Mouthpart structure and function and the feeding mechanisms of *Gerres* (Teleostei)

D.P. Cyrus and S.J.M. Blaber
Department of Zoology, University of Natal, Pietermaritzburg

Members of the genus *Gerres* feed almost exclusively on benthic invertebrates and have evolved efficient protrusible jaw mechanisms and modes of feeding. The methods employed in prey capture and feeding by five species that occur in the estuaries of Natal were studied using slow-motion cine photography and results were supplemented by field observations. All species use visual cues to detect and capture prey on or just below the surface of the substrate.

The protrusible jaw mechanism is the most important feature in prey capture. Bones and muscles involved in jaw movement were studied by dissecting preserved specimens and cleaning jaws and skulls of muscle. The whole mechanism of protrusion of the mouthparts was found to be controlled by two sets of muscles acting on a modified maxilla which together with the cross-palatine ligament forms a groove along which the ascending process of the maxilla can slide when the mouthparts are protruded. The setting up of a suction pressure within the mouth further aids the uptake of items from the substrate. However, whether or not suction pressure is applied depends on the prey type.

S. Afr. J. Zool. 1982, 17: 117 – 121

Gerres-soorte vreet feitlik uitsluitlik bentoniese invertebrata, en het derhalwe doeltreffende•voedingsmetodes en uitstulpbare kaakmeganismes ontwikkel. Die verskillende wyses waarop vyf *Gerres*-soorte, wat in breë riviermonde in Natal voorkom, hul prooi vang en inneem is deur middel van vertraagde tempo rolprente bestudeer, en die resultate is deur waarnemings in die natuur aangevul. Al hierdie soorte maak gebruik van visuele tekens om prooi-organismes op, of net onder, die bodem op te spoor en dan te vang.

Die uitstulpbare kake is die belangrikste faktor in die vang van prooi. Die bene en spiere hierby betrokke is deur middel van ontleding en met behulp van skoongemaakte skedels bestudeer. Die hele meganisme waardeur die monddele uitgestulp word, word gekontroleer deur twee stelle spiere wat inwerk op 'n gewysigde maksillare, wat, tesame met die trans-palatiese ligament 'n groef vorm waarlangs die stygende proses van die premaksillare kan gly wanneer die monddele uitgestoot word. 'n Suigdruk in die mond help verder met die inneem van voedsel vanaf die bodem, maar of so 'n suigdruk gebruik word of nie hang van die soort prooi af.

S.-Afr. Tydskr. Dierk. 1982, 17: 117 – 121

D.P. Cyrus* and S.J.M. Blaber
Department of Zoology, University of Natal, P.O. Box 375,
Pietermaritzburg 3200, Republic of South Africa
*To whom correspondence should be addressed

Received 2 December 1981; accepted 5 March 1982

Gerres Quoy & Gaimard, 1824, is one of seven genera belonging to the family Gerreidae (commonly known as silver biddies, mojarras or pursemouths) (Nelson 1976), which occur in most shallow tropical seas of the world. All members of the genus feed on benthic invertebrates (Cyrus & Blaber in press a). Six species of the genus *Gerres* live in the coastal waters of southern Africa (Smith 1965). They occur in estuaries as far south as the Zwartkops River in the eastern Cape but are uncommon south of the Mtamvuna River in Natal (Cyrus & Blaber 1982). Five species are present in the Kosi system of northern Natal, where three of them are abundant over shallow sandy areas and are of some economic importance to the local population (Blaber 1978; Cyrus 1980).

Little research has been carried out on the genus although Prabhakara Rao (1968) investigated the food and feeding of *Gerres oyena* and *G. filamentosus* in India and Cyrus & Blaber (1982, in press a & b) in Natal covered food and feeding ecology, histology of gonad development and reproductive biology, species identification, distribution and abundance. In this paper the feeding mechanisms and the structure and functioning of the mouthparts of *Gerres* are described in relation to their benthic feeding habits.

Materials and Methods

Modes of feeding of three species were investigated using slow motion (48 f.p.s.) cine photography on fish in an aquarium. The aquarium was divided by a vertical perspex screen fitted parallel to and 5 cm from the front glass. Fish for filming were isolated in this narrow section of the aquarium so that focusing adjustments of the camera were unnecessary. A single food item (live polychaete worm) was placed between the screen and the aquarium wall, resting on the bottom and in the field of view of the camera. The screen caused the fish approaching the food item to swim parallel to the aquarium wall and thus feeding movements could be filmed more easily. Feeding of all five species was observed using snorkel gear in the Kosi system (26° 54'S/32° 53'E) in the shallows of the estuary, shelf areas of the lakes and in the channel areas between the lakes and the estuary.

Jaw protrusion mechanisms of the five species found in the Kosi system were compared by manipulating the jaws of specimens preserved in 10% formalin. The bones and muscles involved in jaw movement were investigated by dissection and by examining cleaned jaws and skulls obtained from heads of large specimens of each species, which were boiled in 10% KOH, placed in acetic acid and bleached in hydrogen peroxide.

Results

Modes of feeding

Cine photography of aquarium specimens (*Gerres acinaces, G. filamentosus* and *G. rappi*) showed that all three species carried out similar feeding movements. It appeared that they observed the movement of the prey provided (usually a polychaete worm lying on a sandy substrate), orientated themselves towards it (Figure 1a), moved forward and pivoted on the tail region as the anterior portion of the body swung downwards until it was at an angle of about 45° to the substrate (Figure 1b). The fish then darted downwards, protruding its mouthparts once it was directly above the prey (Figure 1c). Upon closure, the mouth contained not only the prey but also sand grains and other particulate matter. Next, the fish moved into a horizontal position by moving either forward or backward, at the same time bringing the anterior part of its body upward (Figure 1d). Once back in the horizontal position the food was manipulated inside the buccal cavity by movements of the jaws as well as the opercular region. Rejected items, including most of the sand grains, were passed through the gill rakers and out via the opercular opening. Stomach analyses showed that although little particulate matter other than food items was swallowed, most stomachs contained sand grains. Although the size of sand grains varied, the dominant size was 400 μm.

The duration of feeding movements of *G. rappi* and *G. filamentosus* were calculated from the number of film frames which were exposed during feeding movements using a film speed of 48 f.p.s.. The entire feeding movement (from initial horizontal position back to final horizontal position), occupied an average of 47 frames ($n = 3$) for *G. rappi* and 25 frames ($n = 4$) for *G. filamentosus*. This gives feeding movement times of 0,97s (S.D. = 0,09) and 0,52 s (S.D. = 0,04) respectively. Jaw protrusion time was also calculated from cine frames (from time of opening over prey to time of closing); *G. rappi* occupied an average of 8,5 frames (n = 6) and *G. filamentosus* 5,4 frames (n = 5) giving jaw protrusion speeds of 0,18 s (S.D. = 0,02) and 0,11 s (S.D. = 0,01) respectively.

Gerres acinaces, G. filamentosus, G. oblongus, G. oyena and *G. rappi* were observed feeding in the Kosi system in the estuary, on the shelf areas to a depth of 3 m and in the shallows. The feeding methods of all five species were the same as those observed for three of the species in the aquaria. In a natural situation the prey was not visible to the observer but evidently *Gerres* used sight to detect its prey and was not taking up substrate at random: a fish would 'hover' (remain stationary) in a position approximately 20 cm from the substrate, during which time eye movement was noted, dart to a point on the substrate, take up a 'mouthful' of substrate and return to a horizontal position. This movement would be repeated and at all times the fish darted forward from the 'hovering' position to an apparently selected position on the substrate, from where the food and substrate were taken into the mouth. It was impossible to ascertain on how many occasions food items were obtained, as after each 'mouthful' the procedure was the same with rejection of sand and other particles through the opercula.

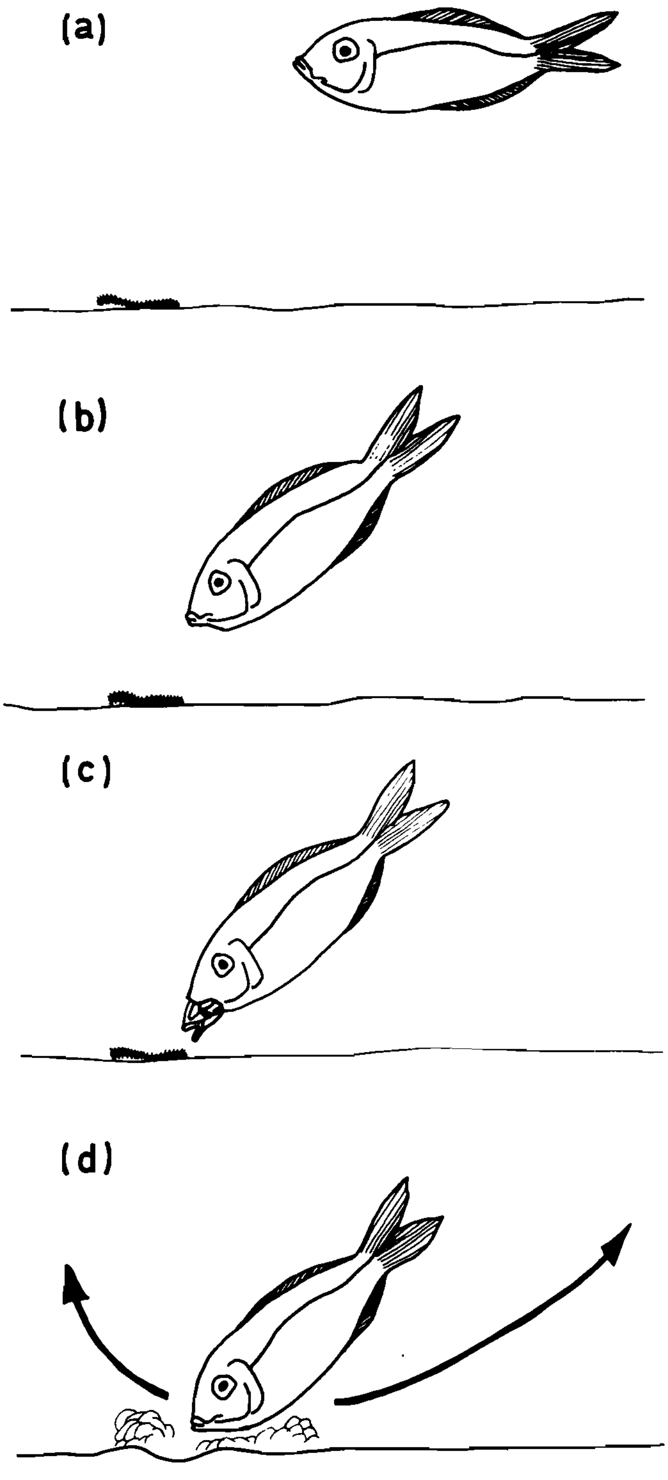

Figure 1 Sequence of prey capture by *Gerres* (a) orientation, (b) downward pivot, (c) protrusion of mouthparts and (d) return to horizontal (drawn from photographs).

The quantity of substrate taken up is determined by the direction in which the mouth opens. Jaw protrusion causes the mouth to open pointing downwards, when the body is at an angle of about 45° from the horizontal. Thus by approaching the substrate at this angle the mouthparts when protruded are at right angles to the substrate and the fish is able to take a 'bite' directly out of it. By sucking up the substrate the quantity taken in is increased. Suction pressure is brought about in the following way: with the mouth closed the buccal and opercular cavities are reduced in volume but when the jaws are protruded and opening of the mouth occurs, these cavities are increased in size by the depression of the hyoid bars and the spreading out of the branchiostegal membrane, the operculum at this stage being closed.

Mouthpart structure and function

The mouthpart structure and function of the five species were found to be similar. Figures 2 & 3 show a superficial view of the head of *G. rappi* with the mouth in the closed and open positions respectively. The shape of the exposed parts of the maxilla (mouthparts protruded) was the only difference noted between the five species (Figures 3 & 4). The difference was visible on specimens of 60 mm S.L. and greater.

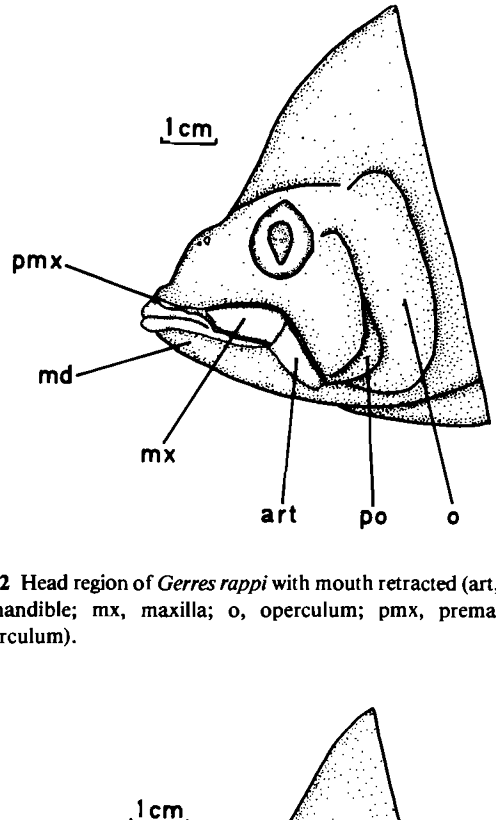

Figure 2 Head region of *Gerres rappi* with mouth retracted (art, articular; md, mandible; mx, maxilla; o, operculum; pmx, premaxilla; po, preoperculum).

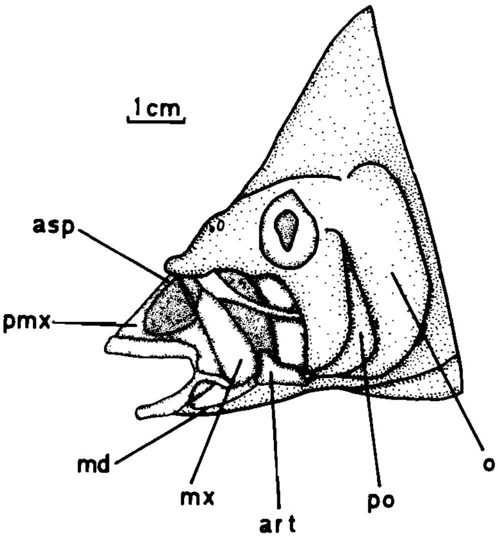

Figure 3 Head region of *Gerres rappi* with mouthparts fully protruded (art, articular; asp, ascending process of premaxilla; md, mandible; mx, maxilla; o, operculum; pmx, premaxilla; po, preoperculum).

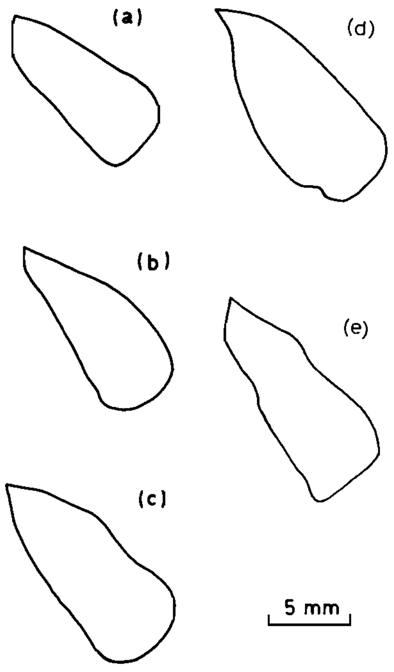

Figure 4 Shape of exposed part of maxilla (mouthparts protruded) of five *Gerres* species (a) *G. rappi*, (b) *G. filamentosus*, (c) *G. acinaces* (d) *G. oyena* and (e) *G. oblongus*.

Jaw structure

Figure 5 illustrates the structure of the protrusible jaw of *Gerres*. The premaxilla is attached at its ventral end to the mandible by the premaxillary-mandibular ligament. The dorsal portion of the premaxilla (ascending process) is greatly elongated and when the mouth is closed extends back over the ethmoid region and the anterior region of the frontals. The maxilla is attached dorsally to the palatine by the palatine-maxillary ligament and ventrally to the mandible by the maxillary-mandibular ligament. A cross-palatine ligament is present and lies over the ascending process of the premaxilla posterior to the maxilla and is attached to the palatines on either side of the head. Two mandibular adductor muscles (external and internal) are present, these both attach posteriorly to the anterior edge of the preoperculum. The external adductor muscle attaches anteriorly at two points on the middle of the maxilla. The internal adductor muscle attachment takes place on the inner side of the mandible. The main body of the mandibular abductor muscle attaches posteriorly to the pelvic girdle and anteriorly to the hyoid arch which in turn is attached to the mandible by the hyomandibular ligament.

Method of jaw protrusion and retraction

Abduction of the lower jaw and contraction of the external division of the adductor muscle causes the maxilla to rotate inwards, this causes the grooved heads to face each other, thus giving the appearance of brackets (Figure 6). These together with the straplike cross-palatine ligament, which lies behind the maxillary heads, forms a grooved trough for the ascending processes of the premaxilla. As the premaxillae are drawn outwards by the downward movement of the mandible, caused by contraction of the abductor mandibular muscle, the ascending process slides forward under the posteriorly situated cross-palatine ligament and within the roughly circular enclosure formed more anteriorly by the opposed grooves of the maxillary heads (Figure 6). Retraction of the jaw occurs with the contraction of the internal division of the adductor muscle and the relaxation of the external muscle. The mandible rotates upwards closing the opening (mouth) between it and the premaxilla. At the same time the premaxilla moves dorsoposteriorly with its long ascending process sliding back over the ethmoid region. On closure of the mouth the maxilla rotates forwards to its pre-opening position.

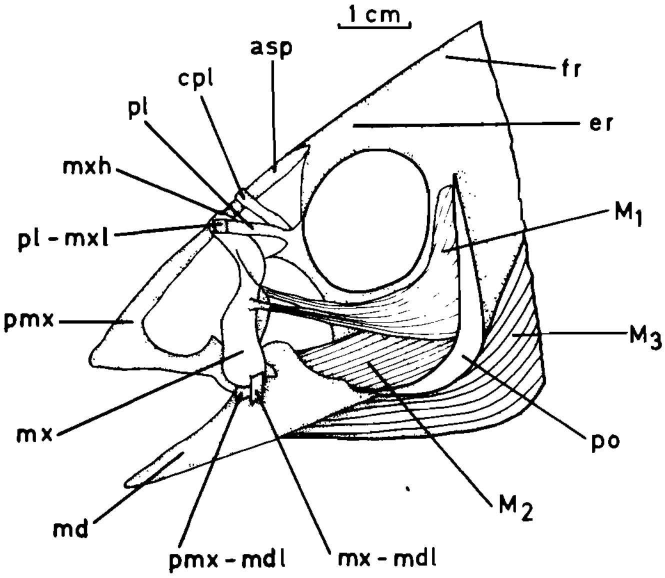

Figure 5 Dissection of bone structure and jaw muscles of the head of *Gerres rappi* (asp, ascending process of premaxilla; cpl, cross-palatine ligament; er, ethmoid region; fr, frontal region; md, mandible; mx, maxilla; mxh, maxillary head; mx-mdl, maxillary-mandibular ligament; M_1, adductor mandibulae muscle (external division); M_2, adductor mandibular muscle (internal division); M_3, abductor mandibular muscle; pl, palatine; pl-mxl, palatine-maxillary ligament; pmx, premaxilla; pmx-mdl, premaxillary-mandibular ligament; po, preoperculum).

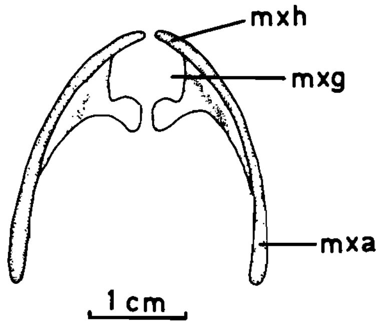

Figure 6 Anterior view of maxillae of *Gerres rappi* showing the groove for the sliding movement of the ascending process of the premaxillae (mxa, maxillary arm; mxg, maxillary groove; mxh, maxillary head).

Discussion

Field and laboratory observations indicate that prey is found by visual cues such as movement on or just below the substrate. It is therefore important for the fish to strike rapidly to ensure successful prey capture. *Gerres* employs a fast feeding movement with rapid jaw protrusion taking place over the point of capture. The setting up of a suction pressure, as described by Alexander (1970) for *Carassius auratus* presumably further aids uptake from the substrate. The accompanying sand grains may assist digestion in the stomach by helping to break up food material.

Millard (1968) stated that jaw protrusion in general is carried out by the downward movement of the lower jaw and either a 'rocking, twisting or lifting' movement of the maxilla, which is attached to the lower jaw. The movement is transmitted to the premaxilla which is thereby thrust forward. Over-protrusion is prevented by the premaxilla-palatine ligament. This is assumed to be a basic mechanism of jaw protrusion. This type of protrusion has been described by Eaton (1935) for *Fundulus* where the twisting movement of the maxilla and its curved shaft assist in sliding the premaxilla forward. The jaw protrusion mechanism of *Pterophyllum* spp. has been described by Alexander (1967) who noted that the palatine-premaxilla ligaments had lost their attachment to the premaxilla and formed a single ligament connecting the two palatines. He concluded that protrusion of the premaxillae as the mouth opened was probably due to the tension in the lip, as the lower jaw swung anteriorly and ventrally. A similar situation has evolved in *Gerres* (Figure 5). Schaffer & Rosen (1961) who examined a specimen of the Gerreidae (species not mentioned), noted that the maxillae no longer act as levers to protrude the premaxillae, which have their own ligaments attaching them to the lower jaw. In the five species of *Gerres* examined from Natal estuaries, similar structures were present; the maxillary heads and the cross-palatine ligament only assist in keeping the ascending processes of the premaxillae in position as they slide forwards and backwards with protrusion and retraction of the mouthparts, respectively. It can, therefore, be concluded that *Gerres*, apart from evolving a protrusible jaw mechanism, has modified the mouthparts to function in a specialized way, which causes rapid jaw protrusion and must improve chances of prey capture. *Gerres* is highly selective in the choice of prey taken (Cyrus & Blaber in press, a), which suggests that after visual detection of movement some form of identification must also take place. In nearly all cases where stomachs examined for feeding analysis (Cyrus & Blaber in press, a) contained only the siphon tips of the bivalve *Hiatula lunulata* (the most favoured food item of the group in the Kosi system), no sand grains were present in the stomach. This tends to indicate that the suction method is not employed when the siphons are being taken. Only the distal 5 mm of each siphon is eaten and it is probable that the rapid contraction of the siphon which is protruding above the substrate, coupled with the 'biting' motion of the fish, causes the siphon tip to break off before the mouth touches the substrate.

Acknowledgements

We are grateful to the Natal Parks Board and KwaZulu Department of Agriculture, Forestry and Nature Conservation for permission to work in areas under their control. The financial assistance of the South African National Committee for Oceanographic Research and the Natal Parks Board is gratefully acknowledged. One of us

(D.P.C.) was the recipient of a C.S.I.R. Post-Honours Bursary.

References

ALEXANDER, R. McN. 1967. The functions and mechanisms of the protrusible jaw of some acanthopterygian fish. *J. Zool., Lond.* 151: 43 – 64.

ALEXANDER, R. McN. 1970. Mechanics of the feeding action of various teleost fishes. *J. Zool., Lond.* 162: 145 – 156.

BLABER, S.J.M. 1978. Fishes of the Kosi system. *Lammergeyer* 24: 28 – 41.

CYRUS, D.P. 1980. The biology of Gerreidae Bleeker, 1859 (Teleostei) in Natal Estuaries. M.Sc. thesis, University of Natal, Pietermaritzburg.

CYRUS, D.P. & BLABER, S.J.M. 1982. Species identification, distribution and abundance of Gerreidae (Teleostei) Bleeker, 1859 in the Estuaries of Natal *S. Afr. J. Zool.* 17:105 – 116.

CYRUS, D.P. & BLABER, S.J.M. In press, a. The food and feeding ecology of Gerreidae Bleeker, 1859 in the Estuaries of Natal. *J. Fish Biol.*

CYRUS, D.P. & BLABER, S.J.M. In press, b. The histology of gonad development and the reproductive biology of Gerreidae (Teleostei) Bleeker, 1859 in the Estuaries of Natal. *Zool. J. Linn. Soc.*

EATON, T.H. 1935. Evolution of the upper jaw mechanism in teleost fish. *J. Morph.* 58: 157 – 169.

MILLARD, N.A.H. 1968. Contributions to the functional morphology of fishes. Part I. Introduction. *Zool. afr.* 2: 31 – 43.

NELSON, J.S. 1976. Fishes of the World. John Wiley & Sons, New York.

PRABKAHARA RAO, A.V. 1968. Observations on the food and feeding habits of *Gerres oyena* (Forskal) and *G. filamentosus* Cuvier from the Pulicat Lake, with notes on the food of allied species. *J. mar. biol. Ass. India.* 10: 332 – 346.

SCHAFFER, B & ROSEN, D.E. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Am. Zool.* 1: 187 – 214.

SMITH, J.L.B. 1965. The sea fishes of southern Africa. 5th edn. Central News Agency, Cape Town.