ON THE FIRST HALOSAUR LEPTOCEPHALUS: FROM MADEIRA

BY

C. M. H. HARRISSON

National Institute of Oceanography

Pp. 441-486 ; *Plate* 1 ; 6 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 14 No. 8

LONDON : 1966

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. 14, *No.* 8 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 9 *September,* 1966 *Price* £1 3*s.*

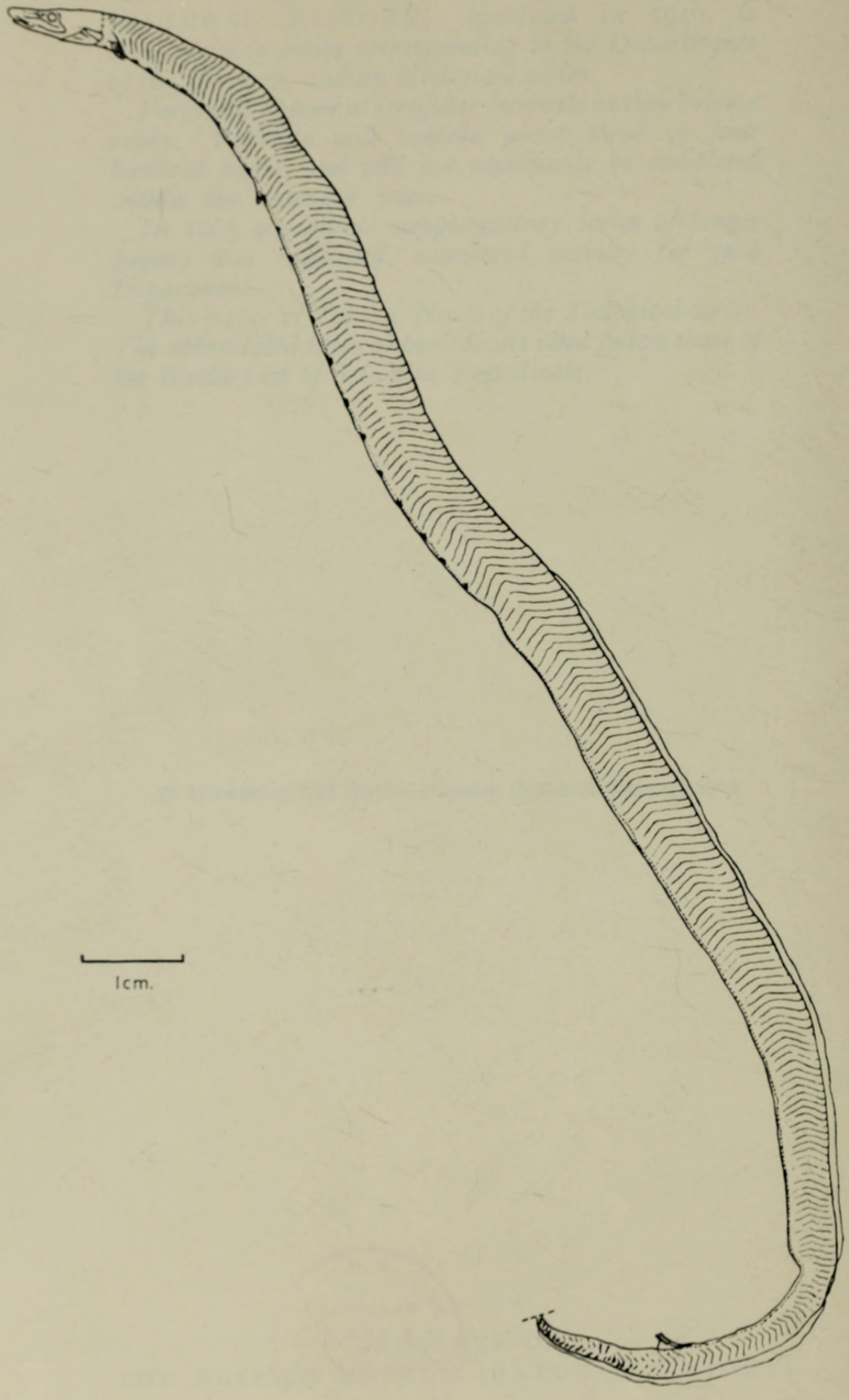

FIG. 1. Whole leptocephalus of an *Aldrovandia* sp. captured off Madeira.

ON THE FIRST HALOSAUR LEPTOCEPHALUS: FROM MADEIRA

By C. M. H. HARRISSON

INTRODUCTION

DURING the autumn of 1961 the R.R.S. Discovery made a series of collections in the Canary Basin of the North Atlantic. Among the fishes examined in the spring of 1964 was an elongate larva taken by an Isaacs-Kidd midwater trawl towed for 2 hours at a mean depth of 1100 m. (601·5 fths.) and a position between 29° 59′ N., 22° 56′ W. and 29° 50′ N., 22° 57′ W. This larva strongly resembled one of the larger ribbon-like eel leptocephali, though after preservation for 2½ years in formalin and subsequent transfer to 70% alcohol, it was somewhat less transparent and of a yellowish tinge. The presence of a pair of small ventral fins combined with the highly characteristic pattern of opercular bones and head canals indicate that it can only be a halosaur. It is indeed the earliest developmental stage yet known for this curious group of largely benthic deep sea fishes.

DESCRIPTION

The larva (Text-fig. 1) is 190 mm. in length though the tip of the " tail " is missing. The original length must have been at least 3 or 4 mm. more. The head is small, 9·5 mm. from snout to basis cranii, 3·5 mm. in maximum depth. The body is flat and ribbon-like, with a gradual dorsoventral broadening behind the head, reaching its greatest depth (7·3 mm.) well behind the ventrals, then tapering away again gradually to the tip of the tail. There are some 250 myotomes, but an exact count is made difficult as the tail is damaged, and the myotomes become less distinct posteriorly. Each myotome consists of a simple V whose apex points forwards (Text-fig. 1). Damage also leaves intact epidermis only on the head, and for a short distance along the body beyond the level of the pectorals (Text-fig. 2). Over this whole area the skin is lightly speckled with black pigment. Summarizing the body proportions, the head length is contained some 20 times in the length and 3 times in the distance from the snout to the origin of the ventral fins, while the maximum body depth is twice the maximum head depth.

The fins consist of (i) a pair of pedunculate pectorals, set somewhat below the mid-line of the lateral profile, and with 10 rays, (ii) a pair of ventrals with 8 rays, and (iii) a larval fin-fold commencing a long distance behind the insertion of the ventrals and confined entirely to the dorsum. The " anal papilla " is close to the tip of the tail, at the level of the 207th myotome, and there is no sign of an anal fin-fold whatsoever, though it must be remembered the tip of the tail is missing. The branchiostegal rays are 10 in number, and there are 9 rakers, 1 on the upper, and 8 on the lower limb of the 1st gill arch. The ray formula so far as can be ascertained is thus: B 10; D —; P 10; V 8; A —.

The head is roughly conical, tapering forwards to a pointed snout that overhangs

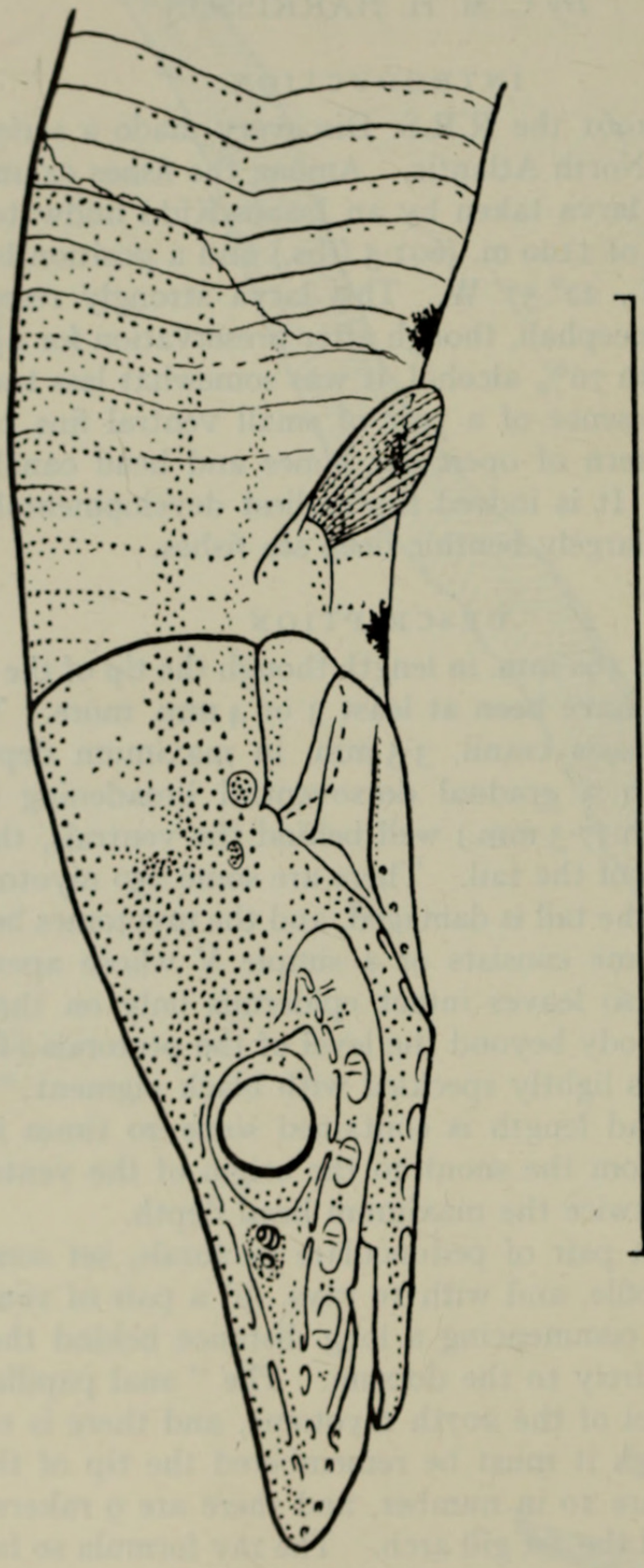

FIG. 2. Head of *Aldrovandia* leptocephalus enlarged to show details of lateral line canals and opercular structure.

the mouth. There are a number of tiny rounded mucus pores on the snout, while a series of pale elongate ovals marks the position of the supraorbital lateral-line canal. A pore just anterior to the nasal capsule marks the posterior limit of the adnasal canal. Much more conspicuous is the very large suborbital canal. Seen by transmitted light the neuromast cushions are visible as opaque dots and above each of these organs in the lateral canal wall is a pale elongate elipse, representing the curled dorsal edge of a developing lateral line scale. Seven such scales are visible, the most posterior, the smallest, lies at the point where the suborbital canal turns upwards behind the eye. Alternating with the cushions are large oval pores connecting the exterior with the canal lumen. A similar series of pores (likewise difficult to see owing to the transparency of the membrane they perforate), marks the position of the mandibular canal. There are no signs of the lateral line along the body. The opercular apparatus (Text-fig. 2) consists of a small shoulder-blade shaped operculum, partly overlain by a very large preoperculum which is perforated by endings of the VIIth cranial nerve. The subopercular is a narrow splint of glassy transparency lying along the lower border of the operculum. The interoperculum is a slender rod passing from the subopercular to the hind border of the mandible. It is connected to the " epihyal ". The suspensorium slopes obliquely upwards to the otic capsule, the dorsal end of the hyomandibular being roughly triangular and having a horizontal edge. The head was somewhat damaged on the right side and the operculum torn outwards allowing an internal view of the opercular apparatus. The lens of the right eye is missing. The left eye remains in better condition, and the diameter of the spherical lens closely approximates to the interorbital width across the frontals. The nasal capsules are placed immediately anterior to the orbits. The nasal rosette has 8 leaflets arranged in pairs. After clearing in glycerine, the structure of the auditory capsule became distinct. Three pale zones, and 2 clearly marked dark zones with the beginnings of a third, were seen in the otoliths.

Turning to details of the body characters there is a conspicuous row of large ventral melanophores spaced at intervals of about 1 pair to every third pair of myotomes, though more closely spaced at the anterior end and more widely separated at the posterior end of the series (Text-fig. 1). These pigment spots discontinue close to the level of the insertion of the dorsal fin-fold. Along the ventral edges of the myotomes is a series of small black dots, while similar minute dots of pigment are arranged close to the myotome septa above the mid-line of the body. This pigmentation is apparently subepidermal (vide supra). There are no signs of developing scales. It is difficult to make out accurate details of the course of the gut, of the kidneys and blood vessels, due to the semi-opacity of the myotomes. Although the viscera are still largely displaced below the body segments, the upper surface of the gut is partly hidden. A thorough examination could not therefore be undertaken without doing what was considered as excessive damage to the specimen. From the partial details visible it seems probable that the duct opening on to the anal papilla is the renal duct. The gut appears to end blindly some 22 segments more anteriorly.

LEPTOCEPHALUS FEATURES AND METAMORPHOSIS

Having described the chief morphological characters, the general importance of the discovery of this larval halosaur may now be considered. Following a discussion comparing modes of development in various groups of fishes, the characters of adult halosaurs will be compared with features in the larva, with a view to interpreting structures from a morphogenetic viewpoint, as well as to consider the larva's probably systematic position.

There is a series of " soft-finned " fishes, including the Tarpons and Lady-fishes (*Tarpon*, *Elops*) ; *Pterothrissus* ; the banana fish and bone fishes (*Albula*, *Dixonina*) ; the eels (*Apodes*) ; and the gulper eels (*Lyomeri*), all of which have a larval stage referred to as a *Leptocephalus*. The question is, whether the halosaurs also have a larva of this rather special type. To enlarge on this, one must first establish what particular features distinguish a *Leptocephalus* from other sorts of larva, then see which of these characters the only available halosaur larva has.

The first description of a *Leptocephalus* was that given by Gronovius in his *Zoophylacium* of 1763. He describes specimens taken in the Irish sea near Holyhead, Anglesey, by William Morris and sent to him by Thomas Pennant. The characters Gronovius gives in his latin diagnosis are : a scaleless body and head, laterally flattened, large eyes and mouth, as well as a long dorsal fin fold. Subsequent to the studies of Delage (1886), and Grassi & Calandruccio (1893) it was realized that the leptocephalus described by Gronovius was in fact a larval eel, while the classical work of Johannes Schmidt made known in great detail the developmental history of *Anguilla*. Later, it was found that the fishes of the groups mentioned above also have transparent larvae, with small pointed heads which are dorsoventrally much narrower than the greatly flattened body. Like eel leptocephali, such larvae also have a long dorsal fin-fold, an anus close to the tip of the tail and large larval teeth borne by the membrane-bones of the jaws. Probably in all, the space between the two lateral myotome sheets, above and below the notochord and bounded ventrally by the low-slung viscera, is filled with an acellular gelatinous tissue, as found by Rasquin (1955) in larval *Albula*. The above, then, may be taken as basic morphological characters common to all leptocephalus larvae.

The halosaur larva has a long and greatly flattened body. Like established leptocephali, it too has a small pointed head. Its anal papilla is close to the tip of the tail, and there is a long dorsal fin fold, while the body broadens to a maximum dorsoventral extent of more than twice the head depth. The simple myotomes form a ribbon down each flank of the body. Above the notochord, and between the nerve chord and the gut, the space is occupied by a gelatinous mass. Only two leptocephalic characters are absent : the transparency of the body and the large larval teeth. The specimen under consideration was yellowish and translucent, but not transparent or glassy-hyaline as are typical leptocephali. However, many Indo-Pacific eel leptocephali are similar to this in appearance, and moreover resemble the halosaur larva in having a ventral series of dark spots. The absence of teeth

seems readily understandable if it is assumed that the halosaur larva has just reached the stage at which it is beginning metamorphosis. This contention is greatly strengthened by the following evidence.

In the great majority of fishes the larval period is a short one, lasting a matter of a few weeks. Prolonged " infantilism " is perhaps a general feature of fishes with leptocephalus larvae. At all events, in *Anguilla anguilla* the leptocephali are in their third year when metamorphosis begins (Schmidt, 1935). They then lose their larval teeth, while the body, following changes in the head, becomes more slender and less leaf-like. It is thus of great interest to find in this halosaur larva with a head of rather adult appearance, and strangely larval body, that the otoliths have three rings. If these are indeed annual rings, then not only does the developmental pattern seem similar, its timing too is alike in both eels and halosaurs. To recapitulate, there is evidence to suggest that the larva to hand was just beginning metamorphosis after a life span of three years. Probably a younger larva would have had large teeth as well as a more transparent and even more leaf-like body. There thus seems excellent justification for stating that the larval halosaur is a leptocephalus.

In the general description, it was remarked that the gut may have ended blindly. This may seem surprising. However one of the features of metamorphosis from the leptocephalus both in eels and elopoids (though probably not in Lyomeri) is the remarkable shift forward of the position of the anus. Bertin (1926), for example, records a shift of some 245–345 myotomes in *Nemichthys scolopaceus*. Now at this period the leptocephali stop feeding. Rasquin (1955) thinks that in *Albula* the gelatinous tissue between the myotome sheets provides the necessary reserves at metamorphosis, and until feeding begins again. This is probably true for other leptocephali. It would not therefore seem strange in a metamorphosing larva to find that the non-functioning gut pinched off a posterior section before retracting, and re-establishing the anus in its definitive position. It seems possible that this is what is happening in the halosaur larva. Alternatively, what appears to be the blind ending of the gut may ultimately prove to be merely a gastric caecum or hepatic lobe. Further material is required before this can be satisfactorily decided. Through the kindness of Mr. Alwyne Wheeler I was able to examine a number of X-ray photographs of adults of 7 species of Halosaur and in all the anus occurs at the level of the 55th–74th vertebra (see Table I, which is further discussed on p. 458). Assuming that the larval halosaur had an anus opening on the anal papilla, at the level of the 207th myotome, there must be a shift in the position of the anus of some 140 myotomes in amplitude during the change from larva to adult. Similar hypermetamorphic phenomena must therefore occur in both nemichthyid eels and halosaurs.

A fuller discussion of the processes occurring at metamorphosis in the halosaurs can only be made after a comparison of larval and adult features. The topic will be resumed after an account of the morphological characters which serve to identify the larva.

TABLE I

a. Adult Segmentation Taken from Vertebral Numbers in Radiographs

Genus and species	Material examined	Standard length (mm.)	Segment numbers: Anterior to pectoral fins	Anterior to ventral fins	Anterior to dorsal fin	Anterior to anus	Anterior to anal fin	Post-cephalic total
Halosaurus Johnson								
ovenii Johnson, 1863	Holotype B.M.N.H.	440 (465)	10	37	45	***74***	76	***274***
johnsonianus Vaillant, 1888	Paratypes B.M.N.H.	381	8	31	39	***62*** ?	64	***265***
		334+	8	31	39	***66*** ?	68	***223***+
	Average number of preanal segments for the 2 spp examined :					***69***		
Aldrovandia Goode & Bean								
rostrata (Günther, 1878)	Holotype B.M.N.H.	495 (507)	8	38	46	***64***	66	***320*** ?
affinis (Günther, 1877)	Syntypes B.M.N.H.	420	8	36	39	***61***	66	***252***
		410	10	36	38	***64***	66	
		(both 421)						
macrochir (Günther, 1878)	Lectotype B.M.N.H.	535 (545)	10	36	37	***61***	64	***260***
phalacra (Vaillant, 1888)	Paratype B.M.N.H.	207+	9	32	40	***60*** ?	62	***169***+
mediorostris (Günther, 1887)	Holotype B.M.N.H.	445 (444)	9	27	35	***55***	56	***216***
	Average number of preanal segments for the 5 spp. examined :					***61***		

b. Larval Segmentation Taken from Myotome Counts

Genus and species	Material examined	Standard length (mm.)	Segment numbers: Anterior to pectoral fins	Anterior to ventral fins	Anterior to dorsal fin	Anterior to anus	Anterior to anal fin	Post-cephalic total
?	Larva from Discovery collections IKMT 4746	190	7	38	Only fin-fold present	***207***	Anal fin absent or missing	***250***+

The larva has ***207*** preanal myotomes. The maximum number of preanal vertebrae found in the adults above was ***74***, the minimum ***55***. It thus seems that the anus migrates over 133–152 segments at metamorphosis.

THE OPERCULAR STRUCTURE AND ITS DEVELOPMENT

In comparing characters shown by the larva with those of adult halosaurs, one may begin with features of the opercular structure and the head canals of the lateral line system. These are the most salient features indicating that this is indeed a halosaur. Adult characters seem well established in the head region long before the body assumes its definitive form.

Taking first the opercular structure. Marshall (1962) has disentangled from a century's terminological controversy the true relation of the opercular bones in halosaurs by examining an *Aldrovandia macrochir*. He showed that all the usual opercular bones are present in halosaurs, but that the preoperculum grows back in the opercular fold to cover the subopercular and the interoperculum more or less completely. Superficially only two bones are visible, a small upper disc, the operculum, and a large lower flange, the preoperculum (Text-fig. 4*c*). This condition, clearly visible in the larva (Text-fig. 2), is unique among fishes. It seems worth a short digression to discuss it in detail.

The fish operculum is a functional unit acting as a respiratory valve and pump (Hughes, 1960), and as a linking mechanism allowing small muscles of the hyoid plate (adductor operculi, Edgeworth, 1935) to help open the lower jaw (van Dobben, 1935). The (dermal) bones are, however, of two sorts: (i) the preoperculum which develops in relation to the lateral line and (ii) the " truly opercular " bones related solely to " cartilage bones " of the hyoid arch. The operculum articulates to a process on the hyomandibular. The subopercular is often attached to the operculum, but in Mormyrids it is hard to distinguish it from a branchiostegal ray and in *Engraulis* it is even connected to the epihyal, increasing its resemblance to a branchiostegal ray (Ridewood, 1904 : 75). This raises the question of the development of the bones. If branchiostegal rays develop as procartilaginous rudiments can they be equated with plates of bone held not to do so? The operculum first appears as a cartilage in eels (Norman, 1926), and the evanescent rudiment in lyomerous larvae is also cartilaginous (Orton, 1963), which suggests they can. There is then the interopercular: commonly it is displaced anteriorly as a triangle of bone. According to van Dobben (l.c.) it is often connected to the interhyal (stylohal). In *Elops* (Ridewood, 1904) the branchiostegal rays all develop into flattened plates of bone so there is a continuous series of similar ossifications from the operculum downwards, but the anteriorly displaced interoperculum does not appear to belong with this series of bones. It is thus interesting to note that in the halosaur larva the interoperculum (Text-fig. 5) develops with all the appearance of a branchiostegal ray. It is attached to the epihyal, with its upper end connected to the subopercular, and linked to the hind end of the lower jaw by a slip of muscle, and a tendon which is shown in Günther, 1887, pl. IX, fig. 2, labelled " lig ". In adult Halosaurs the interoperculum flattens out and enlarges to become a paddle shaped bone (Text-fig. 4*a*). Morphologically then, the interoperculum seems equivalent to a branchiostegal ray. Its forward displacement in many fishes is explained if one accepts that it most often belongs to that part of the hyoid arch kinked anteriorly as the interhyal. The connection of the interoperculum with the

epihyal in halosaurs is thus unusual. In *Anguilla* elvers, too, the interoperculum is paddle-shaped (Text-fig. 3). Further, in eels the opercular fold is supported largely by the branchiostegal rays (Regan, 1912), while the operculum and suboperculum are small. Except for the large preoperculum, the halosaur opercular structure thus resembles the condition found in the eels. The details seen in the larva and described above, correspond closely with those given by Marshall (1962), for an adult halosaur.

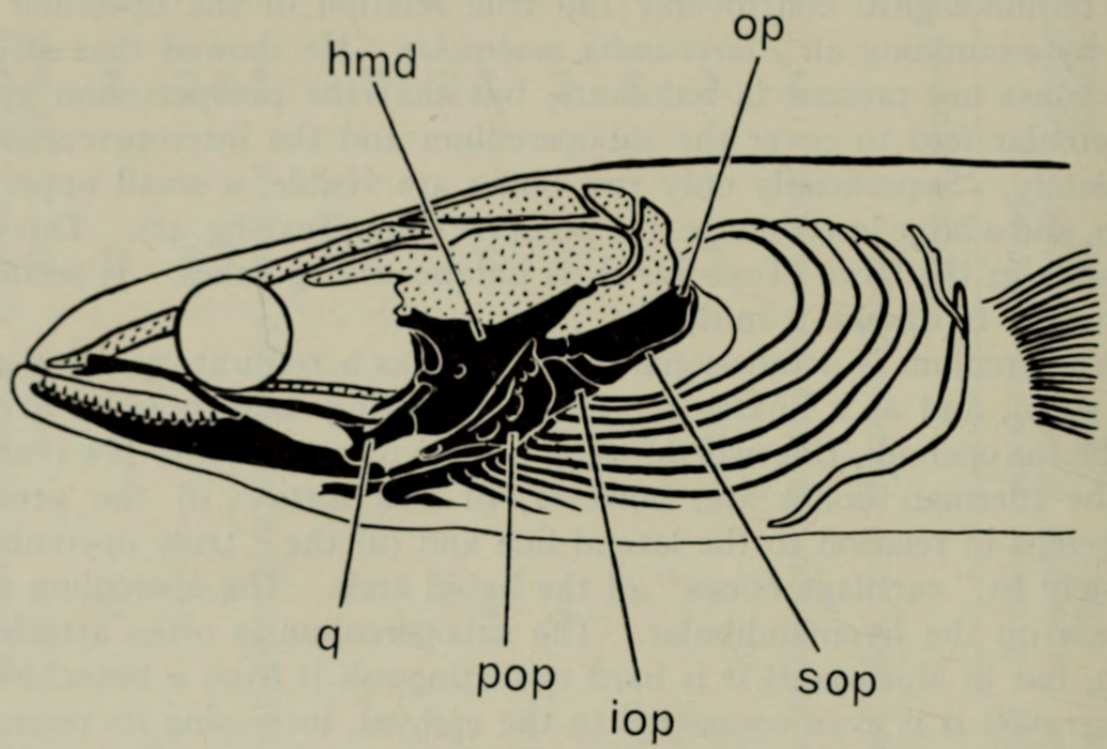

FIG. 3. Head of an *Anguilla* elver showing the bone structure. *hmd.* = hyomandibular, *op.* = operculum, *sop.* = suboperculum, *iop.* = interoperculum, *pop.* = preoperculum, *q.* = quadrate.

THE PREOPERCULUM AND THE HEAD CANALS

The preoperculum may best be considered in relation to the head canals of the lateral line series. Its great size in halosaurs (and in these fishes it has secondarily become the chief support of the opercular fold) seems related to the enormously enlarged mandibular canal (and not to the infraorbital canal as Marshall, 1962, stated). There is no connection between infraorbital and mandibular canals. Figures (pl. LXXXIV : 3–6) by Garman (1899) are misleading in this respect ; they suggest a jugular connection, present in Dipnoi but not known in any Actinopterygian.

The thin walled and greatly expanded canals in the preopercular region are delicate and often damaged in preserved material. In the larva the infraorbital canal stops short of the preoperculum, terminating in a backwardly directed bulge (Text-fig. 2). In several adult *Aldrovandia* examined, the infraorbital canal just extends on to the preoperculum to end blindly in a series of finger-like processes, adhering closely to the preopercular membrane and the wall of the mandibular canal

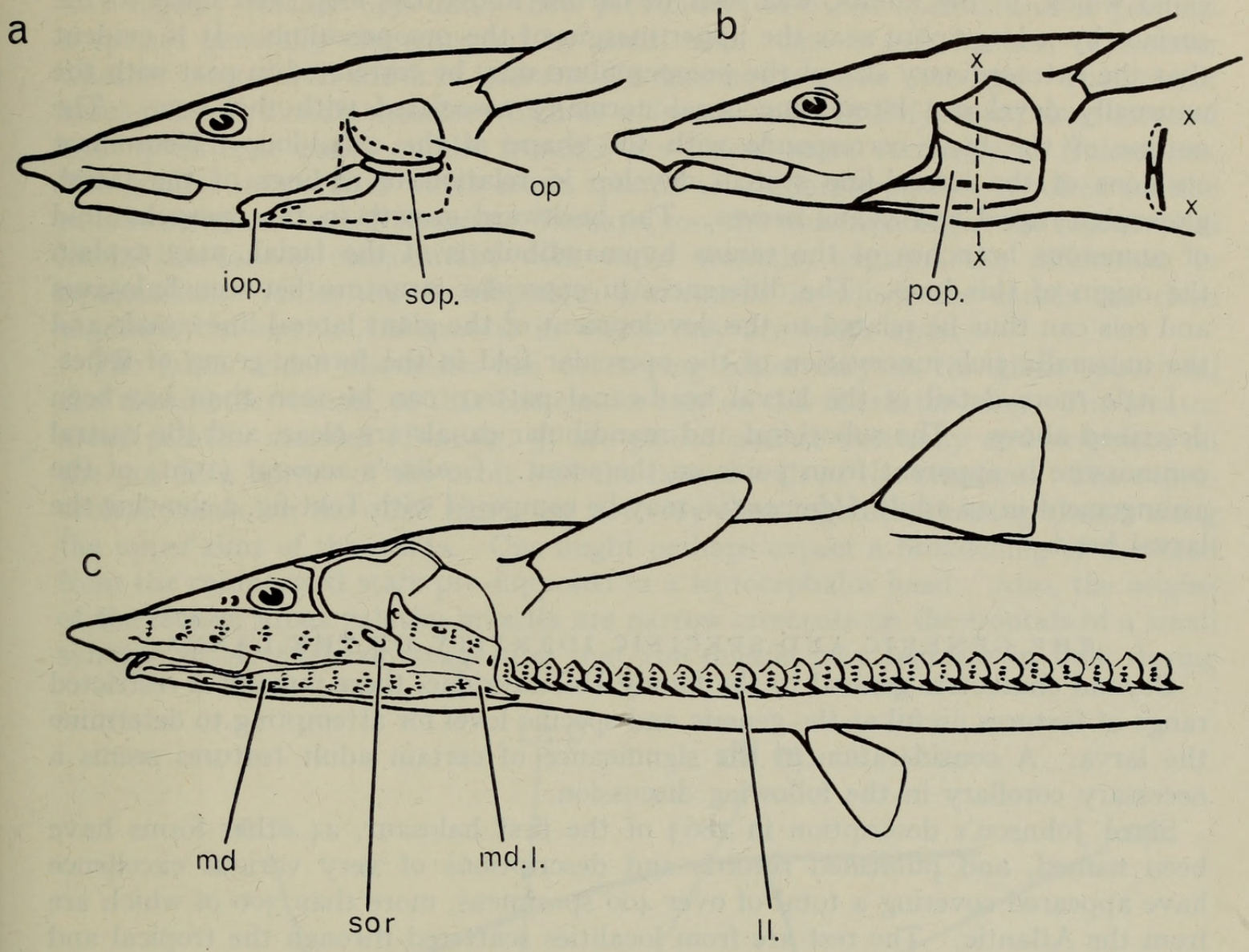

FIG. 4. Diagrams of adult *Aldrovandia* showing features of the lateral line and opercular structure (after Gilbert, 1905). (a) head with preoperculum as stippled outline. *iop* = interoperculum, *sop.* = suboperculum, *op.* = operculum. (b) head with inset vertical section ×——× of the preoperculum = *pop.* (c) head and anterior part of body *md.*=mandibular canal, *sor.*=suborbital canal, *md. l.*=preopercular loop of mandibular canal, *l.l.*=lateral line along body.

below (Text-fig. 4). The larval mandibular canal is evident from the series of large pores along the underside of the lower jaw. It curls round the end of the jaw on to the preoperculum, but further detail is obliterated by damage. In adult *Aldrovandia* the mandibular canal curves back in a broad loop, over the main preopercular flange, and is partly overlain by a thin lamina of bone. This lamina is connected by a delicate strut to the main preopercular flange. The preoperculum thus has an I-girder cross-section with the outer lamina smaller than the main flange (Text-fig. 4*b*). Probably the lamina arises from the fusion back-to-back of two series of curled scale-like ossifications (similar to those in the suborbital canal), formed in the wall of the preopercular loop of the mandibular canal, and additionally fused basally to the flange. The lamina is clearly visible in the larva, as is a part of the

canal which, in the adults, was seen to narrow above the loop, and open to the surface by a large pore near the upper margin of the preoperculum. It is evident that the extraordinary size of the preoperculum may be correlated in part with the unusually developed lateral-line canal normally associated with this bone. The outline of the bone corresponds with the shape of the canal-loop. Neuromast cushions of the lateral-line system develop in relation to endings of the facial, glossopharyngeal and vagus nerves. The backward growth in the opercular fold of numerous branches of the ramus hyomandibularis of the facial, may explain the origin of this loop. The differences in opercular structure between halosaurs and eels can thus be related to the development of the giant lateral line canals and the unusually rich innervation of the opercular fold in the former group of fishes.

Little more detail of the larval head-canal pattern can be seen than has been described above. The suborbital and mandibular canals are clear, and the rostral commissure is apparent from pores on the snout. Gosline's account (1961) of the arrangement in an adult *Aldrovandia*, may be compared with Text-fig. 2 showing the larval head.

THE GENERIC AND SPECIFIC IDENTITY OF THE LARVA

Beyond characters general to the family Halosauridae, there remains a restricted range of features useful at the generic and specific level for attempting to determine the larva. A consideration of the significance of certain adult features seems a necessary corollary in the following discussion.

Since Johnson's description in 1863 of the first halosaur, 24 other forms have been named, and published records and descriptions of very various excellence have appeared covering a total of over 400 specimens, more than 300 of which are from the Atlantic. The rest are from localities scattered through the tropical and subtropical regions: The Prince Edward Islands (Günther, 1878), the Indian Ocean, (Alcock, 1889–98; Brauer, 1908; Norman, 1939), the Malay Archipelago (Weber, 1913), South Australia (McCulloch, 1926), The Philippines (Fowler, 1933), Japan (Günther, 1877, 1887), Hawaii (Gilbert, 1905), and the Gulf of Panama (Garman, 1899). Additional observations have been made from bathyscaphes and by deep-sea photography [e.g. Pérès (1956), Houot (1958)]. Further details are given in Table III, in the map, Text-fig. 6, and in the Gazetteer (Appendix pp. 475–486). There has, however, been no recent review of the family Halosauridae.

Vaillant in 1888 after studying the material brought back by the "Talisman" divided the genus *Halosaurus* into 2 groups according to whether or not the interorbital width was greater than the horizontal diameter of the eye. Vaillant's group of species with a large interorbital width was also characterized by lacking scales on the vertex of the head. His other group, those with a narrow interorbital width, contained, apart from his new species *phalacrus*, only species with a scaly vertex. Goode & Bean (1895) used the criterion of scaled as against scaleless vertices to divide the halosaurs, placing Vaillant's *phalacrus* in their new genus *Aldrovandia*, along with the other smooth-headed species. Now the type of *Aldrovandia phalacra*

was slightly smaller (430 mm.) than previously described species and is perhaps a species generally characterized by small size. One is led, further, to wonder whether interorbital width in *Aldrovandia* does not increase with age. The levator arcus-palatini/hyoidei muscles which in *Aldrovandia* (as in *Polypterus*) slant forward and upwards to insert on the frontals, are placed more vertically in *Halosaurus*. The greater interorbital width seems related to the larger surface required for the muscle insertions in *Aldrovandia*. Perhaps, too, the wider spacing of the supraorbital lateral-line canals, concomitant with wider frontals, explains the differences in squamation. Scales are developed in *Halosaurus* in which the canals are close together, but not in *Aldrovandia* in which they are wider apart.

The larva under discussion has developing scales only in the giant suborbital and mandibular canals, so that one cannot rely on this character here. The levator arcus palatini muscles (Text-fig. 5) are placed almost vertically and originate on the posterior border of the orbit and the lateral wall of the cranium. The supra-orbital canals, on the other hand, are not very close together, running almost along the upper rims of the orbits. One might perhaps expect a broadening of the head from the compressed state pre-supposed in a leptocephalus head. Also, the origins of the levator arcus palatini muscles are narrow crescents on the frontals of a small syntype of *A. phalacra*, suggesting that the muscle may increase in bulk during

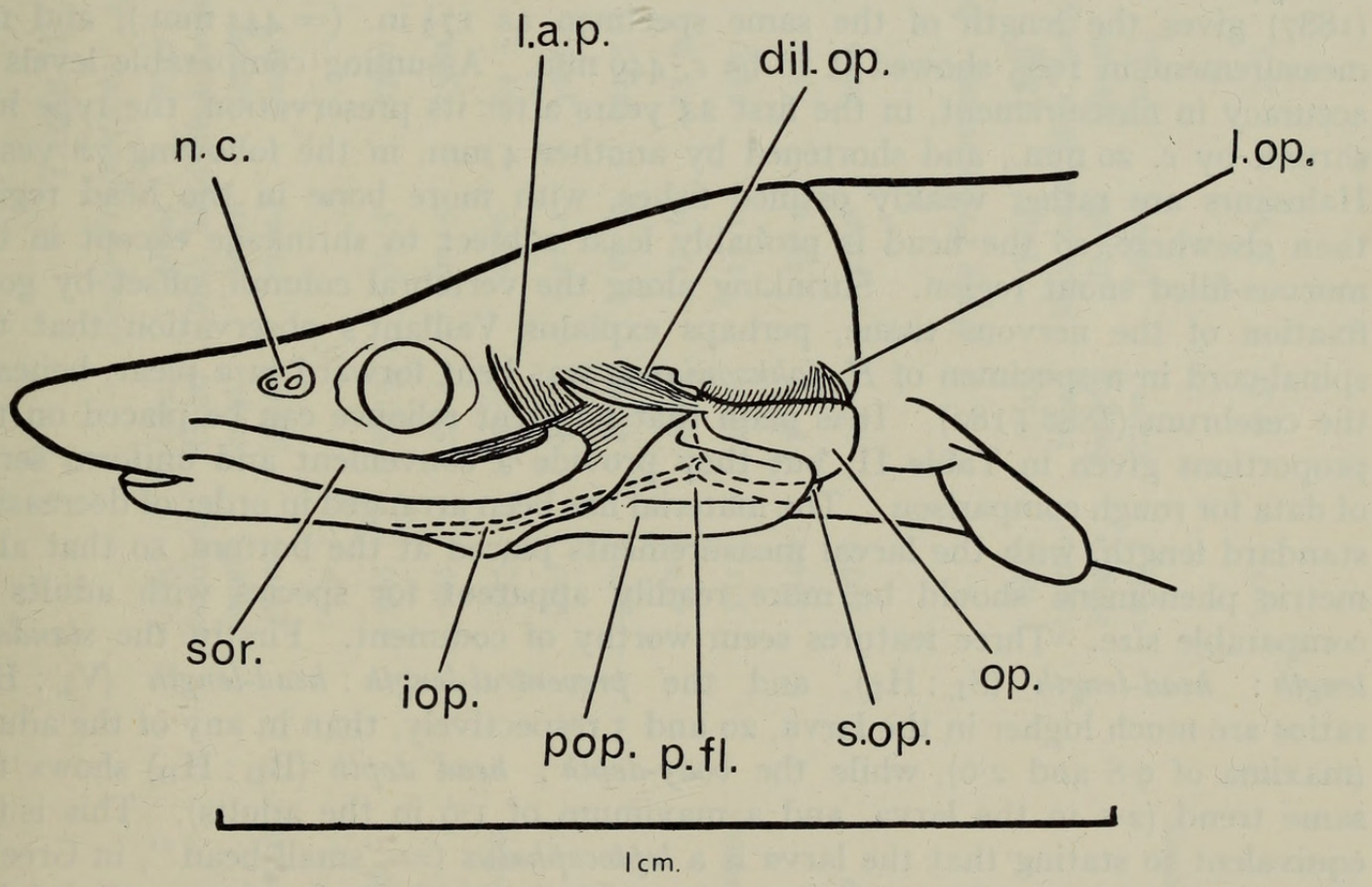

FIG. 5. Head of *Aldrovandia* leptocephalus showing musculature. *n.c.* = nasal capsule, *l.a.p.* = levator arcus palatini, *dil. op.* = dilator operculi, *l.o.p.* = levator operculi, *op.* = operculum, *s.o.p.* = suboperculum, *p.fl.* = preopercular flange, *pop.* = pre-operculum, *i. op.* = interoperculum, *sor.* = suborbital lateral line canal.

development. A shift forward of the origin of the muscle from the wall of the brain case to the dermal bones roofing the orbits, may occur at metamorphosis, and presumably at a time when the larva is not feeding. On the basis of criteria currently used to separate genera it is not possible to decide whether the larva is a *Halosaurus* or an *Aldrovandia*. The facts, that the interorbital width is narrow, and that the levator arcus palatini muscle is placed nearly vertically, seem insufficient for assigning it to the genus *Halosaurus*.

The characters used to separate the species of the family Halosauridae, as adults, are largely valueless when applied to a larva in which the body proportions are altering to such an indisputably major extent. This is best emphasized by a comparison of the body proportions assembled in Table II. Measurements for the 7 species of Halosaur examined are set out, using the same material as detailed in Table I. For specimens that had obviously lost the tip of the tail, the length is given, followed by a plus sign. Since many had stood on their snouts in jars for almost a century, their rostra were bent, so that it is impossible to give reliable length data, irrespective of tail-truncation. Standard lengths are given to the nearest millimetre, but should be interpreted with caution. Lastly there is the factor of shrinkage following preservation. In the last century much material was placed in strong spirit, and " hardened ". Johnson (1863) in his description of the holotype of *H. ovenii* quotes the standard length as 18 $\frac{5}{16}$ in. (= 464 mm.). Günther (1887) gives the length of the same specimen as 17$\frac{1}{2}$ in. (= 444 mm.), and my measurement in 1965 showed it to be *c.* 440 mm. Assuming comparable levels of accuracy in measurement, in the first 24 years after its preservation, the type had shrunk by *c.* 20 mm., and shortened by another 4 mm. in the following 78 years. Halosaurs are rather weakly ossified fishes, with more bone in the head region than elsewhere, so the head is probably least subject to shrinkage except in the mucous-filled snout region. Shrinking along the vertebral column, offset by good fixation of the nervous tissue, perhaps explains Vaillant's observation that the spinal-cord in a specimen of *H. johnsonianus* was bent forward in a pleat, beneath the cerebrum (1888 : 182). It is plain that no great reliance can be placed on the proportions given in Table II, but they provide a convenient and uniform series of data for rough comparison. The material has been arranged in order of decreasing standard length, with the larval measurements placed at the bottom, so that allometric phenomena should be more readily apparent for species with adults of comparable size. Three features seem worthy of comment. Firstly the *standard length* : *head-length* ($S_L : H_L$), and the *preventral-length* : *head-length* ($V_L : H_L$) ratios are much higher in the larva, 20 and 3 respectively, than in any of the adults (maxima of 9·8 and 2·6), while the *body-depth* : *head depth* ($B_D : H_D$) shows the same trend (2·1 in the larva, and a maximum of 1·9 in the adults). This is the equivalent to stating that the larva is a *leptocephalus* (= "small head ", in Greek). The larval head is smaller in all dimensions, relative to the body, than in the adults. Secondly the larval *body depth* : *head-depth* ratio is closer to that of the largest, but more than twice the value for the smaller " adults " measured. It seems that the larva becomes more shallow-bodied following metamorphosis, and the adults

TABLE II

Body Proportions a. *Adults*

Species	(S_L) Standard length (mm.)	(H_L) Head length (mm.)	(H_D) Max. head depth (mm.)	(B_D) Max. body depth (mm.)	(V_L) Length from snout to ventrals (mm.)	$S_L : H_L$	$B_D : H_D$	$H_L : H_D$	$V_L : H_L$
A. macrochir	535	58·3	30·5	37·0	142	9·2	1·9	1·2	2·4
A. rostrata	495	53·4	20·5	25·9	128	9·3	1·3	2·6	2·4
A. mediorostris	445+	51·8	23·6	24·3	105	>8·6	1·0	2·2	2·0
H. ovenii	440	45·1	21·2	31·9	120	9·8	1·5	2·1	2·6
A. affinis	420	44·4	16·5	21·5	107	9·6	1·3	2·7	2·4
	410+	47·2	17·6	23·9	116	>8·7	1·3	2·7	2·5
H. johnsonianus	381	41·2	15·6	14·9	91	9·3	0·9	2·6	2·2
	334+	38·9	13·4	13·4	90	>8·6	1·0	2·9	2·3
A. phalacra	207+	28·0	11·6	10·0	66	>7·4	0·9	2·4	2·4

Body Proportions b. *Larva*

Species	(S_L) Standard length (mm.)	(H_L) Head length (mm.)	(H_D) Max. head depth (mm.)	(B_D) Max. body depth (mm.)	(V_L) Length from snout to ventrals (mm.)	$S_L : H_L$	$B_D : H_D$	$H_L : H_D$	$V_L : H_L$
Sp. ?	190	9·5	3·5	7·3	28·5	20·0	2·1	2·7	3·0

become deep-bodied again after the abdomen has been distended by the gonads. Lastly, the *head-length*: *head-depth* (H_L: H_D) ratios seem to show specific differences. The larval ratio appears comparable with the figures for the adults ; the precocity of the larval head is noted above. But as the adult snouts have been crumpled to such a varying degree, one can only suggest that these figures make it less likely that the larva is one of the following : *A. machrochir*, *A. mediorostris* or *H. ovenii*.

Returning to Table I, the possible systematic value of the segmentation may be considered briefly. Two prefatory remarks are necessary. There is no absolute correspondence between myotomes and vertebral numbers. The myotomes act across the vertebrae, and the first vertebra counted in the radiographs appeared to be a hemicentrum (the basioccipital, fused to the basisphenoid?). One might expect at least one myotome fewer than the vertebral number in the front trunk-region. Also, the thickness and curvature of the body-wall means that the position of the pectoral girdles and the paired-fin insertions, relative to the vertebral column is subject to some variation dependent upon the angle at which the radiograph was taken, the posture in which the specimen was preserved and the state of contraction of the body musculature. For these reasons a direct comparison between vertebral numbers in the adults and myotomes in the larva, seems unjustified where the differences in segmentation over the range of species examined, is so slight. Secondly it should be noted that the lectotype of *A. macrochir* is that chosen by Günther himself, in his final report on the Challenger fishes (1887). In view of the lack of exact information on the effect of muscular contraction on the position of the fins relative to the vertebrae, the information in Table I may simply be regarded as showing a general conformity of the larval segmentation with that in adult halosaurs, in addition to indicating the magnitude of the anal migration at metamorphosis (see p. 449). Perhaps, though, the rather small number of vertebrae anterior to the ventrals makes it less probable that the larva is either *A. phalacra* or *A. mediorostris*. The data in Table I have been arranged with the " adults " of the different species placed in descending order for the number of preanal segments. It will be seen that for the adults the number of segments anterior to the dorsal and ventral fins decreases in this same order, with the exception that the dorsal fin is further from the head in *A. phalacra*. The present standard lengths in this Table are placed above; below them the first published figures, converted to mm., are given in parentheses. The only characters that really might seem available for both adults and larvae are those of the ray formula. Unfortunately almost nothing is known about the range of intraspecific variation, and in relying on published data which have not been adequately reviewed, one is apt to be engulfed in the quicksands of error amassed unfathomed over a century of time. Assuming all published synonymies to be correct, Table III presents the available data for comparison with the larval fin-ray formula and branchiostegal numbers given above. Certain previously unpublished details could be added thanks to Dr. P. H. Greenwood and Mr. N. B. Marshall who allowed me to see type and other material kept in the British Museum. Such details are shown by an asterisk in the Table. Before looking more closely at the ray formulae it may be remarked that the ray count for the larval pectoral fin

given above is probably a conservative figure. The radials and their rays become so small towards the lower border of the fin that they are exceedingly difficult to see.

The species in Table III are arranged in descending order of branchiostegal and fin-ray numbers, except that with *Aldrovandia* the species with a narrow interorbital width (Hawaiian forms, and *A. phalacra*) are placed first, while the species *affinis*, *gracilis* and *rostrata*, which seem to form a natural group, are placed after *A. mediorostris*. Where an author gives an incomplete description of a type specimen, but gives supplementary details for cotypes, such data are given in parentheses. Sizes originally cited in inches have been converted to millimetres. In general only the largest size is given where more than one specimen is treated. Under the head " origin of material " only approximate information is given, as this is often all that is offered by early authors. Full data have been assembled in the Gazetteer (see Appendix). The column " nominal species and genus " shows in brief what changes have occurred in nomenclature. For the sake of brevity and to avoid tedious repetition the full history of transfer from genus to genus is omitted. The next column on the right indicates the author for final recognitions of synonymy and gives additional brief notes where these seem necessary. Where published details are available, all the species of *Halosaurus* have a branchiostegal ray count of 12 or more, whereas in *Aldrovandia* the count is generally smaller, with the exception of Hawaiian forms. Likewise in *Halosaurus* the number of pectoral fin rays tends to be higher, though apparently less markedly so. With respect to the ventral fins the species of both genera have between 7 and 10 rays. The larva has 10 branchiostegal rays (not including the interoperculum) resembling *Aldrovandia*. The remaining ray numbers would fit *A. affinis*, *A. gracilis* or *A. phalacra*. *A. phalacra* has been eliminated on evidence given above, so the larva may probably be referred to as close to the species *A. affinis*. Further than this it seems unwise to venture. As an additional comment one may note as a curiosity that in *Aldrovandia* the enlarged scales of the lateral line are spaced at intervals of roughly 1 to every 3 rows of body scales. The same periodicity was noted above in the distribution of ventral melanophores : 1 about every 3 myotomes, in the larva.

Summarizing the data given above, the larva described is probably a metamorphosing leptocephalus of some species of *Aldrovandia*. Its exact identity will only become clear when more precise accounts of the head morphology of the different halosaurs become available, and when the family has been reviewed. The present tentative determination relies largely on fin-ray and branchiostegal numbers, whose systematic value has not been investigated for this group of fishes.

ON THE RECORD OF A HETEROMOUS LARVA FROM THE INDIAN OCEAN

One may turn at this point to an interesting record published by Mead, 1965 while the present work was in preparation. The title of the paper " The larval form of the Heteromi " is, perhaps, misleading, as the material treated consists of only one larva, stated to be an *Aldrovandia*, and of a juvenile (postmetamorphosis) halosaur. Both specimens were taken in the Indian Ocean. The juvenile specimen

TABLE III

(Explanation : pp. 458-459 of the text)

Genus and species	Branchiostegal rays	Gill rakers (1st arch)	Fin rays P.	V.	D.	A.	Size (S.L.) (mm.)	Origin of material	Author	Nominal species (and genus)	Synonym given by:
Halosaurus Johnson, 1863											
radiatus Garman	21–23	15–17	14	9	11	—	240	Gulf of Panama	Garman, 1899	—	—
	21	16	13	8	10	100	*c.* 125	Peru-Chile trench	Bussing, 1965	—	—
pectoralis McCulloch	18	17	16	10	10 (12)	158	545	Gt. Australian Bight, S. of Eucla	McCulloch, 1926	—	—
güntheri Goode & Bean	—	—	16	10	11	186?	—	W., N. Atlantic	Goode & Bean, 1895	—	—
attenuatus Garman	15	11	15	8	11	—	342	Off the Galapagos Is.	Garman, 1899	—	—
ovenii Johnson	14	16*	11	10	11	191	465	E., N. Atlantic off Madeira	Johnson, 1863	—	—
	15	—	—	10	11	180?	570	E., N. Atlantic	Vaillant, 1888	—	—
	—	—	13	10	11	191	375	S Atlantic off Congo Coast	Poll, 1953	—	—
carinicauda (Alcock)	13	—	15	10	11	—	393	Andaman Sea N. of Cinque Is.	Alcock, 1889	" Halosaurichthys "	Alcock, 1896 : changed to *Halosaurus*
parvipennis Alcock	13	—	12–13	10	9	—	381	Laccadive Sea	Alcock, 1892	Put, together with *carinicauda*, as synonym of *A. mediorostris :* Alcock, 1896 ; opinion revoked Alcock, 1899 ; Norman (1939 : 46) suggests *carinicauda* and *parvipennis* may after all be synonyms.	
	12–13	—	12–13	10	9–10	—	*c.* 394	Laccadive Sea and Arabian Sea off Malabar Coast	Alcock, 1899		
johnsonianus Vaillant	12	—	—	9	11	186	390	East, N. Atlantic	Vaillant, 1888	—	—
	12	—	15	9	10–11	—	408	East, N. Atlantic	Collett, 1896	—	—
	—	16	—	—	9	200?	200 and 363	East, N. Atlantic	Fowler, 1936	—	—
ridgwayi (Fowler)	—	13	12	7	10	140	354	Philippine Islands	Fowler, 1933	" Halosauropsis ". Description ! A scaly head, lateral line scales not enlarged and a narrow interorbital width, are the generic characters of *Halosaurus*.	
Aldrovandia Goode & Bean, 1895								[The case for abandoning " *Halosauropsis* " Collett, 1896 is clear ; and ably put by Barnard (1925 : 167)]			
kauaiensis (Gilbert)	13	23	14–15	9	11	—	655	Vicinity of Kauai, Hawaii	Gilbert, 1905	" *Halosauropsis* "	vide supra.
proboscoidea (Gilbert)	(11)	15	14	9	11	—	422	Kaiwai channel, Hawaii	Gilbert, 1905	" *Halosauropsis* "	vide supra.
verticalis (Gilbert)	12	24	14	9	11	—	295	Vicinity of Kauai, Hawaii	Gilbert, 1905	" *Halosauropsis* "	vide supra.
phalacra (Vaillant)	10	(19)*	(13–14)*	8	10	200?	430	E., N. Atlantic	Vaillant, 1888	" *Halosaurus* "	Goode & Bean, 1895
	—	16–18	9	8	11	—	348	" Indian Ocean "	Brauer, 1908	—	—

Aldrovandia **(contd.)**											
macrochir (Günther)	12	(14)	11–13	10	13	—	545	" Off Gibraltar "	Günther, 1878	(Lectotype chosen by Günther, 1887) " *Halosaurus* "	Goode & Bean, 1895.
	12	—	—	9	12	200?	600	E., N. Atlantic	Vaillant, 1888	—	—
	12	—	11–13	9–10	11–13	190–200?	615	E., N. Atlantic	Collett, 1896	—	—
	12	—	—	9	11–12	—	—	W., N. Atlantic	Gill, 1881	" *goodei* "	Günther, 1887.
	12	—	—	9	12	—	*c.* 608	Off Cape Pt. E., S. Atlantic	Gilchrist, 1906	" *niger* "	Barnard, 1925.
	—	—	—	9–10	12–13	—	650	Cape Pt. and Table Bay, S. Africa	Barnard, 1925	—	—
mediorostris (Günther)	11	17*	8	8	11	—	444	W. of Philippines	Günther, 1887	" *Halosaurus* "	Goode & Bean, 1895.
	11	—	8	9	11	—	—	Indian Ocean, E. of Maldives	Alcock, 1899	—	—
	11	—	8	9	11	—	285	Bali Sea	Weber & de Beaufort, 1922	—	—
affinis (Günther)	10*	13–14*	11–13*	9–10*	10*	—	421	" Japan "	Günther, 1877	" *Halosaurus* "	Goode & Bean, 1895. Alcock, 1896—synonym of *A. mediorostris*—revoked in Alcock, 1899.
	12	14	12	9	12	—	—	Gulf of Manaar (off Ceylon)	Alcock, 1889	" *anguilliformis* "	Barnard, 1925.
	10	8	13	9	11	*c.* 175	533	Laccadives, W. of Mangalore. " Arabian Sea "	Alcock, 1890	" *hoskynii* "	Goode & Bean (1895 : 130) : probably = *affinis* Alcock, 1899 given as = " *anguilliformis* ".
	11	—	13	9	11–12	*c.* 200	482	Laccadives, W. of Mangalore. " Arabian Sea "	Alcock, 1890	—	—
	12	21–22*	9	8	12	—	190	Indian Ocean off Maldives	Alcock, 1898	" *nigerrimus* "	Weber (1913 : 93) ; tentative synonymy (see note p. 462, of the present paper).
	10	—	9–10	8	10–11	—	330	Timor Sea	Weber, 1913	—	—
	—	—	—	9	12	—	—	Off Cape Point E., S. Atlantic	Gilchrist, 1906	—	—
	—	—	—	9	12	—	525	Cape Pt. and Table Bay, S. Africa	Barnard, 1925	—	—
	—	15	13	9	11	*c.* 166	600	Gulf of Mexico	Goode & Bean, 1895	" *pallida* "	Mead, Bertelsen & Cohen (1964 : 583).
	—	14	12–14	—	—	—	512	Gulf of Mexico	Grey, 1958	as " *pallida* "	—
gracilis Goode & Beane	10	14	—	—	—	—	490	Gulf of Mexico and Caribbean Sea	Goode & Bean, 1895	—	—
	—	15	10–11	—	—	—	536	Gulf of Mexico	Grey, 1958	—	—
rostrata (Günther)	9	*c.* 12*	10*	9–10	10	—	507	" Mid Atlantic "	Günther, 1878	" *Halosaurus* "	Goode & Bean, 1895. Günther, 1878 notes the great similarity w. *A. affinis* (p. 242). Regan (in Gilchrist, 1906) suggests they may be identical. Barnard, 1925 notes differences in scale nos. along the lateral line.
Larva	10	9	10	8	0	0	190	E., N. Atlantic " off Madeira "	—	—	—

was tenatively identified as "*Halosaurus nigerrimus*". The latter was synonymized by Weber (1913) with *Aldrovandia affinis* (see Table III), but Dr. S. McDowell (in litt.) suggests an alternative synonymy with *A. phalacra*. This agrees with the fact that Dr. A. G. K. Menon who examined the specimen of *H. nigerrimus* finds a much higher number of gill rakers than in *A. affinis* (see Table III). Thus on first appearance, the material would consist of two specimens (only one a larva), of a single genus of halosaurs, i.e. *Aldrovandia*. No evidence whatsoever is presented concerning the type of larva that either the lipogenyids or the notacanths possess.

The larva is offered as being a leptocephalus, though apart from the comment that it bears a general resemblance to a larval eel, no mention is made of what specifically leptocephalus characters it has. Concerning its ordinal determination, one may remark that the specimen does not appear to possess pelvic fins, which all Heteromi do. Further, the drawings made for Mead show the nasal capsule with one aperture—halosaurs, notacanths, and lipogenyids have two nasal openings. An interesting observation by Mead is that his larva appears to have luminous organs. These organs are probably not present in any of the Heteromi—Brauer, 1908 (p. 119) considers that luminous organs reported by some early observers (e.g. Günther), are in fact only neuromast cushions. The only character given for assigning the specimen to the genus *Aldrovandia* is an obscure reference to jaw characters said to be generically specific. As these have not been used by previous authors, it must be hoped that this point may be clarified when McDowell's revision of the Heteromi (viz. Marshall, 1962 : 261), finally appears in the Sears Foundation series *The Fishes of the Western North Atlantic*. Until then it is not possible to give a proper assessment of this point. In view of the fact that none of the opercular characters typical of halosaurs were found, and that no giant lateral line canals were shown to be present, the statement that the head structure was unmistakably that of a halosaur (Mead, p. 1) thus comes as a surprise. An incomplete ray formula is given, and since details of segmentation are obscured in the available figure by the stipple-shading, there appear to be no reliable characters from which one might settle the identity of Mead's larva. It therefore seems wisest to reject the record, for the present, as representing a heteromous larva. Should it ultimately prove to be that of a halosaur, it would be of great interest, as when fresh it was transparent, and it is a larva with at least one enlarged tooth[1] (cf. p. 449 above). Further discussion must however, be waived, until a better description becomes available, and the identity of the material is properly established.

METAMORPHOSIS IN THE HALOSAURIDAE

After the brief review given above comparing adult characters with those in the larva from Madeira, one may return to the process of metamorphosis. It is not possible on the basis of a single specimen to give a full account of this transition

[1] *Since writing this Dr. Mead has kindly allowed me to see the specimen. It is larger than the halosaur leptocephalus described above, and is badly damaged. This is perhaps to be expected of material from an Isaacs-Kidd tow of nearly twelve hours! Many specimens from hauls lasting two hours are almost unrecognizable. I would suggest that the transparency of the specimen when fresh was due to the almost complete loss of (probably dark black) skin. I was unable to find any enlarged teeth. Other details might have been seen ad clearing and dissection been carried out.*

in the Halosauridae, but additional information may be sought from two other specimens recorded in the literature. These further specimens are Alcock's "*H. nigerrimus*" (1898) of 190 mm. from 905 m. off the Maldives, and Gilchrist's (1908) 120 mm. specimen from North of Cape Point, South Africa, which he provisionally assigned to "*H. niger*". The former was tentatively referred to *A. affinis* by Weber (1913), the latter, in like fashion, to *A. macrochir* by Barnard (1925), (see Table III). Alcock's specimen is apparently an *Aldrovandia* as in his catalogue (1899) he says that there are about 30 much enlarged lateral line scales between the gill opening and the vent. As there are upwards of 60 myotomes anterior to the vent (Table I), this implies 1 lateral line scale per 2 myotome segments and referring back the comment on the usual frequency of lateral line scales (p. 459) suggests that Alcock's "about 30" should be treated with caution.

The forward shift of the anus and renal pore at metamorphosis has been discussed (p. 449, and Table I), as has the proportional increase in the size of the head relative to the body (p. 456, and Table II). Further, the body changes from its laterally compressed ribbon-like leptocephalus shape, to the cylindrical body typical of the adults. The pigmentation of the leptocephalus is confined almost completely to the ventral series of dark spots. Gilchrist's 120 mm. specimen had a black head, and a white body. It seems quite possible that in halosaurs generally, the head darkens before the rest of the body, in contrast to *Anguilla* where the pigmentation spreads forward from the tail, though the ease with which halosaurs seem to lose body skin must be remembered. Alcock's specimen of 190 mm. is described as being uniformly jet black. The small size of both these juvenile halosaurs, and the relatively large size (190 mm.) of the only known leptocephalus, tempts one to wonder whether initially these fishes "grow by shrinking" such as Hollister (1936) has shown to occur in *Albula*. As however, the identity of all three halosaurs concerned is uncertain, since the different species of *Aldrovandia* appear to vary greatly in adult size, and because of the possibility that as in eels (Bellini, 1907, etc.), so in halosarus, small leptocephali may give rise to males and large leptocephali to females, the matter can only be decided when much more material of the young stages becomes available.

Even more striking are the changes in the arrangement of the fins. Consideration of the dorsal and anal fins in the discussion of the adult ray formula above, was omitted. The larva had no anal, and the larval dorsal is merely a long dorsal fold. The changes at metamorphosis are thus considerable in this respect. An adult dorsal fin with a short base and from 10–12 rays (see Table III) appears in front of the larval fin fold. The fold may disappear comparatively late in development in *Aldrovandia*—Alcock's 190 mm. "*H. nigerrimus*" retains a low fold of skin which begins at an enlarged scale two-thirds of a head length behind the dorsal fin and is not continued to the end of the tail—or, in *Halosaurus*, may be retained in the adult. The 394 mm. holotype of *Halosaurus carinicanda* Alcock, 1889 is described as having "a low median fold of skin, (not much more than half a millimetre high) . . . enclosing distant, thin, sharp, irregular indurations", (auct. cit., p. 455). The *Aldrovandia* larva described here did not appear to have "indurations" in the fin fold; this may be a character to be expected in larval *Halosaurus*. From

Alcock's data it seems likely that the larval fin fold is resorbed from the tail end first. After the anus had shifted forward, a long anal fin must develop. No signs of an anal fin could be seen in the present leptocephalus (the tip of the tail was damaged), but in the adults the anal occupies 156–256 segments in *Aldrovandia* (198–201 in *Halosaurus*), on the basis of evidence presented in Table I. Further changes in the fins appear to include an alteration in the " set " of the pectorals ; they are set rather high in the adults, and low in the larva. The change seems concomitant with the development of the swimbladder (cf. Harris, 1937), of which no sign could be detected in the larva. In eels the swimbladder first appears in the elvers.

It is hard to guess at what time the body scales appear in halosaurs. In eels they appear long after metamorphosis has been completed ; 2–4 years later in *Anguilla*, where they first form along the lateral line and in the mid trunk-region (Hornyold, 1937). Alcock (1899), describes his 190 mm. specimen as having scales " on the temples and cheeks ". Those of the lateral line he notes as adherent, the other scales he dismisses as " deciduous ", which might have meant that they had not yet developed were it not for a figure published by Alcock, and Dr. Menon's assurance that body scales are indeed still present. It may still indicate the development of the body lateral-line scales before the others, and in this case the sequence of the appearance of scales would resemble the pattern in *Anguilla*.

Finally there are some metamorphic changes in the arrangement of muscle and bone. In the body the muscles thicken and fold forward at their dorsal and ventral ends so that the myotomes lose their simple V-shape noted in the larva. At the same time the ribs and 2 sets of intermuscular bones (see Plate 1) develop, the space between the larval myotomes disappears as the jelly-filling is resorbed (see p. 449), and the muscles meet ventrally below the viscera as these move up to their definitive position closer to the vertebral column which forms along the notochord. In the head, changes appear to involve the opercular bones, teeth, the dermal roofing of the skull and the musculature of the mandibular-plate. The interoperculum broadens from the narrow branchiostegal-like splint of the larva, to give the paddle-shaped bone seen in the adults. It is likely that a set of larval teeth is shed before the development of the granular adultiform dentition. The present specimen had no teeth, so presumably had already lost its larval set. It is suggested above (p. 456), that the levator arcus palatini muscles shift their insertion at metamorphosis. Dramatic changes including the fusion, degeneration, and the alteration of insertions and origins of various muscles are known to occur in amphibian metamorphosis (Nieuwkoop & Faber, 1956 : 100), which makes it seem probable that analogous changes could occur in fishes. It is also suggested here that the frontals may broaden in *Aldrovandia*, though whether this happens at metamorphosis or after it seems uncertain. Of the smallest known halosaurs all appear to have a narrow interorbital width, and three at least (the Madeira larva, " *H. nigerrimus* " and Weber's (1913) " *H. carinicauda* " of 280 mm.), have long median dorsal fin folds. It seems distinctly possible that a narrow interorbital width in *Aldrovandia*, and a dorsal fin fold in *Halosaurus* may occur as larval features retained in some adults by that process commonly called neoteny.

FOOD, FEEDING AND CLASSIFICATORY FEATURES IN HETEROMOUS FISHES

In a broader setting, the discovery of a metamorphosing halosaur leptocephalus makes clearer the ties between the Apodes and " the Lyopomi " (Berg's Halosauriformes), but what of the notacanths? The latter share many osteological peculiarities in common with the halosaurs. Likewise the notacanths have an eel-like swimbladder (Marshall, 1962). There seem good grounds for believing that notacanths eels and halosaurs derive from a common stock, and all 3 may be regarded as members of a natural group of eel-like fishes. The bone structure of eels perhaps serves to isolate them somewhat from notacanths and halosaurs. A third family of heteromous fishes, the Lipogenyidae, is omitted from the following discussion : the author can add no new information on its status.

The major differences between notacanths and halosaurs lie in the structure of the lateral-line canal-system and the operculum. As Marshall (1962) has shown the intergradation between spines and soft rays in the notacanths, and there are frequent references in the literature to spines in halosaurs, the justification disappears for separating the notacanths as spiny fishes from the halosaurs as soft-finned. Gosline (1961 : 36) states that the pelvic structure of notacanths is unique. This is not clear from his previous discussion in the same paper (pp. 17–21). If based on the " pungent " elements in notacanths, it should be borne in mind that halosaurs are also reported as possessing pelvic spines by many authors. Halosaurs have lateralis canals lying external to the scales and the opercular apparatus (cf. Günther, 1887 : 238–239 : " luminous organs ") and have large free branchiostegal folds. Notacanths have a larger operculum, suboperculum and interoperculum, and the preoperculum small, while the lateral line canals lie internal to the scales, both on the head and the body. These are considerable differences, but one may ask how far they are related to functional requirements.

Baglioni (1907) divided marine fishes into four main groups according to their habits and noticed accompanying differences, chiefly in the branchiostegal apparatus, when considering respiratory mechanisms. Bottom living fishes tend to have a large branchiostegal apparatus, while in pelagic fishes the opercular apparatus is large and the branchiostegal flap small. These differences parallel those between notacanths and halosaurs. The following is offered as a possible interpretation, considering the differences in relation to feeding requirements in the two groups.

Actively swimming pelagic fishes pursue their prey, and whether or not they catch it may be thought of as depending largely " on who swims fastest ". Assuming this is the predator, all that is required is for it to open its mouth at the right moment, when, if the victim is of a suitable size, it will pass down the gullet of the oncoming pursuer. Water can flow over the gills automatically during swimming, and no extra pumping is needed. For a bottom living fish the situation is different. An excess of guile over muscle may be advantageous, but of no less importance is the possession of a large branchiostegal flap. Potential food animals crawling over the bottom may disappear into places not accessible to the predator. A rapid gulp, involving a sudden intake of water through the mouth, is thus important, and is

one function of a well developed flexible branchiostegal flap. The fold can be fanned forwards and down by the hyohyoid muscles in the web between the rays, so that the extrabranchial cavity expands. A flick of the web, produced by relaxation of the muscles joining the tips of the rays, and by a rotation of the hyoid bar by muscle joining it to the mandible, suddenly pushes back water from outside and behind the gill cavity resulting in an inrush of water through the rictus as the mouth-floor sinks. The development of the branchiostegal flap may therefore be important as part of a complex mechanism, [also involving the mouth, the shoulder girdle and the operculum (Tchernavin, 1953)], for the purpose of catching moving prey, in addition to the need for pumping water over the gills (Hughes, loc. cit.). Where the opercular fold is supported chiefly by the branchiostegal rays a highly flexible and much more readily expansible structure is achieved than when the opercular bones are larger and the branchiostegal flap smaller.

Both halosaurs and notacanths are benthic fishes, but whereas notacanths can browse at leisure on banks of sessile sea anemones, the halosaurs appear to feed almost exlusively on benthic microcrustacea. Notacanth stomachs are packed with fragments of actinians (Tucker & Jones, 1951 ; Wheeler, personal communication). Records of food from halosaur stomachs have suggested that they were catholic feeders. Collett (1896 : 151) records 2 *Rossia* of 28 mm. from the stomach of one *A. macrochir* ; mud, sand, foraminifera, sponge spicules and a *Cleodora* shell from the intestine of another. The *Rossia* were described as " well preserved " and may have been swallowed in the trawl-bag as it was hauled in by the yacht Hirondelle. Günther (1887 : 233) records " shrimp-like crustaceans " from the stomach of a third *A. macrochir* apparently from the Marion Islands, while Bell (1887) describes a trematode parasite from the ureter of a halosaur and gives the provenance of the material as " off Cape St. Vincent . . . 1,090 fths. ", (= 1,993 m.). This seems to be an error, as only one halosaur was taken by the Challenger at Station V, off Cape St. Vincent, and this was Günther's lectotype of *A. macrochir*, which shows no signs of having been dissected. Bell's apparent mistake has been reproduced elsewhere (Manter, 1934 : 262 ; Dogiel, 1964 : 285). Günther more probably dissected one of the 4 *A. macrochir* from the Marion Islands (taken at Stn. 146—1,365 fths. = 2,515 m.) prior to its preparation as a skeleton! Mr. Prudhoe, who has kindly examined the material of " *Distomum halosauri* ", Bell, kept in the British Museum, suggests that it may be a *Phyllodistomum*, and in this genus those species whose life history is known (species from freshwater fishes etc.) always have a larval stage whose host is a lamellibranch. This parasite record thus suggests that *A. macrochir* may also feed on bivalve molluscs. It is likely that the sloping levator-arcus-palatini muscles in *Aldrovandia* help rock the palatoquadrate back and forth, and a grinding mechanism of this type would seem well suited to triturating lamellibranchs. Zugmayer (1911) records crustaceans and sand from the stomach of another *A. macrochir*. An *Aldrovandia* among material collected by the Rosaura expedition from the Atlantic had its stomach packed with fragments of Cumacea, tanaids etc. recalling Günther's " shrimp-like crustacea ". A remarkable number of recognisably crustacean fragments could also be seen in the radiographs of a

series of halosaurs. An astonishingly clear image of a whole tanaid is shown in the hind gut of the type specimen of *A. rostrata* (Plate 1). This evidence suggests that crustacea form, at least, the basis of the halosaurs' diet. The Tanaidacea live in tubes which they spin for themselves. While the Cumacea are highly active little crustaceans which swim for short distances, then burrow back rapidly into the silt in which they live. The great development of the sense organs of the lateral line, and the large contribution to the support of the opercular fold by the branchiostegal rays, may thus be features connected in halosaurs with catching moving prey, and the chief differences (vide supra) between the two groups of heteromous fishes would then resolve themselves as functional devices related to their markedly divergent food requirements. A possible difference remains in the mode of development. Whether or not notacanths have a leptocephalus larva, remains an unanswered question. N. B. Marshall (pers. comm.) has found in the British Museum collections a 115 mm. notacanth from Messina which is laterally flattened and is perhaps a young post-larva. Earlier stages remain unknown.

REPRODUCTION IN HALOSAURS AND OTHER FISHES WITH LEPTOCEPHALUS LARVAE

A prolonged period of development implies a small number of generations over a long time-span, hence provides less material for genetic variation or natural selection to act upon than would be so were development and maturation more rapid, given in both cases a similar level of fecundity. It is thus not surprising to find in the groups of fishes with slow developing leptocephalus larvae a range of morphological oddities otherwise associated with extinct or ancient forms. (The gular plate of *Elops*, the rostral commisures of *Pterothrissus*, Elopidae, Megalopidae, *Albula* and halosaurs, the valved conus arteriosus also in *Albula* and *Megalopidae* and perhaps the extra gill bars in *Saccopharynx*, may serve as examples). The simple myotomes of the larva resemble those of the *Acrania*, and perhaps too the anomalous Silurian fossil *Jamoytius kerwoodi* White (1946), in which Ritchie (1960) shows that the V-shaped smears are probably scales. (Presumably they nonetheless correspond to the underlying myotomes). Nor is it strange that fossil halosaurs, very like the living forms, are known from the Cretaceous. Balancing the long life-span, it appears that in those fishes with leptocephalus larvae, for which data are available, prodigious numbers of eggs are produced. Thus estimates of the egg numbers in *Anguilla anguilla* vary between 20 millions (quoted without reference in Bigelow & Schroeder, 1953) and 5–10 millions (Bertin, 1956 : 77), while J. T. Nichols counted 12,201,94 eggs from a 142 lb. *Tarpon atlanticus* (cited by S. F. Hildebrand, 1963 : 115). This must allow a maximum of genetic recombination at meiosis, for gametes from a single parent, but the effect will be enhanced if, as in *Anguilla*, the adults congregate to spawn, since then the recombination possible in the zyogote may be as between a larger number of adults assuming that the freely shed eggs of any female may be fertilized by sperm from a number of different males. This may explain how the eels which congregate to spawn have acquired many

striking adaptive modifications of basic teleost body form in the adult in spite of their longevity, whereas *Tarpon* which probably spawns in pairs, retains many "primitive" unmodified characters, in addition to a few advanced ones such as its secondary lung-like swim bladder. Acting against the variation to be expected from such enormous fecundity, is the length of vulnerable larval life. Only a very few of the immense numbers of leptocephali produced will survive to adulthood. Indeed the sunfishes find leptocephali sufficiently palatable to feed solely upon them when opportunity allows, preferring them to their more usual diet of jellyfishes. Grassi (1896 : 263) found sunfishes with their stomachs packed with eel-leptocephali in the Straits of Messina. The low "survivorship" and slow rate of development are probably the two most important factors producing the assortment of "advanced" and "primitive" characters in the fishes with leptocephalous larvae. Now these fishes seem in the main to be of sedentary habit. Gosline (1959), for instance, considers that the chief characters of eels are related to their living in crevices. Halosaurs are benthic, gulper eels are probably not powerful swimmers. The whole complex appears to have renounced higher rates of evolution, and acquired instead, pelagic larvae that act largely as a distributive phase in the life cycle. It is remarkable how widespread many of the fishes with leptocephalus larvae are.

What little information is available on breeding in halosaurs is scattered through the literature. It seems worth summarizing it briefly. All the records of halosaurs fall between the latitudes of 40° North and South of the equator, except for Günther's record of *A. macrochir* from the Prince Edward Islands (Marion Islands), reports of *H. güntheri* and *A. gracilis* from the North West Atlantic where the Gulf Stream carries northward water masses of more southerly characteristics, and a specimen of *A. macrochir* from off Ireland, (see Map, Text fig 6). Within these boundaries of latitude, the halosaurs are world-wide. The depth range for the group appears to be between a record maximum of 5029 m. (= 2750 fths.) for an *A. rostrata* (N. Atlantic), and a record minimum of 383 m. for an *A. affinis* (Timor Sea). The author is not aware of records of halosaurs in nets fished at shallower levels. Most of these fishes were not found in hauls taken above 900 m. or below 3,000 m. and are distributed around the lower edges of the continental shelves and along oceanic ridges. Bathyscaphe observations and deep-sea photographs show that halosaurs normally swim just above the bottom (e.g. Pérès l.c., Marshall & Bourne, 1965). There are records of more than twenty-four halosaurs with eggs. At least five of these females can be referred to the genus *Halosaurus*, and some nineteen to *Aldrovandia*. In *Halosaurus* Johnson's 465 mm. genotype of *H. ovenii* 1863, collected in February had eggs, some of which measure 1·0 mm. in diameter after more than a century in spirit. The specimen came from off Madeira, i.e. at a latitude of c. 32° N. Poll (1953) records a 375 mm. specimen of the same species taken on October 14th, 1948 at 5° 39′ S., which also had ripe eggs, whereas Vaillant, 1888 whose samples covered the period from June to August records that all the females of *H. ovenii* taken by the Talisman had small eggs. A specimen of *H. johnsonianus*, taken on 18th August, 1888 is reported by Collett as having eggs at different stages of development. In some other fishes this condition is indicative of a prolonged spawning period. The

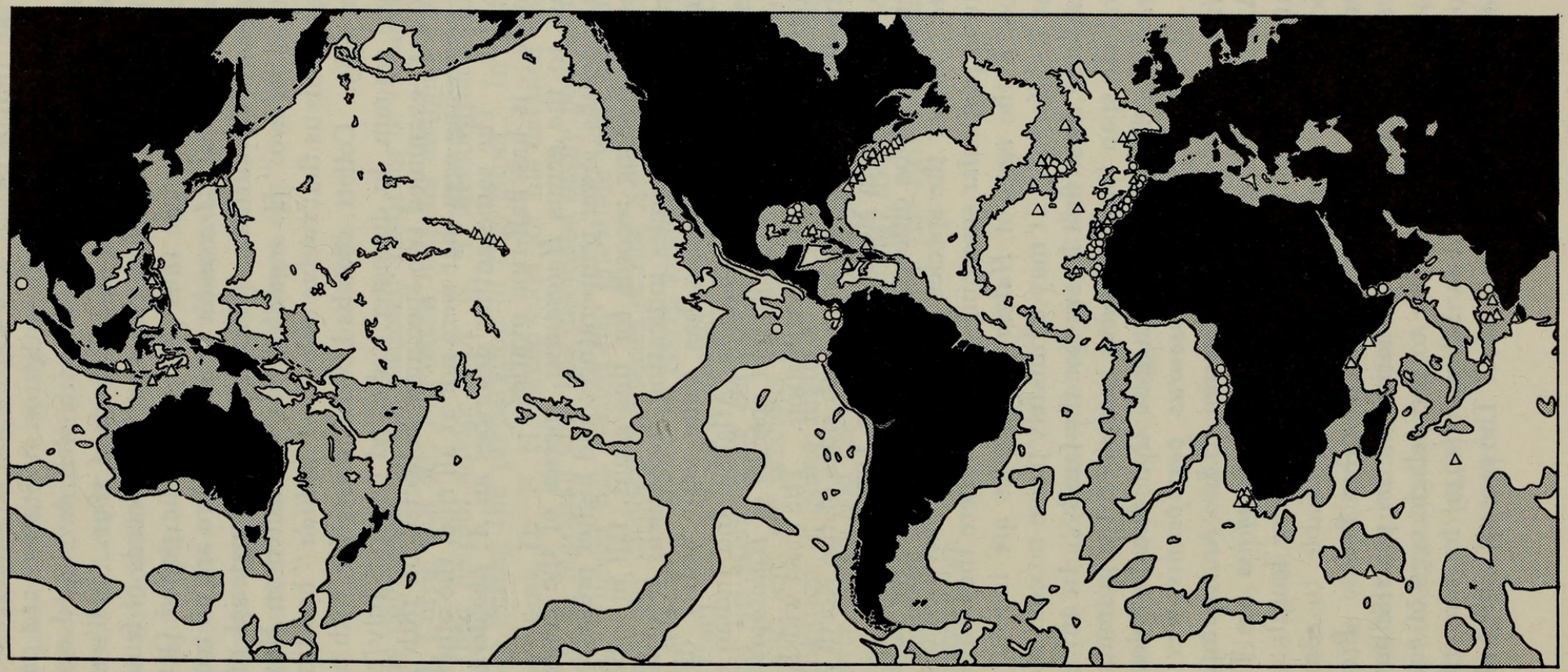

FIG. 6. Map showing the distribution of halosaurs from published records. Land shown in black. The stippled area indicates water of a depth of 2,000 fathoms (= 3658 m.) or less. Circles indicate records of *Halosaurus* species, triangles show records of members of the genus *Aldrovandia*.

picture for the Indian Ocean and the Pacific is similar. A gravid female of *H. parvipennis* was taken by the Investigator at Station 122 on October 21st, 1891, while in the Pacific, an *H. radiatus* with well developed eggs was taken by the Albatross expedition in February, or March of 1891. Poll's record is the only one for the southern hemisphere (see Gazetteer). Records of females with ripe eggs in the Northern hemisphere are thus grouped in the period October to March.

Turning to the genus *Aldrovandia* one finds there are no records at all of females with ripe eggs. Two authors apparently report material of *A. affinis*: Alcock, (1889) says that his two "*H. anguilliformis*" collected on May 5th, 1886 had eggs, and Grey (1958) tells us that twelve of her "*A. pallida*" had tiny eggs when collected on May 26th, 1955. Collett, 1896 had two *A. macrochir*, with unripe eggs, the largest of which were 0·5 mm. in diameter, collected on 31st July/1st August, 1888, and Zugmayer, (1911) examined two specimens collected on 18th August, 1910, one he describes as possessing eggs that were not at all ripe, the other bore eggs considered as not fully ripe. The same author describes an *A. phalacra* collected on the last mentioned date: it has half-ripe ovaries.

In contrast to the genus *Halosaurus*, species of the genus *Aldrovandia* mostly live at greater depths, lower temperatures and higher pressures. Thus on the map, the triangles symbolizing records for this genus, fall in a belt closer to the deep ocean basins, while the circles indicating *Halosaurus* records, are almost all close to the continents. *Aldrovandia* has some very widely distributed species, for example, *A. macrochir* and *A. phalacra* (Atlantic and Indian oceans), and *A. affinis* (all oceans), whereas there are different species of *Halosaurus* for each ocean, and these are often of limited known distribution. The most widely dispersed *Halosaurus* appears to be *H. ovenii* known from both sides of the North Atlantic, and reported from points reaching from Morocco to Cape Town.

There seem then to be differences in the reproductive biology within the family *Halosauridae*. Either the species of *Aldrovandia* have very much smaller eggs, or they migrate to particular spawning-grounds, where they have not yet been caught. Possibly, too, if the eggs of *Halosaurus* species are indeed larger, their mode of development is different. It may ultimately prove no coincidence that leptocephali of *Aldrovandia* are those first known for the family. In any case one may expect a shorter larval life span for *Halosaurus* species on the grounds of their more limited distribution. The data available suggest that female halosaurs mature early in life. Thus Alcock's type of *Halosaurus parvipennis* was 381 mm. long, while Garman's *H. radiatus* was only 356 mm. S.L. An example for *Aldrovandia* is given by Alcocks "*H. anguilliformis*" (= *A. affinis* see Table III) which were ovigerous at *c.* 356 mm. S.L. (this is not a precise length: both specimens were brought aboard in fragments). It seems justifiable to compare the eggs of the genus *Halosaurus*, at least, with those of other fishes. Presuming that the eggs swell after oviposition and the formation of the perivitelline fluid they might be expected to be comparable in size to the pelagic eggs of eels, where diameters of 2·40 to 2·70 mm. are recorded by Schmidt (1930) for *Nessorhamphus*, and 3·3 mm. for an unidentified eel by Beebe (1936). The present record of a larva from 1,110 m.

(bottom at *c.* 3,000 m.) suggests that oviposition may be followed by a larval existence within the horizontal plane inhabited by the adults.

If distribution is associated with length of larval life in fishes not otherwise thought to be powerful swimmers or of migratory habit, perhaps the almost ubiquitous occurrence of the notacanths may be taken as weak circumstantial evidence that they, too, have leptocephalus larvae. Be that as it may, the discovery of a metamorphosing halosaur larva adds another tessera to the mosaic showing the lower teleosts, as a diverse group that has at the same time frequently retained a basic similarity in the pattern of development from egg to adult.

ACKNOWLEDGEMENTS

I am grateful to my colleagues at the National Institute of Oceanography, and especially to Mr. R. I. Currie and Mr. P. Foxton both for enabling me to work on the material and for their helpful advice. Dr. N. A. Mackintosh kindly provided me with working-space during the preparation of this paper. In addition it is a pleasure to be able to thank Dr. P. H. Greenwood for his detailed reading of the manuscript, and Mr. N. B. Marshall who has discussed many points and corrected several errors. Mr. A. Wheeler has earned my gratitude with his editorial skills in addition to placing at my disposal the series of fine X-radiographs, from among which Plate I has been selected. Mr. R. H. Harris kindly lent me one of his beautiful alizarin preparations from which I have drawn Text-fig. 3. To Dr. S. McDowell my thanks are due for his stimulating correspondence. Dr. Giles Mead and Mr. M. J. Penrith have both lent me precious specimens, while Dr. A. G. K. Menon carried out an investigation of some material in the Indian Museum. Miss S. Hiddleston has patiently typed and checked my manuscript. To all these people I am most grateful. There remains finally to record my indebtedness to the library staffs of the British Museum at Bloomsbury, and the British Museum (Natural History) at South Kensington.

SUMMARY

1. A single specimen of a halosaur leptocephalus is described, and its characters compared with those of the leptocephali of other fishes.

2. The distinctive features of the specimen are compared with details observable in adult halosaurs.

3. A review is made of such systematic characters in the adults as can be observed in the leptocephalus. Notes of previously unpublished details based on a re-examination of type material are given. It is concluded that the leptocephalus is an *Aldrovandia*, close to *A. affinis*.

4. An attempt is made to outline the processes occurring at metamorphosis.

5. The feeding of adult Heteromi is considered in relation to their systematic status.

6. The reproductive biology and distribution of the halosaurs is discussed.

7. An effort has been made to gather together as full a series of data as possible, relating to published records of halosaurs. These are given in the form of a gazetteer.

REFERENCES

AGASSIZ, A. 1892. Reports on the dredging operations off the west coast of central America . . . II. General sketch of the expedition of the " Albatross " from February to May 1891. *Bull. Mus. comp. Zool. Harvard* **23** : 1–90.

ALCOCK, A. W. 1889. On the bathybial fishes of the Bay of Bengal and neighbouring waters . . . *Ann. Mag. nat. Hist.* (6) **4** : 450–461.

—— 1890. On the bathybial fishes of the Arabian Sea . . . *Ann. Mag. nat. Hist.* (6) **6** : 295–311.

—— 1892. On the bathybial fishes collected during the years 1891–1892. *Ann. Mag. nat. Hist.* (6) **10** : 345–364.

—— 1894. An account of a recent collection of bathybial fishes from the Bay of Bengal and the Laccadive Sea. *J. Asiatic Soc. Bengal* **63**, Pt 2 : 115–137.

—— 1896. A supplementary list of the Marine fishes of India. *J. Asiatic Soc. Bengal* **65** (2) : 304–339.

—— 1898. A note on the deep-sea fishes with descriptions of some new genera and species. *Ann. Mag. nat. Hist* (7) **2** : 137–156.

—— 1899. A descriptive catalogue of the Indian deep-sea fishes in the Indian Museum. Calcutta 211 + viii pp.

BAGLIONI, S. 1907. Der Atmungsmechanismus der Fische. *Z. allg. Physiol.*, Jena **7** : 177–282.

BARNARD, K. H. 1925. A monograph of the Marine Fishes of South Africa. Pt. I *Ann. S. Afr. Mus.* Cape Town **21** : 418 pp.

BEEBE, W. 1936. The egg-life of a deep-sea Eel. *Bull. New York zool. Soc.* **39** : 60–66.

BELL, F. J. 1887. Description of a new species of *Distomum*. *Ann. Mag. nat. Hist.* (5 ser.) **19** : 116–117.

BELLINI, A. 1907. Expérience sur l'élevage de l'anguille en stabulation à Comacchio. *Bull. Soc. cent. Aquic. Pêche* **19** : (quoted by Bertin 1956).

BERTIN, L. 1926. Les migrations de l'anus au cours de la métamorphose chez les poissons apodes. *Bull. Soc. zool. France* **51** : 327–344.

—— 1956. Eels : a biological study. Cleaver-Hume Press, London, 192 pp.

BIGELOW, H. B. & SCHROEDER, W. C. 1953. Fishes of the Gulf of Maine. Fish. *Bull. U.S. Fish & Wildlife Serv.* **53** : 577 pp.

BRAUER, A. 1908. Die Tiefsee-Fische 1.Syst. Teil. wiss. *Ergebn. Deutsch. Tiefsee Exp.* **15** (1) : pp. 420.

BUSSING, W. A. 1965. Studies of the midwater fishes of the Peru-Chile Trench. *Antarctic Res. Ser.* (*Am. Geophys. Union*) **5** : 185–227.

COLLETT, R. 1896. Poissons provenants des Campagnes du yacht l'Hirondelle 1885–1888. *Rés. Camp. Sci. Albert Ier Monaco* **10** : 198 pp.

DELAGE, Y. 1886. Sur les relations de parenté du Congre et du leptocephale. *C. r. hebd. Séanc. Acad. Sci., Paris* **103** : 698–9.

DOGIEL, V. A. 1964. General Parasitology. Oliver & Boyd : Edinburgh and London. 516 pp.

EDGEWORTH, F. H. 1935. The Cranial muscles of vertebrates. Cambridge University Press. 493 pp.

FOWLER, H. W. 1933. Description of new fishes obtained 1907–1910, chiefly in the Philippine Islands and adjacent seas. *Proc. Acad. nat. Sci. Philadelphia* **85** : 233–367.

—— 1936. The Marine Fishes of West Africa. *Bull. Am. Mus. nat. Hist.*, **70** : 1493 pp.

GARMAN, S. 1899. Reports on an exploration off the west coasts of Mexico Central and S. America and off the Galapagos, 26. The Fishes. *Mem. Mus. comp. Zool. Harvard* **24** : 431 pp.

GILBERT, C. H. 1905. The aquatic resources of the Hawaiian Islands, Section II. The Deep Sea Fishes. *Bull. U.S. Fish. Commn.* for 1903 **23** (2) : 297 pp.

GILCHRIST, J. D. F. 1906. Descriptions of fifteen new South African fishes, with notes on other species. *Mar. Invest. S. Afr.* **4** : 143–171.

——& VON BONDE, C. 1924. Deep Sea Fishes procured by the s.s. "Pickle" Pt. II. *Fish. Mar. biol. Surv.* (*S. Afr.*) *Rep.* **3**, (*Spec. Rep.* 7) : 24 pp.

GILL, T. N. 1881. Diagnosis of new genera and species of deep-sea fish-like vertebrates. *Proc. U.S. natn. Mus.* **6** : 257.

GOODE, G. B. & BEAN, H. T. 1895. Oceanic Ichthyology. Washington and Cambridge.

GOSLINE, W. A. 1959. Mode of life, functional morphology and the classification of teleost fishes. *Syst. Zool.* **8** (3) : 160–164.

—— 1961. Some osteological features of modern lower teleostean fishes. *Smithson. misc. Collns.* **142** (3) : 42 pp.

GRASSI, B. 1896. The reproduction and metamorphosis of the common eel (*Anguilla vulgaris*). *Proc. Roy. Soc.* **60** : 260–271.

—— & CALANDRUCCIO, S. 1893. Ancora sullo sviluppo dei Muraenoidei. Terza nota preliminare. *Bull. delle sedute Acc. Gioenia Catania.* **34** & **35** : 2–4.

GREY, M. 1958. Descriptions of abyssal fishes from the Gulf of Mexico. *Fieldiana* (*Zool.*) **39** (16) : 149–183.

GRONOVIUS, L. T. 1763. *Zoophylacium.* Leiden.

GÜNTHER, A. 1877. Preliminary notes on new fishes collected in Japan during the expedition of H.M.S. Challenger. *Ann. Mag. nat. Hist.* (4) **20** : 433–446.

—— 1878. Preliminary notices of deep-sea fishes collected during the voyage of H.M.S. Challenger. *Ann. Mag. nat. Hist.* (5) **2** : 248–251.

—— 1887. Report on the deep-sea fishes collected by H.M.S. Challenger during the years 1873–1876. *Challenger Rep.* (*Zool.*) **22** : 335 pp.

HARRIS, J. E. 1937. The mechanical significance of the position and movement of the paired fins in the Teleostei. *Pap. Tortugas Lab.* Carnegie Instn. **31** : 171–189.

HILDEBRAND, S. F. 1963. in: Fishes of the Western North Atlantic Part 3. *Mem. Sears Foundation for mar. Res.*

HOLLISTER, G. 1936. A fish which grows by shrinking. *Bull. New York zool. Soc.* **39** : 104–109.

HORNYOLD, A. G-. 1937. Recherches sur l'âge et la croissance de 260 petites anguilles . . . *Bull. Inst. oceanogr. Monaco.* **718** : 15 pp.

HOUOT, G. S. 1958. Four years of diving to the bottom of the sea. *Natn. geogr. Mag.* **113** (5) : 715–731.

HUGHES, G. M. 1960. A comparative study of gill ventilation in marine teleosts. *J. exp. Biol.* **37** : 28–45.

JOHNSON, J. Y. 1863. Descriptions of three new genera of fishes obtained at Madeira. *Proc. zool. Soc. London* pp. 403–410.

MCCULLOCH, A. R. 1926. Report on some fishes obtained by the F.I.S. Endeavour . . . *Biol. Res. "Endeavour"* **5** : 157–217.

MANTER, H. W. 1934. Some digenetic trematodes from deep-water fish of Tortugas, Florida. *Pap. Tortugas Lab.* Carnegie Inst. **28** : 257–345.

MARSHALL, N. B. 1962. Observations on the Heteromi, an order of Teleost fishes. *Bull. Br. Mus. nat. Hist.* (*Zool.*) **9** (6) : 251–270.

—— & BOURNE, D. W. 1965. A photographic survey of benthic fishes in the Red Sea and Gulf of Aden. *Bull. Mus. comp. Zool. Harvard* **132** (2) : 223–244.

MEAD, G. W. 1965. The Larval form of the Heteromi (Pisces). *Breviora* No. 226.

——BERTELSEN, E. & COHEN, D. M. 1964. Reproduction among deep-sea fishes. *Deep Sea Res.*, **11** : 569–596.

NIEUWKOOP, P. D. & FABER, J. 1956. Normal Table of *Xenopus laevis* (Daudin). *North Holland Publ. Co., Amsterdam;* 243 pp.

NORMAN, J. R. 1926. The development of the chondrocranium of the eel . . . *Phil. Trans. Roy. Soc. B* **214** : 369–464.
—— 1939. Fishes. *John Murray Exp. Sci. Rep.* **7** : 116 pp.
ORTON, G. L. 1963. Notes on larval anatomy of fishes of the order Lyomeri. *Copeia* 1963 : 6–15.
PÉRÈS, J.-M. 1958. Résultats Scientifiques des Campagnes du bathyscaphe F.N.R.S. III 1954–1957 V Remarques générales . . . *Annls. Inst. océanogr., Monaco* **35** : 259–285.
POLL, M. 1953. Poissons III. Téleostéens Malacopterygiens. *Exp. Oceanogr. Belge eaux côt. Afr. Atl. Sud.* **4** (2) : 258 pp.
RASQUIN, P. 1955. Observations on the metamorphosis of the bonefish *Albula vulpes* (Linnaeus). *J. Morph.* **97** : 77–118.
REGAN, C. T. 1912. The osteology and classification of the teleostean fishes of the order Apodes. *Ann. Mag. nat. Hist.* (8) **10** : 377–387.
RIDEWOOD, W. G. 1904. On the cranial osteology of the Fishes of the families Elopidae and Albulidae . . . *Proc. zool. Soc. London* 1904 : 35–81.
RITCHIE, A. 1960. A new interpretation of *Jamoytius kerwoodi* White. *Nature, Lond.* **188** : 641–9.
SCHMIDT, E. J. 1930. *Nessorhamphus*, a new cosmopolitan genus of oceanic eels. *Vidensk Meddr. dansk. naturh. Foren.* **90** : 371–375.
—— 1935. Danish Eel Investigations. Carlsberg Foundn. Copenhagen ; 16 pp.(Trans. fm. "*Danas Togt omkring Jorden*").
TCHERNAVIN, V. V. 1953. The feeding mechanisms of a deep-sea fish *Chauliodus sloani* Schneider. London, British Museum (Natural History) : 101 pp.
TUCKER, D. W. & JONES, J. W. 1951. On a rare deep-sea fish *Notacanthus phasganorus* Goode. *Bull. Br. Mus. nat. Hist. (Zool.)* **1** : 67-79.
VAILLANT, L. 1888. Poissons. *Exp. Sci.* "*Travailleur et Talisman*". G. Masson & cie. Paris. 406 pp.
VAN DOBBEN, W. H. 1935. Uber den Kiefermechanismus der Knochenfische. *Archs. Néerland. Zool.* **2** : 1–72.
WEBER, M. 1913. Fische der Siboga Expedition. *Siboga Exped.* **57** : 710 pp.
—— & DE BEAUFORT, L. F. 1922. The fishes of the Indo-Australasian archipelago. IV. Heteroni—Microcyprini. Leiden. E. J. Brill. 410 pp.
WHITE, E. I. 1946. *Jamoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire. *Geol. Mag.* **83** : 89–97.
ZUGMAYER, E. 1911. Poissons . . . des campagnes du yacht "Princesse Alice" *Res. Camp. Sci. Albert I^er Monaco* **35**, 174 pp.

SUPPLEMENTARY REFERENCES

(Selected references not quoted in the text and used solely for data on distribution).

ALCOCK, A. W. 1902. A naturalist in Indian Seas. London.
ESCHMEYER, W. A. 1965. Station data errors for fishes collected by the steamer Blake. *Copeia* 1965 (No. 2) : 236–238.
KOEFOED, E. 1927. Fishes from the sea bottom. *Rep.* "*Michael Sars*" *N. Atl. Deep-Sea Exped.* 1910, **4** (1) : 1–148.
PARFAIT, J. T. 1884. Mission Scientifique du Talisman dans l'océan Atlantique *Annls hydrager. Paris.* 1883. **5** (2^ème Sér) : 258–311.
PARR, A. E. 1937. Concluding report on fishes. *Bull. Bingham oceanogr. coll.* **3** (7) : 79 pp.
RICHARD, J. 1939. Liste générale des stations des campagnes scientifiques du Prince Albert de Monaco. *Rés. Camp. Sci. Albert I^er Monaco* **89**. 348 pp.
ROUCH, J. 1948. Stations Hydrologiques des Campagnes Scientifiques du Prince Albert I^er. *Rés. Camp. Sci. Albert I^er Monaco* **108**. 26 pp.

ROULE, L. 1919. Poissons provenant des campagnes du yacht Princesse-Alice 1891–1913, et du yacht Hirondelle II (1914). *Rés. Camp. Sci. Albert Ier Monaco* **52** : 190 pp.

—— & ANGEL, F. 1933. Poissons provenant de Campagnes du Prince Albert Ier de Monaco. *Rés. Camp. Sci. Albert Ier Monaco* **86** : 115 pp.

SMITH, S. (et al.). 1889. Appendix E. pp. 1–144. Lists of the dredging stations . . . in the Atlantic and Arctic oceans. *Rep. U.S. Fish Comm.* 1886.

SPRINGER, S. & BULLIS, H. R. 1956. Collections by the " Oregon " in the Gulf of Mexico 1950–1955. *Spec. scient. Rep. U.S. Fish & Wildlife Serv.* **196** : 134 pp.

TANNER, Z. 1886. Report of the work of the U.S.F.C. steamer Albatross for the year ending December 31st 1884. *Rep. U.S. Fish Comm.* 1884.

TOWNSEND, C. H. & NICHOLS, J. T. 1925. Deep-sea fishes of the " Albatross " Lower California Expedition. *Bull. Am. Mus. nat. Hist.* **52** : 20 pp.

TUCKER, D. W. 1954. 4. Report on the fishes collected by S.Y. " Rosaura " in the North and Central Atlantic, 1937–38. *Bull. Br. Mus. nat. Hist.* (*Zool.*) **2** : 163–214.

APPENDIX

A GAZETTEER TO HALOSAUR RECORDS

In order to summarize the fragmentary information on the reproductive biology of the Halosauridae it was found desirable to gather together as full a series of data as possible from published records. The immense labour of piecing together these results from station lists, hydrographic papers, studies on bottom deposits, annual reports and charts, leads to the conclusion that it would be valuable to print what has been gathered in this way, if only to save others from this onerous task in the future. Considerations of space preclude the listing of all the papers consulted for this part of the work. A selection of the most important works is given above after the main body of references. Special notice should however be given to the following points. As Eschmeyer (1965) has shown, many of the stations assigned to Blake material by Goode & Bean (1895) and printed in roman numerals in " Oceanic Ichthyology ", are in fact erroneous. Probably the same applies to specimens from " Albatross " stations. It has not been possible at present to trace all such errors. In general the roman numerals have simply been sought against the equivalent arabic numbers given in the lists of Smith (1899). An additional record of *A. macrochir* which does not appear in Goode & Bean, has been added from Tanner's (1886) report on the work of the " Albatross ". Gill's records of " *Halosaurus goodei* " have been combined with Goode & Bean's data for *A. macrochir* : Gill states how many specimens he saw, Goode & Bean do not. This means that the numbers of *macrochir* for the stations concerned are minimal figures, as in some cases specimens formerly separated into the supposedly different forms *macrochir* and " *goodei* ", occurred together, but only Gill's data for numbers of " *goodei* " are available. It should be noted that the Talisman station-numbers given by the biologists concerned with working up the material from the 1883 expedition, are printed in roman type, and include secondary substations. The numbering given by the hydrographers (Parfait, 1884) is, on the other hand, in a simple continuous series of arabic numerals. Caution is therefore necessary in tracing data when referring to the hydrographic lists, from a series of biological records. In spite of

the agreement at the Washington meridian conference in 1884 to quote longitudes from Greenwich, the publications on this expedition, even though they appeared some years later than this date, still quote longitude from Paris. Smith gives correct longitude data for both conventions in most (not all) instances, but follows the French hydrographers in printing simplified station numbers which thus differ from those given in Vaillant's (1888) account of the fishes. The early reports on the expeditions of Prince Albert I of Monaco, also quote station-position longitudes from Paris, but corrected data quoted from Greenwich are to be found in Richard (1934). It will be seen that the species occur in the tables in the order of their first discovery in the relevant ocean, with data for species of *Aldrovandia* following records for the genus *Halosauras*. Finally, the asterisks against some bottom temperatures given in parentheses indicate information cited from a different, but closely adjacent station, of comparable depth.

KEY TO ABBREVIATIONS

r.	red	cl.	clay
br.	brown	m.	mud
ye.	yellow	for	foraminifera
gn.	green	glob. oz.	globigerina ooze
ol.	olive	oz.	ooze
blu.	blue	r	radiolaria
gy.	grey	bar. nods.	barytes nodules
bl.	black	mang.	manganese
wh.	white	bm.	bottom
-sh.	ish	hd.	hard
spkd.	speckled	shay.	shaley
lt.	light	bkn.	broken
dk.	dark	shlly.	shelly
rks.	rocks	cs.	coarse
sts.	stones	th.	thick
sha.	shale	sy.	sandy
shr. deb.	shore debris	my.	muddy
shs.	shells	sft.	soft
cor. s.	coral sand	fn.	fine
vol. s.	volcanic sand	reg.	region
s.	sand	w.	with

A Gazetteer to Halosaur Records

Atlantic Ocean

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom temp.	Number of Halosaurs taken
1. *Halosaurus ovenii*							
Johnson, 1863	—	Off Madeira	Feb.	—	—	—	1 ♀ (± ripe)
Vaillant, 1888	Talisman XIX	33° 42′ N., 8° 01′ W.	14.vi.1883	920	ye. m.	10° C.	1
	XXXIII[2]	32° 31′ N., 9° 48′ W.	17.vi.1883	834	r.-sh. m.	11° C.	3
	XLV	29° 08′ N., 12° 26′ W.	26.vi.1883	1,235	sft. ye. m.	8·5° C.	1
	L	28° 35′ N., 13° 10′ W.	27.vi.1883	975	ye. m.	7·2° C.	4
	LII	28° 33′ N., 13° 19′ W.	27.vi.1883	946	s. spkd. bl.	—	1
	LXXII	25° 39′ N., 16° 02′ W.	9.vii.1883	882	my. s.	—	2
	LXXXII	23° 00′ N., 17° 30′ W.	12.vii.1883	932	gn. my. s.	7·0° C.	1
	LXXXIV	22° 54′ N., 17° 26′ W.	12·vii·1883	860	gn. my. s.	7·5° C.	1
	LXXXV	22° 52′ N., 17° 23′ W.	12.vii.1883	830	gn. my. s.	7·5° C.	1
	LXXXVII	22° 03′ N., 17° 33′ W.	13.vii.1883	1,113	gn. my. s.	7·0° C.	20
	XCIII	20° 44′ N., 18° 07′ W.	14.vii.1883	1,495	gn.-sh. my. s.	4·5° C.	1
	XCV	20° 38′ N., 18° 19′ W.	14.vii.1883	1,230	gn. my. s.	—	10
	XCIX	17° 12′ N., 17° 07′ W.	17.vii.1883	1,617	shay. cl.	—	1
	C	17° 16′ N., 16° 59′ W.	17.vii.1883	1,550	gn.-sh. m.	—	1
	CXXVII	38° 38′ N., 28° 21′ W.	15.viii.1883	1,257	gy. m.	11·5° C.	1
Good & Beane, 1895	Blake Ag. 67	Off Havana	1878	439	—	—	—
	Ag. 68	Off Havana	1878	838	—	—	—
	Albatros 2181	39° 29′ N., 71° 46′ W.	23·vii·1884	1,267	gy. m., fn. s.	3·8° C.	2
Gilchrist & von Bonde, 1924	Pickle 517	33° 35′ S., 17° 00′ E.	8·xi·1921	1,097	—	—	10
Poll, 1953	Noordende III 45	5° 39′ S., 11° 25′ E.	14·x·1948	470	br. sy. m.	7·8° C.	1 ♀ (ripe)
	88	10° 45′ S., 13° 07′ E.	12·xii·1948	500	gn. sy. m.	—	1
	97	11° 53′ S., 13° 20′ E.	18·xii·1948	510	gn. m.	8·0° C.	1
	125	8° 28′ S., 12° 45′ E.	7.ii.1948	500	sy. m.	7·28° C.	1
Tucker, 1954	Rosaura 49	28° 25′ N., 13° 34′ W.	1.ii.1938	1,300	—	—	1
					Species total (for Atlantic)		>69

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
2. *Halosaurus johnsonianus* Vaillant, 1888							
Vaillant, 1888	Talisman XIII	35° 07′ N., 7° 18′ W.	11.vi.1883	1,216	m. & cor.	10° C.	1
	XXXII	32° 34′ N., 9° 49′ W.	16.vi.1883	1,590	th. m.	—	1
	XXXIII	32° 31′ N., 9° 49′ W.	17.vi.1883	1,350	r. m.	—	10
	XXXIII[2]	32° 31′ N., 9° 48′ W.	17.vi.1883	834	m.	11° C.	1
	XLI	30° 01′ N., 11° 46′ W.	24·vi·1883	2,115	gy. m. bkn. shs.	—	6
	XLII	29° 58′ N., 11° 41′ W.	25.vi.1883	2,104	m. & bkn. shs.	—	3
	XLV	29° 08′ N., 12° 26′ W.	26.vi.1883	1,235	sft. ye. m.	8.5° C.	1
	XLIX	28° 37′ N., 13° 02′ W.	27.vi.1883	865	ye. m.	7·0° C.	1
	L	28° 35′ N., 13° 10′ W.	27.vi.1883	975	ye. m.	7·2° C.	1
	LXXII	25° 39′ N., 16° 02′ W.	9.vii.1883	882	my. s. cor. shs.	—	18
	LXXIX	23° 53′ N., 17° 16′ W.	11.vii.1883	1,232	gy. m.	5·8° C.	33
	LXXXI	23° 50′ N., 17° 17′ W.	11.vii.1883	1,139	gy. m.	6·2° C.	7
	XCIII	20° 44′ N., 18° 07′ W.	14.vii.1883	1,495	gn.-sh. my. s.	4·5° C.	13
Collett, 1896	Hirondelle 112	38° 34′ N., 28° 06′ W.	1.vii.1887	1,287	fn. s.	—	1
	233	38° 33′ N., 28° 08′ W.	18.viii.1888	1,300	m. & s.	9·8° C.	1
Roule, 1919	Pr. Alice 553	37° 42′ N., 25° 05′ W.	3.vii.1895	1,385	my. s.	—	3
Koefoed, 1927	M. Sars 23	35° 32′ N., 07° 07′ W.	6.v.1910	1,215	ye. m.	<10·2° C.	16
Tucker, 1954	Rosaura 49	28° 25′ N., 13° 34′ W.	1.ii.1938	1,300	—	—	1
Pérès, 1958	F.N.R.S. III bathyscaphe	38° 17′ N., 09° 13′ W.	23.viii.1956	1,690	r. m.	*c.* 4° C.	" many "
						Species total (for Atlantic)	>118
3. *Halosaurus guentheri* Goode & Bean, 1895							
Goode & Bean, 1895	Albatross 2722	39° 13′ N., 72° 01′ W.	20.ix.1886	1,086	gn. m.	—	1
Springer & Bullis, 1956	Oregon 349	29° 09′ N., 87° 38′ W.	22.v.1951	914	blu. m.	—	—
	640	29° 01′ N., 88° 24′ W.	19.ix.1952	869	—	—	—
						Species total (for Atlantic)	>3
						Total number of the genus *Halosaurus* (for Atlantic)	>190

4. *Aldrovandia macrochir* (Guenther, 1878)

Guenther, 1878	Challenger V		35° 47′ N., 8° 23′ W.	28.i.1873	1,993	glob. oz.	3·5° C.	1
Vaillant, 1888	Talisman XXXIX		30° 08′ N., 11° 42′ W.	23.vi.1883	2,200	th. m.	*(4·0° C.)	9
		CXXX	37° 55′ N., 27° 02′ W.	16.viii.1883	2,235	sft. gy. m.	*(*c.*4·0° C.)	1
		CXXXI	38° 38′ N., 25° 06′ W.	22.viii.1883	2,995	sft. wh. m.	3·4° C.	1
Gill, 1881	Blake Ag. 308		41° 24′ N., 65° 35′ W.	29.vi.1880	2,271	dk. gy. m.	3·2° C.	—
(" H. goodei ")		Ag. 325	33° 35′ N., 76° 00′ W.	14.vii.1880	1,183	glob. oz.	3·8° C.	—
Goode & Bean,	Albatros	2035	— — N., — — W.	17.vii.1883	2,491	glob. oz.	*(3·2° C.)	3
1895		2037	38° 53′ N., 69° 23′ W.	18.vii.1883	3,166	glob. oz.	3·2° C.	1
		2051	39° 41′ N., 69° 20′ W.	1.viii.1883	2,023	bl. m. & oz.	3·8° C.	>11
		2052	— — N., — — W.	1.viii.1883	2,008	glob. oz.	7·2° C.	>10
		2074	41° 43′ N., 65° 21′ W.	3.ix.1883	2,257	m. & sts.	4·4° C.	—
		2077	41° 09′ N., 66° 02′ W.	4.ix.1883	2,295	blu. m.	3·8° C.	—
		2106	37° 41′ N., 73° 03′ W.	6.xi.1883	2,738	glob. oz.	5·7° C.	—
		2111	35° 09′ N., 74° 57′ W.	9.xi.1883	1,715	gn. m.	—	—
		2116	35° 45′ N., 74° 31′ W.	11.xi.1883	1,624	bl. m. & fn. s.	3·8° C.	—
		†2140	17° 36′ N., 76° 46′ W.	11.iii.1884	1,767	s.	4·3° C.	—
(Tanner, 1886 p. 46)			38° 27′ N., 73° 02′ W.	12.ix.1884	2,136	—	—	" a few "
		2533	40° 16′ N., 67° 26′ W.	15.vii.1885	1,514	br. oz.	3·7° C.	—
		2550	39° 44′ N., 70° 30′ W.	9.viii.1885	1,977	br. m.	3·5° C.	—
		2562	39° 15′ N., 71° 25′ W.	11.viii.1885	2,623	gy. oz.	2·9° C.	—
		2563	39° 18′ N., 71° 23′ W.	11.viii.1885	2,601	by. oz.	3·0° C.	—
		2564	39° 22′ N., 71° 23′ W.	11.viii.1885	2,452	gy. oz.	2·9° C.	—
		2571	40° 09′ N., 67° 09′ W.	1.ix.1885	2,480	gy. glob. oz.	3·2° C.	—
Collett, 1896	Hirondelle 209		39° 18′ N., 31° 02′ W.	31.vii/1.viii.1888	1,372	my. s. w. bkn. shs.	—	2
Roule, 1919	Pr. Alice	575	38° 27′ N., 26° 30′ W.	13.vii.1895	1,165	my. s.	6·8° C.	1
		698	39° 11′ N., 30° 44′ W.	18.vii.1896	1,846	gy. sy. m.	*>5·5° C.	1
		738	37° 40′ N., 26° 26′ W.	7.viii.1896	1,919	sy. m.	4·0° C.	1
	Pr. Alice II	1331	38° 40′ N., 26° 00′ W.	9.viii.1902	1,805	my. s.	*>3·8° C.	4
		1334	39° 30′ N., 29° 02′ W.	13.viii.1902	1,900	glob. oz.	4·1° C.	2
Zugmayer, 1911	Pr. Alice II	2990	43° 45′ N., 9° 41′ W.	18.viii.1910	2,320	glob. oz.	3·7° C.	2
Roule & Angel, 1933	Hirondelle II	3150	38° 01′ N., 25° 21′ W.	27.viii.1911	1,740	—	—	1
Gilchrist 1906,	P. Fauré	Shrimp Trawl No.						
		16,893	34° 44′ S., 17° 45′ E.	Sept. 1903	1,646	gn. m. & rks.	—	1
		16,937	34° 44′ S., 17° 45′ E.	Sept. 1903	1,646	gn. m. & rks.	—	1
		17,257	34° 30′ S., 17° 39′ E.	Sept. 1903	1,701	gn. m. & rks.	—	1
		17,293	34° 29′ S., 17° 41′ E.	Sept. 1903	1,628	gn. m. & rks.	—	1
Gilchrist & von Bonde, 1924	Pickle 526		33° 17′ S., 16° 24′ E.	17.xi.1921	2,560	—	—	2

† And a large earthenware jar (Tanner, 1886 : 20).

* At neighbouring Stations.

Atlantic Ocean

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
Koefoed, 1927	M. Sars 25	35° 46′ N., 8° 16′ W.	8.v.1910	2,055	ye. m. (glob. oz.)	<5·27° C.	5
	35	27° 27′ N., 14° 52′ W.	18.v.1910	2,603	ye. glob. oz.	—	2
	53	34° 59′ N., 33° 01′ W.	8.vi.1910	2,615	wh. glob. oz.	<4·4° C.	7
	88	45° 26′ N., 25° 45′ W.	18.vii.1910	3,120	wh. glob. oz.	—	1
	95	50° 22′ N., 11° 44′ W.	26–27.vii. 1910	1,797	gy. glob. oz.	—	3
					Species total (for Atlantic)		>92
5. *Aldrovandia phalacra* (Vaillant, 1888)							
Vaillant, 1888	Talisman XVI	34° 01′ N., 8° 32′ W.	13.vi.1883	2,190	m.	4·5° C.	1
	XXII	33° 47′ N., 9° 03′ W.	14.vi.1883	1,635	m.	6·5° C.	2
	XXXI	32° 37′ N., 9° 47′ W.	16.vi.1883	1,103	m.	*(3·5° C.)	2
	XLII	29° 58′ N., 11° 41′ W.	25.vi.1883	2,104	gy. m. & bkn. shs.	*(5·0° C.)	1
	LXXIII	25° 39′ N., 17° 15′ W.	9.vii.1883	1,435	gy. m.	—	1
	LXXIX[2]	23° 53′ N., 17° 17′ W.	11.vii.1883	1,250	gy. m.	6·0° C.	3
	CXXI	37° 35′ N., 29° 26′ W.	12.viii.1883	1,442	gy. m.	7·0° C.	1
	CXXIX	38° 00′ N., 27° 03′ W.	16.viii.1883	2,220	sft. gy. m.	*(4·0° C.)	1
Roule, 1919	Pr. Alice 703	39° 21′ N., 31° 05′ W.	19.vii.1896	1,360	—	—	1
	Pr. Alice II 1123	27° 41′ N., 17° 53′ W.	15.vii.1901	1,786	hd. bm.	5·2° C.	3
	1209	16° 34′ N., 23° 03′ W.	18.viii.1901	1,477	—	4·7° C.	1
Zugmayer, 1911	Pr. Alice II 2989	43° 45′ N., 9° 41′ W.	18.viii.1910	2,320	glob. oz.	3·7° C.	1
					Species total (for Atlantic)		18

6. *Aldrovandia affinis* (Guenther, 1877)

Goode & Bean, 1895	Blake Ag. 29	24° 36′ N., 84° 05′ W.	(Jan?) 1878	1,746	—	4·1° C.	—
	Albatross 2072	41° 53′ N., 65° 35′ W.	2.ix.1883	1,569	gy. m.	3·8° C.	—
	2181	39° 29′ N., 71° 46′ W.	23.vii.1884	1,267	gy. m., fn. s.	3·8° C.	—
	2216	39° 47′ N., 70° 30′ W.	22.viii.1884	1,761	gn. m.	4·1° C.	—
	2231	38° 29′ N., 73° 09′ W.	12.ix.1884	1,765	gy. oz.	2·6° C.	—
	2380	28° 02′ N., 87° 43′ W.	2.iii.1885	2,615	br. m.	4·4° C.	—
	2381	28° 05′ N., 87° 56′ W.	2.iii.1885	2,432	lt. br. m.	—	—
	2533	40° 16′ N., 67° 26′ W.	15.vii.1885	1,514	br. oz.	3·6° C.	—
	2729	36° 26′ N., 74° 32′ W.	25.x.1886	1,242	dk. gn. m.	—	—
Gilchrist, 1906	P. Fauré						
	Ref. no. 17714	34° 28′ S., 17° 43′ E.	?9.ix.1903	1,152	reg. of	—	2
	Ref. no. 17742	34° 28′ S., 17° 46′ E.	?9.ix.1903	914	gn. m. & rks.	—	1
Gilchrist & von Bonde	Pickle 77	33° 48′ S., 17° 07′ E.	11.v.1920	1,381	—	—	1
	251	33° 43′ S., 17° 24′ E.	23.xi.1920	1,116	—	—	1
	522	33° 24′ S., 16° 38′ E.	15.xi.1921	2,195	—	—	8
	526	33° 17′ S., 16° 24′ E.	17.xi.1921	2,560	—	—	3
	534	33° 30′ S., 16° 45′ E.	29.xi.1921	1,847	—	—	2
	542	33° 41′ S., 17° 09′ E.	8.xii.1921	1,061	—	—	1
Grey, 1955 (Springer & Bullis, 1956)	Oregon 1303	28° 47′ N., 87° 50′ W.	26.v.1955	2,195	gy. m.	—	20
					Species total (for Atlantic)		>48

6a. *Specimens of uncertain identity ;* probably *A. affinis*

Gilchrist, 1906 (p. 171)	P. Fauré	34° 57′ S., 17° 51′ E.		1,390		—	1
Parr, 1937	Pawnee 54	21° 16′ N., 71° 18′ W.	12.iv.1927	*c.* 1,321? (1,981 m. of wire out)	—	—	4
Harrisson, 1966	Discovery 4745	29° 50′ N., 22° 57′ W.	23.ix.1961	1,100 (bottom at *c.* 5,200 m.)	Midwater trawl	—	1 lepto-cephalus
					Species total (for Atlantic)		6

Atlantic Ocean

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
7. *Aldrovandia rostrata* (Guenther, 1878)							
Guenther, 1878	Challenger 63	35° 29′ N., 50° 53′ W.	19.vi.1873	5,029	glob. oz.	—	1
Roule, 1919	Pr. Alice II 1193	15° 17′ N., 23° 01′ W.	15.viii.1901	1,311	gn. my. s.	5·8° C.	1
					Species total (for Atlantic)		2
8. *Aldrovandia gracilis* Goode & Bean, 1895							
Goode & Bean, 1895	Blake 163 Ag.	16° 03′ N., 61° 52′ W.	20.i.1879	1,406	oz. & s.	4·3° C.	1
	Albatross 2380	28° 02′ N., 87° 43′ W.	2.iii.1885	2,615	br. m.	4·4° C.	1
	2381	28° 05′ N., 87° 56′ W.	2.iii.1885	2,432	lt. br. m.	—	1
Roule & Angel, 1933	Hirondelle II 3476	42° 31′ N., 63° 40′ W.	6.ix.1913	1,380	—	—	1
Grey, 1955	Oregon 1303	28° 47′ N., 87° 50′ W.	26.v.1955	2,195	gy. m.	—	21
					Species total (for Atlantic)		25
					Total number of the genus *Aldrovandia* (for Atlantic)		>191

Indian Ocean

1. *Halosaurus carinicauda* (Alcock, 1889)							
Alcock, 1889	Investigator 10	*c.* 11° 23′ N., 92° 42′ E.	12.iv.1888	896	—	—	1
Weber, 1913	Siboga 18	7° 28′ S., 115° 24′ E.	18.iii.1899	1,018	fn. m.	—	1
					Species total (for Indian Ocean)		2

2. *H. parvipennis* Alcock, 1892							
Alcock, 1892	Investigator 122	12° 05′ N., 71° 33′ E.	21.x.1891	1,609	glob. oz.	4·4° C.	1
1899	177	13° 47′ N., 73° 07′ E.	5.v.1894	1,163	gn. m.	6·7° C.	1
	217	6° 56′ N., 72° 53′ E.	21.x.1896	839	s.	—	1
Norman, 1939	Mabahiss 33	13° 41′ N., 48° 17′ E.	15.x.1933	1,295	gn. m.	—	1
	143	5° 16′ S., 73° 23′ E.	30.iii.1934	797	gn. s.	<7·9° C.	1
2a. Probably *H. parvipennis*							
Marshall & Bourne, 1965	Atlantis 1	12° 51′ N., 45° 57′ E.	vi.1958	1,240	—	—	<4
					Species total (for Indian Ocean)		<9
3. *H. pectoralis* McCulloch, 1926							
McCulloch, 1926	Endeavour	Gt. Australian Bight S. of Eucla	13.v.1913	823	—	—	3
					Species total (for Indian Ocean)		3
					Total number of the genus *Halosaurus* (for Indian Ocean)		14
4. *Aldrovandia macrochir* (Guenther, 1878)							
Guenther, 1878	Challenger 146	46° 46′ S., 45° 31′ E.	29.xii.1873	2,515	glob. oz.	2·0° C.	4
					Species total (for Indian Ocean)		4
5. *A. affinis* (Guenther, 1877)							
Alcock, 1889	Investigator 2	6° 32′ N., 79° 37′ E.	5.v.1886	1,234	gn. m. & bar. nods.	—	2
1890	104	11° 12′ N., 74° 25′ E.	3.v.1890	1,829	ol. gn. m.	3·6° C.	4
1896	217	6° 56′ N., 72° 53′ E.	21.x.1896	839	s.	—	1†
Weber, 1913	Siboga 286	8° 50′ S., 127° 02′ E.	19.i.1900	883	m.	—	1
	300	10° 48′ S., 123° 23′ E.	30.i.1900	918	m.	—	1
Norman, 1939	Mabahiss 118	4° 06′ S., 41° 10′ E.	17.i.1934	1,789	glob. oz.	—	1
	158	4° 42′ N., 72° 42′ E.	7.iv.1934	1,117	—	—	1
Mead, 1965	Anton Bruun 349 B	26° 44′ S., 65° 05′ E.	26.vi.1964	1,470	Isaacs-Kidd	—	1†
			bottom at:	4,571	midwater trawl		
					Species total (for Indian Ocean)		12

† "*H. nigerrimus*" see note on p. 462.

Indian Ocean

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
6. *A. mediorostris* (Guenther, 1887)							
Alcock, 1894	Investigator 150	7° 05′ N., 75° 04′ E.	29.xi.1893	1,315	fn. cor. s.	—	1
Weber, 1913	Siboga 18	7° 28′ S., 115° 24′ E.	18.iii.1899	1,018	fn. m.	—	1
					Species total (for Indian Ocean)		2
7. *A. phalacra* (Vaillant, 1888)							
Brauer, 1908	Valdivia 257	1° 48′ N., 45° 42′ E.	27.iii.1899	1,644	fm. gy. br. glob. oz.	—	1
					Species total (for Indian Ocean)		1
					Total number of the genus *Aldrovandia* (for Indian Ocean)		19

Pacific Ocean

1. *H. radiatus* Garman, 1899							
Garman, 1899	Albatross 3354	7° 09′ N., 80° 50′ W.	23.ii.1891	589	gn. m.	3·8° C.	—
	3394	7° 21′ N., 79° 35′ W.	10.iii.1891	934	dk. gn. m.	5·4° C.	—
	3396	7° 32′ N., 78° 36′ W.	11.iii.1891	474	gy. m. & s.	8·5° C.	—
Bussing, 1965	Eltanin 34	7° 48′ S., 81° 23′ W.	6.vii.1962	680	midwater trawl (bottom at 5,050 m.)	—	1
					Species total (for Pacific)		>4

2. *Halosaurus attenuatus* Garman, 1899							
Garman, 1899	Albatross 3413	2° 34′ N., 92° 06′ W.	5.iv.1891	2,487	glob. oz.	2·2° C.	1
Townsend & Nichols, 1925	Albatross 5676	25° 31′ N., 113° 29′ W.	17.iii.1911	1,180	gn. m. fn. s. glob.	3·8° C.	1
					Species total (for Pacific)		2
3. *H. ridgwayi* (Fowler, 1933)							
Fowler, 1933	Albatross D. 5527	9° 23′ N., 123° 43′ E.	11.viii.1909	717	glob. oz.	11·8° C.	7
					Species total (for Pacific)		7
					Total number of the genus *Halosaurus* (for Pacific)		>13
4. *Aldrovandia affinis* (Guenther, 1877)							
Guenther, 1877	Challenger 235	34° 07′ N., 138° 0′ E.	4.vi.1875	1,033	gn. m.	3·3° C.	2
					Species total (for Pacific)		2
5. *A. mediorostris* (Guenther, 1887)							
Guenther, 1887	Challenger 207	12° 21′ N., 122° 15′ E.	16.i.1875	1,280	blu. m.	10·9° C.	1
					Species total (for Pacific)		1
6. *A. verticalis* (Gilbert, 1905)							
Gilbert, 1905	Albatross 3985	22° 04′ N., 159° 15′ W.	10.vi.1902	872	gy. s. w. shr. deb.	4·4° C.	—
	4141	22° 04′ N., 159° 16′ W.	2.viii.1902	1,156	vol. s. w. foram.	4·9° C.	—
	4151	23° 16′ N., 161° 46′ W.	5.viii.1902	1,593	cor. s.	3·2° C.	—
					Species total (for Pacific)		>3
7. *A. proboscoidea* (Gilbert, 1905)							
Gilbert, 1905	Albatross 4111	21° 25′ N., 157° 25′ W.	24.vii.1902	859	fn. s., rks.	4·4° C.	—
					Species total (for Pacific)		>1

Pacific Ocean

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
8. *A. kauiensis* (Gilbert, 1905)							
	Albatross 3887	21° 17′ N., 156° 41′ W.	17.iv.1902	1,479	fn. ye. s. & glob. oz.	4·1° C.	—
	3977	23° 07′ N., 162° 12′ W.	2.vi.1902	1,602	cor. s. for r.	3·3° C.	—
	3989	22° 07′ N., 159° 15′ W.	11.vi.1902	914	cor. s. for r.	3·0° C.	—
	4018	22° 03′ N., 159° 14′ W.	21.vi.1902	1,470	foram. shs. & mang.	2·8° C.	—
	4019	22° 16′ N., 159° 14′ W.	21.vi.1902	1,006	gy. s. for r	3·2° C.	—
						Species total (for Pacific)	>5
						Total number of the genus *Aldrovandia* (for Pacific)	>12

PLATE 1

X-radiograph of type of *Aldrovandia rostrata*, showing intermuscular bones and the clear image of a tanaid (=*t*), in the hind-gut.