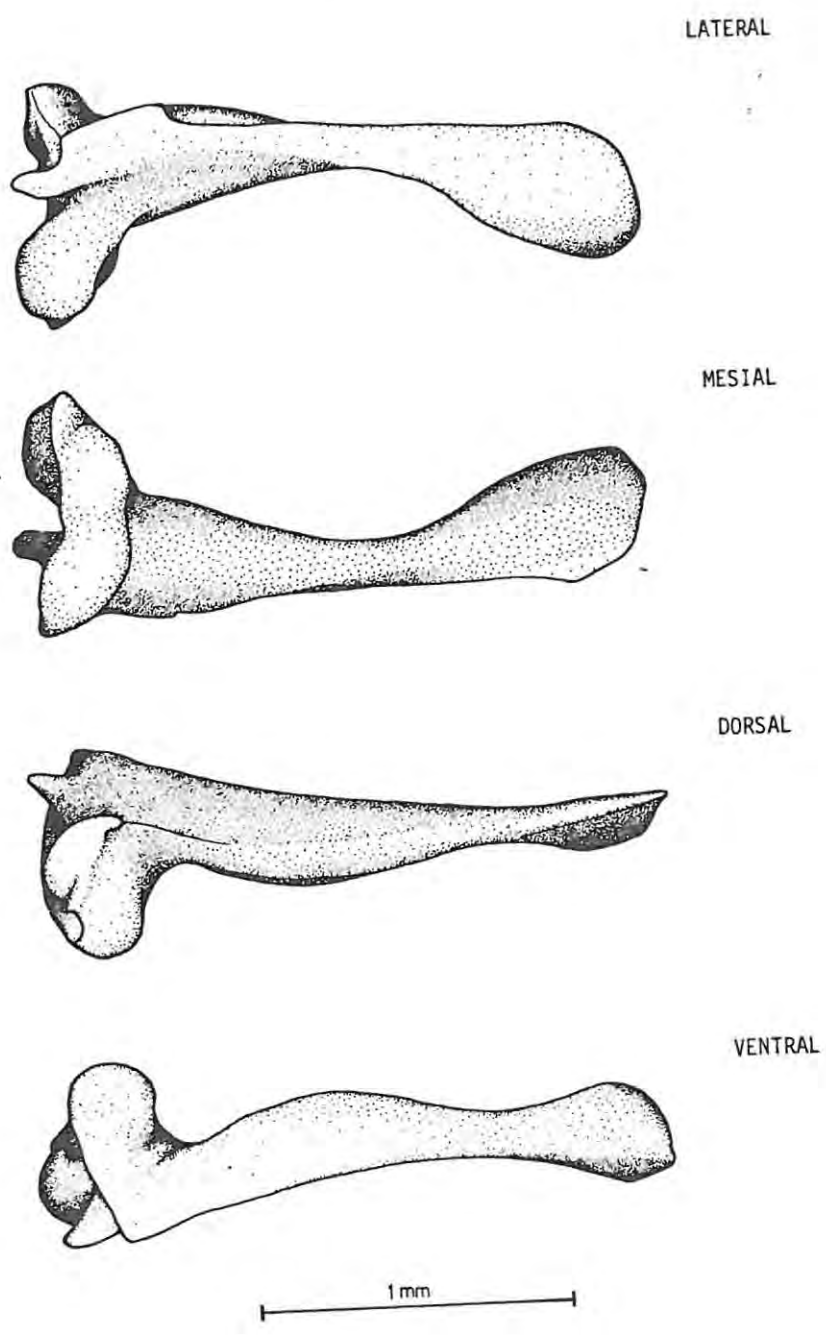


FIGURE 18 LEFT MAXILLA

This thickening forms an articulation facet on its mesial surface for the maxilla, the maxillad articulation facet of Barel et al., (1976).

The two dentigerous arms are firmly joined anteriorly at their median symphysis by a ligament. The ascending processes are more loosely bound to each other, and in situ extend posterodorsally to lie between the ventral ends of the nasals.

Each premaxilla bears a single row of large, slightly recurved coniform teeth on the outer edge. The teeth decrease in size posteriorly. Inside this row is a patch of smaller coniform teeth. The width of the patch decreases from a maximum at the symphysis to a single row at the back of the jaw.

Maxilla. (Figure 18). The paired maxillae are heavy bones which extend from their anterior articulation with the articular process of the premaxillae to cover the coronoid wing of each dentary laterally. They are thus included in the gape.

Each maxilla consists of a ventrally concave, slightly curved shank and a complex head which articulates between the anterior end of the palatine and the premaxilla. The posterior end of the shank is laterally flattened and widened and connected by ligament to both the coronoid wing of the dentary and the posterodorsal margin of the premaxilla.

The major portion of the head consists of a large kidney-shaped condyle curving mesiad and separated dorsomesially by a saddle from the shank. The anterior end of the palatine articulates in this saddle. A short conical process extends anteriorly from the lateral anterior end of the head. Mesial to this process is a depression.

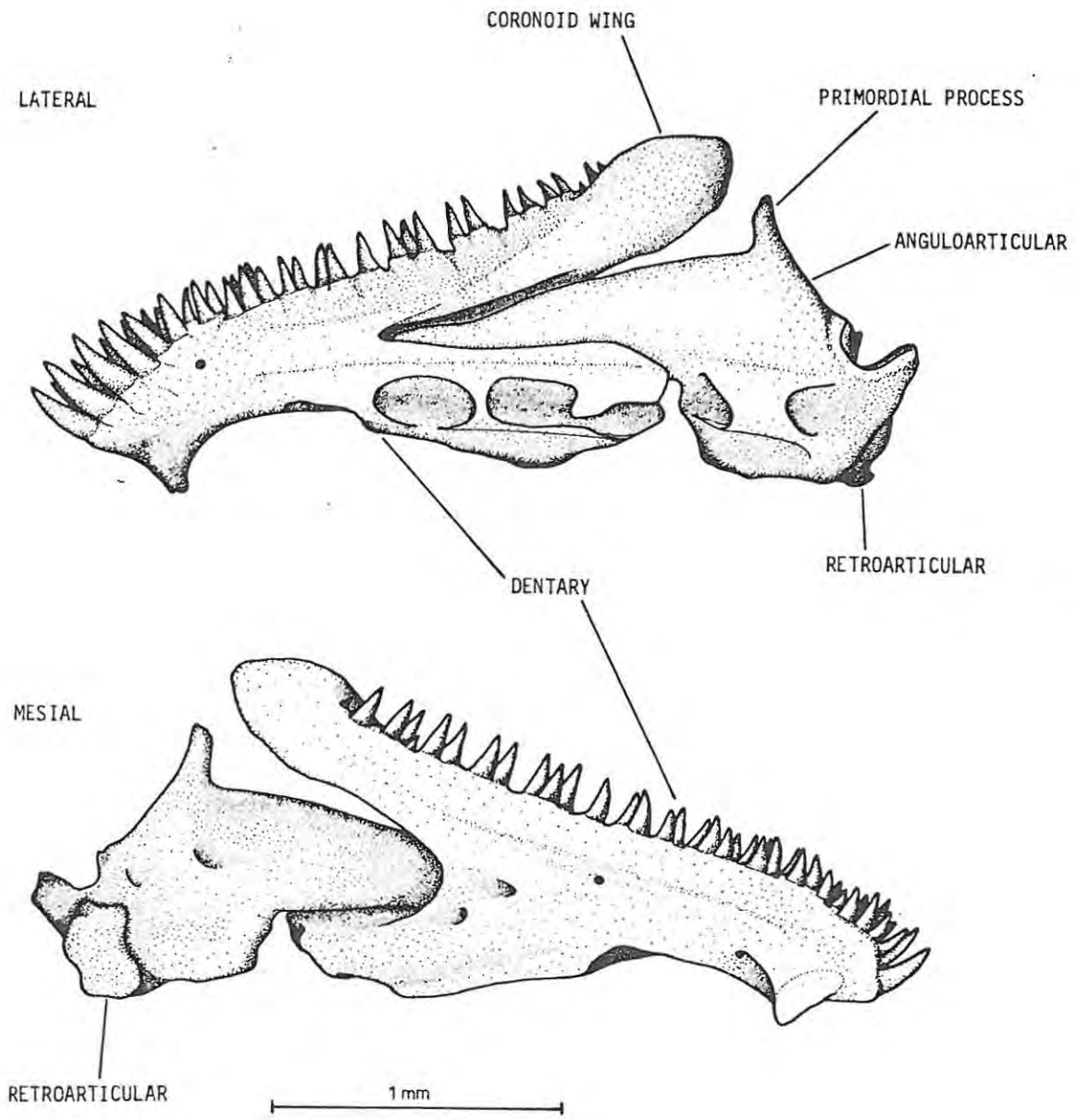


FIGURE 19 LEFT LOWER JAW

A ligament connects the anterior end of the head to the mid-ventral surface of its respective nasal. A ventral groove extending onto the shank separates the anterior process and the ventral portion of the condyle. The dorsal margin of the articular process articulates in this groove. The premaxillad articulation facet (Barel et al., 1976), that portion of the condyle ventral to the groove, articulates with the maxillad articulation facet of the premaxilla.

Dentary. (Figure 19). Each dentary is a 'V'-shaped bone which lies with the apex of the 'V' anterior and the two arms posterior. The anterior end curves inward to suture at their median symphysis. The angle between the dorsal arm (coronoid wing) and ventral arm, which carries the mandibular sensory canal, is termed the 'reentrant angle' by Barel et al., (1976). The dentary fossa which accomadates the anterior of the anguloarticular lies at the apex of the reentrant angle.

Each dentary carries slightly recurved coniform teeth on the dentigerous area. The teeth are largest on the outer anterior edge and decrease in size posteriorly and toward the inner margin of the bone. The smallest teeth occur as a single row along most of the length of the coronoid wing.

There are three small foramina on the mesial surface of each dentary for nerves and blood vessels.

Anguloarticular. (Figure 19). There is some inconsistency in the literature in the terminology used for the anguloarticular and the retroarticular (see below). Gosline (1963) refers to these bones as the 'articular' and the 'angular', as do Springer (1968) and

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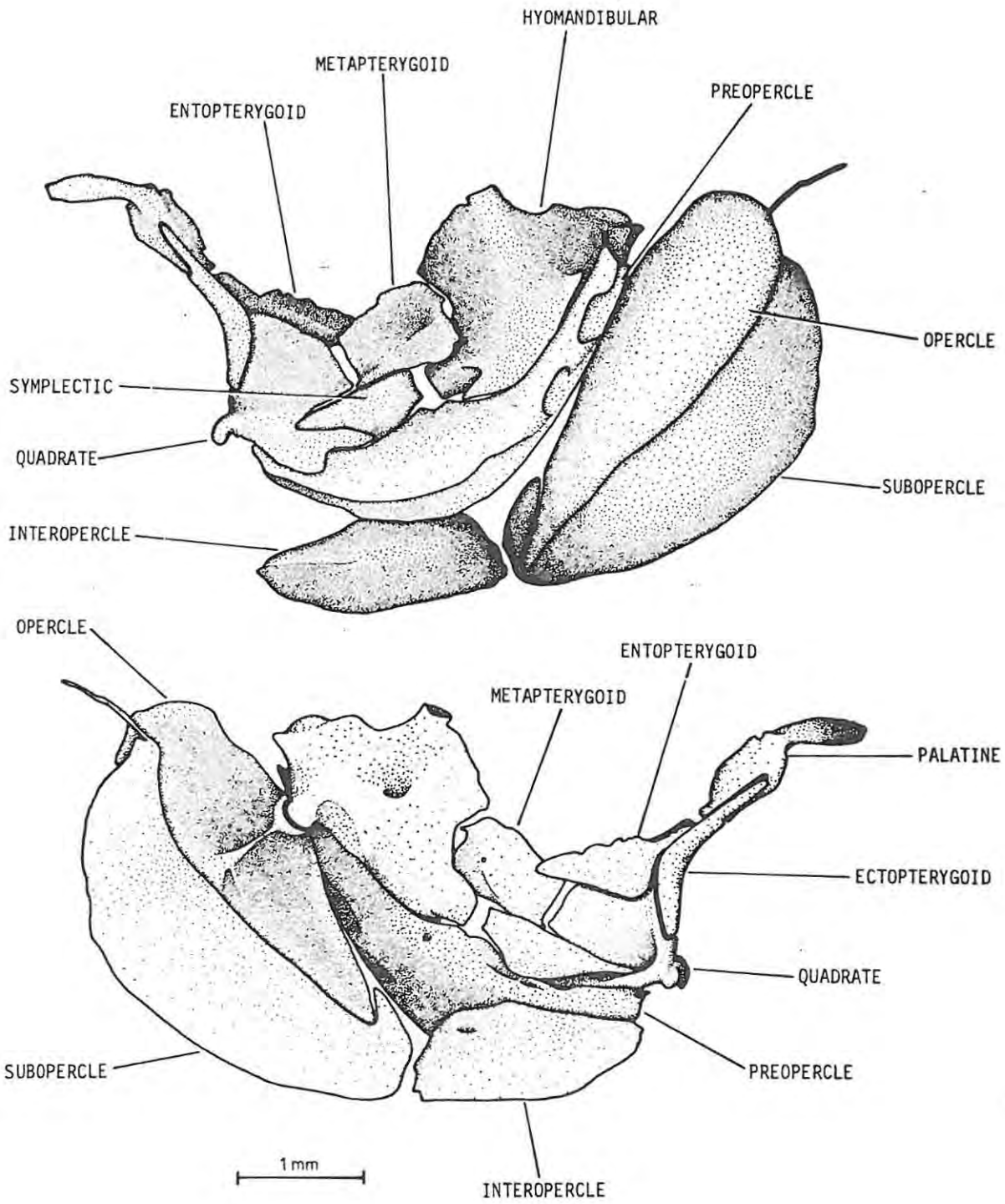


FIGURE 20 LEFT SUSPENSORIUM, PALATINE ARCH AND OPERCULAR SERIES

Springer & Freihofer (1976). Both Harrington (1955) and Collette & Chao (1975) name these bones the 'angular' and 'retroarticular' respectively. The terminology of Patterson (1977) is used here.

Each anguloarticular consists of a hollow posteroventral portion which carries the posterior part of the mandibular sensory canal (the 'coulter area' of Barel et al., 1976), and a large, sharply pointed anterior and dorsal area. The point fits into the dentary fossa. A narrow pointed primordial process (Barel et al., 1976) extends dorsally from the posterodorsal margin of each anguloarticular.

The broad, dorsally concave articulation facets for the quadrates lie at the posterior end of each anguloarticular. These facets are bounded posteriorly by a fairly large postarticular facet.

Retroarticular. (Figure 19). The two retroarticulars are small, almost rectangular, flattish bones closely attached to the mesial posteroventral corner of each anguloarticular. They protrude a small distance posterior to the margins of the anguloarticulars.

Meckel's Cartilage. A small, elongated cone-shaped Meckel's cartilage lies in a shallow groove on the midmesial surface of each anguloarticular.

Palatine Arch (Figures 12,20).

The palatine arch consists of paired palatines, ectopterygoids and entopterygoids.

Palatine. The main portion of each palatine is irregular in shape and is clasped ventrally by the ectopterygoid (see below). Anteriorly it extends anterolaterally as a cylindrical process (the maxillary process of Barel et al., 1976) which is about equal in length to the main body of the palatine.

The maxillary process articulates between the ventral edge of the lateral ethmoid and the saddle of the maxilla. The process is attached by ligament to both the lateral ethmoid and maxilla.

The palatines of S. conspicuus are edentate. Those of S. abeli have a single row of 3-5 teeth, continuous with the row of vomerine teeth.

Ectopterygoid. The ectopterygoids are crescent-shaped bones which are deeply grooved posteriorly. The dorsal anterior margin of a quadrate fits into the ventral half of the groove, and the anterior end of the entopterygoid fits into the dorsal half. Anterior to the grooved portion the bone projects as two long, narrow flanges which clasp the ventral end of its palatine. The palatines in turn have shallow grooves to accommodate these flanges.

Entopterygoid. Although Springer (1968) and Springer & Freihofer (1976) use the term 'mesopterygoid' for the bone lying dorsal and mesial to the quadrate and ectopterygoid, the name 'entopterygoid' appears to be more frequently used (Harrington, 1955; Makushek, 1958; Collette & Chao, 1975).

The entopterygoids are irregular bones firmly attached in the dorsal part of the ectopterygoid groove anteriorly, and to the quadrate ventrally. Each bone forms a wide flange mesial to the quadrate.

The posterior end of each entopterygoid lies mesial to the anterior corner of the metapterygoid.

Suspensorium (Figures 12,20).

The suspensorium is taken as the chain of bones on either side of the neurocranium which support the lower jaw: the hyomandibulars, metapterygoids, symplectics and quadrates.

Hyomandibular. The hyomandibulars are flattish, irregularly shaped bones which join the preopercles along the posterventral margins and the symplectics and metapterygoids along the anteroventral margins.

There is a semicircular notch in the posterior margin of the hyomandibular to accomodate the posterior margin of the metapterygoid. The two bones are joined by a broad sheet of connective tissue. The anteroventral corner is thickened and joins the posterior end of the symplectic via a cartilage. The interhyal articulates with the suspensorium on the ventromesial surface of this cartilage. A shallow groove extends along the posterior margin of each hyomandibular. The rounded dorsal anterior edge of the preopercle lies in this groove.

Each hyomandibular has three condyles, two on the dorsal margin and one on the dorsoposterior margin. The anterior dorsal condyle is concave and bears a semi-spherical cartilage which articulates with the anterior hyomandibular socket of the neurocranium. The

posterior dorsal condyle is convex and articulates in a socket on the ventrolateral side of the prootic. The third condyl is convex and articulates in a socket on the anteromesial surface of the opercle.

An opening on the internal surface of each hyomandibular between and below the two dorsal condyles leads to a ventral passage which exists on the external surface of the bone near its ventral margin. This is a passage for the hyomandibular branch of the facial nerve (VII).

Metapterygoid. These are semirectangular, thin and flat. They are bounded posteriorly and ventrally by the hyomandibulars and symplectics, and anteriorly by the quadrate.

Symplectic. Each symplectic is a well developed bone, squared posteriorly and tapered anteriorly. The anterior end fits into a deep fossa in the quadrate. Ventrally it slightly overlaps the margin of the preopercle medially.

Quadrate. These are fan-shaped, each with a notch and a deep 'V'-shaped fossa in the posterior margin to accommodate the anterior end of the symplectic. A flange along the ventral margin lies lateral to the anterior end of the preopercle. The dorsal anterior edge of the quadrate fits into a deep groove in the ectopterygoid. The dorsal edge overlaps the entopterygoid laterally. Anteriorly the quadrate is thickened and bears a broad, double-headed condyle with which the anguloarticular articulates.

Opercular Series (Figures 12,20).

The opercular series each consist of three large flattish bones, the opercle, subopercle and interopercle, and a fourth, the preopercle, which bears the preopercular sensory canal.

Opercle. These are thin, slightly laterally convex bones which taper to a point ventrally. The posterior margin overlaps the anterior margin of the subopercle, and the ventral point fits into a shallow groove in the latter bone.

A bone ridge extends parallel to the short axis of the opercle across the anterior half of its mesial surface. The anterior end of the ridge widens to form the shallow socket for the hyomandibular condyle.

Subopercle. The subopercles are thin crescentic bones also slightly laterally convex. The anterior margin of each is concave with a hook at its ventral end. A shallow groove for the ventral point of the opercle extends from the base of the hook almost to the ventral margin. A slender filament projects posterodorsally from the dorsal margin of the bone. The length of the filament is about equal to the maximum width of the subopercle and extends to just posterior of the posttemporal.

Interopercle. These are comparatively short, broad and blade-like. Each lies mesial to the ventral portion of the preopercle with only its ventral edge projecting when in situ. The anterior end is attached by a strong ligament to the posteroventral corner of the anguloarticular. Posteriorly it is also firmly attached by ligament to the anterior point of the opercle. The interopercle

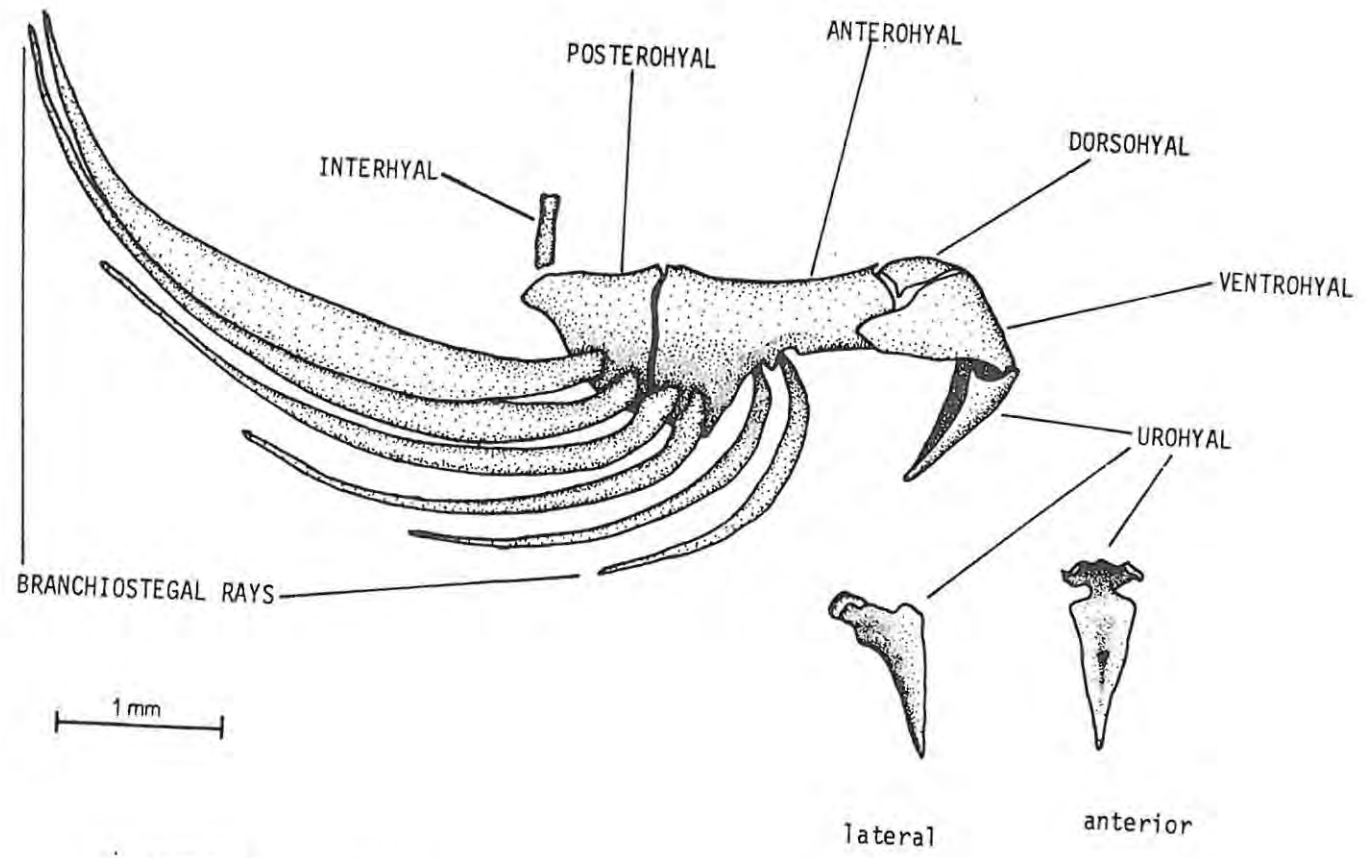


FIGURE 21 HYOID ARCH

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is fairly loosely fixed by connective tissue to the preopercle. It is closely attached by connective tissue to the lateral face of the posterohyal.

Preopercle. The dorsal end of each anteriorly concave, crescent-shaped preopercle lies lateral to the dorsoposterior corner of the hyomandibular. Ventral to this its anterior margin lies in a shallow groove in the posterior edge of the hyomandibular. Anteriorly it is laterally covered by the ventral flange of the quadrate. Posteriorly and ventrally each preopercle covers the margins of the opercle and interopercle respectively.

The preopercular portion of the preoperculo-mandibular sensory canal extends along the entire posterior and ventral margin of the bone. The canal is posteriorly partially enclosed and ventrally open. Dorsally the canal continues to the lateral extrascapular and anteriorly to the anguloarticular.

Hyoid Arch. (Figure 21).

The hyoid arch as discussed here consists of a median urohyal, and paired dorsohyals, ventrohyals, anterohyals and posterohyals. There are six branchiostegal rays on either side. The terminology used follows that of McAllister (1968) and Nelson (1969).

The urohyal is the shape of a three-sided wedge with concave faces. The bone points posterioventrally with a face ventral and an edge dorsal. Two short wings extend laterally from the anterior end of the dorsal edge. These wings articulate between the ventrohyals.

The dorsohyal and ventrohyal on either side join each other ventro-

mesially by an overlap joint. Dorsally and laterally they abut. The two ventrohyals are joined at a median symphysis. Ventral to the symphysis each dorsohyal bears a notch on its anterior dorso-mesial surface. The first basibranchial is clasped between these notches.

The anterohyal and posterohyal are sutured. Together these two bones form an anterior shank and a posterior ventrally extending blade. Dorsally the anterior end of the shank is synchondrally joined with the dorsohyal. Laterally, mesially and ventrally the anterohyal forms overlap joints with the dorsohyal and ventrohyal.

The first four branchiostegal rays articulate on the anterohyal. The first articulates in a notch in the ventral margin of the anterior end of the shank, and the second in a notch in the ventro-mesial margin at the origin of the blade. The third and fourth articulate on the ventrolateral surface of the bladed portion of the anterohyal. The last two branchiostegal rays attach to the ventrolateral surface of the posterohyal.

At the anterodorsal corner of the posterohyal is a small articulation surface where the ventral end of the interhyal attaches.

A short cylindrical interhyal articulates ventrally with the posterohyal and dorsally with the cartilage which lies between the symplectic and hyomandibular. This cartilage is ventrally convex to accommodate the dorsal end of the interhyal.

Branchial Arches (Figure 22).

The branchial arches of the Tripterygiidae are very similar to those of the Blenniidae as described by Springer (1968). Terminology

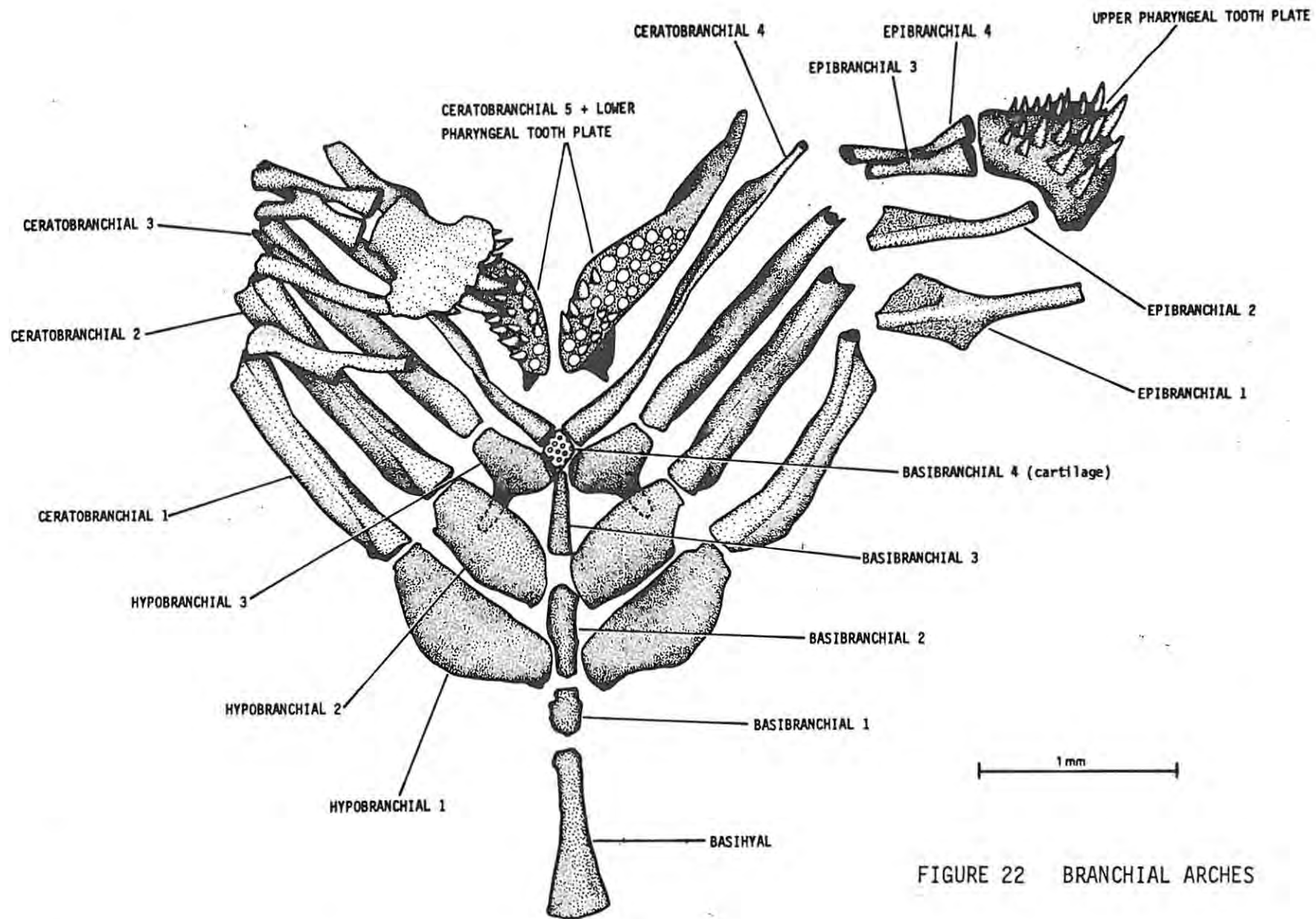


FIGURE 22 BRANCHIAL ARCHES

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follows that of Nelson (1969). The proximal end of a paired element is the one closest to the basibranchials.

The arches comprise an anterior median basihyal followed by four basibranchials, the fourth being cartilaginous; three pairs of hypobranchials; four pairs of ceratobranchials which bear gillrakers, and a fifth pair of ceratobranchials to which the lower pharyngeal tooth plates are fused. Dorsally there are four pairs of epibranchials, the last two pairs articulating with a pair of upper pharyngeal tooth plates. The epibranchials do not have gillrakers.

The first arch is connected to the neurocranium by ligaments from the first epibranchials. Epibranchials 2-4 are connected to the upper pharyngeal plates which are connected by ligaments to the neurocranium.

The basihyal is relatively long, posteriorly round and anteriorly dorsoventrally flattened and widened to about twice its posterior width.

Basibranchial 1 is a short irregularly shaped bone which lies in two notches on the dorsohyals. Basibranchials 2 and 3 are roughly cylindrical, about twice the length of basibranchial 1 and a little more than half the length of the basihyal. Basibranchial 4 is unossified and is represented by a thick, diamond-shaped cartilage lying between the mesial ends of the third pair of hypobranchials and the fourth pair of ceratobranchials. There is a small ossification between basibranchial 1 and 2.

Hypobranchials 1 and 2 are dorsally convex, broad, thin bones. The first hypobranchials have broadly convex anterior margins.

The third hypobranchials are 'T'-shaped with a broad cross-piece and a narrow stem anteriorly which lies ventral to hypobranchial 2. A ligament attaches the anterior tip of hypobranchial 3 to the mid-anteroventral margin of hypobranchial 2. The first three ceratobranchials are relatively long (one-and-a-half to twice as long as their respective hypobranchials). They are curved outward, and each bears two flanges running the length of the outside of the curve. The fourth ceratobranchial is as long as the third ceratobranchial and hypobranchial together. This fourth ceratobranchial is twisted and bears a single flange along its outer edge.

There are two rows of gillrakers along each ceratobranchial. Each gillraker consists of a small dome surmounted by two to four small spikes. There are five gillrakers in each row on the first ceratobranchial of S. conspicuus.

The lower pharyngeal tooth plates are the posteriormost paired elements. The two plates are closely attached at their anteromesial margins. At its anterior end each tooth plate bears a large ventral process. A ligament runs from the tip of each process, join, and attach to the cartilagenous fourth basibranchial as a single ligament. Dorsally each tooth plate has a roughly oval dentigerous area with three irregular rows of slightly recurved coniform teeth. The teeth decrease in size posteriorly; the largest are on the median margins.

The epibranchials are shorter than the ceratobranchials. The first epibranchial is more or less straight with a flange on either side of its proximal end. The second is slightly curved at its distal end, and bears a single flange at its proximal end. Epibranchials 3 and 4 are bent midway along their length. The third

bears a hooked flange proximal to the bend, whereas the fourth has no flanges. Epibranchial 2 to 4 articulate with the upper pharyngeal tooth plate.

The upper pharyngeal tooth plate is irregular in shape, broader and thicker distally than proximally. At its proximal end are two adjacent articulation surfaces for epibranchials 3 and 4. The second epibranchial articulates in a small cusp on the mid-antero-ventral margin. The whole ventral surface of each plate is dentigerous and bears irregularly spaced coniform teeth, most of which are about twice the size of those on the lower pharyngeal tooth plate. There is a single row of smaller teeth on the posterior margin.

Section 2 - Vertebral column and unpaired fins.

The vertebral column and unpaired fins of Scoliosolen (and all other Tripterygiidae) are very similar to those described for the Blenniidae by Springer (1968). The major difference between these two families is that the dorsal fin of the Blenniidae is divided into a spinous and a rayed portion, whereas the dorsal fin of Tripterygiidae has two distinct spinous dorsal fins and a rayed dorsal fin.

VERTEBRAL COLUMN (Figures 23,24).

Scoliosolen conspicuus has 32-33 vertebrae. The complete range for the genus cannot be given since few authors have determined vertebral counts. The ranges for six species of Scoliosolen are given in table VII.

The choice as to which vertebrae to count as the first caudal vertebra poses a problem. Springer (1968) took the first vertebrae bearing a well developed haemal spine as the first caudal vertebra for the Blenniidae. In this family the first proximal anal pterygiophore is associated with the first haemal spine. Certain authors (e.g. Lagler, Bardach & Miller, 1962) consider the first vertebra with a closed haemal arch as the first caudal vertebra.

The first 'well developed' haemal spine of Scoliosolen (and most other Tripterygiidae) is distally forked (figure 23), and the subsequent centrum has a conventional haemal spine (figure 23). The first two proximal anal pterygiophores fall between the forked haemal spine and the first proper haemal spine. The third anal pterygiophore is associated with this last mentioned haemal spine. The first closed haemal arch is usually coincident with the forked

haemal spine, but closure may occur in one or two preceding vertebrae. As closure of the haemal arch is extremely difficult to determine from radiographs, it is expedient to consider the centrum with the forked haemal spine as the first caudal vertebra. This is most easily determined as the vertebra with a haemal spine immediately anterior to the first anal pterygiophore. This criterion for the first caudal vertebra is adopted in this study.

Clark (in press) does not state which vertebra was counted as the first caudal vertebra. She records between 10 and 12 precaudal vertebrae for six of the Red Sea species of Enneapterygius (table VII). (Four of these species have been referred to Scoliosolen). Four of the species show a range of 2 in the count which this study does not confirm.

Gosline, writing on Blennioid classification, states that "members of the Tripterygiidae all are recorded with 10 abdominal (precaudal) vertebrae" (1968:51). If the first caudal vertebrae is counted as defined above, it would appear that Gosline is correct. For 12 species in 7 genera this has been found to be true.

The centra are amphicoelous, constricted mid-laterally, lack longitudinal struts, and have a notochordal canal through their centres. The first four are about equal in length and shorter than the remaining centra, which are again about equal in length.

The anterior end of the first centrum articulates with the basi-occipital condyle, and the neural prezygapophyses are enlarged and directed dorsally to articulate with the exoccipital condyles.

The first three centra bear lateral posteriorly directed processes which overlap the succeeding centrum. On the first centrum these are dorsally situated, dorsolaterally on the second and midlaterally on the third. According to Springer (1968), who described similar processes for the Blenniidae, these are not serially homologous with either neural or haemal postzygapophyses.

All vertebrae except the first and last have a neural spine. The spine on the second is very small, and those on the third and fourth, though well developed are smaller than the remainder. The neural arch on the first vertebra is closed.

The first recognisable neural postzygapophyses are on the fifth centrum, and the first haemal postzygapophyses are on the ninth. The first haemal prezygapophyses are on the 15th vertebra, but these remain small until the 20th.

The third and fourth vertebrae bear concave parapophyses laterally with which the heads of the first two pairs of pleural ribs articulate. The parapophyses on the 5th to 7th vertebrae are unmodified. The heads of 3rd to 5th pleural ribs bear two small anteriorly projecting processes which clasp the distal ends of their parapophyses from behind. The parapophyses of vertebrae 8 to 10 are also unmodified, but extend more ventrally with each successive vertebra. Those on vertebra 10 nearly meet in the sagittal plane. The heads of ribs 6 to 8 are flattened and articulate on the mesial surface of the distal end of the parapophysis, the head of the 8th pair of ribs lying next to each other between the parapophyses. The parapophyses on vertebra 11 meet to close the haemal arch and then divide again to form the forked haemal spine referred to above. This is the first caudal vertebra. It bears no pleural ribs. The proximal end of the first proximal anal pterygiophore is attached by

ligaments between the two sides of the forked haemel spine.

The first epipleural ribs articulate in small concavities midway on either side of the neural arch of the first vertebra. The second pair also articulate on their neural arch, but more ventrally. The 3rd through seventh epipleural ribs articulate on the first through fifth pleural ribs, close to their proximal ends, the eighth pair articulates at the heads of its pleural ribs, and the 9th to 11th (last) epipleurals articulate laterally on the parapophyses of vertebrae 9 to 11. A further 6 intramuscular bones are associated with vertebrae 12 through 17.

DORSAL FINS.

The name Tripterygiidae is derived from the tripartite division of the dorsal fin.

The first dorsal fin of Scoliosolen consists of 3 spines, each supported by broad proximal pterygiophores. The first two pterygiophores lie close together just posterior to the skull; there are no predorsals. The third is separated from the first two, and the fourth (the largest), supporting the first spine of the second dorsal fin, is separated by a gap which could be occupied by a pterygiophore. Gosline (1963) suggested that the anterior 3 spines have appropriated the usual percoid supra-neurals as their supporting bases as a result of the forward movement of the soft dorsal (third dorsal) fin.

The second dorsal fin of S. conspicuus has 11 or 12 spines. The range for the six species assigned to the genus is 11-14.

There are no distal pterygiophores in either of the first two dorsal

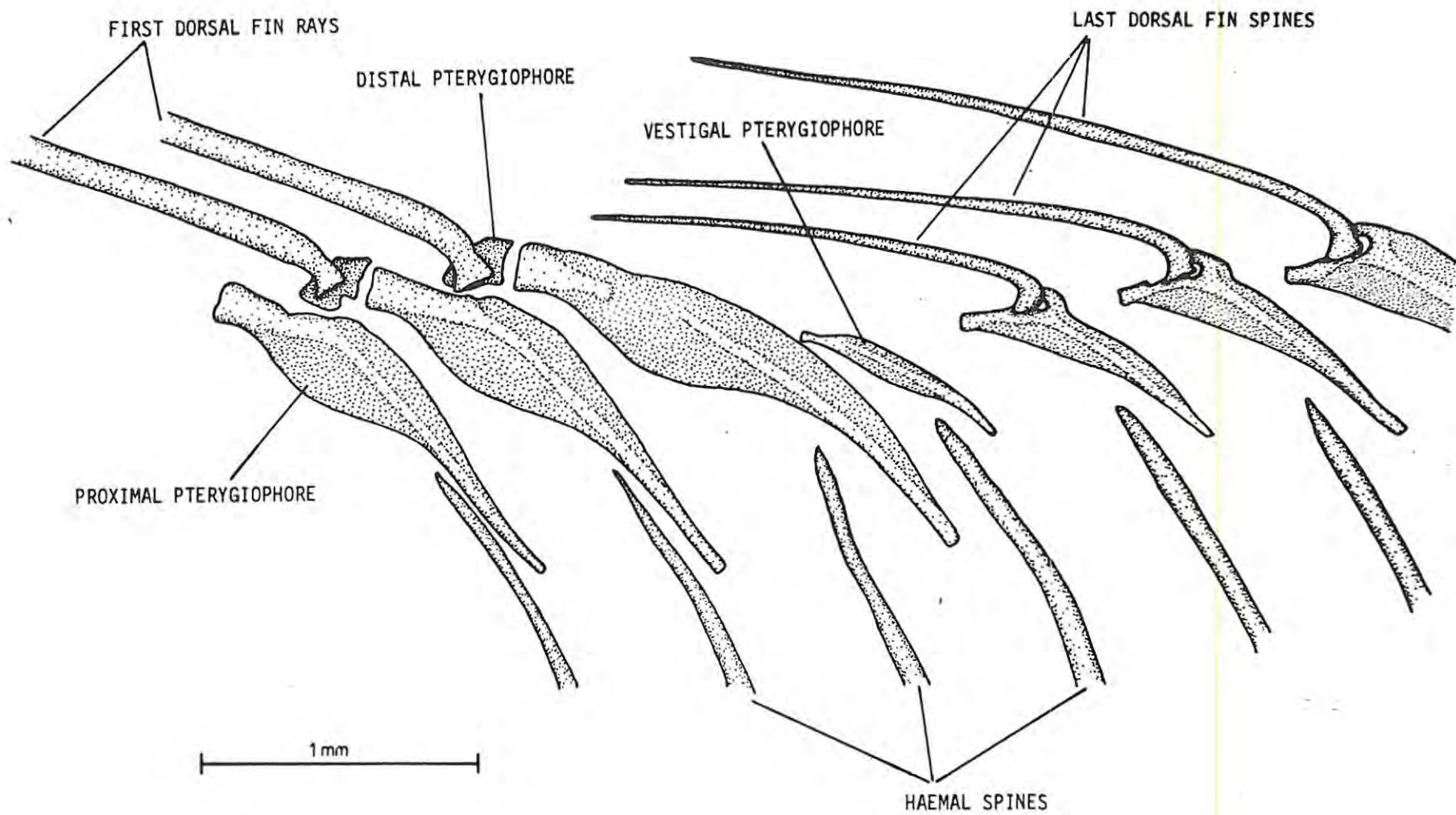


FIGURE 24 DETAIL OF JUNCTION BETWEEN SECOND AND THIRD DORSAL FINS

fins. The spines are attached to their pterygiophores by ring joints. Gosline (1963) considered that this unit consists of fused distal and proximal pterygiophores.

The third dorsal fin comprises 8 or 9 undivided, segmented rays, except the terminal ray which is usually divided to its base (double) (see below). The range for the six species is 8-11 rays.

The rays are bilaterally paired, segmented structures which, with the exception of the terminal ray, attach to bilaterally paired distal pterygiophores. These in turn are attached anteriorly to the expanded distal end of an unpaired proximal pterygiophore, and posteriorly to a subterminal prominence of the succeeding proximal pterygiophore. The last pterygiophore usually bears a double ray, which is counted as a single element (Hubbs & Bardach, 1947). Where divided the anterior portion attaches directly to the expanded distal end of the last proximal pterygiophore, while the posterior portion attaches via paired distal pterygiophores postero-ventrally to the expanded end of the proximal pterygiophore.

One or two vestigial pterygiophores occur between the second and third dorsal fins (figure 24). Although these vestigial pterygiophores are similar to the proximal pterygiophores of the rayed, third dorsal fin, the presence of either one or two appears to be determined by the number of spines in the second dorsal fin. There is only one vestigial pterygiophore if the second dorsal has 12 spines, but two vestigial pterygiophores if the second dorsal has 11 spines.

ANAL FIN (Figure 23).

S. conspicuus has a single anal fin spine and 16 or 17 rays. The range for the six species assigned to the genus is one short spine and 16 to 18 rays.

Both the spine and the first ray articulate with the first pterygiophore. The spine is attached by a ring joint and the ray (as are all subsequent rays) via bilaterally paired distal pterygiophores. The anal fin rays are also bilaterally paired, segmented structures which, except for the terminal (double) ray, are undivided. Each ray articulates with a pair of distal pterygiophores attached anteriorly to the expanded distal end of its proximal pterygiophore, and posteriorly, to a saddle-shaped subterminal prominence on the anterior of the subsequent pterygiophore. The two portions of the terminal ray articulate with the last pterygiophore in an identical manner to that of the last dorsal fin ray.

The proximal end of the first proximal pterygiophore is attached between the arms of the forked haemal spine of the first caudal vertebra (as defined above). The second pterygiophore lies between the forked haemal spine and the subsequent spine, and the third is associated with the spine of the second caudal vertebra.

CAUDAL SKELETON AND FIN (Figure 25).

The nomenclature used in this section is that of Rosen (1973) and Clark (in press). The penultimate and antepenultimate vertebrae are referred to as PU_2 and PU_3 . The ultimate vertebra is regarded as the fusion of the original ultimate vertebra (PU_1) and the first urostylar element (U_1). A uroneural is presumed to be fused to this unit, forming a low crest on the dorsum of the

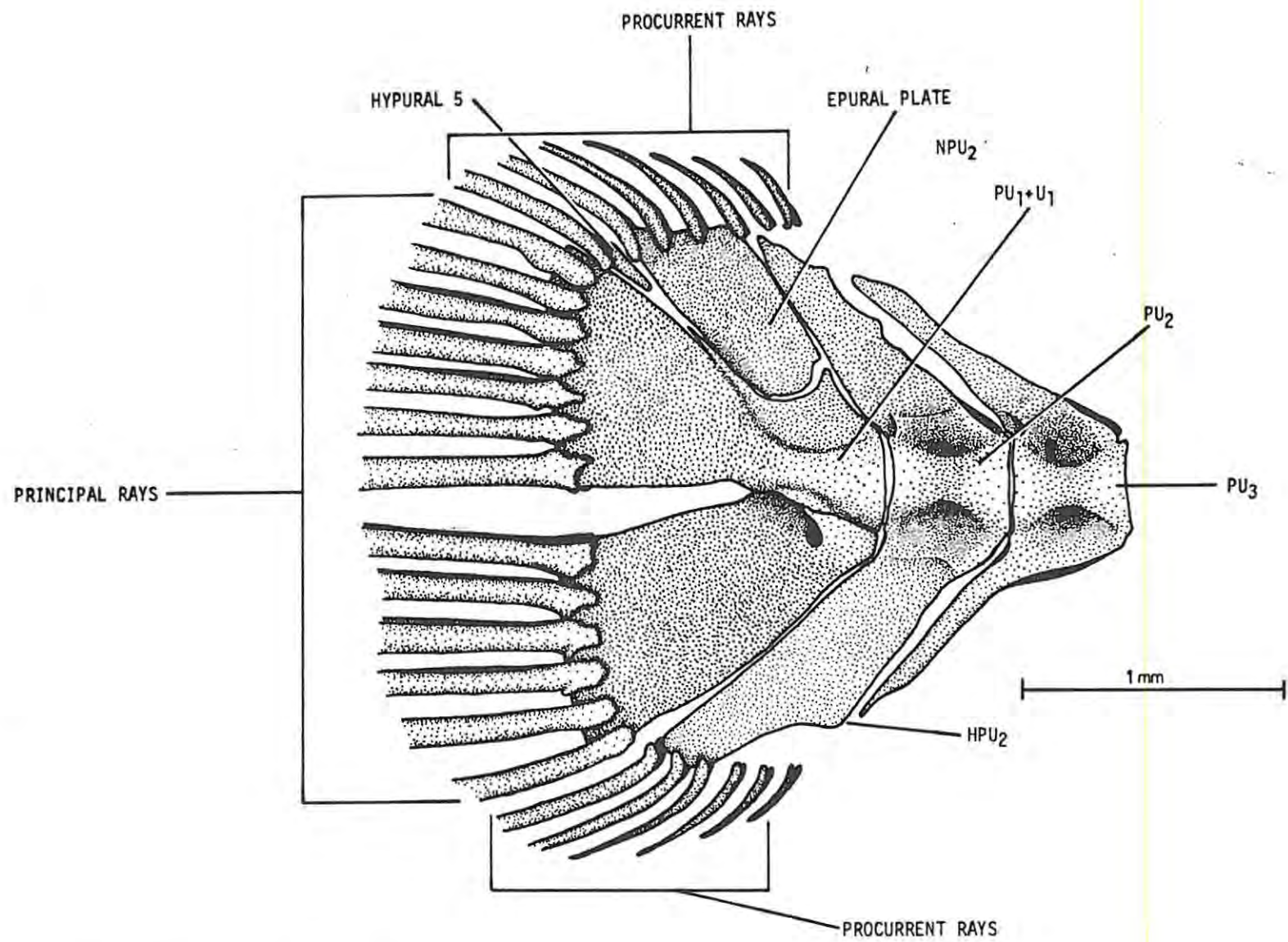


FIGURE 25 CAUDAL SKELETON

element. The dorsal and ventral hypural plates are also fused to this element. The dorsal plate if regarded as comprising a fused second uroneural (U_2) and hypurals 3 and 4 (H_3-H_4), and the ventral plate as a parhypural (PHYP) plus H_1+H_2 . A small hypural is attached posterodorsally to the dorsal hypural plate. A small hypural is also present in the Blenniidae and is termed the 'minimal hypural' by Springer (1968). Clark (in press) considers this as H_5 . There is a broad epural plate which, since there are two epurals present in other genera, is taken as two fused epurals. The posterior edge of the epural plate slots into a shallow groove in the anterior margin of the dorsal hypural plate. There is an opening on either side of the ventral plate where the two branches of the caudal artery exit.

PU_2 bears long, broad neural (NPU_2) and haemal (HPU_2) spines, which participate in the support of the most anterior procurrent rays. S. conspicuus normally has 7 dorsal and 5 ventral unsegmented, paired procurrent rays. Some specimens have 7 and 6 or 8 and 6 rays. Counts for procurrent rays known for the genus (table VIII) generally fall between 6 and 8 dorsal and 5 and 7 ventral. The first (posteriormost) dorsal procurrent ray is supported by the dorsal hypural plate, the next four by the epural plate and the last two or three by NPU_2 . Ventrally the most posterior procurrent ray is attached in the gap between the ventral plate and HPU_2 . The remaining four or five are supported by HPU_2 .

TABLE VIII

Numbers of procurrent rays for various species
of Tripterygiidae.

	Dorsal Proc. Rays.	Ventral Proc Rays.
<u>Scoliosolen abeli</u>	7-8	7-8
<u>S. altipinni</u> (Red Sea)	6-8(7)	5-7(6)
<u>S. conspicuus</u>	6-8(7)	5-6
<u>S. destai</u> (Red Sea)	5-7(7)	5-7(6)
<u>S. obscurus</u> (Red Sea)	6-7	4-6(6)
<u>Enneapterygius pallidus</u> (Red Sea)	7	6
<u>E. pulcherrimus</u>	7-8(8)	6-8(7)
<u>E. pusillus</u> (Red Sea)	6-8(8)	4-7(6)
<u>E. traingulus</u>	7-8(8)	6-7
<u>Helcogramma fuscopinna</u>	9-10	9-10
<u>H. obtusirostre</u>	8-10(9)	8-10(9)
<u>H. steinitzi</u> (Red Sea)	8-9(8)	7-9

Figures for Red Sea species taken from
Clark (in press).

There are 13 segmented rays. The middle 9 are divided once; the uppermost and lowermost two are undivided. The upper 7 rays articulate with the dorsal plate and the lower 6 with the ventral plate.

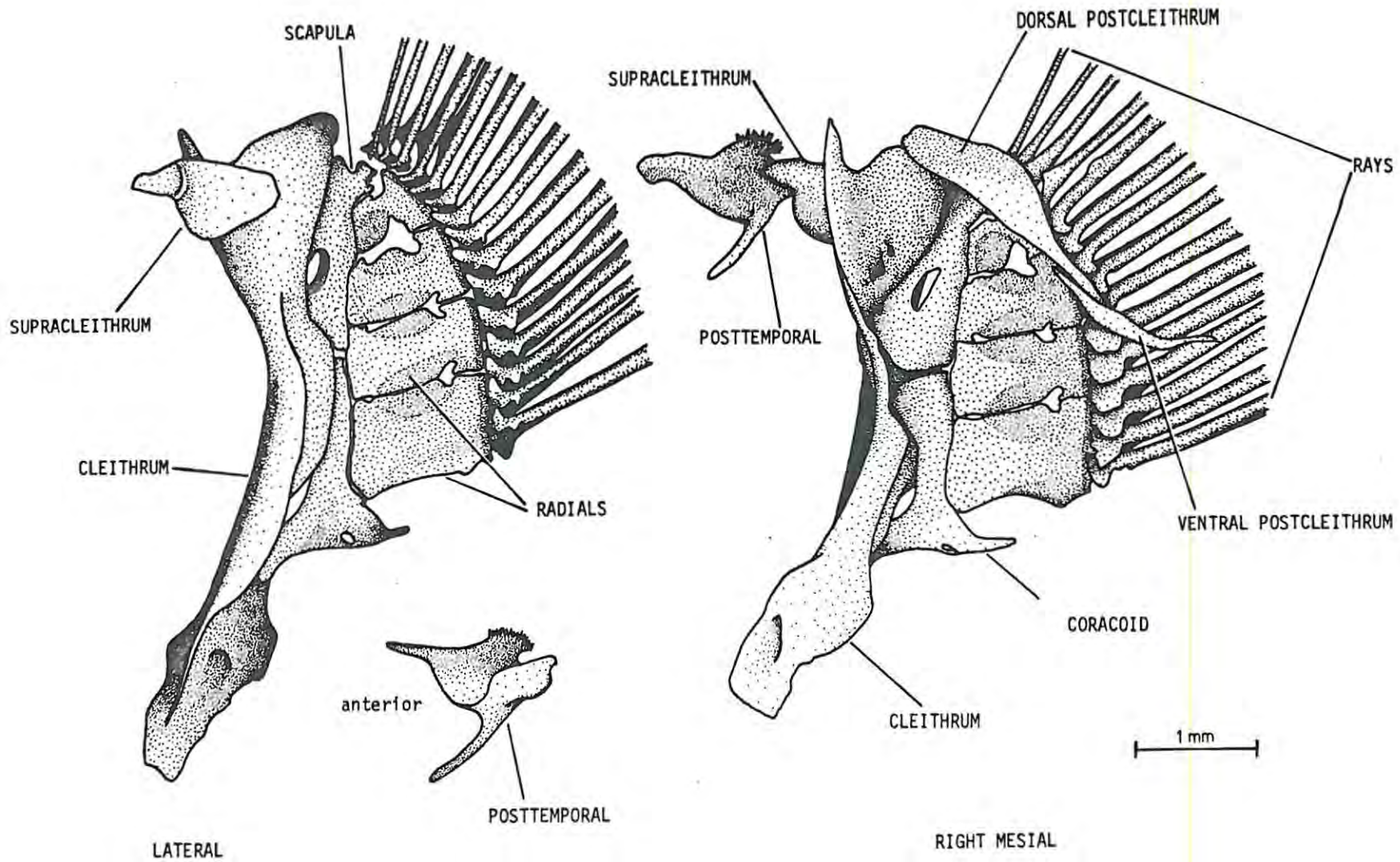


FIGURE 26 PECTORAL GIRDLE AND FINS

Section 3 - Pectoral and pelvic girdles and fins.

PECTORAL GIRDLE AND FINS (Figure 26).

Each half of the pectoral girdle consists of a posttemporal, supra-cleithrum, cleithrum, scapula, coracoid, a postcleithrum divided into dorsal and ventral portions, and four radials. S. conspicuus has 15 segmented pectoral fin rays.

The posttemporal is forked in the vertical plane. A dorsolaterally open channel for the cephalic lateralis sensory canal runs between the upper and lower portions of the fork. The posterior margin of the inner side of the channel is toothed and is exposed so that externally this portion of the bone resembles a ctenoid scale.

The upper portion of the fork is dorsoventrally flattened and articulates with the epioccipital wing. The anterior end of the lower portion is connected by a short ligament to the centre of the intercalar. A condyle on the posterior mesial surface of the bone articulates with a depression on the external surface of the supra-cleithrum.

The supracleithrum is a pear-shaped bone with the tapering end anterior. A laterally raised process at the junction of the narrow and wide portions of the bone bears the concave articulating surface referred to above. The narrow anterior portion lies flat against the posteromesial face of the posttemporal. The supra-cleithrum is loosely attached to the upper lateral surface of the cleithrum.

The cephalic lateralis canal does not continue along the supra-cleithrum as it does in the Blenniidae (Springer, 1968) but continues

from the posttemporal to the first lateral line scale lateral and slightly dorsal to the supracleithrum.

The cleithrum is a large, anteriorly concave, crescentic bone. There is a laterally extending flange running along the anterior margin of the center of the arc. A shorter flange extends posteriorly. The dorsal portion of the cleithrum is widened and laterally convex, and the ventral end has flanges extending laterally, mesially and posteriorly so that in section it resembles a 3-pointed star. The ventral margins of the two cleithra join to form a 'V'-shaped cradle in which the pelvis lies. The scapula and coracoid are joined to the posterior margin of the cleithrum.

Postcleithrum. There are two slender postcleithra on either side lying mesial to the girdle. The dorsal end of the upper (dorsal) postcleithrum is flattened and is loosely attached to the postero-dorsal corner of the cleithrum on its mesial surface. The ventral third of the dorsal postcleithrum lies adjacent and loosely attached to the dorsal third to half of the ventral postcleithrum.

Both the coracoid and scapula are well-developed. The scapula is flat and constricted about a third down from its dorsal end. There is a large oval foramen mid-anteriorly in the ventral portion of the bone. The anterior edge of the dorsal end abuts the dorso-posterior edge of the cleithrum. The widened ventral portion partially overlaps the cleithrum mesially. On the dorsal edge of the scapula is a single articulation for the uppermost two pectoral rays.

The coracoid is the shape of an inverted 'T'. The end of the stem is broadened and overlaps the mesial face of the cleithrum abutting

the ventral margin of the scapula. The anterior end of the cross-piece of the 'T' is attached to the external surface of cleithrum ventral to the central posterior flange. There is a small foramen close to the ventral edge of the coracoid.

There are four flat radials on either side. The uppermost is 'T'-shaped with a bulbous stem. It articulates with the scapula and supports pectoral rays 3 to 6. The next two radials are rectangular bones with notches in their dorsal and ventral margins. The second also articulates against the scapula and supports rays 7 to 9 and part of 10. The third radial, which articulates against both the scapula and the coracoid, supports rays 11, 12 and portion of 13. The last radial is rectangular, except for a notch only in its dorsal margin. It articulates against the coracoid and supports the lower two to three rays.

The rays are bilaterally paired structures. The uppermost 1-3 and lowermost 7 are undivided; the remaining rays are divided once. They are connected by cartilage and connective tissue to the radials (or scapula). The bases of both halves of each ray, forming a dorsally extending process externally which overlaps the base of the next ray dorsally, and a ventrally extending process internally which overlaps the base of the next ray ventrally.

The second to fifth uppermost rays have a second dorsal extension on the external half of the ray which overlaps the next ray dorsally. These extensions increase in size from ray 2 to 5.

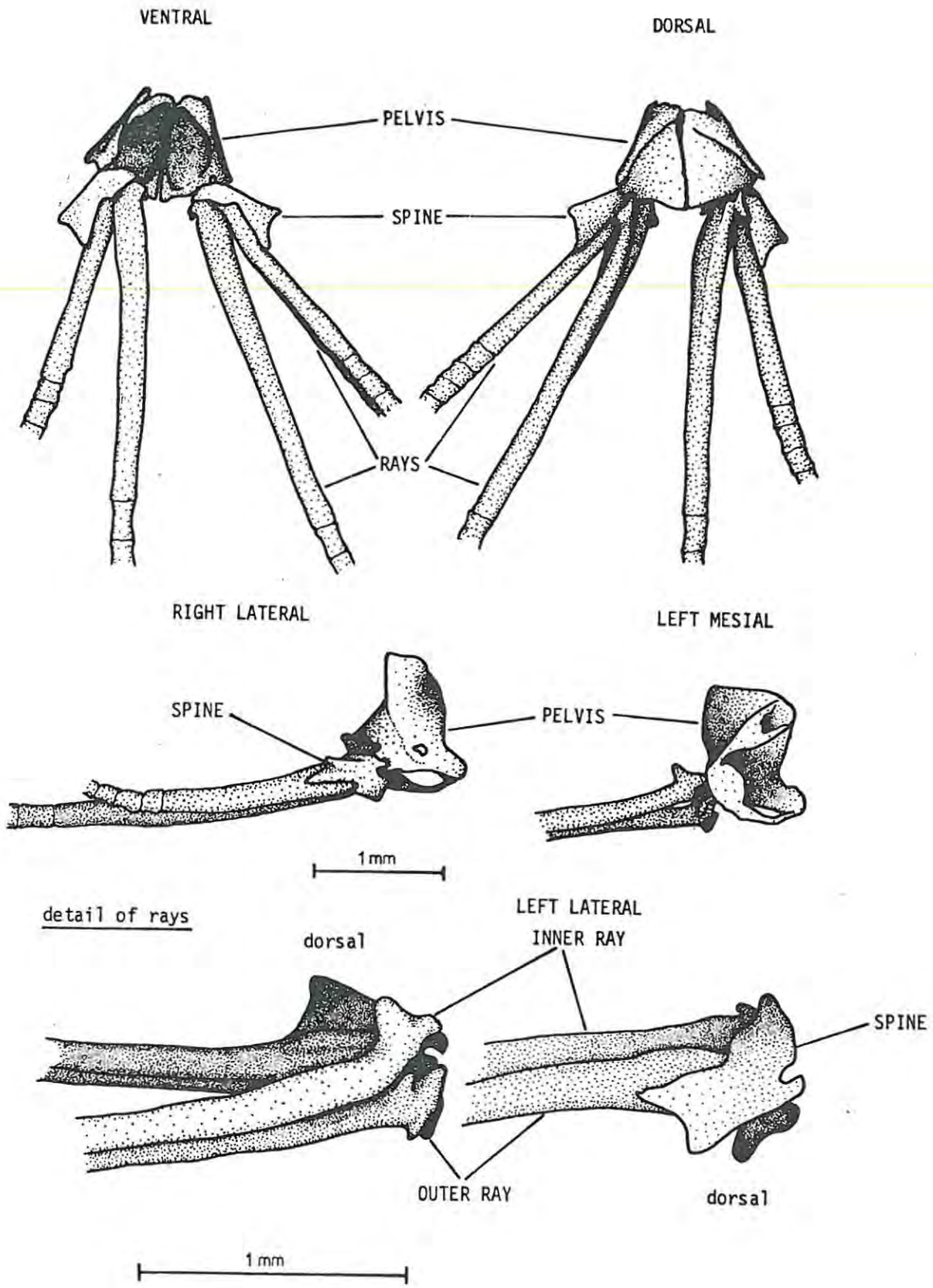


FIGURE 27 PELVIC GIRDLE AND FINS

PELVIC GIRDLE AND FINS (Figure 27).

Each Pelvis is a laterally convex bone with a thin triangular flange which extends dorsally from its lateral surface. The two bones lie with their edge joined in the midline to form a hollow pod which lies in the angle between the two cleithra. The triangular flanges lie flat against the mesial surfaces of the cleithra. A thin, flat strut connects the mesial anteroventral corner of each pelvis to the posteromesial corner of its dorsal surface. The two struts lie joined along the sagittal section. Anteriorly is a foramen formed by the concave anteriomesial margin of each pelvis.

Two segmented, bilaterally paired rays and a single short spine are attached to each pelvis. The spines are very short, and lie hidden under the skin. They clasp the pelvises' posterolateral corners. The rays lie median to the spines. The two halves of the innermost rays also clasp the pelvises, but the outer ray on either side appears to rely on its attachment to the pelvis by its close connection to its respective spine. At the base of the inner ray, each half of the ray bears a process directed away from the junction of the two halves.

In the following chapter selected features of the osteology of Scoliosolen are compared with similar features in the other four South African genera.

COMPARATIVE OSTEOLOGY OF TRIPTERYGIID GENERA, WITH EMPHASIS ON
THOSE OCCURRING IN SOUTH AFRICAN WATERS.

This chapter is not a detailed osteological comparison, but rather the comparison of selected characters of the five genera which occur in South African waters (Scoliosolen, Enneapterygius, Norfolkia, Helcogramma and Cremnochorites) with further reference to eight genera which do not occur in these waters viz. Tripterygion, Enneanectes, Vauclusella, Lepidoblennius, Gilloblennius, Brachynectes, Notoclinus and Notolinops. The particular characters were selected because they appear to be consistent in a number of species of a particular genus, and have thus been assumed to be consistent for the genus. Where only one species of a genus has been available, the same characters as those used in genera where more than one species was available, were selected.

In the preceding chapter the choice of Scoliosolen was explained, and that it was reasonable to assume that this is a generalized genus. The term 'generalized' must however not be interpreted to have any phylogenetic significance. No attempt has been made to establish the phylogeny of the genera, since only a small proportion (five of 16 or more) of the genera have been dealt with in some detail. A summary of the characters discussed or mentioned is given in table IX at the end of this chapter.

Neurocranium

The neurocrania of the majority of tripterygiid genera are similar in overall appearance and structure to that of Scoliosolen.

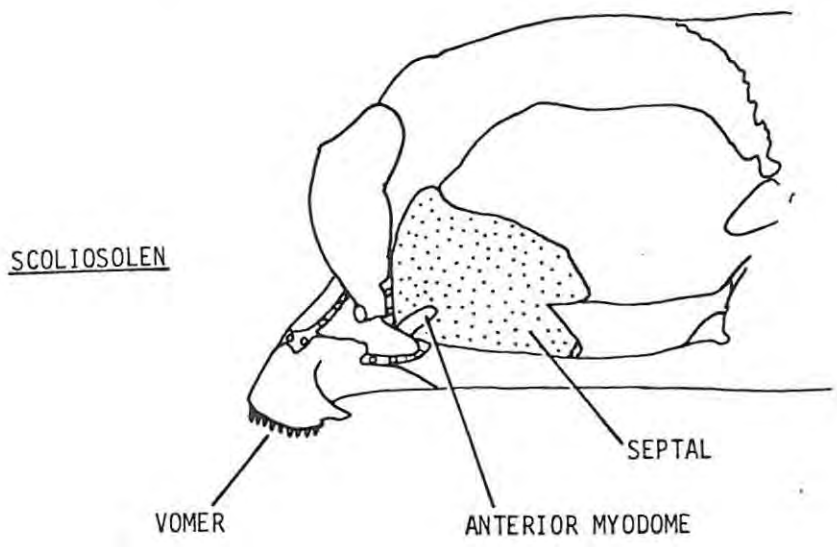
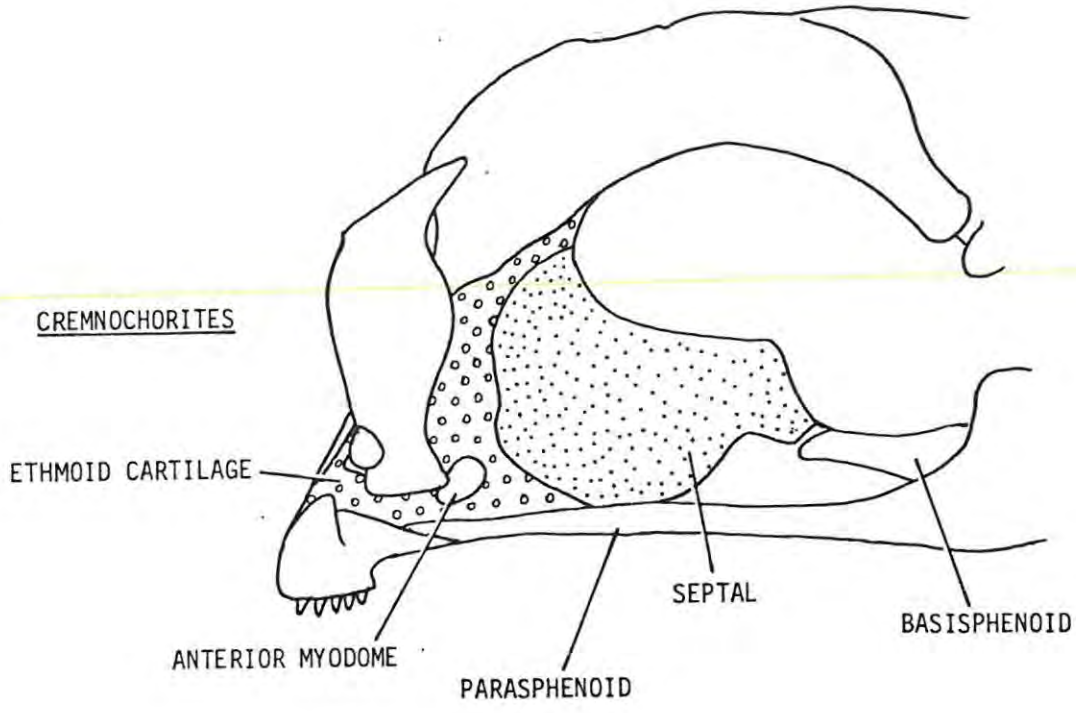


FIGURE 28 LATERAL ANTERIOR PORTION OF NEUROCRANIA OF CREMNOCHORITES AND SCOLIOSOLEN.

The first and most obvious difference is that not all genera have a septal in the neurocranium. Of the 'South African' genera, only Norfolkia lacks a septal. This condition is shared at least by Notoclinus, Brachynectes, Lepidoblennius and possibly Enneanectes. If a septal is present in Enneanectes, it is very small. A more detailed investigation of this genus is necessary to confirm its presence or absence.

Cremnochorites was the only genus in which the septal does not impinge on and form part of the border of the anterior myodome, or join the frontals and lateral ethmoids as it does in other genera where it is present (figure 28). In some specimens of Cremnochorites the septal does not extend ventrally to join the parasphenoid. The length of contact between the septal and parasphenoid of Cremnochorites is very short compared to that of Scoliosolen.

Brachynectes and Notoclinus are further distinct in having a very broad interorbital compared to that of other Tripterygiid genera.

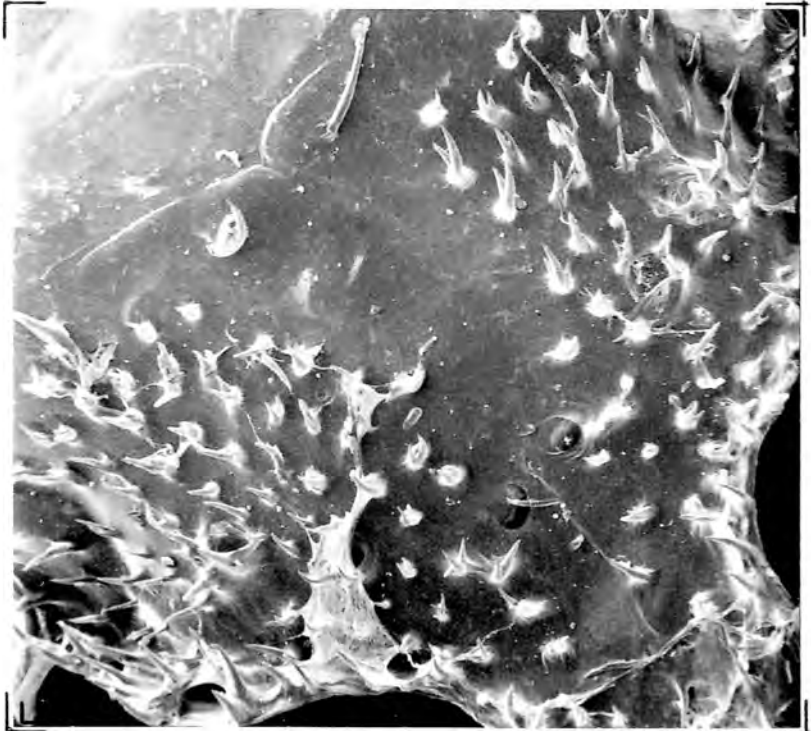
The basis for the division of Enneapterygius into two genera, Enneapterygius and Scoliosolen, is the shape of the supraoccipital sensory canal and associated osteology.

The supraoccipitals of all 'South African' genera are similar in shape. They are overlapped anteriorly by the frontals and laterally by the parietals. In four of the genera the median margins of the parietals lie close to each other. However, in Enneapterygius the supraoccipital is relatively longer than in the other genera, separates the parietals widely, and extends forward to between the posterior ends of the frontals (figure 29).

108a

PLATE 7

parietal



orbit

30X

frontal



110X

Stereoscan photograph of dorsum of Cremnochorites neurocranium.

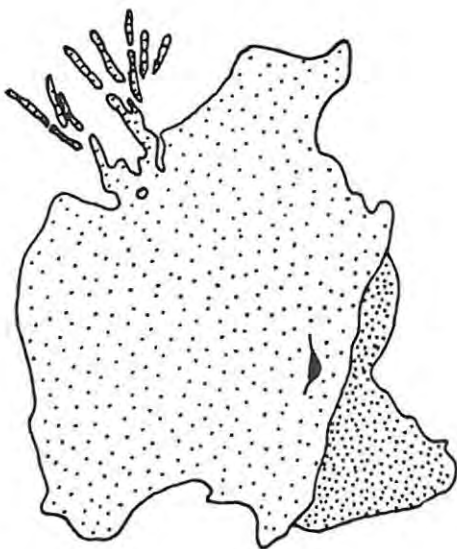
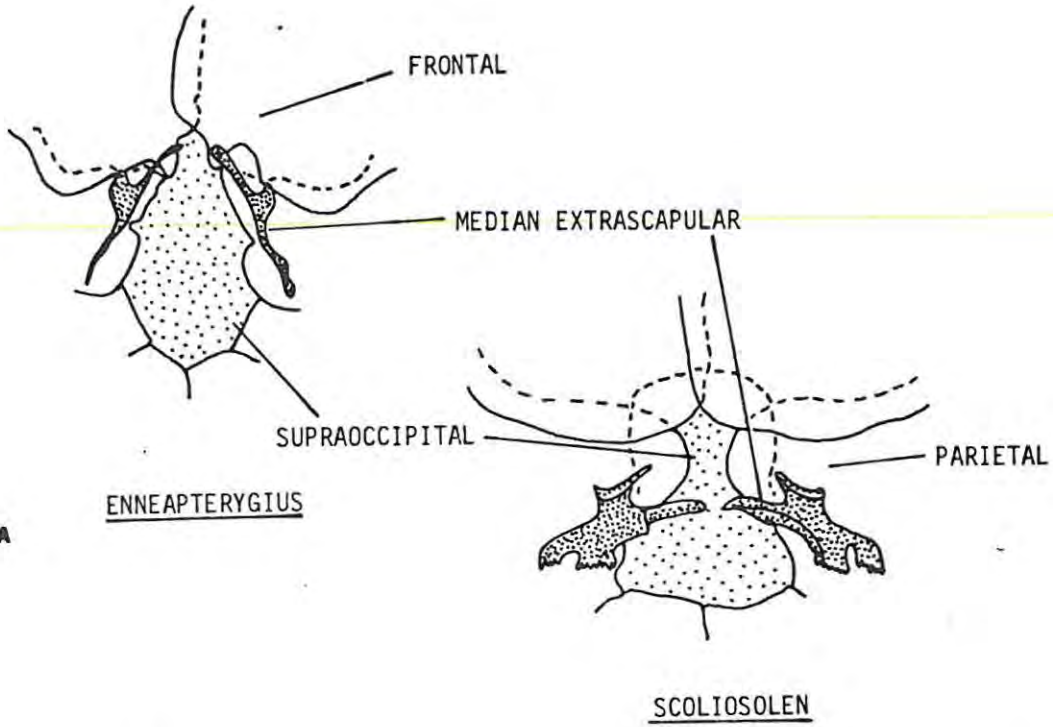
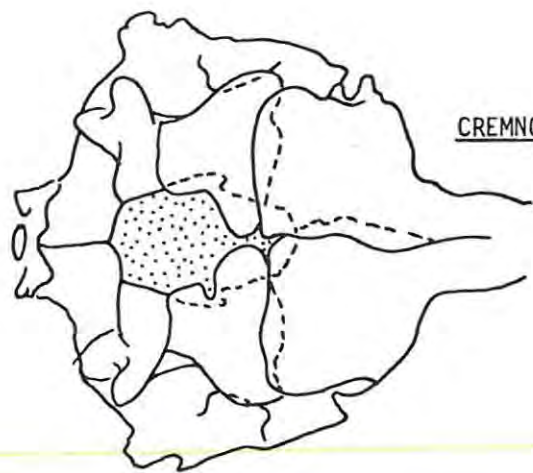


FIGURE 30A DIAGRAM TO SHOW POSITION OF MEDIAN EXTRASCAPULARS OF SCOLIOSOLEN AND ENNEAPTERYGIUS

B ANTERIOR VIEW, RIGHT LATERAL ETHMOID OF NORFOLKIA



CREMNOCHORITES



NORFOLKIA



HELCOGRAMMA

EPIOCCIPITAL

PARIETAL

FRONTAL

SUPRAOCCIPITAL

EXOCCIPITAL



ENNEAPTERYGIUS

FIGURE 29 DORSAL POSTERIOR PORTION OF NEUROCRANIA OF NORFOLKIA, HELCOGRAMMA, CREMNOCHORITES AND ENNEAPTERYGIUS.

Furthermore, the supraoccipital of Enneapterygius is dorsally slightly concave, suggesting that the first dorsal fin has moved forward over the back of the head, and the supraoccipital has become depressed to accommodate the first three dorsal pterygiophores.

The real or apparent forward movement of the dorsal fin has displaced the median extrascapulars from their 'normal' position, from the posterior margins of the parietals and across the supraoccipital, forward to lie parallel to the median margins of the parietals, and onto the posteromesial margins of the frontals (figure 30A).

Both Gilloblennius and Lepidoblennius have long supraoccipitals, widely displaced parietals and a supraoccipital canal curved similarly to that of Enneapterygius. The anteriormost dorsal pterygiophores are accommodated by a depression of the supraoccipital, again as in Enneapterygius. These two genera do, however, differ from Enneapterygius in that the supraoccipital does not extend so far forward as to lie between the posterior ends of the frontals. The supraoccipital of Brachynectes is also depressed to accommodate the anteriormost dorsal pterygiophores, but the genus lacks the deeply curved supraoccipital canal of Gilloblennius, Lepidoblennius and Enneapterygius.

The margins of the frontals of Norfolkia and Enneanectes bear spine-like projections above the eyes. The surface of the frontals and parietals of Cremnochorites are covered with small spine-like projections (plate 7). Similar, though smaller 'spines' are present on the frontals of Enneanectes pectoralis (but are absent in E. altivelis), and to a lesser degree in Norfolkia.

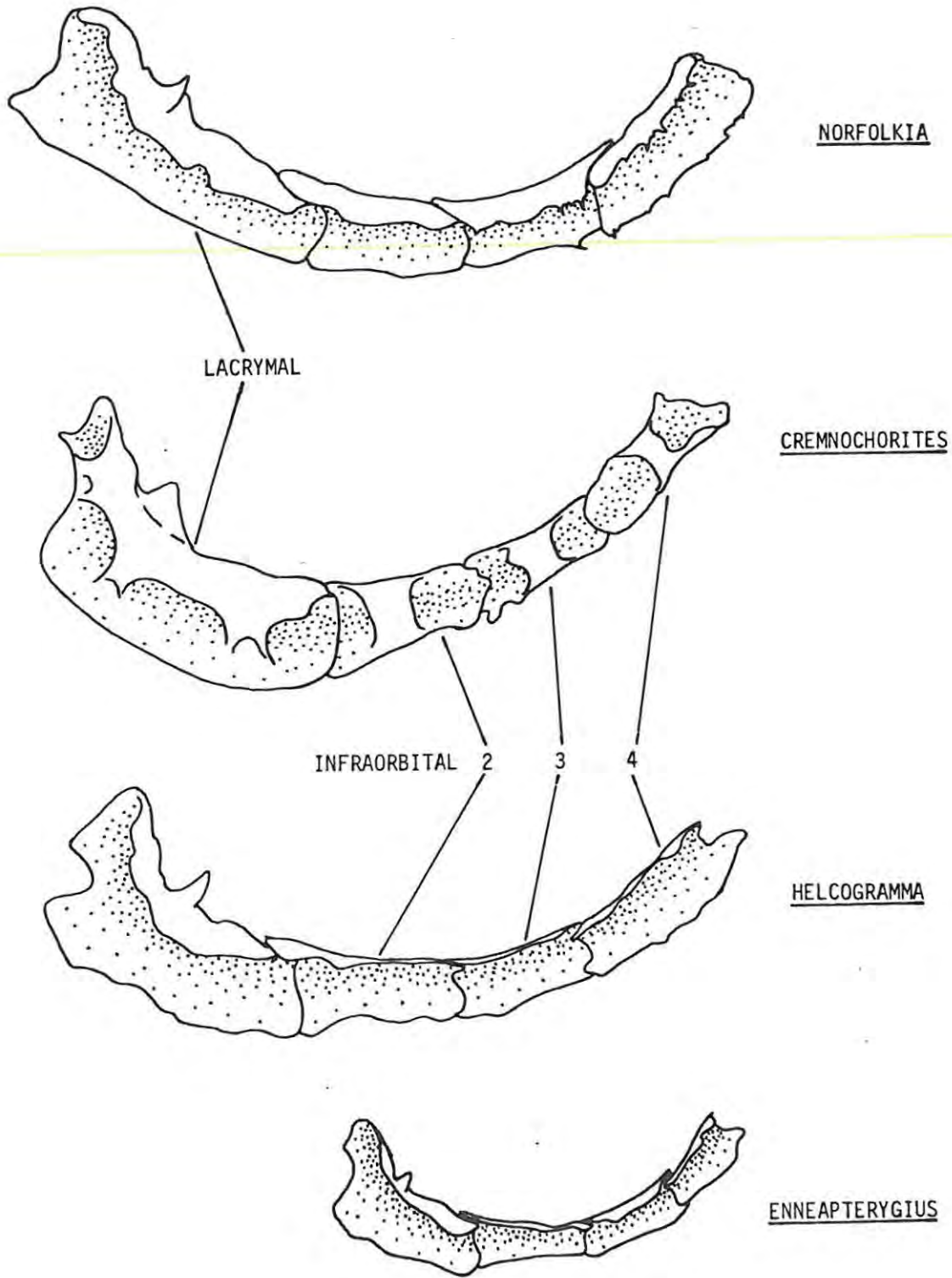


FIGURE 31 INFRAORBITALS OF NORFOLKIA, CREMNOCHORITES, HELCOGRAMMA AND ENNEAPTERYGIUS.

In both the Enneanectes species and Norfolkia these 'spines' are well developed on the margins of the frontals above the orbits, and extend to the dorsolateral margins of the lateral ethmoids. The ornamentation of the lateral ethmoid margins of Norfolkia and Enneanectes differs from the 'spines' of the frontal margins, in that the bone is partially excavated to produce dendritic filaments on the margin (figure 30B). The margins of the third and fourth infraorbitals of Norfolkia squamiceps also carries 'spines'.

The gap between the parasphenoid and basioccipital through which two pairs of rectus eye muscles pass was described for Scoliosolen in the preceding chapter. This gap is absent in Notoclinus and Brachynectes, but present in the other genera named in this chapter.

All tripterygiid genera appear to have five infraorbital bones. In most of the genera they are as described for Scoliosolen: a laterally open trough comprising a lacrymal which is longer and broader than the second through fourth infraorbitals, and a small fifth infraorbital which is generally firmly attached behind the posterior wing of the sphenotic. The infraorbitals of Cremnochorites are similar in shape and relative size to those of Scoliosolen but are bridged (figure 31). The lacrymal has three 'bridges', and the second to fourth each one 'bridge'. The fifth is open. The fifth infraorbital of Notoclinus appears fused to the sphenotic. Lepidoblennius and Notoclinus have large, complex lacrymals bearing greater similarity to that of the Blenniidae described by Springer (1968). The fifth infraorbital of Lepidoblennius is relatively large, and the canal is enclosed, with pores through the bones. The infraorbitals of Gilloblennius are best termed 'semi-closed'; the margins fold over as though to close the canal but have irregular edges which leave a narrow, meandering gap along the

length of the canal. Notoclinus has curious narrow, tube-like infraorbitals quite unlike those of other tripterygiids.

The other bones which carry cephalic sensory canals may also be either open or bridged. The canals of the pterotics, preopercles, posttemporals and nasals of Cremnochorites, Notoclinus, Brachynectes and Gilloblennius are closed; the nasals of Tripterygion are closed, and the nasals of Norfolkia may have a narrow bridge.

The bridging of the mandibular sensory canal does not follow the same pattern as the other sensory canals, and in all five genera the mandibular canal may or may not be bridged posteriorly, but always carries a bridge behind the anteriormost opening.

The presence or absence of palatine teeth appears to be consistent for most genera. Cremnochorites, Helcogramma, Gilloblennius, Tripterygion and Notoclinops have palatine teeth. Norfolkia, Brachynectes, Lepidoblennius, Enneanectes and Enneapterygius lack palatine teeth, whereas Scoliosolen and Vauclusella may or may not have them. Specimens of Vauclusella have been seen with one to three teeth on only one of the palatines.

Branchiocranium.

With the exceptions of Lepidoblennius, Brachynectes and Notoclinus, the jaws, branchial arches, and jaw supporting elements of the other genera are very similar. There appear to be only two noteworthy features which can be used for comparison. The jaws the abovementioned genera are very different to other genera and will not be discussed any further.

The premaxillae have long ascending processes, and shorter, blade-like articular processes. In Scoliosolen, Helcogramma, Enneanectes, Tripterygion, Vauclusella, Gilloblennius and Cremnochorites these two processes are separated by a narrow gap. Those of Norfolkia are partially fused, and in Enneapterygius they are completely fused.

Enneapterygius, Scoliosolen, Vauclusella, Gilloblennius, Notoclinops and Norfolkia bear long, narrow primordial processes on the posterodorsal edge of anguloarticular. This process is short in Helcogramma and Cremnochorites, and of intermediate length in Tripterygion and Enneanectes.

All tripterygiids appear to have an opercular filament (figure 20). Norfolkia has the upper posterior 'corners' of both opercle and subopercle toothed. Enneanectes and Cremnochorites have small teeth on the opercle only.

The structure of the branchial arches is conservative and shows no noteworthy differences between the different genera.

Axial Skeleton and Unpaired Fins.

The most obvious consistent difference between genera is the number of spines in the first dorsal and anal fin. With the possible exception of Notoclinops, the number of spines appears to be constant within a genus.

Enneapterygius, Helcogramma and Scoliosolen each have three first dorsal fin spines and a single anal fin spine, whereas Norfolkia and Cremnochorites have four and two respectively. Among the non-

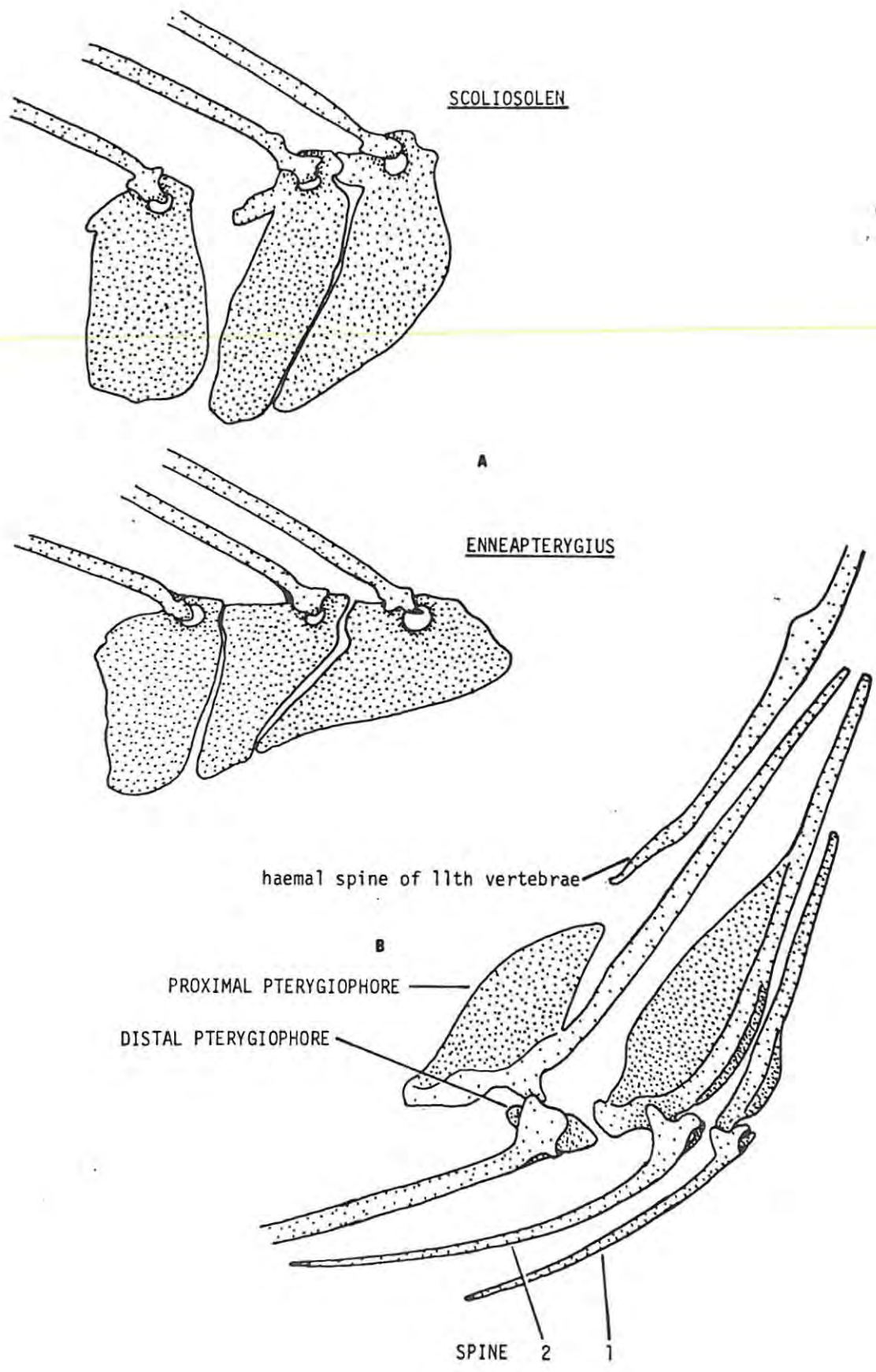


FIGURE 32 A FIRST DORSAL FIN ELEMENTS OF SCOLIOSOLEN AND ENNEAPTERYGIUS.
B FIRST ANAL FIN ELEMENTS OF NORFOLKIA.

South African genera Tripterygion, Gilloblennius, Enneanectes and Brachynectes have three first dorsal fin and two anal fin spines, Vauclusella has three and one, Notoclinus has four and one, and Lepidoblennius has three first dorsal fin spines, but lacks anal fin spines. Notoclinops, the possible exception, has been recorded with a single anal fin spine, and four to six first dorsal fin spines. Two newly described species, Forsterygion multiradiatum Scott (1977) and Forsterygion gymnotum Scott (1977) have seven and one, and seven and two spines respectively. Forsterygium varium (Forster), a valid species (Springer, pers. comm.) has five first dorsal fin spines and two anal fin spines.

Each first dorsal fin spine is supported by a separate pterygiophore, to which the spine is fixed by a ring-joint. The first two (or three) pterygiophores are close to each other and separated from the third (or fourth) by a gap of about half a pterygiophore-width (figure 23). The last pterygiophore of the first dorsal fin is separated by a gap about the width of a pterygiophore from the first pterygiophore of the second dorsal fin. The pterygiophores of the first dorsal fin of Enneapterygius are deflected backwards by the apparent movement of the first dorsal fin forward over the back of the skull (figure 32A).

Where a single anal fin spine is present, it is attached to the anterior of the first anal pterygiophore which also supports the first anal fin ray by a ring joint. If two spines are present, the first is supported by a small, separate pterygiophore while the second is attached as when only a single spine is present (figure 32B). Notoclinus is an exception here in that the single anal fin spine is supported by its own pterygiophore.

Vertebral counts cannot be used to separate one genus from another. The counts of species within one genus overlap those of species in other genera (table VII).

Of some significance is the presence or absence of the vestigial pterygiophore between the second and third dorsal fins. Of the five South African genera, Enneapterygius lacks a vestigial pterygiophore, and there are merely one or two 'blanks' between the last pterygiophore of the second dorsal fin and the first of the third dorsal fin.

Caudal skeleton Clark (in press) made fairly detailed observations of the structure of the caudal skeleton of the Red Sea Tripterygiidae. Differences between genera lie in the presence, size or absence of hypural 5 (H_5), the length of the second preural neural spine (NPU_2) and the number of epurals present. (It is relevant here that Clark found H_5 as either present or absent in Red Sea Enneapterygius species. The presence or absence of H_5 is another of the characters separating Enneapterygius and Scoliosolen.)

Norfolkia, Cremnochorites, Vauclusella and Brachynectes have a large H_5 ; H_5 is small in Scoliosolen, Tripterygion, Enneanectes, Lepidoblennius, Gilloblennius and Notoclinus, and absent in Enneapterygius, Helcogramma and Notoclinops. Those genera with a large H_5 have two epurals, and so have Helcogramma and Notoclinops. There is a single epural (two fused epurals?) in Scoliosolen, Enneapterygius, Gilloblennius and Notoclinus. NPU_2 may be either long, participating in the support of the most anterior dorsal procurrent rays, or short. It is long in Scoliosolen, Enneapterygius and Gilloblennius. Although NPU_2 is also long in Brachynectes and

Notoclinus it is comparatively narrow compared to the long NPU_2 of the other genera noted. It must here be noted that the caudal skeleton of Lepidoblennius, Brachynectes and Notoclinus differs in other aspects from those of the other genera here discussed, but this will not be discussed any further.

Paired fins.

The structure of the pectoral girdle and fins of the Tripterygiidae appears to be conservative, no noteworthy differences were observed.

The pelvic girdle and fins show some variation, although not in South African genera. The five South African genera, as well as the majority of the others, possess two segmented rays and a short, hidden spine. Gilloblennius, Lepidoblennius, Brachynectes and Notoclinus each have three pelvic fin rays. The innermost ray of Brachynectes and Notoclinus is considerably thinner and shorter than the other two.

As noted in the opening paragraph of this chapter, only salient features which obviously differ between genera have been selected and discussed. In the following chapter these differences are used to provide definition of the five South African genera.

TABLE IX - Summary of Osteological Characters.

	<u>Cremnochorites</u>	<u>Norfokia</u>	<u>Helcogramma</u>	<u>Enneapterygius</u>	<u>Scoliosolen</u>	<u>Tripterygion</u>	<u>Enneanectes</u>	<u>Vauclusella</u>	<u>Lepidoblennius</u>	<u>Gilloblennius</u>	<u>Brachynectes</u>	<u>Notoclinus</u>	<u>Notoclinops</u>
1. Septal	present	absent	present	present	present	present	?	present	absent	present	absent	absent	present
2. Supraoccipital	short	short	short	long	short	short	short	short	long	long	short	short	short
3. Parietals	close	close	close	wide	close	close	close	close	wide	wide	close	close	close
4. Margin lateral ethmoid	smooth	ornamnt	smooth	smooth	smooth	smooth	ornamnt	smooth	smooth	smooth	smooth	smooth	smooth
5. Basioccip/basisphen gap	present	present	present	present	present	present	present	present	present	present	absent	absent	present
6. Infraorbitals		open	open	open	open	open	open	open	closed	semi-cl	closed	closed	semi-cl
7. Preopercular canal	closed	open	open	open	open	open	open	open	closed	closed	closed	closed	closed
8. Posttemporal canal	"	"	"	"	"	"	"	"	"	"	"	"	"
9. Pterotic canal	"	"	"	"	"	"	"	"	"	"	"	"	"
10. Nasals	"	"	"	"	"	"	"	"	"	"	"	"	"
11. Opercular margin	some tth	toothed	smooth	smooth	smooth	smooth	smooth	smooth	hooked	smooth	smooth	smooth	smooth
12. Subopercular margin	smooth	toothed	"	"	"	"	"	"	smooth	"	"	"	"
13. Ascend & pmxy processes	sep	/ fused	sep	fused	sep	sep	sep	sep	/ fused	sep	/ fused	sep	sep
14. Anguloartic primord proc	short	long	short	long	long	intermd	intermd	long	short	long	lng/brd	int/brd	intermd
15. First dorsal fin spines	4	4	3	3	3	3	3	3	3	3	3	4	4-6
16. Anal fin spines	2	2	1	1	1	2	2	1	0	2	2	1	1
17. Pelvic rays	2	2	2	2	2	2	2	2	2-3?	3	3	3	2
18. Hypural 5	large	large	absent	absent	small	small	small	large	small	small	large	small	absent
19. Epurals	2	2	1/2	1	1	2	2	2	2	1	2	1	2
20. NPU ₂	short	short	short	long	long	short	short	short	?	long	lng/narw	lng/narw	short
21. Palatine teeth	present	absent	present	absent	prs/abs	present	absent	prs/abs	absent	present	absent	absent	present

DISCUSSION AND DEFINITIONS OF SCOLIOSOLEN, ENNEAPTERYGIUS,
HEICOGRAMMA, NORFOLKIA AND CREMNOCHORITES.

In the introduction to this study the confusion surrounding the use of various tripterygiid genera was pointed out, and the necessity to define the genera of the Tripterygiidae was stressed. In the first part, which dealt with the taxonomy of the South African representatives of the family, two genera, Cremnochorites and Scoliosolen, were described as new. The diagnoses of these genera were based on external morphological features - those which the field worker must use to identify a particular genus.

In the second part of the study the osteology of Scoliosolen was described to provide a basis against which other genera may be compared, and, in the preceding chapter, characters which are considered consistent within genera were described. What remains to be done is to combine the external morphological features and the osteological characters, and to use these to provide definitions of the South African genera.

The simplest way to provide the definitions is to list the characters in point form. A listing also makes comparisons easier. External features are noted first, followed by osteological characters.

Genus Cremnochorites.

1. First dorsal fin with four spines.
2. Anal fin with two spines.
3. Lateral line divided with anterior series of pored scales, and a posterior series of notched scales.
4. Head, cheeks, and snout covered with small denticle-like,

ctenoid scales. A ring of 'ctenii' on the perimeter of the eyeball. Throat papillose with 'ctenii' embedded in the papillae.

5. Frontal area of head with small 'ctenii' or spines attached to the bone.
6. Palatine teeth present.
7. Septal present but does not form part of the border of the anterior myodome.
8. Infraorbitals and nasals are bridged, as are those portions of the preopercle, posttemporal and pterotic which carry sensory canals.
9. Ascending and articular processes of premaxillae separate.
10. Primordial process of anguloarticular short, forming a small protruberance on dorsal surface of anguloarticular.
11. Large hypural 5 and two free epurals present in caudal skeleton. Haemal spine on second preural centrum short, and does not participate in supporting dorsal procurrent rays.
12. Vestigial pterygiophore present between last pterygiophore of second dorsal fin and first pterygiophore of third dorsal fin, if there is a gap between the two fins.

Genus Norfolkia.

1. First dorsal fin with four spines.
2. Anal fin with two spines.
3. Lateral line divided, with anterior series of pored scales and posterior series of notched scales.
4. Body entirely covered with ctenoid scales, as is nape, opercles, preopercles and pectoral fin bases. Throat, snout, interorbital area and cheeks directly below eyes naked.
5. Palatine teeth absent.

6. Septal absent.
7. Infraorbitals open, as are those portions of the preopercle, posttemporal and pterotic which carry sensory canals; the nasal may have a narrow bridge.
8. Ascending and articular processes of premaxillae fused for about the half length of the articular process.
9. Long, narrow primordial process present on anguloarticular.
10. Large hypural 5 and two free epurals present in the caudal skeleton. Haemal spine on second preural centrum short, and does not participate in supporting dorsal procurrent rays.
11. Vestigial pterygiophore present between last pterygiophore of second dorsal fin and first pterygiophore of third dorsal fin, provided that there is a gap between the two fins.

Genus Helcogramma

1. First dorsal fin with three spines.
2. Anal fin with single spine.
3. Lateral line single consisting only of an anterior series of pored scales.
4. Body scales ctenoid. Head, abdomen and pectoral fin bases naked, nape may be scaled.
5. Palatine teeth present.
6. Septal present, and forms part of border of anterior myodome.
7. All bones bearing cephalic lateralis sensory canals open.
8. Ascending and articular processes of premaxillae separate.
9. Primordial process of anguloarticular short, forming a small protruberance on the dorsal surface of the anguloarticular.
10. Hypural 5 absent from, and two free epurals present in caudal skeleton. Haemal spine of second preural centrum short, and does not participate in supporting dorsal procurrent rays.

11. Vestigial pterygiophores present between last pterygiophore of second dorsal fin and first pterygiophore of third dorsal fin, if there is a gap between the two fins.

Genus Scoliosolen.

1. First dorsal fin with three spines.
2. Single spine in anal fin.
3. Lateral line divided, with an anterior series of pored scales, and a posterior series of notched scales.
4. Supraoccipital sensory canal crescent-shaped.
5. Body scales ctenoid, Head and nape naked, abdomen may be scaled and one species, S. conspicuus, is known with a single row of cycloid scales on the pectoral fin base. In all others the pectoral fin base is stated to be naked.
6. Palatine teeth present or absent.
7. Septal present and forms part of border of anterior myodome.
8. All bones bearing cephalic lateralis sensory canals open.
9. Ascending and articular processes of premaxillae entirely separate.
10. Primordial process of anguloarticular long and narrow.
11. Small hypural 5 and a single broad epural (2 fused epurals) present in caudal skeleton. Neural spine of second preural centrum long, and participates in support of dorsal procurrent rays, if there is long series of rays.
12. Vestigial pterygiophores present between pterygiophores of first and second dorsal fins, if there is a gap between the two fins.

Genus Enneapterygius

1. Three spines in first dorsal fin.
2. Single spine in anal fin.
3. Lateral line divided, with an anterior series of pored scales and a posterior series of notched scales.
4. Supraoccipital sensory canal 'U'-shaped, wrapping around first dorsal fin.
5. Body with ctenoid scales. Abdomen, head, nape, and pectoral fin bases naked.
6. Palatine teeth absent.
7. Septal present, and forms part of border of anterior myodome.
8. All bones bearing cephalic lateralis canals open.
9. Supraoccipital large and dorsally concave to accommodate pterygiophores of first dorsal fin. Anterior of supraoccipital lies between median posterior corners of frontals.
10. Ascending and articular processes of premaxillae entirely fused.
11. Primordial process of anguloarticular long and narrow.
12. Hypural 5 absent. One broad epural (2 fused epurals) present. Neural spine of second preural centrum long and participates in support of dorsal procurrent rays.
13. Vestigial pterygiophores absent from gap between second and third dorsal fins.

The above definitions show that each genus can be clearly separated from another, albeit by a relatively small number of characters.

It must again be noted that it is beyond the scope of this study to deal with and define all the genera of the family. The primary reasons are the time available, and that a broader and more detailed study of a larger number of species in each genus is required. Considerable difficulty was experienced in obtaining

material from New Zealand. Moreland has some 30 undescribed species and at least two new genera in his collections (pers. comm., 1977). It is also known that there are six new genera described by Rosenblatt (1959) which have not been published. Not until such time as Moreland's and Rosenblatt's material become available, or their results are published, can an entire analysis of the family be undertaken.

It must be stressed that the list of osteological characters presented in this study is by no means exhaustive. There are numerous characters, such as the condition of the basisphenoid, posttemporal, lateral and median extrascapulars, which have not been mentioned. A complete list of characters would probably result in such cumbersome generic definitions that they may be unusable. There is no doubt that the list would have to be expanded when an entire revision of the family is undertaken, and certainly would have to be expanded if any assessment of phylogenetic relationships is to be made.

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