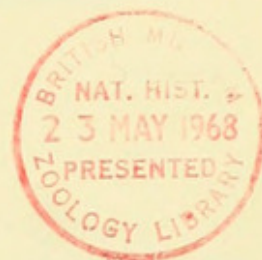


ON THE NEOTYPE OF *RADIICEPHALUS*
ELONGATUS OSÓRIO WITH REMARKS
ON ITS BIOLOGY



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BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY

Vol. 16 No. 5

LONDON: 1968

THE BULLETIN OF THE BRITISH MUSEUM
(NATURAL HISTORY), *instituted in 1949, is
issued in five series corresponding to the Departments
of the Museum, and an Historical series.*

*Parts will appear at irregular intervals as they become
ready. Volumes will contain about three or four
hundred pages, and will not necessarily be completed
within one calendar year.*

*In 1965 a separate supplementary series of longer
papers was instituted, numbered serially for each
Department.*

*This paper is Vol. 16, No. 5 of the Zoological
series. The abbreviated titles of the periodicals cited
follow those of the World List of Scientific Periodicals.*

*World List abbreviation:
Bull. Br. Mus. nat. Hist. (Zool.).*

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 24 May, 1968

Price Twelve Shillings

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By C. M. H. HARRISSON & G. PALMER

SYNOPSIS

The demonstration that *Radiicephalus elongatus* Osório 1917 does not belong to the Trachipteridae, (to which family it has recently been relegated as *incertae sedis*), is offered in completion of a review of the dealfishes of the Eastern Atlantic and Mediterranean. A need is shown for selecting a neotype for *R. elongatus*, and a male specimen from the same locality as the lost holotype is so designated. (No full description of an adult female exists). Two further specimens, smaller in size, are considered, and notes on the biology and development of the species are offered. *R. elongatus* is tentatively reinstated in Osório's family Radiicephalidae, and the position of this family with reference to the other families of taeniosome allotriognaths is discussed. A full translation of the species description (originally published in Portuguese) is given in an appendix.

INTRODUCTION

A SHIP'S engineer, Senor José da Glória, on his return from a voyage with the Portuguese distant water fleet to the Moroccan shelf, went in Lisbon to the Bocage Museum, taking with him a strange fish 760 mm. long, caught off Salé at 200 m. (110 braças). A published account of the specimen was subsequently produced by Osório (1917) who described it as the only known representative of a wholly new family of dealfishes, the Radiicephalidae, with a single genus and species *Radiicephalus elongatus*. The description appears to have remained without further notice until 46 years later brief reference was made to it as an anomaly "*incertae sedis*" (Walters 1963b), but during a cruise of R.R.S. "Discovery" in 1966, three new specimens were caught: one of 304 mm. S.L. off São Miguel in the Azores, an even smaller example of 154 mm. S.L. close to Fuerteventura, and a third, the largest, of 597 mm. S.L. (692 mm. total length) off Morocco, close to Osório's type locality.

OSÓRIO'S TYPE

In order to understand any apparent discrepancies between Osório's type and the material to be described here, a critical analysis of the case-history of José da Glória's specimen is essential. First, it must be stressed that this specimen has disappeared without trace. We take this opportunity of thanking Professor Saccarão and Senor Luiz Saldanha for their thorough but fruitless searches for it in the Bocage Museum. All the required information must therefore be drawn from the rather brief description which Osório published in Portuguese. Secondly, when Osório first saw it, his specimen was already badly damaged. He thought that the fact that most of the body was quite devoid of scales was "by virtue of the mischances the specimen underwent before it entered the museum" (Osório, p. 113, lines 14, 15). The tail appears to have been incomplete, (as the caudal seemed to have been destroyed), (p. 113, line 24) and ended in "a length of vertebrae almost completely stripped of

soft parts " (p. 114, lines 2, 3) with two long rays remaining a certain distance from the tip. The anal fin was represented by only a small "remainder of spines" (p. 113, line 35) which nevertheless seemed to Osório to represent what had been a long fin. The ventrals "should have been thoracic" (p. 113, line 27), but were missing (p. 113, line 35–p. 114, line 1). Even the first ray of the dorsal fin was broken (p. 114 line 24) while the rest of the dorsal lacked any connecting membrane as it had "disappeared, naturally decomposed whilst the specimen was exposed to the air, and perhaps to the sun" (p. 114, lines 26–28).

The impression given is that José da Glória put the specimen carefully aside, but left it dry, and either lying on decking smeared with blood, scales and scraps of offal, or else wrapped in a piece of the sacking used to wipe gutted fishes from the catch prior to salting. Osório's figure shows a rather shrivelled dealfish with a sunken eye, yet considering how difficult it is to keep such material in good condition even with all the facilities of a modern research vessel, the specimen was in a remarkably good state, and must have been well tended aboard the small fishing vessel on its journey back to Lisbon. As will be shown subsequently, the characters of Osório's specimen agree in almost every respect with the new material, but a primary difference we ascribe to handling prior to its arrival in Portugal. Osório believed that his specimen "must have been covered with scales" (p. 144, line 11) even though "in our example it is almost completely devoid of them" (p. 113, line 16), because there were some "though in very small numbers, in the dorsal region near the dorsal fin". It seems likely, for reasons adduced later (p. 201 this paper), that these scales belonged to other fishes, and having stuck to the specimen as it dried, became inseparably attached to the dessicated fish finally deposited in the Bocage Museum. Alternatively, it is quite possible that the scales in *Radiicephalus* are very delicate and dissolve in formalin, in which case they might have disappeared in the neotype.

DESCRIPTION OF THE 1917 HOLOTYPE

Stripped of such evident reservations, what Osório described (c.f. Appendix) was a long, laterally compressed fish of 760 mm. total length, with a gently curved dorsum. The height of the body contained $c.8\frac{1}{2}$ times, the greatest thickness 38 times, in the total length. The head with an oblique profile and a long snout, the mouth a little protracted to lie sub-obliquely, and bearing small, strong, pointed teeth in both jaws. These teeth directed inwards and arranged in two rows with those of the inner row larger than those of the outer in either jaw. The broad inferior maxillary was striated. Eyes were rather large, their diameter 3 times in the length of the head. There were 4 gill arches, and pseudobranchs were present. The operculum, suboperculum and interoperculum were striated (like the maxilla). The lateral line began above the orbit at more than $\frac{2}{3}$ the maximum body height, and sloped gradually towards the ventral profile which it reached "just beyond the anus, without having shown any curvature along its length. The anus was situated at about $\frac{2}{3}$ of the total length measured from the snout". The skin was covered with rounded silvery bodies resembling pinheads, the silvering confined to linear areas and forming a pattern, like bricks in a wall, especially visible in the abdominal region. A long

dorsal fin commencing just behind a vertical drawn through the anterior border of the orbit ended well before the tail. The first few rays were the longest and were very long and thin, shorter rays followed and the rays numbered about 159 in total. The pectorals were small, set close to the angle of the opercular flap and contained c.9 rays. The ventrals were absent or missing, but a thoracic base was present. The anal fin was represented by a few rays. The tail ended in a filament borne by two rays originating on a preterminal vertebra.

From this critical appraisal and condensed summary of Osório's original diagnosis one may turn to the new material which shows virtually all but one of the features listed in the above paragraph, and allows, in addition, observation of details not visible in the damaged specimen which is now lost. It is therefore considered necessary to select a neotype of *Radiicephalus elongatus* Osório. The specimen chosen is the largest individual taken by "Discovery" and a description of it is followed by an amplified definition of the family Radiicephalidae and the genus *Radiicephalus*, using the two smaller "Discovery" specimens as evidence for such variation, (in meristic and other characters), as occurs within the species and during the course of development.

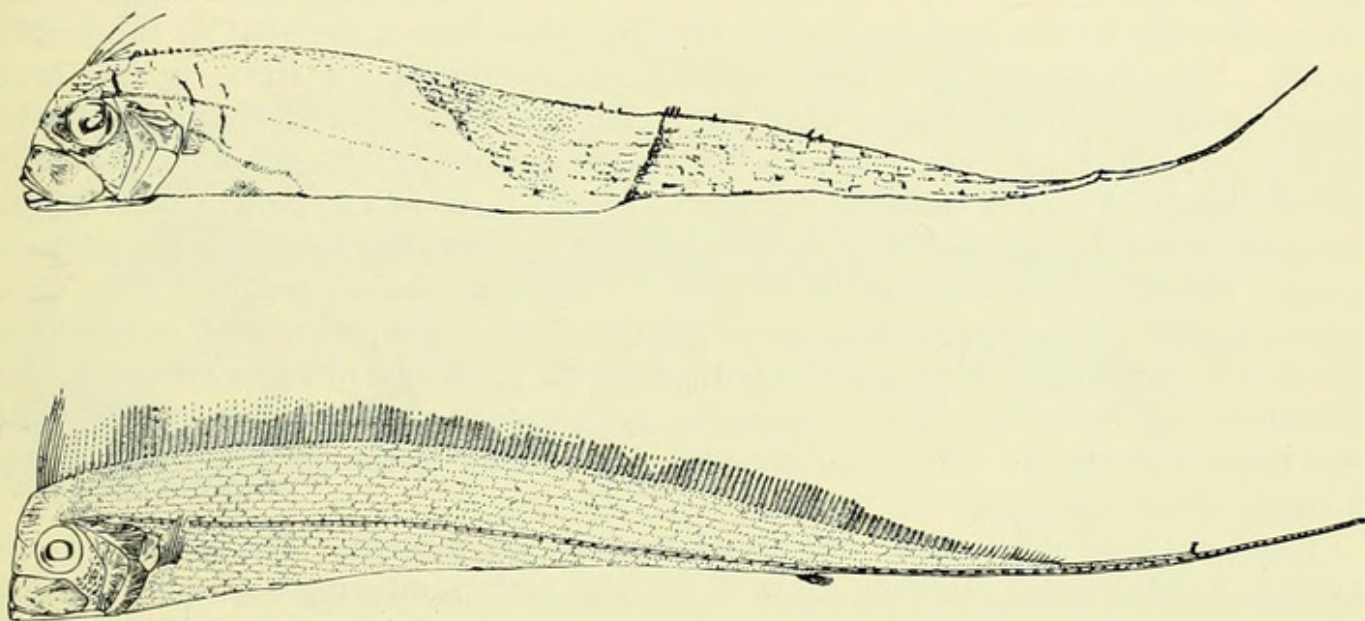


FIG. 1. The holotype of *Radiicephalus elongatus* (above) 760 mm. T.L. (after Osório, 1917) compared with the 1966 "Discovery" neotype (below) 692 mm. T.L. The course of the postcleithra in the holotype is held to be shown by the curved shadow bending towards the ventral profile (c.f. with the neotype, Fig. 2).

THE NEOTYPE OF *RADIICEPHALUS ELONGATUS* OSÓRIO

In accordance with the International Code of Zoological Nomenclature 74-75 (1964), adopted by the XV International Congress of Zoology, a neotype may be designated only if the holotype is lost or destroyed, and no lectotypes or syntypes exist. This is the case with *R. elongatus*. The present paper is offered in completion of revisionary work (Palmer, 1961) on the dealfishes of the Mediterranean and Northeast Atlantic, and the proposition of a neotype is considered necessary in the

interests of stability of nomenclature, as it will avoid the proliferation of names for material demonstrably belonging to a single species, and prevent future confusion involving the identity of any other members of the same family that may subsequently be discovered. The neotype of *R. elongatus* has been deposited in the British Museum (Natural History) London, registration number: 1967.10.2.1.

The specimen of 692 mm. T.L. (597 mm. S.L.) was taken off the Moroccan coast with an Engel's trawl (Harrison 1967) fished between 570 and 0 m. on November 17th, 1966 at a position, $34^{\circ} 17' 3''$ N, $8^{\circ} 00'$ W, (Table 2) very close to where the holotype was caught. Its general shape (Text-fig. 1) is a tapered triangle broad at the head and narrowing to a thin caudal filament. The dorsum is gently curved, and the body is laterally compressed. The maximum dorsoventral "height" (depth) of the body is contained 8.9 times in the total length, and its maximum thickness nearly 41 times.

The head and the body closely resemble Osório's specimen (see Text-fig. 1.) The dentition consists of a single row of retrorse premaxillary teeth, and in the lower jaw a symphyseal tooth is followed on either side by two rows of teeth bordering the mouth, each formed of four small pointed teeth, those of the inner row being slightly larger than those of the outer in either jaw. There is a large striated maxilla, and the premaxilla has an anterior process reaching more than $\frac{4}{5}$ the way up the frontal profile. The jaws are protrusile. The eye is contained 3.4 times in the head length, with an orbital diameter of 26 mm. The lens fully fills and slightly protrudes from the pupillary aperture. The iris is silvered presumably with guanine. X-radiographs taken at 20 KV with an exposure of some 1,200 m.a.s. show a faint streak running obliquely across the orbit towards a pale semilunar patch at the postero-ventral margin of the orbit (see Text-fig. 2.). These streaks are assumed to be the 4 rectus muscles of the eye running down towards the posterior myodome, represented by the pale patch, and the bar dividing this from the main area of the orbit would then constitute the basisphenoid bar separating the apertures of the muscle canals of the two sides of the head. The nasal capsule lying anterior to the orbit appears to have a single round aperture.

There are four gill arches, and pseudobranchs are present. The gill rakers are longish, tooth-bearing papillae, those of the first arch numbering $2+0+7-8$. The lower part of the hyoid arch consists of a reflexed interhyal nearly as long as the following rather short epihyal, which bears 4 branchiostegal rays. The ceratohyal is elongate, with a narrow anterior shank carrying two more branchiostegals. The preoperculum, operculum, suboperculum and interoperculum are striated (like the maxilla). The suboperculum has a pectinate postero-dorsal border. An elongate, pallid, cylindrical body marked with brown protrudes from beneath the opercular flap of the left side, and probably represents a copepod parasite (possibly related to *Cardiodectes*) with its anterior head processes in, or close to, the ventral aorta.

The pectoral girdle is seen in the x-radiographs to consist of flattened cleithra, like tilted hockey sticks, bearing posteriorly a pair of very long slender postcleithra (running above and just beyond the pelvics) and the ventrally directed pistol-shaped scapulocoracoids, with the horizontally set pectoral fins borne on the upper borders of the scapulae.

The lateral line canal of the body begins above the operculum and slopes down towards the ventral profile which it closely approaches in the region of the anal fin. It continues beyond the vertebral column, where the canals of either side are closely joined, flattened, and form the major part of a long caudal filament supported by some 7 very elongate dermatrichia of the lower caudal lobe and receiving additional strength basally from some of the long haemal spines of the first few preural vertebrae anterior to the fifth (using the terminology of Nybelin, 1963). One hundred and twelve tubular scale elements were counted in the canal wall of the left flank, 92 along the body and 20 in the caudal filament. The posterior elements are longer than the anterior ones, but become shorter again in the caudal filament as one approaches the smoothly rounded tip. The canal scales are smooth but more posteriorly they bear spots of dark pigment. The lateral line canals of the head are not visible superficially. Traces in radiographs with the diameter of the body canal suggest supra- and suborbital systems extending respectively to just above and below the nasal capsule. Scales, other than the tube elements of the lateral line, are absent.

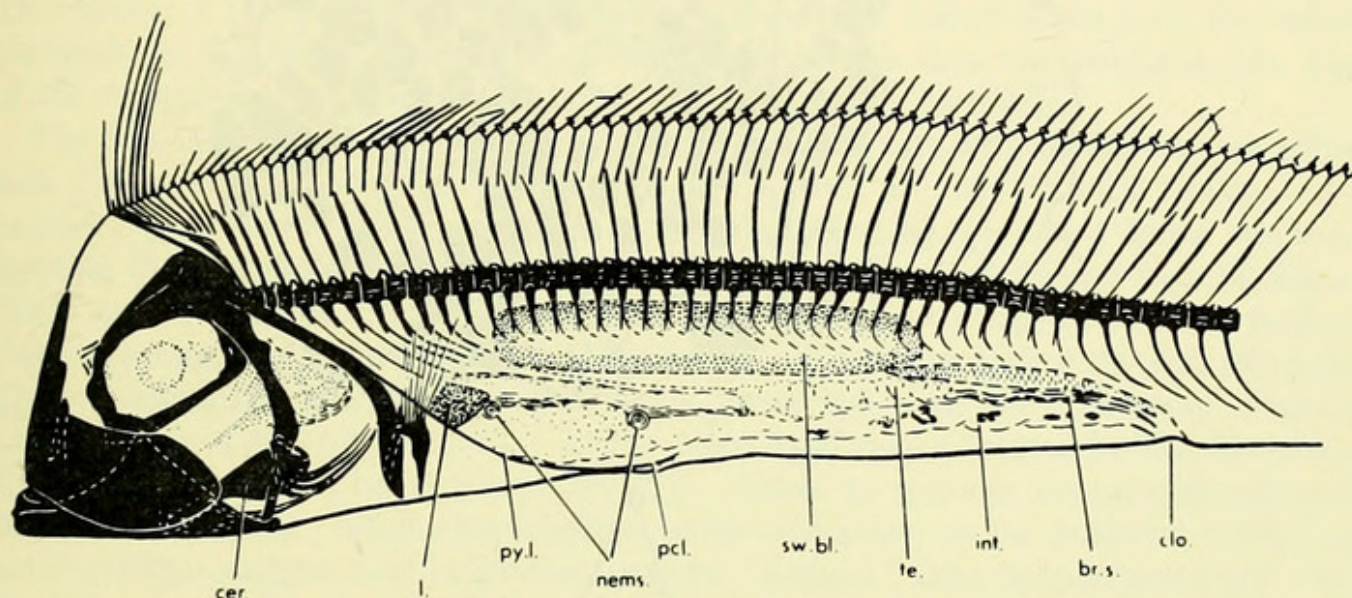


FIG. 2. Internal anatomy of the neotype of *R. elongatus* Osorio. Details visible from x-radiographs are shown in solid black, those seen externally or in dissection are stippled or shaded. The figure is semi-diagrammatic, particularly in the details of the hyoman-dibular arch. The posterior ribs are represented as truncated to avoid obscuring the soft anatomy of the body cavity. *cer.* = ceratohyal; *l.* = liver; *p. cl.* = postcleithrum; *nems.* = nematode cysts in gut mesentery; *py. l.* = pyloric loop; *sw. bl.* = swim bladder; *te.* = testis; *int.* = intestine with faecal material visible in x-radiographs; *br. s.* = brown sac; *clo.* = cloaca.

The anus is situated at the level of the 44th vertebra, opposite dorsal ray no. 70, 2.8 head lengths along the body from the snout, and opens into a cloaca that receives the urinogenital ducts and the opening of a brown sac. This sac appears to be an unpaired median structure. Dissection of the left side of the neotype showed that the sac extended forward, between the gonads, and was suspended by a mesentery below presumed kidney tissue, to the level of the 31st vertebra. The gonads were

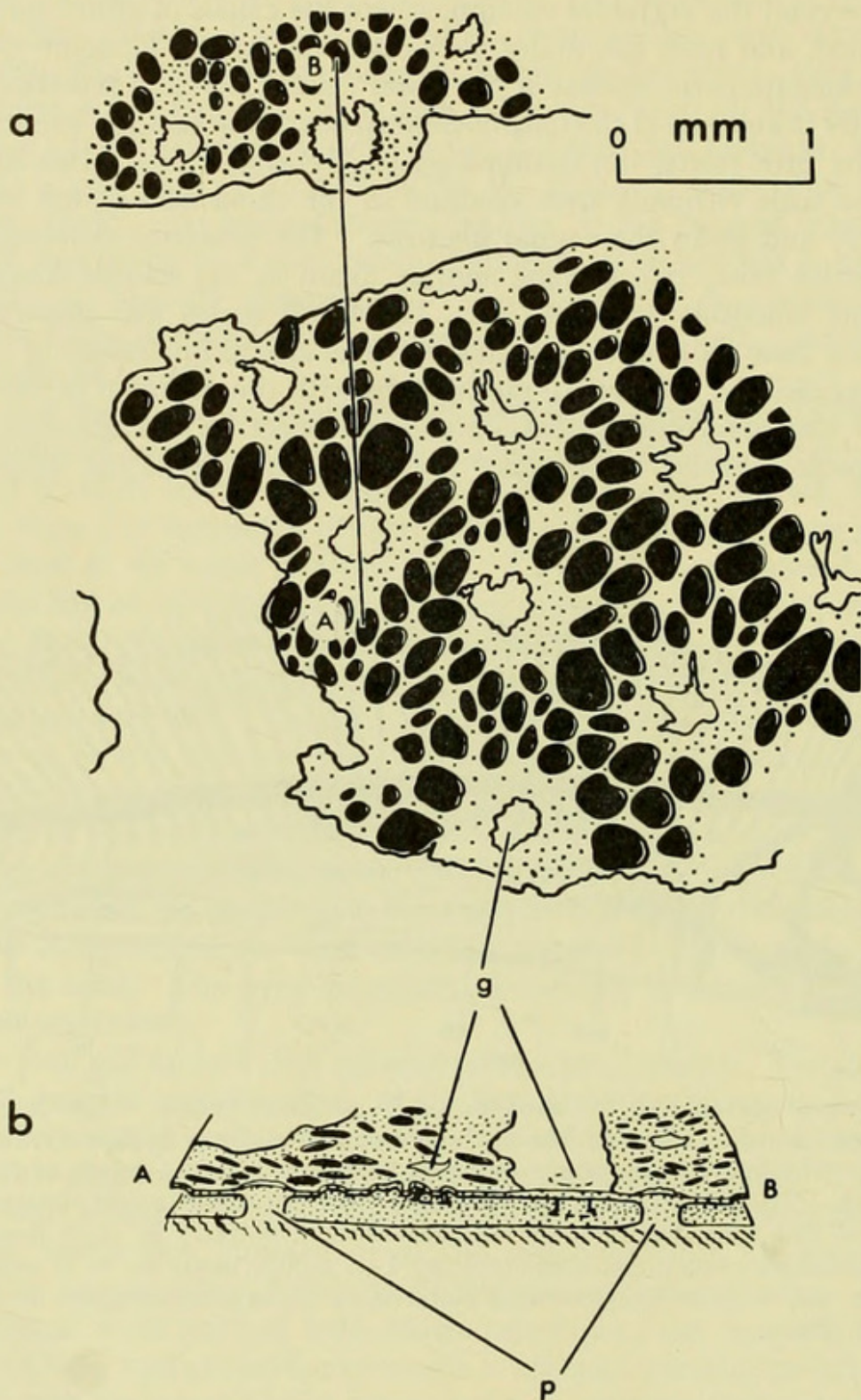


FIG. 3. Skin from the flank of the neotype, in an area just below the lateral line and behind the pectoral fin. a. Surface view with pores shown in black, skin stippled and areas with guanine silvery left white. b. Diagrammatic section along the line A-B (in fig. 3a). *g.* = guanine patches; *p.* = papillae.

well developed, showing the neotype to be a male, and suspensory filaments reached forward to the anterior end of an elongate and well developed swim-bladder with a silvery wall, probably invested with guanophores. This bladder extends from the level of the 14th vertebra to the end of the 33rd centrum (see Text-fig. 2). It is closely appressed to the broad parapophyses and limited laterally by the fine pleural ribs in the wall of the peritoneum. An orange lobe of liver extends beyond the level of the postcleithrum to near the vertical from the anterior margin of the swimbladder. The gut consists of a sac-like stomach with a reflexed pyloric section without caeca.

The skin has a guanine layer with, beneath it, a mesh punctured with elliptical pores radiating from mushroom shaped papillae which support the poreweb from the basal dermis (Text-fig. 3). As the guanine is developed along lines forming a parallelogram brickwork-pattern, in the unsilvered "brick areas" the pores are exposed, and appear to connect the exterior with a dermal space interrupted only by the bases of the papillae. Drops of aniline blue dye passed freely from one area to those around it. (It must be remembered that if in the fresh animal this space was filled with a mucopolysaccharide jelly, this could be lost during fixation in formalin). The heads of the papillae bear a guanine spot which makes them look like silver pinheads in the skin. Where the silvered lines on the skin are damaged, the tops of the underlying papillae remain, and resemble further pinheads.

The fins include a long dorsal of 156 rays, pectoral fins with a short upper splint and 9 rays, ventrals with (only the bases of) c.9 rays, an anal fin with 7 rays, and a caudal with 4 short rays in an upper section (see Text-fig. 4) and a lower filament bearing the continuation of the body lateral-line canals, containing 7 rays (as far as could be ascertained from radiographs). The dorsal fin commences at a vertical drawn through the anterior border of the orbit. Eight rays articulate with pterygiophores associated with a Y-shaped bone connected with the forwardly directed neural spine of the 1st vertebra. The Y-bone itself seems formed by the fused two first interneurals and bears 2 rays distally. These 10 anterior rays are slender and form a nuchal crest. Rags of epithelium borne terminally on the posterior borders of some of them, suggest that in life they may be "flagged" (like the pennant rays of the nuchal crest in *Regalecus*). The neural spines of vertebrae 1 to 101 have pterygiophores associated with them, some spines (apart from the first) carry one (posteriorly), others have two interneurals, before and behind them. The pectorals are set close below the angle of the operculum, just above the juncture between the suboperculum and the interoperculum. The ventrals appear to lie directly below the tips of the postcleithra, at the level of the 21st vertebra, and are thus more nearly abdominal than thoracic. The anal fin is borne by interhaemals associated with the haemal spines of vertebrae 72-75, a considerable distance (0.7 of a head's length) caudad from the external opening of the cloaca. It is difficult to interpret the structure of the caudal (Text-fig. 4). The neotype is the only specimen with all the tail present. It is already very slender at the caudal peduncle, and tapers further into the caudal filament. The caudal cockade appears to be borne on a terminal plate (c.f. *Stylephorus*). It is assumed that the ural vertebrae have fused together in a terminal complex. The preceding centrum bears a neural arch and is therefore presumed to be a preural element. As it bears two rays ventrally it may represent the fusion

of preurals 1 and 2. The preceding element may likewise be equivalent to preurals 3 and 4. The element bearing the last well developed haemal spine would then be designated the fifth preural.

The axial skeleton is composed of 118 vertebrae and the terminal element, discussed above. The centra composing it consist of 4 short discs behind the skull followed by a series remarkably constant in length. The 6th vertebra is 4.8 mm. long anteroposteriorly, and the antepenultimate vertebra is longer (5.5 mm.) by just less than one millimetre.

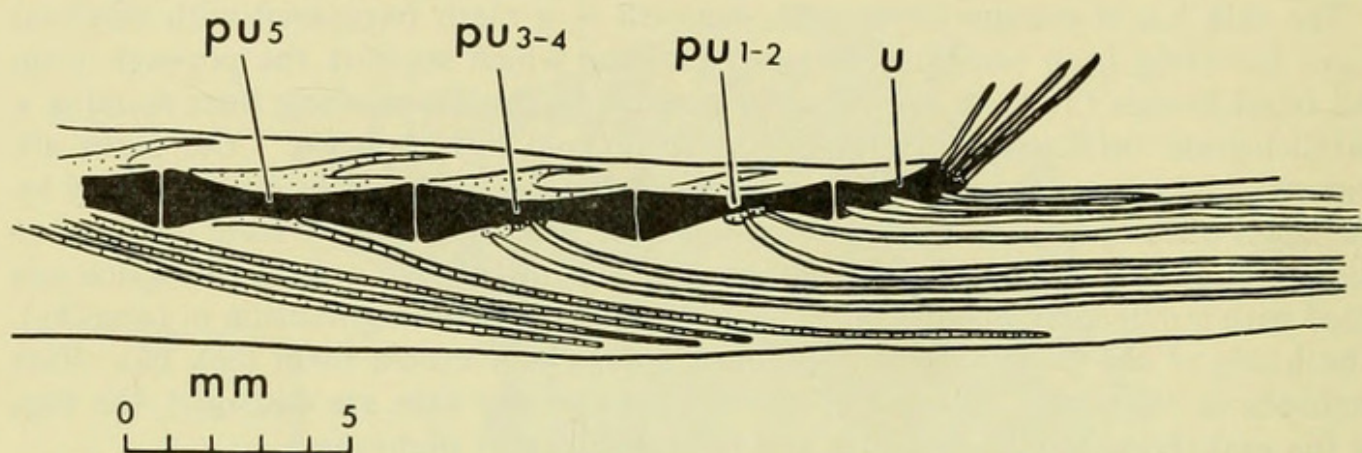


FIG. 4. Diagram of the caudal structure in the neotype of *R. elongatus*, drawn from soft x-radiographs. Paired caudal rays white, unpaired median structures black. The overlying lateral line canals are omitted. Standard lengths quoted in the text are taken to the insertion of the posteriormost ray of the upper part of the caudal. Total lengths are taken to the tip of the lower filament. PU 1-5 = pre-ural centra; U = ural complex.

The first 25 centra bear neural arches inclined anteriorly, the 27th neural arch and all the arches on the more posterior centra are directed backwards. There are well developed pre- and postzygapophyses on vertebrae 4-95 though the prezygapophyses are stronger in the more posterior part of the caudal region. There are well developed blade-like parapophyses which appear to be fused to the centra, and are present on the 3rd-39th vertebrae. The parapophyses on centra 4-16 point backwards and down, those on centra 21-39 forwards and down. There are long slender pleural ribs borne by the parapophyses of vertebrae 4-39. The first haemal spine is carried on the 40th centrum, the last on centrum 116.

Having presented an extract of the characters visible in the type and the new specimen one may now weigh the evidence for their conspecific identity. Much of the matter may be best displayed in tabular form. Further information about development and biology can then be drawn from an examination of the two smaller "Discovery" specimens. Finally the position of the family may be examined in relation to the other taeniosome fishes known to science, and distinguishing characters can then be set out in the manner of a formal diagnosis.

THE CONSPECIFICITY OF THE LARGEST "DISCOVERY" SPECIMEN WITH OSÓRIO'S TYPE

Both from the descriptions and from the figures (Text-fig. 1) it will be clear that the "Discovery" specimen is very like Osório's fish. A summary of similarities is

drawn up in Table 1. Further marked resemblances will be seen between even the minute details of bone sculpture of the maxilla and opercular bones as figured by Osório and the pattern seen in the present individual. The shape, the colour pattern, the "pinheads" of the skin, the teeth, gill arches and such meristic details as are available all correspond closely. Although Osório believed he could make out truly thoracic bases for the ventrals, his figure (Text-fig. 1, above) shows the course of the postcleithra to have been identical with that in the neotype. There remains but one difficulty, as stated above.

Osório, (on his p. 114, line 22) says "the anus is situated at approximately two thirds of the total length measured from the head". In the "Discovery" specimen the anus lies at about $\frac{1}{3}$ the total length from the head.

Osório's specimen was the larger, and one might imagine an allometric shift back of the anus, were there not good evidence to the contrary (see p. 196). If, though, one takes into account Osório's remarks about the damaged caudal region, and the fact that the anal fin was so battered that it was impossible, from what remained, to tell whether it had been a long or a short fin (p. 113), then it seems more likely that either partial evisceration had made it hard to judge just where the anus came or that, dried and wrinkled, the position of the anus was as hard to determine as in Günther's *Lophotes fiski* (Günther 1890, p. 246). In such an event it might have been reasonable to suppose it lay just in front of the anal fin.

If one assumes that this is indeed what Osório supposed, then the proportions for the position of the anal fin are in good accord for both specimens (Column 10, Table 1). In fact the anus of the original type specimen, before it was damaged, probably lay well in advance of the anal fin just as in the "Discovery" specimen. In that case one should read "anal fin", not "anus" in the appropriate passage cited from Osório's description. As all the other characters of the two fish agree so well, this seems a reasonable assumption to make and it may then be allowed that the second specimen, caught after a lapse of nearly half a century, is in fact conspecific with the first one taken off Salé.

THE DEVELOPMENT, DISTRIBUTION AND BIOLOGY OF *RADIICEPHALUS ELONGATUS* OSÓRIO

One may now turn to the two smaller specimens collected by R.R.S. "Discovery" in 1966. The position of their capture is shown in Text-fig. 6, and details for comparison with the features seen in the neotype are summarized in Table 2. Like the larger neotype, both of the smaller individuals had a well developed gas-filled swimbladder identifiable in radiographs. Dissection of the medium sized specimen was expertly done by Dr. N. B. Marshall who found a ventral blood supply passing to 7 unipolar retia on either side, each rete c.2 mm. long being associated with a separate pad of the gas gland (Text-fig. 5). These specimens, too, possessed ribs. Where the skin was undamaged the colour pattern was similar, the dentition agreed, so did the structure of the cloaca, while the uniformity of the meristic features detailed in Table 2 is, likewise, most apparent. Some minor differences and supplementary observations from both the additional individuals allow one to construct a fuller picture of the biology and development of the species, while further suggestions

are offered about its geographical distribution together with its vertical range in the Atlantic Ocean.

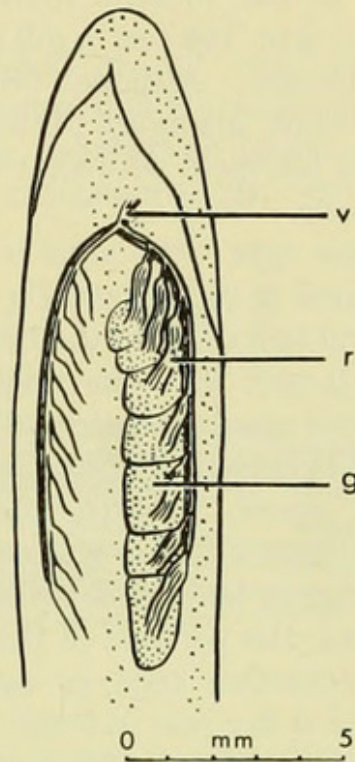


FIG. 5. Diagram of the inside of the swimbladder in the medium-sized "Discovery" specimen of *R. elongatus*, after a drawing by N. B. Marshall. Only the retia and gas-gland pads of the right side are shown in detail. *r.* = retia; *g.* = gas gland; *v.* = vascular system.

The figures for body proportions, Table 2 (Column 3), suggest a decrease in body depth relative to standard length, a common feature in fishes where the myotomes become folded progressively from the originally flat sheets in the larva. The same table (Column 9) shows that the position of the cloaca remains unchanged during growth from a small postlarva to a relatively large and mature fish: in the smallest specimen it was located beneath the 44th vertebra (counted from the head) just as in the large neotype, while in both the neotype and the medium sized specimen the cloaca lay beneath the 5th vertebra that bore a haemal arch.

There is no evidence for a significant alteration in the size of the eye relative to the head during growth, but the available figures suggest a reduction in head size relative to the body length in the transition from post-larva to juvenile. A marked change which may also be assumed to occur at this time involves the ventral fins. In the smallest specimen they are composed of long slender rays nearly a quarter of the fish's standard length, yet in the juvenile and the neotype there are only rudimentary skin-covered stubs, so there seems to be an almost total loss of the ventral fins during development. The position of the pelvic bases on the body appears to remain constant, abdominal, and close to the tips of the postcleithra.

Round blobs visible in the x-radiographs of the medium sized individual from São Miguel were juxtaposed to incomplete, lightly ossified lengths of fish vertebral

columns. Dissection yielded the remains of at least three small fishes, and the otoliths with round borders carrying a single notch (for the point where the saccular nerve supplies the macula) resemble those of either a species of sternoptychid or some lantern fish. For fishes of comparable sizes the sagittal otoliths are generally larger in lantern fishes, so that from the size of those in the *Radiicephalus* stomach and from the other bones in the stomach contents, it seems most likely that the blob-shaped otoliths belong to a lantern fish of the genus *Lampanyctus*. The advanced state of digestion strongly suggests these myctophids are natural prey, and not chance specimens swallowed in the trawl-bag as the catch was brought in. The damaged state of the specimen when brought aboard also reduces the likelihood that feeding occurred subsequent to capture.

It may, then, be assumed that small lantern fishes form part of the natural diet of *Radiicephalus elongatus*. The large eyes suggest that it hunts by sight, aided also by the well-developed lateral line, and as the captures were made at depths of less than 700 m., that is, shallower than the daytime occurrence of *Lampanyctus* species in the area (Harrison 1967 and in press), then it seems probable that predation either occurs by night, possibly when the lantern fishes produce bioluminescent display, or during dusk and dawn vertical migrations of the myctophids through the layer which *R. elongatus* normally inhabits.

Text-figure 6, which shows the sites of capture of the *Radiicephalus* specimens, also includes, tentatively, data for some taeniosomes taken on a cruise of the S.S. "Walther Herwig" which Dr. G. Krefft (in litt.) suggests may represent six further individuals of *R. elongatus*. If this surmise is correct, then the depth distribution would appear to be centred on the upper mesopelagic zone. Five out of six specimens from night time hauls came from depths less than 400 m. and three of these were taken in depths of less than 330 m. The sixth was from somewhere between 600 m. and the surface. The geographical range of the species stretches nearly the full length of the eastern basin of the North Atlantic.

Having thus considered what information is currently available on the anatomy and biology of *Radiicephalus*, the data can be compared with features of the structure and behaviour of the other taeniosomes in an attempt to assess the status of Osório's family Radiicephalidae.

THE STATUS OF THE FAMILY RADIICEPHALIDAE

The rediscovery of material of *Radiicephalus* poses almost as many problems as it provides hints about the relationships within the taeniosome allotriognaths (Regan, 1907). Currently, Regan's group may be said to include the Trachipteridae with three genera and of the order of ten species, (most of them in *Trachipterus*), the Lophotidae with two genera and three species, the Regalecidae with two genera and two or more species, and the Stylephoridae with at least two species in a single genus. The question to be answered is whether the genus *Radiicephalus* shows a sufficient number of unique features to be retained in the separate family erected by Osório. A proper appraisal can only be made by taking into consideration such features as development, biology, feeding, digestive physiology and swimming behaviour if

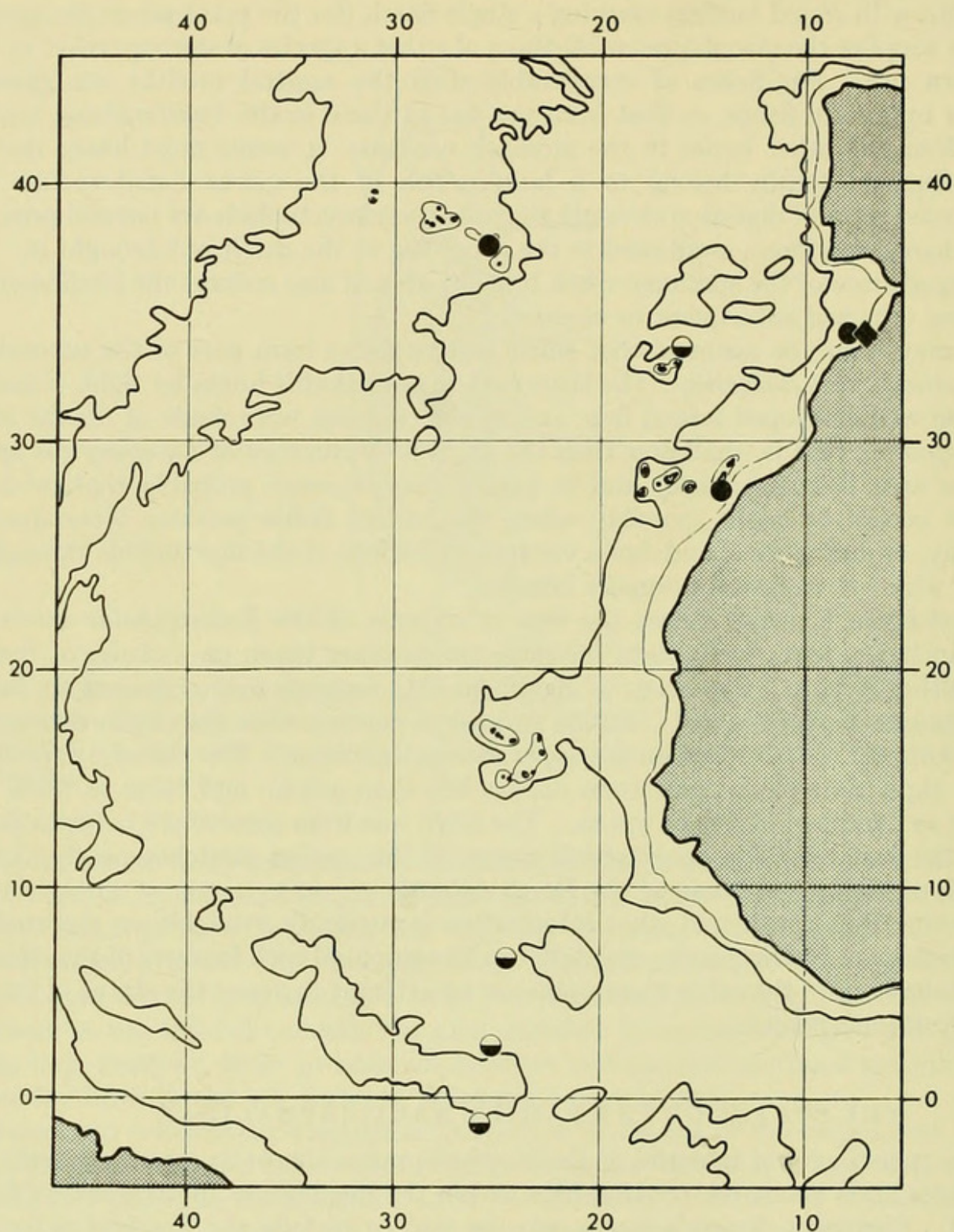


FIG. 6. Map of the central region of the eastern basin of the North Atlantic, showing stations at which specimens of *R. elongatus* are supposed to have been taken.

◆ = 1917 holotype which coincides with the solid disc indicating the collection position of the "Discovery" neotype.

● = the two smaller "Discovery" specimens.

◐ = "Walter Herwig" stations for unsorted taeniosome material believed to be *R. elongatus* (Kreff in litt.).

Shaded areas indicate land. 100 and 2,000 fm. contours are shown.

structural features are to be given their appropriate relative importance. As comparatively little is known about any one family of taeniosomes, such conclusions as are drawn at present must remain but partially satisfactory guesses. Dealfishes have seldom been caught by past oceanographic expeditions, and only the use of giant trawls appears to be accelerating the rate at which new species are being found. The material in older collections largely represents specimens washed ashore, or else taken accidentally in large commercial set-nets or by line-fishing.

Regan's Allotriognathi includes a range of brightly coloured fishes with many features oddly intermediate between "berycoids" and percomorphs. The Opah is blue and red with white spots, *Velifer hypselopterus* is green, and many taeniosomes have silver bodies with red fins. Oddities in structure and colour may be used together in the light of recent work to orientate features noted in *Radiicephalus*.

Walters (1963b) decided that there was no criterion to distinguish the Radiicephalidae from the Trachipteridae. A closer reading of Osório's paper shows that *Radiicephalus* has an anal fin. The additional information offered above indicates that other differences are to be found in the presence of a well developed gas-filled swimbladder, ribs, the possession of a sac filled with a brown fluid, and a higher number of vertebrae in *Radiicephalus* as compared with *Trachipterus*, *Zu*, or *Desmodema*.

Further clarification may be obtained from a developmental feature noted by Parker (1886); Meek (1890). In regalecids and trachipterids, the posterior caudal centra became 2-5 times longer than anterior centra, altering greatly the body proportions and the relative positions of skeletal and soft parts. In the Lophotidae and the Stylephoridae the vertebrae are of nearly identical length along the axial skeleton, throughout the life history. *Radiicephalus* resembles the latter group, all its vertebrae are of almost the same length. Like *Stylephorus* it has a caudal filament carrying back the lateral line canals beyond the vertebral column, but unlike *Stylephorus* the eyes are directed laterally, and the anterior crest borne by a Y-shaped bone connected to the 1st neural arch prevents the head being thrown back. Also, the neural spines in *Radiicephalus* are strong, the body shape flattened, rather than sub-cylindrical.

From this it is clear that *Stylephorus* has diverged from most taeniosomes. *Radiicephalus* would appear to share more features in common with the Lophotidae, as it has a "brown sac", an anal fin, a cloaca, smooth lateral line plates, a large swimbladder, strong ribs, and the body pattern an exaggerated form of that seen in *Lophotes*. However, lophotids have an exceptionally long gut with the anus only just anterior to the caudal fin in both *Eumecichthys* and *Lophotes*, while the few haemal spines that are left, crowded in the short caudal zone, are expanded hockey stick like laminae that stiffen the caudal fan to which the anal fin contributes. In *Radiicephalus* the gut is short, with the cloaca only $\frac{1}{3}$ along the total length of the body (Table 1), and there is a large number of normal unexpanded haemal spines. Further, the crest formed by an exaggerated development of the Y-bone, carries the dorsal fin well anterior to the eye in *Lophotes* and by hypertrophy forms an unicorn-like spike in *Eumecichthys*, but is not pronounced in *Radiicephalus* where the dorsal fin begins behind the anterior border of the eye.

Structure thus suggests that *Radiicephalus* lies outside the limits of the other taeniosome families as currently defined. As an interim measure, pending a full review of all the allotriognath fishes, (which is much needed), it seems justifiable to reestablish Osório's family for the single genus and species known at present. The Radiicephalidae could then be defined as laterally compressed taeniosomes with vertebrae of equal length, a gas filled swimbladder, ribs, smooth lateral-line scales, laterally directed eyes, no body-scales, a cloaca (enclosing genital, renal, intestinal and brown-sac apertures) at about $\frac{1}{3}$ along the total length from the snout, and with lateral line canals borne back on a long slender lower caudal filament supported by 7 rays.

One may turn to such conjectures as can reasonably be made about distribution, behaviour and physiology to try to ratify this position. It seems necessary to try to interpret the functional significance of a confusing array of both structures and colours. It is possible, however, that the taeniosomes may be regarded as a series progressively adapting to a deep-sea mode of life. Were this so, one would expect plain silver shallow living species with well ossified skeletons and large swimbladders passing into dusky chocolate forms with reduced skeletons and poorly developed swimbladders, and finally violet or black species with slightly ossified skeletons and, perhaps, telescopic eyes. Such a series could be compared to sequences of genera and species in the gonostomatids, sternoptychids and their relatives among the stomiatoids, or the lantern fishes among iniomes.

This scheme at first sight appears to fit the families of taeniosomes supremely well. *Radiicephalus* is silver with a pale dorsal fin, *Lophotes* (among Lophotids) is also silver but resembles *Regalecus* and certain *Trachipterus* species in having a red dorsal fin. *Radiicephalus* has a large swimbladder in which the 14 short retia resemble those of an upper mesopelagic species, while in *Lophotes*, which also has a well developed swimbladder, the rather longer retia resemble those of a deeper living form, (Marshall, pers. comm.). Some authors (Starks, 1908) report the absence of a swimbladder in *Stylephorus*. The small specimen examined by Marshall (1960, p. 44) had a regressed bladder with one unipolar rete. In at least one large individual of a *Trachipterus* species that has been properly examined, the swimbladder was minute (Palmer, 1961), while dissection of other individuals and several other species showed the swimbladder was further reduced, and absent. In the genus *Regalecus* there is apparently no swimbladder (Gunther, 1891). Apart from predominantly silver-bodied forms, there are *Trachipterus* species which have brown pigment, silvering, and crimson fins (*T. trachyurus* Leapley, 1953), or are black headed (*T. nigrifrons* Smith, 1956). *Desmodema* is chocolate brown, while *Stylephorus* is violet and silver with large telescopic eyes, which have three superimposed layers of retinal rods giving great visual sensitivity combined with binocular acuity of sight (Munk, 1966, p. 32), and reduced ossification, though a small swimbladder is retained in one species at least. The presence or absence of ribs and swimbladder seem correlated. Their absence may be regarded as an economy feature fitting deep-sea existence (cf. Denton and Marshall, 1958).

Probably all taeniosomes live in the mesopelagic zone as defined by Hedgepeth (1957, p. 18) or above it. If *Desmodema*, which is dark-coloured, is in fact a deeper

living form by day, then it probably performs considerable vertical migrations. It has been taken by night at depths of less than 50 m. (Krefft in litt.). Fitch (1964, p. 238) suggests vertical migration by *T. fukuzakii* while Sardou (1966, p. 199) reports migration by other *Trachipterus* species without providing the evidence. Smitt (1893, p. 318) and Palmer (1961, p. 342) both cite near surface observations of *Trachipterus*, while Fitch (1964) suggests a broad depth range for *T. altivelis*.

As in other mesopelagic fishes scale reduction appears to have gone hand in hand with a lightening of ossification. *Zu* retains modified cycloid scales. Histological sections of skin from material lent by Dr. G. Krefft showed a thin layer of silvering above and below each scale pocket. This makes it improbable that Osório's dried specimen could have lost its scales yet retained its silvering intact. However, there are reasons for caution in reporting the presence or absence of scales. *Zu cristatus* is possibly the most epipelagic of the family Trachipteridae. Few other taeniosomes appear to have retained scales. Fitch (1964) describes thin scales with two divergent keels in *Desmodema*, but Walters (1963a, fig. 1) assumes modified scales which cannot occur in their normal taeniosome position, or the hydrodynamic system he elegantly describes would have the pore apertures inconveniently blocked. Nishimura (1964, p. 127) reports that the scales of *Trachipterus ishikawai* disappear after preservation in formalin. It has been pointed out above (p. 193) that polysaccharide slime may also dissolve during preservation. It then becomes clear that any observations on pores, scales and hydrodynamics, need to be made on very fresh fish. As regards pores, genera of taeniosomes usually assumed to be scaleless, like *Trachipterus* and *Regalecus*, do have the intra-dermal canal system, but the pores are either partially exposed or lie wholly covered by a layer of epidermis with guanine. When this is removed the pores come to lie at the surface. Existence of an exposed pore system thus depends on the whole or partial failure of the guanine layer to develop (see Text-fig. 3), or else upon skin abrasion. The question of pores and swimming dynamics, together with scale formation and degeneration, thus needs further study.

The fact that severe storms coincide with strandings of *Regalecus* (Gunther, 1887, p. 73) suggests that these fishes swim in the upper layers of the ocean. Further, they must frequently approach the surface. During a cruise of R.V. "Atlantis II" in 1964, Mr. P. J. Herring saw two specimens by day off Mozambique, swimming round a water-bottle which was being hauled to the surface. *Regalecus* sp. is apparently commonly taken during trawling operations off the Cape of S. Africa (M. J. Penrith, in litt.). If the ink produced by *Lophotes* (Griffin, 1934, p. 243; Kershaw, 1909, p. 79) really acts as a blind to would-be predators, then fishes of this genus probably live in the photic zone too. The ink's chemical composition is that of a melanin compound, resembling squid ink (Fox, 1957, p. 371), and it seems likely that it serves the same function. The brown sac of *Radiicephalus elongatus* liberated into the preserving alcohol a yellow tint with a maximal light absorption in the ultraviolet. This may probably be compared with Fox's yellow extract from *Lophotes*. Again, King and Ikehara (1956) report that their specimen of *Eumeciichthys* was taken at the surface by day. What is intriguing about taeniosome swimming, with reference too to depth distribution, is that Nishimura (1964) has

TABLE I

OSÓRIO'S HOLOTYPE OF *RADIICEPHALUS ELONGATUS*

	1	2	3	4	5	6	7
	Shape	Colour markings	T.L. in mm.	Depth in T.L.	Head in T.L.	Eye in head	Teeth
Osório's specimen	Laterally compressed with a gently curved dorsum	Silvery lines forming a brickwork pattern	760	8.5 times	7.6 times	3 times	Sharp in 2 rows, the inner being the larger
"Discovery" specimen	as above	as above	692	8.9 times	7.7 times	3.4 times	as above

COMPARED WITH THE "DISCOVERY" NEOTYPE

8		9	10		11		
Gill arches and pseudobranch	Position of "anus"	No. head lengths from snout of anal fin	D.	P.	Fin Ray counts V. A. C.		
4 gill arches and a pseudo- branch	at about $\frac{2}{3}$ of total length from snout (5 head lengths)	ca. 5	159	9	bases only	Present. Few rays	Only lower lobe remaining, this forming a slender caudal filament
as above	at about $\frac{1}{3}$ of total length from snout (2.8 head lengths)	4.8	156	9	bases of c. 9 rays	Present. 7 rays	Small upper lobe of 4 rays + lower lobe with ca. 7 rays forming a slender filament

TABLE II.

MERISTIC AND OTHER CHARACTERS AND PROPORTIONS OF THE THREE

	S.L.	Depth in S.L.	Head length	Head in S.L.	Eye in head	Position of cloaca	No. of vert.	Position of anal fin	Branch. rays	Gill rakers
Neotype	597 mm	8.9 times	90 mm	6.7 times	3.4 times	In approx 1st $\frac{1}{3}$ of body beneath 44th (= 5th caudal) vert. 2.8 head lengths from snout	118 (39+ 79)	407 mm from front of orbit 4.8 head lengths from snout	6	2+ 0+ 7-8 large
Juvenile	304 mm	8.4 times	44 mm	6.8 times	3.5 times	c.f. above. below 41st (= 5th caudal) vert. 2.8 head lengths from snout.	114 (36+ 78)	182 mm from front of orbit 4.13 head lengths from snout	6	2+ 0+ 7 large
Postlarva	154 mm	6.7 times	28 mm	5.5 times	3.4 times	c.f. above. below 44th (= 7th caudal) vert. 2.5 head lengths from snout	114 (37+ 77)	85 mm from front of orbit 3.04 head lengths from snout	6	2+ 0+ 7 large

"DISCOVERY" SPECIMENS OF *RADIICEPHALUS ELONGATUS* OSÓRIO

P.	V.	D.	A.	C.	Discovery Station	Position	Date	Depth m.	Net
9	9 bases only of rays left	156 (ends above the 99th vert.)	7	4+7	6187	34° 17' N 8° 00' W (off Morocco)	17 XI 1966	570 -0	Net EMT
11— 12	9 bases of rays only	157	7	4+? (broken)	6117	37° 36' N 25° 13' W off São Miguel, Azores	17 X 1966	400 -0	EMT
10	9 rays very long ca. 60 mm long	152	7	?4 with a very long filament	6173	28° 04' N 14° 04' W (off Fuerte- ventura, Canary Islands)	10 XI 1966	725 -0	N113(H)

observed live *Trachipterus* propel themselves by passing ripples along the dorsal fin, in the manner of a *Notopterus* using its anal fin. If those taeniosomes with red fins live chiefly in the zone where blue light predominates, then the red pigment, by blacking out the fin, will eliminate the flicker of scattered light as waves shimmer back and forth along the dorsal during swimming, and so give these species the advantage of concealment both from prey and predators alike.

Information on feeding behaviour in the taeniosomes might yield much of interest. A radiograph of *Zu cristatus* showed it had eaten fish, as did others of *Trachipterus* species (see also Palmer, 1961, p. 348). The type of *Lophotes cristatus* was reported by Johnson (1863) to contain fish and squid remains. Further probing of this specimen has now produced an additional small trichiurid from the stomach, while in the intestine (which has a backwardly directed valve flap about half way along it) was the beak of a small squid (possibly a small *Architeuthis*). *Radiicephalus elongatus* is, at least in part, piscivorous (see p. 197). For the present the differences in digestive physiology (implied by strongly contrasting differences in gut length) between lophotids and radiicephalids, must remain obscure. *Regalecus* like *Lophotes* has a long gut laid down in the embryo. In *Regalecus*, though, it is the stomach which stretches back, and by far overreaches the anal aperture (Vayssi re, 1917). In a small *Regalecus* caught from R.R.S. "Discovery" off Fuerteventura (Canary Isl.) the anus opened at 29% of the standard length measured from the snout, yet the stomach tapered back to a point at 53% along the same length. The short intestine was bent forwards in a pyloric loop bearing very large numbers of caeca, and the greatly elongate stomach was packed along its entire length with small shrimp-like euphausiids.

From this sketchy survey of additional data, *Radiicephalus elongatus*, which has pale fins, appears the least specialized of all the taeniosomes. It does seem to have lost its scales, yet it shares features in common with each of the other families. The axial skeleton, fin structure and colour pattern, show various similarities with stylephorids or lophotids; the body form and the structure of the haemal spines, together with the anterior insertion of the dorsal fin, are of the type seen in trachipterids. The number of pterygiophores forming the nuchal crest, and perhaps, too, the pennanted nature of the first few dorsal rays, are most like these features in regalecids. *Radiicephalus elongatus* likewise appears to be least adapted among the taeniosomes to a fully mesopelagic existence, and has retained a large swimbladder of a type common among epipelagic fishes. Further collection combined with observations on live animals, and a better examination of its histology and anatomy must show whether or not these conclusions are substantially correct.

ACKNOWLEDGMENTS

We should like to thank Dr. Luiz Saldanha for a photocopy of Os rio's paper (in addition to his searches for the holotype of *R. elongatus* see p. 187). Mr. G. E. Maul kindly checked the accuracy of our translation of Os rio's description (see appendix). Mr. K. Twinn and Miss Joy Smith at Guys Hospital provided a fine series of x-radiographs taken with soft x-rays, and Mr. Arnold Madgwick skilfully made prints and enlargements from these negatives. Miss Pam Verity of the

Nuffield Institute of Comparative Medicine at Regent's Park provided additional x-radiographs of the neotype and of a specimen of *Regalecus*. Dr. G. Krefft supplied us with information about a cruise of the "Walter Herwig" and with material of *Zu cristatus* for an investigation of skin structure. Dr. Bruce Collette, Dr. J. King, Mr. R. Lavenberg, Dr. M. Cohen, Mr. M. Penrith and Dr. J. Fitch either lent material, answered queries by letter, or offered helpful suggestions, as did Dr. V. Walters. We are grateful to all these people who contributed in their different ways to the construction of a difficult paper. Dr. P. H. Greenwood, Dr. N. B. Marshall and Mr. P. M. David have all offered constructive criticism of the text. Dr. N. A. Mackintosh sheltered both authors for varying periods, and we should like to thank him and the other members of the Whale Research Unit of the National Institute of Oceanography for their warmly appreciated hospitality.

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